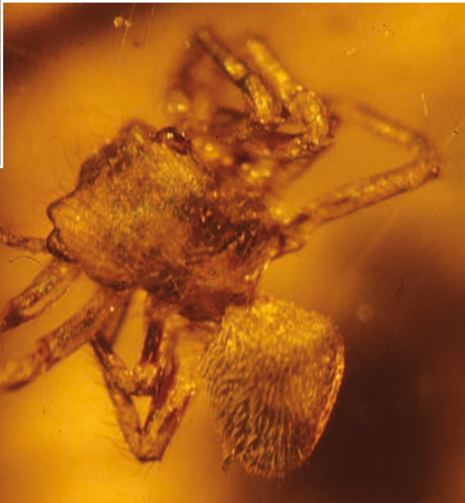
BEITR. ARANEOL., 5 (2008)

FOSSIL AND EXTANT SPIDERS (ARANEAE)

FOSSILE UND HEUTIGE SPINNEN

Joerg Wunderlich



BEITR. ARANEOL., 5 (2008)

BEITRAEGE ZUR ARANEOLOGIE, 5 (2008). – ISBN 978-3-931473-11-2.

FOSSIL AND EXTANT SPIDERS (ARANEAE)

Photos on the front cover of the book (the bodies of four extraordinary fossil spiders):

Photo ABOVE ON THE LEFT: Male spider of the extinct family Spatiatoridae in Eocene Baltic amber, body length 4.3 mm. This spider existed 40 to 50 million years ago. Note the raised "caput". See photo 139.

Photo ABOVE ON THE RIGHT: Male spider of the family Borboropactidae in Baltic amber, body length 3.5 mm. This is a relict family of the tropics. Note the powerful anterior "capture legs". See photo 380.

Photo BELOW ON THE LEFT: Male spider of the family Pumiliopimoidae in Baltic amber, body length 1.9 mm. The family is almost extinct; a single extant species, which I regard as related, has recently been described from North America. See photo 156.

Photo BELOW ON THE RIGHT: Juvenile spider of the extinct family Lagonomegopidae in Lower Cretaceous amber from Burma, body length 1.2 mm. The spider existed about 100 million years ago. Note the very large eyes in a lateral position. See photo 90.

Fotos auf dem Buchdeckel (Körper vier außergewöhnlicher fossiler Spinnen):

Foto OBEN LINKS. Männliche Spinne der ausgestorbenen Familie Spatiatoridae in Baltischem Bernstein, Körper-Länge 4.3 mm. Diese Spinne lebte vor 40–50 Millionen Jahren. Ihr "Kopfteil" ist deutlich erhöht. Siehe Foto 139.

Foto OBEN RECHTS: Männliche Spinne der nahezu ausgestorbenen tropischen Familie Borboropactidae in Baltischem Bernstein, Körper-Länge 3.5 mm. Ihr vorderes Beinpaar ist als mächtige Fangbeine ausgebildet. Siehe Foto 380.

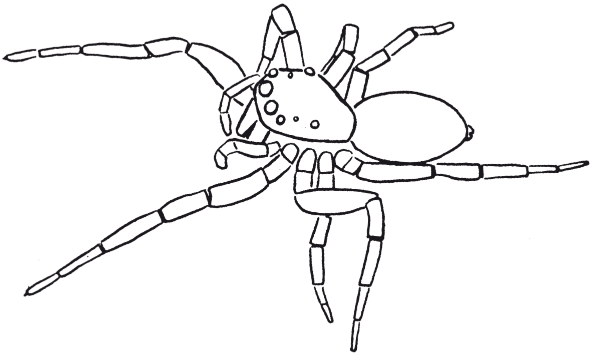
Foto UNTEN LINKS: Männliche Spinne der nahezu ausgestorbenen Familie Pumiliopimoidae in Baltischem Bernstein, Körper-Länge 1.9 mm. Eine vermutlich verwandte Art wurde kürzlich aus Nord-Amerika beschrieben. Siehe Foto 156.

Foto UNTEN RECHTS: Junge Spinne der aus der Unteren Kreidezeit bekannten ausgestorbenen Familie Lagonomegopidae in Burmesischem Bernstein, Körper-Länge 1.2 mm. Diese Spinne lebte vor etwa 100 Millionen Jahren und besaß ein Paar enorm entwickelte Augen in seitlicher Position. Siehe Foto 90.

Photos on the backcover of the book: Photo above: An extant Cretaceous spider from Brazil (Zygiellinae). Photo below: An extant spider from Australia (Theridiidae).

BEITR. ARANEOL., 5 (2008)

FOSSIL AND EXTANT SPIDERS (ARANEAE)



Editor and author:
Joerg Wunderlich

Joerg Wunderlich, 69493 Hirschberg, Germany

Print:
GROSCH! Druckzentrum, 69214 Eppelheim

Orders for this volume:
Publishing House JOERG WUNDERLICH
Oberer Haeuselbergweg 24, 69493 Hirschberg, Germany
E-Mail: joergwunderlich@t-online.de

ISBN 978-3-931473-11-2

BEITR. ARANEOL., 5 (2008)

FOSSIL AND EXTANT SPIDERS (ARANEAE)

Phylogeny, diversifications, extinctions, biogeography, ecology and ethology; with descriptions of new fossil and extant taxa

JOERG WUNDERLICH

Remark: Unfortunately just before the printing of this volume a defect in the software caused some trouble with the manuscript, e. g. some letters and words were lost or changed, and some corrections as well.

CONTENTS

KEY WORDS OF MOST PARTS OF THIS VOLUME
(see also the key words in the paper no. 5 on Cretaceous spiders):

Allometric growth, Anelosiminae, ants, Araneae, Araneidae, Araneomorpha, Archaeoidea, ballooning, Baltic amber, behaviour, biodiversity, biogeography, Bitterfeld amber, blood, Borboropactidae, Burma, Burmascutidae, Burmese amber, burmite, camouflage, Canada, capture web, China, cladistics, clasping spur, computer cladistics, co-evolution, colulus, connecting link, copal, cope’s rule, Corinnidae, C-Pg boundary events, courtship behaviour, Cretaceous, cribellum loss, decomposition, Deinopidae, diversification, dragline, dwarfism, ecology, Eocene, Eocene, Eopsilodercidae, epiandrous gland spigots, erroneous determinations, European amber forests, evolution, evolutionary trend, extinction, fakes of inclusions, “faunas connecting fossils”, Formicidae, fossil resins, fossils, France, fungi, Gamasomorphinae, Gondwanaland, healing events, healing system, Hersiliidae, historical biogeography, hot spot of biodiversity, hybrids, inclusions, intraspecific variability, Jordan, key, Kurnub, K-T (=C-Pg) boundary events, Lacunaucheniinae, Laurasia, Lebanoecobiinae, Lebanon, Lebansegestriinae, leg amputations, leg autotomy, leg injuries and healing events, leg regenerations, Linyphiidae, linyphioid branch, Liocranidae, Loxoscelidae, lumper, Lycosidae, Mecysmaucheniinae, Metinae, Micropalpimanidae, Microsegestriinae, mimesis, Mimetidae, mimicry, Miocene, Mizaliinae, morphological connecting (“missing”) links, Myanmar, Mygalomorpha, new taxa (subfamilies, tribus, genera, species), New Jersey, *Nanoa*, Ochyroceratidae, Oligocene, Oonopidae, orb web, Orchestininae, origin of taxa, palaeobiogeography, palaeofaunistic, palaeoecosystem, Paleogene, Palpimanidae, Palpimanoidea, Pangaea, parasites, pedipalpus, phylogeny, Pimoidae, Pisauridae, Plumorsolidae, Praeterleptonetidae, Praetheridiini, preservation, prey of spiders, Protheridiidae, radiation, relict taxa, resurrected genera, Psilodercinae, Pumiliopimoidae, Salticidae, Salticoididae, Segestriidae, Selenopidae, Sinopimoidae, Spain, spiders, splitter, stridulatory organs, surviving taxa, syninclusions, Synotaxidae, taxonomy, tendency, Tetragnathidae, Theridiidae, Thomisidae, trend, Uloboridae, USA, Zarqa river, Zodariidae, Zoridae, Zygiellidae.

ACKNOWLEDGEMENTS: See the different papers of this volume especially p. 531. I thank ALEX BEIGEL very much for scanning and reworking the slides/photos and some drawings and WALTER STEFFAN for helping me with the layout and preparing the final print!

INTRODUCTION

My aim twenty five years ago was to publish not more than three books on fossil spiders, but during the last five years more and more material (it includes quite strange Cretaceous spiders in amber) and new findings made me write a further paper on this matter, which has continuously been growing to a large volume of its own.

In this volume mainly fossil spiders are treated but also numerous extant taxa, including some new families, a large paper on spiders in Cretaceous ambers, a voluminous part on fossil Eocene as well as extant European Combfooted Spiders (family Theridiidae (*)), and another one on fossil and extant Zoridae s. l./Liocraninae. I always try to link the work on fossil spiders with related extant taxa.

(*) During the last years I have been intensively involved mainly with the study of extant and fossil European Combfooted Spiders (Theridiidae) – one of the worldwide most diverse spider families –, especially with their taxonomy and evolution as well as with the relationships of fossils and their extant kin. My curiosity was mainly caused by the fossil animals: Most of them are strange; only very few genera survived the Oligocene cooling period. Early Tertiary members of the subfamily Asageninae – which I take as an example here – possess a mosaic of ancestral and advanced structures. Their fossil taxa may play an important role in distinguishing ancestral and derived characters, e. g. in structures like the kind of the paracymbium; see also the family Tetragnathidae (paper no. 2). A change in the ecology of members of the theridiid subfamilies Asageninae and Enoplognathinae during the Tertiary – from the preference of higher strata of the vegetation and probably more tropical regions to ground dwellers of more temperate regions – became more and more distinct during my study.

Finds of – and findings on – inclusions in amber are undoubtedly “an endless story”; an unknown – surely high – number of taxa has still to be discovered in the future: Conspecific specimens have to be studied (a) to find the second sex which is unknown in most species, (b) to recognize more structures which are not or only inexactly observable in the specimen(s) which were already studied, and (c) to discover (e. g.) syninclusions like spider’s threads, egg sacs, prey, parasites, enemies and injuries. Thousands of undetermined fossil species of my private collection (now SMF), as well as of numerous private and museums collections are waiting for further studies.

According to my investigation the Early Tertiary European amber forests were “hot spots” of spiders diversity/diversifying, the Eocene faunas were quite more diverse than the extant European fauna, their study is a fascinating matter, and too much work for few investigators only. It is a pity that almost none of the taxonomical specialists of spider families – a dozen were asked by me – were interested or felt able to work on fossil spiders in amber; exceptions are DANILO HARMS (Mimetidae), BERNHARD HUBER (Pholcidae) and PETER JÄGER (Sparassidae).

In my books on fossil spiders in amber I want to give only a survey, and future generations of arachnologists and palaeontologists may profit by taking information and some hints from my work, may correct errors as well as conclusions, and may complete more and more our knowledge of the fossil spider faunas, revising family by family and/or genus by genus, e. g. the difficult Oonopidae: Orchestininae or the difficult genera

Episinus and *Lasaeola* of the family Theridiidae. The results of the first closer – but still quite fragmentary – study on the CRETACEOUS spider faunas are exciting and very promising; see the paper no. 5 on these spiders in this volume.

In some respect my descriptions of new fossil taxa may seem almost perfect but surely some are not. If I had several lives I would probably have the motivation – and the time – to work more intensively and accurately on certain fossils and on this matter in general; but my aim was mainly to give an introduction and overview on certain amber faunas and to draw new conclusions from the fossils on the biogeography, biodiversity, diversification, ecology, ethology, phylogeny, and taxonomy of spiders.

Thirteen papers of this volume are written in English, nos. 12 and 14 (more popular) in English and in German as well, and are placed near the end of this book.

Can fossils teach much about evolution, taxonomy, biogeography and behaviour? The answer – with respect to extant animals, too – is clearly "yes", and therefore fossils must not be ignored furthermore by revisers of extant generic or suprageneric spider taxa or by authors e. g. of catalogues of spiders. Certain structures – compared to structures and behaviour (fig. 1) of today's animals – allow conclusions on the behaviour of extinct spiders. Special and remarkable patterns of the mating behaviour: See below, the family Theridiidae. Parasitized spiders as well as spiders which are preserved with their prey – within their webs or not – demonstrate "frozen behaviour" of a world which existed 40 or even 140 million years ago, photos 1–46.

Peculiar fossil spiders in amber – e. g. so-called "missing links" – may provide the key for the understanding of evolutionary processes, for example in the families Archaeidae s. l., in the Combfooted Spiders (Theridiidae: e. g. of the relationships of their subfamilies), in Golden Silk Orb-weavers Nephilinae (Araneidae), in the Tetragnathidae (see paper no. 2), in Hackled Band Orb-Weavers (Uloboridae), Zoridae, and Jumping Spiders (Salticidae). The investigation of fossil spiders may give more important and more sure results on their evolution than the study of extant species or computer cladistics of extant taxa. For example certain fossils ...

(1) make it possible to establish the geological age of a taxon and the area of its origin, see papers nos. 3 and 5;
(2) can prove the extinction of a taxon (probably in a special area and era, paper 3);
(3) can help to recognize plesiomorphic/ancestral characters of a taxon (see e.g. the family Tetragnathidae, paper no.2, can give hints concerning the phylogeny, e. g. on the origin of families and subfamilies (*),"evolutionary trends" and co-evolution,
(4) can help to reconstruct
  – the palaeobehaviour (see the photos 1–46, fig. 1 below and the Orchestininae),
  – the palaeoecology (fig. 1), the frequency, and the palaeoenvironment,
  – the palaeobiogeography (see e. g. the paper no. 5 and the Spatiatoridae),
  – the palaeodiversity (see e. g. the papers nos. 3 and 5),
  – the palaeoclimate.

(*) Remarks on nominate subfamilies of spiders: (1) See e. g. WUNDERLICH (2004: 242–244) on Gondwanan spider taxa as well as the the papers on the Theridiidae and the Cretaceous spiders in this volume. Undoubtedly the Cretaceous spiders are much more important in this respect than the Tertiary spiders. – (2) Several nominate spider subfamilies – e. g. Tetragnathinae (Tetragnathidae), Theridiinae (Theridiidae) and Salticinae (Salticidae) – are the most diverse and most "typical" ones of their families today, and – as shown by their rareness or even absence of fossils in Eocene ambers – they are the geologically youngest, and at the same time – shown by their characters – they are the most derived subfamilies in contrast to ancestral and geologically old subfamilies. Examples of (relatively) old subfamilies are the Asageninae of theTheridiidae, the Linyphiinae of the Linyphiidae, and the Cocalodinae of the Salticidae, which all were frequent already in the Eocene European amber forests. – (3) Most ancestral groups of spiders occur in the tropics but for two hundred years most "classical" workers on spider taxonomy have studied the spiders of Europe and North America more intensively. So the most derived subfamilies of these continents have frequently been chosen as nominate subfamilies and not the more ancestral tropical ones; see also PLATNICK in FORSTER & FORSTER (1999: Foreword). Such derived subfamilies – like the Tetragnathidae: Tetragnathinae may even be quite "untypical" for their families; see paper no. 2 below.

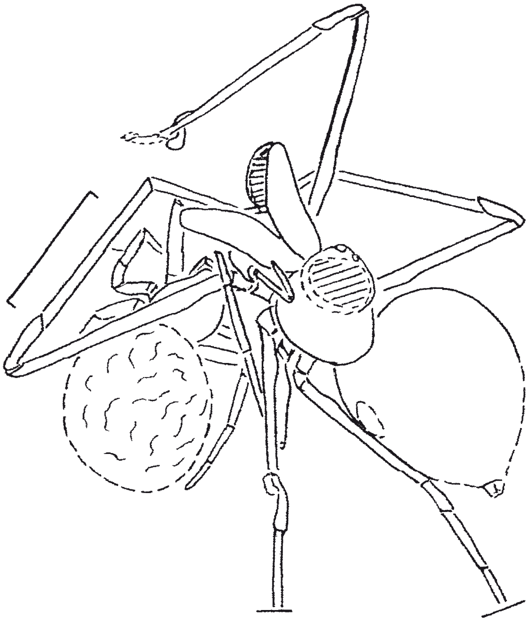


Fig. 1) Prey of a fossil spider, and a proof of fossil spiders as enemies of spiders: A female *Archaea* sp. indet. of the family Archaeidae (F 713/CJW) (at the right side) in Baltic amber, holding a juvenile spider of the Combfooted Spiders (family Theridiidae) as its prey. The opisthosomal folds of the Theridiidae indicate that this spider has been sucked out, and really was the prey of the archaeid spider. The long "teeth" of the chelicerae (which are recognizable on the right chelicera of the archaeid spider), and its strongly diverging chelicerae are – like in extant relatives – adaptations, which indicate the prey capture behaviour of these spiders. This pair of spiders demonstrates that already 40–50 million years ago members of the Archaeidae preyed on spiders as they do today; see WUNDERLICH (2004: 93–94, 98, fig. 5, photo 626). – Scale bar = 1 mm.

BEITR. ARANEOL., 5 (2008)

CONTRIBUTION ON FOSSIL AND EXTANT SPIDERS

JOERG WUNDERLICH, D–69493 Hirschberg.

Abstract and key words: See the contents and the key words above.

CORRECTIONS AND SUPPLEMENTS REGARDING VOL. 3 BEITR. ARANEOL. (2004) ("SPIDERS IN AMBER AND COPAL" BY J. WUNDERLICH)

In the following I want to correct some mistakes and errors of papers of the Beitr. Aranol., vol. 3 (2004); I also will add some remarks and several new findings/results.

Vol. 3A:

P. 8 (contents): Please add "Agelenidae. . . .1483" and "Zoropsidae. . . .1489".
P. 20: During the last four years I got not a single specimen which I wanted to get. Now I furthermore would like to spend 1000 Euros for a correctly determined CRETACEOUS spider which is noted in that list, and I enlarge the list by Lower and Mid Cretaceous members of the salticid subfamily Cocalodinae.
P. 110: F1306: With the ant a theridiid female is preserved which may be a member of the genus *Lasaeola* SIMON.
P. 154: Add to the photos the nos. 351 and 606–612.

P. 177: Add to the parthenogenetic extant spiders *Theotima minutissimus* (PETRUNKEVITCH 1929) (Ochyroceratidae), see EDWARDS et al. (2003).
P. 184: Add “photo 67” (*Baltarchaea*) to the paragraph (4) Mimesis.
P. 229: Micronetinae are rare but present in the Baltic amber.
P. 266 below: No fig. c) is published here.
P. 283: Correct terms: Add “pedicel” = “petiolus”. Theridiidae: *Lasaeola* not *Dipoena*.
P. 296: Tengellidae: Probably only some taxa are cribellate.
P. 640: Add to 13(12)...”Unpaired tarsal claw absent”, and to 13(12) –: “Unpaired tarsal claw present or absent (no. 16)”.
P. 641: Ochyroceratidae: In the present volume I upgrade the Psilodercidae from the subfamiliar rank; in contrast to the Ochyroceratidae the Psilodercidae possesses lungs.
P. 645: (1) Oonopidae: Add “converging labium”; (2) Leptonetidae: Their position may be wrong here: An egg carrying behaviour is absent, see COKENDOLPHER (2004) (correct also on p. 713), and a cribellum exists in certain taxa according to GRISWORLD (unpubl.). This family may be the sister group to the remaining families of the “branch of egg-carrying females”; (3) Ochyroceratidae: Add “a single spigot of the median spinnerets only”; (4) Pholcidae: Add: “Ventral comb of tarsus IV, and sticky droplets in the capture web” (“comb” has also to add on p. 737).
P. 658: (1) Delate the character of the labium; (2) add the character “position of the median eyes”: “between the anterior lateral eyes” in the Segestriinae and “between the posterior lateral eyes or between anterior and posterior lateral eyes” in the Ariadninae.
P. 661, relationships of *Vetsegestria*: Substitute “the labium is fairly wide” by “labium distinctly longer than wide”.
P. 761: (1) The name of the superfamily may be Archaeoidea (= Palpimanoidea) more likely than Eresoidea; see the note in the paper on Cretaceous spiders in this volume; (2) Lagonomegopidae: Add as diagnostic character “loss of the posterior median eyes”; (3) upgrade Stenochilinae to Stenochilidae; (4) Palpimaninae: (a) upgrade it to Palpimanidae, and (b) add “reduction of spatulate hairs of leg II”.
P. 768 below the middle: Substitute “pedipalpus” by “femur with a ventral hump and prolaterally...”.
P. 769: Add below the last line the character “size of ♀-pedipalpus"; Archaeinae: "weak, distinctly < femur III"; Mecysmaucheniinae: "ca = femur III or longer".
P. 777: change “fig. 25” to “fig. 42” (the bulging dorsal femoral structure).
P. 845 (fig. 11): Substitute “calamistrum” by “pseudocribellum”.

Vol. 3B:

P. 809: *Praetermeta* is a member of the Metinae, not of the Diphyinae.
P. 909: The number of metatarsal I–II bristles turned out to be 2 in *Anameta*.
P. 927 and 935: *Guizygiella* is not a member of the Zygiellidae but of the Araneidae.
P. 937: *Chrysometata palaearctica*: Figs. 53–57 (not 75–79).
P. 955: ?Zygiellidae gen. & sp. indet.: The spider may be a member of the family Protheridiidae; see the paper on Cretaceous spiders in this volume. The fig. was taken from PENNEY & SELDEN (2002).
P. 962: *Miraraneus*: Figs. 1–7 concern this genus.

P. 1031: Most probably the Micropholcommatinae has to add here.

P. 1033, add at the end of the key:

– Femoral organ absent, prosoma strongly raised, “peg teeth” exist at least on the cheliceral promargin. (= Textricellinae). . . . . .Micropholcommatinae
See also the end of p. 1043. Questionable proof of this taxon in Eocene French amber according to PENNEY (2007).

P. 1045: Add “Femur IV frequently thickened” before “*Fossilanapis*”.

P. 1058: 1 –: “Metatarsus I not dsitinctly thickened (fig. 81). . . . . .2”

P. 1078: *Dominicanopsis grimaldii*: The extant related species *Patu marplesi* FORSTER 1959 from Samoa is even slightly smaller, its body length is only 0.3 mm.

P. 1118: Mygalomorpha: Add the character “cuspules in labium and gnathocoxae”.

P. 1119: (1) RTA-clade, at the end: Substitute “bristles” by “Trichobothria”.
(2) Dionycha: Delate “presence of tarsal and 1 metat. trichobothria”.

P. 1134: Add to the diagnosis of the family Protheridiidae: “Convex prosomal profile, most probably all tarsal claws toothless.”.

P. 1141: Add to the diagnosis of the Protheridiini: “2–3 apical tibial bristles present.”

P. 1387: Hahniinae: a “scinny conductor” exists in this taxon.

P. 1539: The figs. 1–4 are taken from PETRUNKEVITCH (1958). Remark: The clypeus is really longer than shown in fig. 2.

P. 1585 and 1587: Lachesinae = Lachesaninae. The genus *Anniculus* is a member of the subfamily Storenomorphinae.

P. 1590: Storenomorphinae: Add “Dwellers of higher strata”.

P. 1613: Diagnosis of the family Clubionidae: Add “posterior median eyes circular, gnathocoxae long”.

P. 1614: *Massula*: Male, not juvenile.

P. 1623–1624: See the description of fossil and extant taxa of the family Zoridae (= Liocranidae auct.) in this volume.

P. 1656: *Protoorthobula bifida* WUNDERLICH 2004: I gave the male F7 as a present to the British Museum (A. ROSS).

P. 1659: Diagnosis of *Cryptoplanus*: Add “Clypeus long, position of the legs probably mediograde.”. The genus may be a member of the Family Zoridae (= Liocranidae).

P. 1737: Borboropactidae: See the revision in this volume.

P. 1749: Diagnosis of the family Thomisidae: Add “Chelicerae above the fangs with a row of strong hairs, as pointed out already by SIMON (1895: 950, fig. 1020); cuticula frequently granular; colulus usually reduced but large and hairy in *Epidius* THORELL 1877.”

P. 1767: I want to modify the chronocladogram: (1) The Lyssomaninae may be the basal sister group to the remaining taxa in which the median apophysis has been lost (but see the fossil genus *Almolinus*); (2) a synapomorphy of the Cocalodinae is the existence of a “SUBTEGULAR apophysis” which has been formerly mistaken as a median apophysis. Please correct the diagnosis of the Cocalodinae p. 1771–1772 in this sense. – Still no cretaceous salticid taxon has been reported.

P. 1825: *Succinero rovnoensis* WUNDERLICH 2004 is most probably a member of the extant genus *Ero* according to DANILO HARMS (person. commun.).

P. 1844: ?*Anyhops cortex* WUNDERLICH 2004 in copal from Madagascar is a junior synonym of the extant taxon *Gorcorops jadis* BOSSELAERS 2004.

P. 1864–1865: The female “Linyphiidae” (fig. 1) may be a member of the family Protheridiidae WUNDERLICH, see the paper on Cretaceous spiders in this volume.
P. 1894ff: Additional names of the index: Araneoidea. . . .1112f, Archoleptonetinae. . . .713, *Epidius*. . . .1750, Eresoclada. . . .1116, Eutychurinae. . . .1613, add photos 123–125 of *Graea*, Sternodini. . . . 1259, *Tegenaria* (photos 309–310). . . .1485.
P. 1907: Comarominae WUNDERLICH 2004 has to replace Balticorominae (nom. nud. by an error of the present author).

Remarks on J. DUNLOP’s (2005, 2006) reviews of J. WUNDERLICH’s (2004) “Fossil Spiders in Amber and Copal”:

I (JW) thank JASON DUNLOP – as well as other authors like G. BECHLY, O. KRAUS and G. POINAR (Jr.) – for reviewing my books (2004) – undoubtedly hard works! – Apparently J. DUNLOP overlooked some paragraphs within my books, and misunderstandings seem to exist within his review which I want to partly comment on:

(1) Long lists on specimens only, e. g. p. 100–112: (a) The list on p. 100–112 presents the diversity of fossil spiders’ prey in Baltic and Dominican amber in detail for the first time, including spiders’ webs, partly the condition of the prey and bite marks as well as the storage of the material. Such a list may be quite important for further palaeontological and entomological studies in various respects and for statistics. The underlined names of insects help quickly to find the order which is looked for. Therefore I think the many hours of work on this list were not superfluous. (b) Furthermore every piece/specimen of a fossil shows unique features/structures – as injuries, hidden or excellently recognizable structures, as well as emulsions and syninclusions – which all may be important for further studies and for borrowing a certain specimen, and only this one. (Such implications may not be easily understood by a palaeontologist who is working mainly on the taxonomy of taxa which are represented by single specimens only).
Remark: I think that most of the readers will be clever enough to recognize that my books are different from novels and so will skip special lists (as well as certain paragraphs in German).

(2) Figures taken from other publications: The origin of the figs. which are taken from other authors is noted. The photos were taken partly in exchange with photos from my private collection. Except for figs. which were published more than fifty years ago I personally asked most of the authors (e. g. BELLMANN, DEELEMAN, MURPHY, ROBERTS, WEITSCHAT and ZSCHOKKE), who allowed the publication of photos and figs., and I told this to the reviewer but he was not willing to delete this – and some other incorrect parts – of his review. J. DUNLOP overlooked or ignored apparently furthermore a paragraph on this matter on p. 18 within the chapter “Acknowledgements”.

(3) Absence of standards of modern systematics : According to DUNLOP numerous taxa are (a) based solely on extinct species and are (b) rarely compared with extant species (!). (a) As published by several authors by far most of the Early Tertiary spider genera are extinct, – according to WUNDERLICH (2004: 206) 88% –, and therefore almost 9/10 of the spider genera in Baltic amber are based on extinct species which possess no known congeneric extant relatives.
(b) A major part of my work during the last thirty years was to find relationships between fossil and extant spiders. I found such relationships within numerous families and subfamilies – e. g. in the Borboropactidae, Comarominae, Corinnidae, Hahniinae, Leptonetidae, Mimetidae, Nesticidae, Pimoidae, Salticidae, Segestriinae, Uloboridae and Zygiellidae – but I failed to find sure closer relatives for example of or within the Baltsuccinidae, Copaldictyninae, Ephalmatoridae, Insecutoridae, Protheridiidae, Thomisidae, Trochanteriidae as well as close relatives of most genera of the Synotaxidae and the Zodariidae. Probably no close extant relatives exist any more or they live hidden/unknown in tropical rain forests; of course some taxa may have been overlooked by me. I am glad to leave numerous questions and answers to further generations of araneologists...
(c) If “standard of modern systematics” sensu DUNLOP means computer cladistics: See below, the chapter “Methods”, and the paper on the family Theridiidae in which I discuss the apparently wrong main results regarding the relationships of theridiid subfamilies which were based on this method, see also Beitr. Araneol., 3 (B): E. g. p. 1493, and BECHLY (2000).

(4) “One-man Show”: (a) Co-work of other authors: Apparently the reviewer overlooked my regretful remarks on potential co-workers, p. 12; see also above (no interest of workers on extant taxa like Salticidae, Theridiidae or Zodariidae). – (b) Publishing House of my own: A publication in another Publishing House would have caused at least the double price of the volumes in question.

(5) Storing the fossil material in an institution. (a) DUNLOP overlooked the explicit note regarding the SMF (p. 19) among institutions which have already got – and will get more – type material which was published by me. He criticized the absence of numbers of (pieces of) the collection but numbers of my collection (CJW) were actually published by me. In some Museums it takes some time to place numbers of their type collection but via computer it is no problem to find type material in the future. Material from my private collection – stored in my private laboratory – is available directly from me by posting in contrast to some museums, e. g. the Geological Museum Copenhagen and the Museum Palanga (Lithunia); I had to visit the first museum to study type material. – (b) According to DUNLOP (p. 34) the reader may know in a hundred years to which museum(s) I will give my fossil material. It is great to know that in one hundred years I will be still alive and able to present my collection of fossil spiders to a museum of my choice. Thank you, dear Jason, for your optimistic view of my longevity! The reader may know herewith that the type material of spiders which were described by me has been deposited in the meantime mainly in the Senckenberg-Museum, Frankfurt a. M., in the Museum für Naturkunde in Görlitz, and in the Palaeontological Institute of the University Hamburg as well.

Final note: My books deal with for the most part on spider taxonomy and phylogeny. Is’n it really a shame that the editors of the “Arachnologische Mitteilungen” did not find an araneotaxonomist as a reviewer of the “Fossil Spiders in Amber and Copal”? K. THALER started to prepare a review but he unfortunately passed away so early.

MATERIAL

(1) Origin of the material and the collectors

Extant material: Most extant spiders were collected by the present author in various parts of the world, mainly in Europe, numerous species on the Canary Islands.

Eocene fossils: The material comes usually from the Kaliningrad (Koenigsberg) area if not otherwise stated than “Baltic amber”, but the origin of certain material is not quite sure because dealers may have mixed material from other deposits – e. g. from Poland and even from Germany (Bitterfeld) – and changes by mistake may happen, see WUNDERLICH (2004: 33). I got most spider inclusions from dealers from Germany, Lithunia, Poland and Russia, numerous pieces from private collectors and friends and some pieces (type material) from different institutions, e. g. Ukrainean (Rovno) amber – mainly Theridiidae; see the paper on this family in this volume – from E. PERKOVSKY (Museum Kiew).
Cretaceous fossils: See the paper no. 5 on Cretaceous spiders in this volume.

(2) Storing the material and main Institutions:

BMNH = British Mueum of Nastural History London,
CJW = private collection of J. WUNDERLICH, Laboratory of Arachnology in 69493 Hirschberg, Germany. – Note: Most parts of my present and previous collections have been given to three museums in Germany: (a) to the SMF, (b) to the SMNG, and (c) to the GPIUH (fossil spiders only); the remaining Theridiidae will most probably go to the SMF;
ERMNH = Eternal River Museum of Natural History in Jordan (Amman) (still in construction) (H. F. KADDUMI),
GPIUH = Geological-Palaeontological Institute, University Hamburg, Germany (W. WEITSCHAT),

GZUG = Geowissenschaftliches Zentrum Univ. Göttingen (M. REICH) (*), previously:
MGG = Museum für Geowissenschaften Göttingen (now GZG),
MGMC = Mineralocical and Geological Museum Copenhagen (see also ZMC),
MNHUB = Museum für Naturkunde der Humboldt Universität Berlin,
MNHNP = Musem National d'histoire Naturelle Paris (fossils: D. AZAR),
NHMLP = Natural History Museum London, dept. of Palaeontology, England (A. ROSS),
OSU = Oregon State University, Corvallis, USA (G. POINAR jr.),
PMHU = Paläontologisches Institut (Museum für Naturkunde) der Humboldt Universität Berlin (C. Neumann),
SMF = Senckenberg-Museum, Frankfurt a. M., Germany (P. JÄGER),
SMNHS = Staatl. Mus. f. Naturkunde Stuttgart (G. BECHLY),
SMNG = Staatliches Museum für Naturkunde Görlitz (A. CHRISTIAN),
ZMC = Zoological Museum Copenhagen,
ZMHU = Zoological Museum of the Humboldt University Berlin.

(*) The coll. M. KUTSCHER (amber from Bitterfeld) is now kept in the GZUG.

(3) Preservation of the material

During the deposition of ca. 40–50 million years within the “Blue Earth” of Kaliningrad (In German: “Blaue Erde” von Königsberg) the surface of amber pieces changed to a brown or redbrown colour and became more or less fissured, crumbly and destroyed. Also certain organic inclusions as plants, insects or spiders – which had contact to the amber’s surface – may have been destroyed by “aging” (e. g. oxidation and drying out), see the photos 22–23. This photos – the piece no. F1602 of the collection JW – shows a juvenile fossil spider in Baltic amber, body length 2.7 mm, which is so strongly destroyed that a close determination is impossible. Some leg articles were in contact with the amber’s surface so that the destruction – oxidation, drying out – of the inclusion happened already during million of years of deposition within the “Blue Earth”. The surface of the spider’s body and legs consists of numerous small cracks and irregular honeycomb-shaped structures; only most of the leg bristles are preserved.

Out of their deposit – and especially in pieces which were polished by man – similar processes may take place in a relatively short time of few decades (younger Dominican amber may change much faster); pieces of amber and their organic inclusions may break in small particles. Type material of arthropods which were described by KOCH & BERENDT ca. 150 years ago has been strongly darkened so that the sclerites of spiders bulbi are very difficult or even not recognizable any more, structures altered irreversibly, see WEITSCHAT & WICHARD (2002: Figs. 20a, b), the photos 166–167. Some Inclusions which were “mounted in clarite” by PETRUNKEVITCH – see PETRUNKEVITCH (1942: 133, 141) half a century ago are also strongly darkened by heating – see the photos 169, 189 and 263 – and frequently male genital structures are not recognizable any more; the colour of the amber changed partly to red brown and dark brown, increasing in direction to the surface of the amber. This is a very seri-

ous situation: A very large number of important scientific material – including numerous holotypes – is lost forever for a detailed revisional study! Apparently certain curators were not interested in the protection of scientific material and ignored their responsibility. In my opinion this is nothing else than a cultural shame and comparable with the destruction of works of Picasso or Monet. Recently certain – ignorant – humanities scholars proposed to scan instead preserve fossils but there is a strong and evident different in these matter: It is much easier to document pictures than fossils: A scanned reproduction of a drawing, painting or a photo – besides of all original material which would be lost in both cases – may show much more details than a scanned document of a three-dimensional fossil in amber in which microscopic structures as well as molecular structures are not preserved and may be lost forever with the original piece.
In contrast to most other material which is preserved for a longer time the “hypotype” of *Episinus longimanus* (photos 306–307), kept in the AMNH for more than half a century, is still in a very good condition. The medium in which this piece of amber has been embedded is unknown to me.
The preservation of amber and its inclusions within artificial resin was proposed, described and manualed e. g. by GRÖHN and by HOFFEINS (2001). Although we have no information on long-term effects with this medium this may be an acceptable or even optimal method of preservation of amber inclusions.
Regarding the preservation: See also the chapter on “Preservation of selected structures of the inclusions” below.

(4) Selection of holotypes and the importance of paratypes in fossils

If there exist more than a single specimen of a new species – usually it is a male – I selected as the holotype the best preserved specimen and – most important! – the peculiar male which possesses the best recognizable structures of the bulbus.

Remark: Paratypes are quite more important in fossils than in extant material: Besides findings on the intraspecific variability, the position and the kind of preservation, paratypes may allow conclusions e. g. on the mode and season of their embedding and the behaviour of a certain species, syninclusions may tell about their biotope and habitat, their enemies, their prey and their method of prey capture, as well as the kind of their capture webs. Microstructures as sense organs, hairs of the colulus, spinules, and structures of the bulbus are never well preserved alltogether in a single specimen. Finally a paratype may be identified as a species of its own by a revising author.

TECHNIQUES OF STUDY AND DOCUMENTATION

Remark: The chapter on “techniques” is mixed and confused with the chapter “methods” by most authors.

Polishing, handling, preparation: See also WUNDERLICH (2004: 21).
For polishing the amber an instrument of the firm HAMAG was used which allows cooling with the help of water. The photos – slides Kodak professional 100 – were taken with the help of a Minolta camera SRT 101 and a binocular microscope of LEITZ.
To get a plain and smooth surface of the amber I drew and photographed some of the pieces under paraffin or coated them with a thin layer of paraffin, oil or glycerine.
I did not use a REM; a REM cannot be used for studies of inclusions in amber except the amber is broken off and structures are free from the fossil resin. But – under a high magnification – fine structures like colular hairs, emboli or epiandrous gland spigots are well recognizable with the help of the light microscopes which I used.
Some dealers used and use an autoclave to clear inclusions in amber by heating and by pressure, see the photo 287. The result may be a helpful reduction of the white emulsion on the surface of an inclusion including its genital structures, but the inclusion may be more or less darkened, deformed or even partly destroyed, the genital structures, too, and a wrong determination of the taxon may result. This technique is also used to produce fakes, see the photo 12, and the photo 83 in the book of WUNDERLICH (2004).
Benzylium benzoicum (C14H12O2) may be used to “clear” fissures in pieces of amber; frequently it enters the gaps of the layers (mainly in material which is freshly polished). Unfortunately certain fine structures – like wings of Diptera – may be darkened or modified otherwise by this substance, compare the photos 688 and 689 in the book of WUNDERLICH (2004: 590). One has to be very careful with this substance.

METHODS OF THE STUDIES

The aims of a study determine their main methods. I tried to find out the range of the diversity of fossil spiders faunas which are preserved in different ambers, as well as indications on spiders phylogeny and palaeobiogeography, “frozen behaviour”, spiders webs, parasites, injuries, decompositions etc. Therefore I tried to study more or less closely all the material which was available, the incredible number of more than 100 000 specimens of fossil spiders in amber and copal (subrecent).

For the taxonomic work I endeavered to study as many as possible adult spiders and compared them with type material and related extant species. So in many cases I was able to document numerous characters of the species which are not recognizable solely in the holotype (but in paratypes), and in numerous cases I found the intraspecific variability of certain taxonomically relevant structures, e. g. the number of hairs on the colulus (paper no. 3).

Regarding the descriptions of the species I focused on the documentation of the genital organs which are most important in identifying and distinguishing most species of spiders. Therefore I described only very few new species which are based on juveniles, but I selected males whose genital structures are more proper for a differenciating diagnosis (see the photos 168, 327), and which are usually better visible than genital organs of the rare females which most often are covered with a white emulsion and whose internal structures are only exceptionally recognizable. On the other hand taxonomic important non-genitalic structures have never to ignore, especially sensory hairs like trichobothria.

Computer cladistics and “traditional” methods: Regarding conclusions on the relationships of higher taxa I tried mainly to find out and want to consider such structures which are most important in a taxonomical sense: Structures which are very peculiar and rare, probably more constant within a taxon and connected with other particular structures. Convergences as well as the intrageneric and intrasubfamiliar variability of certain structures had to cheque; an example: The discovery of quite different kinds of paracymbia in well related taxa – see the theridiid subfamilies Asageninae and Episinae – restricted evidently the taxonomical value of this structure(s). The use of FOSSILS: With the help of fossil spiders I became aware and discovered the existence of a colulus in members of certain Theridiidae like Anelosiminae and Episinae probably for the first time. I tried to identify (a) convergences – which may be caused by ecological reasons like the kind of prey – and (b) reversals, which may be difficult to realize. Based on fossils the diagnosis of higher taxa may change: Eocene Nephilinae possess a median apophysis in contrast to extant kin, in fossil *Pimoa* are cheliceral stridulatory files absent in contrast to extant *Pimoa*; see also the papers nos. 3–5 and 13.

I did not focus on the numberless simple structures which cause useless/stupid conclusions to computer cladists; see WUNDERLICH (2004: 114) and BECHLY (2000). Computer cladistics do not (enough) evaluate the COMBINATION and CONNECTIONS of important taxonimic characters.

Finally: In recent papers of computer cladists a very restricted number of species is used which is not representative for the whole group – e. g. the family Theridiidae – which is studied in this book, see below: The intra-subfamiliar variability of the colulus (including its hairs), the shape of the labium as a subfamily character of the Hadrotarsinae or shape and position of the paracymbium within the Asageninae, Enoplognathinae and Episinae. The main conclusions of a whole paper may be incorrect if it includes only a very restricted number of taxa, if the variability of taxonomic important structures is not chequed in a wide range, and if convergences are not closely discussed. Incompetent reviewers with a special inclination (to a peculiar author) “overlook” very often such faulty methods, see WUNDERLICH (2004: 114).

PRESERVATION OF SELECTED STRUCTURES OF THE INCLUSIONS

Preservation of external and internal structures, organs and remains of fossil Theridiidae: Remains of muscles in leg articles are occasionally preserved, see the photo 17 and WUNDERLICH (2004: 27–31, photos 151, 184). – Structures of the vulva of *Lasaeola* sp. indet. (F1675/BB/CJW, fig. below and the photos 282 and 284) (Theridiidae) are preserved and visible in a unique way including the receptacula seminis and the introductory ducts. See also the vulva structures of *Protoorthobula bifida* WUNDERLICH 2004 (Corinnidae), photo 381 in the book of WUNDERLICH (2004). – Male genital organs and spematozoa: The structures of the bulbus are excellently preserved in numerous fossil spiders, see the figs. and e. g. the photos 168, 327. – Questionable remains of sperm are preserved at the tip of the embolus of a male of *Eomysmena crassa* (PETRUNKEVITCH 1958) and *Hirsutipalpus varipes* n. gen. n. sp. (Theridiidae: Asageninae), see the drawings. – In certain cases spigots of epiandrous glands and of spinnerets are well preserved (*), see e. g. *Succinomus duomammillae* n. gen. n. sp (Zoridae s. l.), and *Sosybius kochi*, see WUNDERLICH (2004: 1725, figs. 7–10) (Trochanteriidae). – Occasionally remains of blood are preserved at the stumps of autotomized legs beyond the coxa, e. g. in the male paratype of *Lasaeola sexsetosa* n. sp. (Theridiidae) (F1544/BB/ AR/CJW) (photo 278), and in a member of the family Linyphiidae, see WUNDERLICH (2004: 435, photo 254). Remains of questionable poison: See *Hirsutipalpus varipes* and WUNDERLICH (2004: 29, fig. 2, photo 389). Remains of spider's threads are not rare: Parts of capture webs including remains of sticky droplets and prey which is spun in (in members of the superfamily Araneoidea), egg-sacs and – frequently overlooked – draglines (e. g. photos 45–46) are preserved for example in numerous members of the family Theridiidae (paper no. 3) and below ("Frozen behaviour").

Original colour of the body: See e. g. photo 238, *Succinura* sp. (Pholcommatinae).

Healing events may (have) exist(ed) in fossils of the family Theridiidae (see below): Enoplognathinae (e. g. *Hirsutipalpus varipes*), Hadrotarsinae and Asageninae (e. g. *Eomysmena* sp. indet., F1703/CJW), photos 9–11, see below – as well as in the family Zodariidae; see WUNDERLICH (2004: 154–157). (Extant spiders: Photos 1–7).

I observed few cases of a natural break in the fossil resin right through an organic inclusion. Such a break is present in the small piece, F1683/BB/AR/CJW, which includes a Theridiidae indet.. This piece of amber is of special interest because it allows conclusions on the process of fossilization. It was heated by man, has a size of 14 x 8.5 x 2.2 mm and consists of ca. 6 floods of resin within the height of only 2.2mm. 3 mm below and right behind the spider a spider's thread is preserved which is 3 mm long and bears small droplets; it may be part of a former capture web of the spider, a juvenile male which is 2.1 mm long and is probably a member of the family Theridiidae. The dorsal half of its opisthosoma as well as the right patellae II and III are cut off (photo 21). Apparently the opisthosoma has eaten out – probably by an ant – and has been broken almost longitudinally through the middle of the piece of resin and the opisthosoma as well; both halfs drifted sidewards. The gap is up to 0.1 mm wide and is continuing beyond the margins of the opisthosoma. A flood of resin filled the opisthosoma and the gap. Later on another flood covered the piece at least dorsally of the spider; remains of this layer are preserved on the surface of the amber behind the spider's opisthosoma. Finally – 40 or 50 million years later – the piece of amber was polished by man; so we do not know its original size.

From this piece we may conclude that the resin has been quite liquid and that – because of the presence of the gap within the amber – the resin may have hardened very fast.

(*) According to the erroneous note of PENNEY & ORTUNO (2006: 3) spigot morphology is "not visible in fossils" but even spinning tubes are well recognizable in various specimens; see WUNDERLICH (2004: E. g. the photos 92–93, 305 and 547).

"Frozen behaviour" and ecology. I focus on members of the family Theridiidae; see also e. g. the paragraph above, the paper no.1 below (the rarity in fossil members of the family Tetragnathidae), and the paper on Cretaceous spiders (paper no. 5):
Conclusions from the kind of preservation and from syninclusions: (a) Frequently the Eocene amber spiders are partly covered with a WHITE EMULSION, mainly the opisthosoma (photo 30), and most often the ventral side. The emulsion results from tiny bubbles of liquid, which get out from the spider's body. This white emulsion may disappear during heating which may have caused by sunshine on the fresh resin or artificially by men with the help of an autoclave (a process of "clearing"). Most spiders moved with their ventral side to the sticky resin, and therefore only the dorsal side was cleared by the sun in contrast to the ventral side in the shaddow of the body. The holotype of *Euryopis nexus* n. sp. – see the photo 293 – is one of the exceptions; apparently it was captured by the resin with its dorsal side, and only its ventral side was cleared, but probably this spider was embedded below the bark and only the ventral side was artificially cleared by men. – (b) INJURED fossil spiders in which the opisthosoma was impressed by a blow – and the spider was killed – are not so rare in Baltic amber, e. g. in Theridiidae; examples are some specimens of the rare species *Kochiuridion pecten* n. gen. n. sp (Theridiidae), see the photos 339–340. Some of those spiders which became enclosed by the resin a short time after killing are more or less decomposed, photos 18–21. – (c) Syninclusions with some specimens of *Kochiuridion pecten* are coffee-pear shaped POLLEN GRAINS (photos 341–342) which originate from oaks or related Fagaceae – which do not produce resin – but not from the resin-producing needle-trees (Pinaceae). From the rarity of these spiders in Baltic amber, their frequently injured specimens and the relatively frequent syninclusions of Fagaceae pollen grains I conclude that these spiders were dwellers of Fagaceae which occasionally were transported by a storm to the resin-producing needle-tree. – (d) PARASITISM: See the photos 26 and 359. – (e) PREY: See the family Theridiidae; e. g. the photos 27–38.

Amputations of legs in fossil Theridiidae (photos 8–11), especially in the Asageninae and the Hadrotarsinae, are more frequent than in all other fossil members of the superfamily Araneoidea; examples are preserved e. g. in members of the genera *Clya* PETRUNKEVITCH, *Eomysmena* PETRUNKEVITCH (Theridiidae: Asageninae), *Hirsutipalpus* n. gen. (Enoplognathinae), and in *Episinus nasuticymbium* n. sp. (Episinae). These spiders feed mainly on ants which is a dangerous prey and which may cut off spiders legs with the help of their powerful mandibles.

Cannibalism (photos 29–30): See below, Synotaxidae: *Acrometa ?cristata*, Theridiidae: *Clya obscura*, *Eomysmena* sp. indet. (F1698/CJW), *Hirsutipalpus varipes* n. sp., and WUNDERLICH (2004: 113).

Remains of capture webs are occasionally preserved with fossil spiders, sticky droplets for example with members of the Theridiidae: Asageninae (paper no. 3), e. g. *Eomysmena* sp. indet., F1698/CJW, see the photos 40–41, 52–59.

Fossil draglines, bridging threads and ballooning lines. Draglines with fossil spiders in Baltic amber are not too rare – see the photos 45–46, WUNDERLICH (2004: 67–70, photos 565–573) and below, e. g. Theridiidae – but they are sometimes hard to recognize and easily to overlook. – Up to now I failed to find a sure ballooning (aeronautic) line in a fossil spider; I found only threads which originates from the anterior spinnerets. According to FOELIX (1996: Fig. 97) bridging threads may be build by the anterior AND the median spinnerets as well.
Already about one hundred years ago (!) the famous French entomologist J. H. FABRE – Souveniers entomologiques; translation into German in "Kosmos", (1911: 380, fig. 2) – described the behaviour of ballooning spiderlings, and he showed the production of – really ballooning? – threads by the median spinnerets in a member of the family Araneidae, see fig. 2.

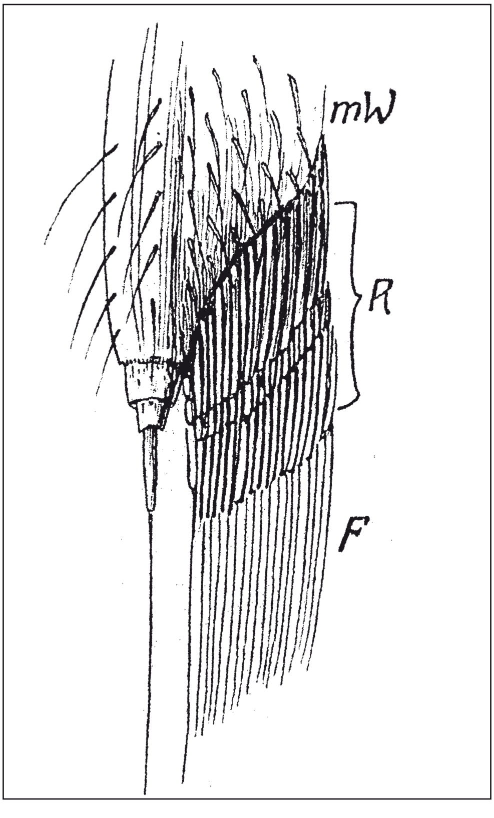


Fig. 2) A thread-producing median spinneret of a member of *Araneus diadematus* (family Araneidae). – mW = median spinneret, R = two strong and numerous fine spinning tubes, F = threads which originate from these spinning tubes. – Taken from a figure which was drawn by J. H. FABRE ca. 100 years ago.

FAKES OF INCLUSIONS, IMITATIONS AND CHANGES BY MISTAKE

See also WUNDERLICH (2004: 33–41).

(1) A Wolf Spider (Lycosidae) in “Baltic amber” (photos 15–16)

Material: A piece of amber as well as artificial resin which contains an extant juvenile female of the family Wolf Spiders (Lycosidae), coll. ERNST/NORDMANN in Skagen (Denmark). According to P. ERNST the origin of this piece is Lithunia or Poland; it was sold to him as an imitation.

Description and discussion: The piece (photos 15–16) is a chimera, 7.3 cm long: One part is Baltic amber; this part was sticked on a yellowish piece of artificial resin which contains the spider. I identified the spider as *Alopecosa* sp. indet. of the family Lycosidae. It is a juvenile female and has a body length of 6 mm. Spiders of this family prefer open/sunny biotopes and such spiders are only scarcely expected in Baltic amber. A member of the Lycosidae has never been found in Baltic amber and probably will never be found because it supposingly is a geological young family, see WUNDERLICH (2004: 20, 1557–1558). A member of the subfamily Argyrodinae (Theridiidae) has also never been found in Baltic amber, see below (paper no. 3).

(2) An Orb Web Spider (Araneidae) in “Baltic amber” (photo 14)

Material: *Araneus* ?*diadematus* CLERCK 1757, ?ad. ♀ in artificial resin which is mixed with pieces of Baltic amber, bought by me as "Baltic amber" on Mallorca (Pollenca) in 2006, a faked inclusion which has probably been produced in Poland or Lithunia, FF1840/AR/CJW.

The size of the piece – a chimera, too – is 53 x 36 x 16 mm, the spider is complete and has a body length of 10.5mm; the dorsal side of its opisthosoma is strongly deformed (injured and probably dried out), the ventral side is hidden, the legs are spread out on a layer of artificial resin or plastic. In the layer below of the spider six pieces of Baltic amber are enclosed (well observable against light) which bear a stellate hair and some oxidated crusts on their surfaces. The orange pieces of amber give the piece a colour which is similar to Baltic amber. The underside of the piece is rough, contains numerous bubbles and appears at first sight like a piece of amber. Determination: I identified the spider as a probably adult female of the genus *Araneus* CLERCK 1757 (Araneidae) which is unknown from Baltic amber, and probably as a member of the well-known and widely distributed species *diadematus* CLERCK 1757.

(3) A Combfooted Spider (Theridiidae) which is said to be preserved in Baltic amber but more likely is embedded in heated copal from Madagascar

(Photos 12–13, fig. 445)

Material: *Argyrodes* sp. indet., 1♀, in a piece of resin among ca. 1000 pieces of Baltic amber of the Mus. Copenhagen; coll. BORGE MORTENSEN I–II 1964.

Preservation and syninclusions: The piece of resin has been broken into two pieces and has a drilled hole at one end; the small piece has been used for investigations, see below. Its size is 2.6 x 1.7 x 1.2 cm, its surface has distinct fissures, its colour is orange-brown. The spider is situated just below the surface at a corner of the piece, most parts of its anterior prosomal part, the anterior legs and the pedipalpi are cut off, its body and legs are deformed and darkened probably by heating, remains of a white emulsion are absent, few bubbles are preserved but no stellate hairs or other syninclusions.

Description of the spider which is partly cut off, darkened and deformed, see above: The legs are slender, femur I is 1.5 mm long, dorsal tibial bristles are absent, the opisthosoma (fig. 445) is 2 mm long, slender and widely extending beyond the spinnerets, the epigyne is protruding.

Discussion: The shape of the opisthosoma and the bristle-less tibiae are typical for members of the theridiid subfamily Argyrodinae, tribus Argyrodini, the extant cosmopolitical – mainly tropical – genus *Argyrodes* SIMON 1864. The shape of the opisthosoma may be fairly similar to *Caudasinus* n. gen. (Theridiidae) in Baltic amber but in *Caudasinus* the tibiae bear bristles and the opisthosoma is shorter. – From my test of the piece which include the specimen of *Argyrodes* in 95% ethanol – three times a droplet was given on the surface of the piece in question – resulted a distinct solving and a grey cover similar to copal but this is similar to old and darkened pieces of Baltic amber.

Results from investigations of Dr. N. VAVRA (Wien): No amber acid, terpene or borneol were found. The piece is surely a natural resin, not an artificial resin, and was most probably heated; the origin of Baltic amber can not be excluded.

Among ca. 100 000 spiders in Baltic amber a member of *Argyrodes* and the Argyrodini SIMON has never been found (besides this specimen of questionable origin). I know similar spiders of *Argyrodes* in copal from Madagascar (CJW) and in Dominican amber. Since a long time heated copal from Madagascar has been sold as Baltic amber, see WUNDERLICH (2004: 33ff). Remains of a white emulsion and stellate hairs as syninclusions – both are characteristical for most inclusions in Baltic amber – are absent in this piece but a white emulsion is frequently absent in heated Baltic amber.

Conclusion: From these findings I conclude that this piece of natural resin is most probably not Baltic amber but very likely heated copal from Madagascar. I suppose that it is a fake. Such a fake was a great surprise to me because it has been mixed among a very large number of pieces of true Baltic amber several decennia ago.

(4) A probable fake or a change by mistake

The holotype of the armoured ?*Stenoonops rugosus* WUNDERLICH 2004 (Oonopidae) was described in questionable Baltic amber but it may be changed by mistake from Dominican amber, see WUNDERLICH (2004: 33, 692) or from copal. All the remaining spiders of the family Oonopidae in Baltic amber – a saw thousands of specimens – are members of the genus *Orchestina* SIMON but an apparently related armoured species has been reported from Dominican amber.

PHYLOGENETICS and BIOGEOGRAPHY

Origin of certain (sub)families of the superfamily Araneoidea: See below (the family Theridiidae, paper no. 3, and paper no. 5 on Cretaceous spiders).

Evolutionary "trends": See below (papers on theTheridiidae and on Cretaceous amber spiders). A "trend" seems to exist to evolve a larger body size within certain phylogenetic branches of spiders, similar to "Cope's rule" in mammals. Apparently the smallest members of several taxa – e. g. certain genera of the Segestriidae and Theridiidae (like certain members of *Episinus* (Episinae) and of the Asageninae) as well as of the family Zygiellidae – became extinct during the Tertiary; the reasons are unknown. The largest males of the diverse family Salticidae in Baltic amber are less than 5 mm but extant European bark-dwelling Jumping spiders like *Marpissa muscosa* possess a body length of 7.5–10 mm. On the other hand exists dwarfism which concerns whole families; an example: The quite tiny Dwarf Spiders (Erigoninae) were still absent in the Eocene but they are today the most diverse subfamily; members of the remaining subfamilies of the Linyphiidae are larger spiders. – In the theridiid evolution – like in other families – the trends exist to reduce the size of colulus and leg bristles, and probably of sticky droplets within the capture web, too, as well as to shift an ectal to an internal paracymbium, see below (Theridiidae, paper no. 3).
Eyes: Reduction of certain – basically eight – eyes is not rare, even among non cave-dwelling spiders. Most often it concerns the loss of the "main eyes" (the anterior median eyes) in/among small or tiny spiders. The basic position of the eyes in spiders is similar to the related Amblypygi and to *Pholcus*: A pair of anterior median ("main") eyes possess everted rhabdomeres, the remaining six ("secondary") eyes build two groups of lateral triplets and have inverted rhabdomeres. The consequence of the "drifting" apart from the secondary eyes – and their new position in two rows – was a widening of their range of vision. The posterior median eyes "moved", apparently simultaneously, and usually onto the former position of the lost anterior median eyes, especially in the superfamily Dysderoidea, see WUNDERLICH (2004: 643, 650–651) (the genus Dys-

dera LATREILLE 1804 – in which the anterior lateral eyes moved to the middle – is an exception). A loss of the anterior median eyes existed already in (most of the) Lower Cretaceous spiders, see the paper on spiders in Cretaceous ambers (paper no. 5); frequent is the "segestriid position" of the eyes in which the posterior median eyes did not shift to an anterior position. – Such a loss of the anterior median eyes is frequently connected with dwarfism, e. g. in numerous Anapidae s. l., certain Theridiidae, and most Dysderoidea (up to a single eye in a species of the Tetrablemmidae!); it is quite rare among the "advanced" members of the RTA-clade (reductions/losses exist e.g. in certain small or tiny members of the Dictynidae).– The reason(s) for the reduction/loss of the anterior median eyes may be connected (a) with a dwarfism of the spiders in question (the body size may have increased secondarily in some of these taxa during the Tertiary after the loss of the anterior median eyes, e. g. in Dysderidae, Loxoscelidae, Segestriidae, Sicariidae as well as in certain Pholcidae and Scytodidae), (b) with the function of certain mouth parts – see WUNDERLICH (2004: 650) –, and (c) with a process of functional concentration/specialisation to a smaller number of eyes, and with the evolution of only a single type of eyes, the inverted ones.

The size of the lenses of the POSTERIOR MEDIAN EYES decreased during the early evolution of the Salticidae (their anterior median eyes increased at an unknown era before that); they were still large in most spiders of the Early Tertiary Baltic amber forest, see WUNDERLICH (2004: 1766), but today large posterior median eyes exist – almost without exceptions – only in certain tropical taxa of this family. – The size of the posterior median eye lenses is reduced in the Trochanteriidae of the Baltic amber forest, see WUNDERLICH (2004: 1699ff). The size of the anterior as well as the posterior median eyes decreased during the evolution of the Thomisidae; they were already small in certain Eocene genera (the lateral eyes increased apparently simultaneously).

Sexual dimorphisms: Extremely large male chelicerae exist in some extant members of the Tetragnathidae (e. g. *Tetragnatha*), and Theridiidae (e. g. *Enoplognatha*) but they are absent in Early Tertiary relatives of the Baltic amber forest in which only fairly modified (enlarged/toothed) chelicerae exist, e. g. in *Praetermeta*; see WUNDERLICH (2004: 947, fig. 29) of theTetragnathidae, and in *Hirsutipalpus* n. gen. of the Theridiidae. These may be called "morpholocical links" to extant taxa. Large male chelicerae – like in extant *Tetragnatha* – existed already in the Miocene Dominican amber spiders, see WUNDERLICH (1988) (2004: 948, fig. 35). *Enoplognatha* and *Tetragnatha* may be relatively "young" genera which – as far as known – did not yet exist in the Early Tertiary (Eocene). – Conspicuously long/dense hairs of the anterior male legs or the male pedipalpal articles are known from numerous extant species, but they were still rare in Eocene spiders in which they are known from certain members of the Salticidae, the genus *Almolinus*, see WUNDERLICH (2004: Fig. 414). – Female gigantism (which may be connected with male dwarfism) – like in the genus *Latrodectus* (Theridiidae) and in numerous Araneidae – evolved in spiders probably not before the Oligocene (an Eocene proof is wanted). – Clasping spurs/spines of the modified anterior male legs are not rare in extant spiders of several (sub)families like the Segestriidae (Ariadninae), but in Cretaceous and Early Tertiary Segestriidae such spurs/spines were still completely absent. They existed already in Eocene Anapinae. See the paper on the family Theridiidae.

Certain stridulatory organs – like cheliceral files – evolved apparently relatively late, after the Eocene, e.g. in the families Pimoidae, Hahniidae, and certain Mimitidae, in contrast to Eocene Archaeidae and Linyphiidae in which such files were already existing.

Phylogenetic relationships: Morphological/taxonomical connecting ("missing") links, **the taxonomical importance of fossil/extinct spider taxa, the concepts of genera and remarks on spider's diversity**: See WUNDERLICH (204: 265–266) and below: Borboropactidae (the sensory structures of the anterior tarsi), Zoridae (e.g. the position of the eyes), Cretaceous amber spiders, and Theridiidae.

The different position of the paracymbium in the theridiid subfamily Asageninae: In all fossil taxa of the Baltic amber forest exist the plesiomorphic (ecto-marginal) position of the paracymbium, in almost all of the extant members its position is more or less inside the cymbium (internal). During the Tertiary the paracymbium changed its position in this subfamily. In respect to the variability of this important taxonomical character the diagnosis of the subfamily has to adapt; see the paper no. 3 on the Theridiidae. – See also below, *Eochorizomma* n. gen. (Araneidae).

From today's spiders we know numerous ant-shaped spiders, most conspicuous in Corinnidae and Salticidae. Ant-shaped spiders are unknown from the Cretaceous, and ants were very rare in this period. From the Early Tertiary we still know no distinct myrmecomorphic spiders but weakly or fairly ant-shaped spiders existed already in the Eocene Baltic amber forest as "links" to the quite unusual shape of certain today's extremely myrmecomorphic spiders, see WUNDERLICH (2004: 189–196). The Eocene was the first period in which ants were very frequent (much more frequent than in the Palaeocene), and apparently there was a co-evolution of spiders and ants. (Members of *Myrmecarchaea* more likely have been wasp-imitating spiders or were mimetic, see the paper no. 14 in this volume).

According to my estimation we may know less than 50 percent of the probably about 100 000 extant spider species but probably only ca. 0.1 promille or less (fewer than 1 000) of the millions of fossil/extinct spider species. Therefore – and from other reasons – it is not estonishing that we still found only very few examples of fossil connecting ("missing") links of these animals, and most of such peculiar fossils must be missed forever.

The percentage of extinct spider genera in Baltic amber (~90%) is higher than expected by earlier authors and seems to be higher than in most groups of insects, see WUNDERLICH (2004: 252ff). The Dolichopodidae (Diptera) possesses apparently a low percentage of extinct genera in Baltic amber, but such results were questioned by ULRICH (2003: 321): "Apparently the stem species of most of the recent genera lived after the Baltic amber period, and the species in Baltic amber may have been common ancestors of several genera. Where recent genera appear to be older, it should be considered that THE CONVENTIONAL CONCEPTS OF GENERA are not based on objective criteria and may change with increasing knowledge of the recent fauna." This opinion seems to be correct, and the study of fossil taxa may be helpful in this matter. In numerous fossil taxa of spiders we may have a similar situation which may explain the high percentage of almost 90% of extinct genera in Baltic amber spiders. The situation may be comparable in fossil Acari in which the most important taxonomical characters are usually not observable, and therefore most species are regarded as members of extant genera. In contrast to fossil Acari and most fossil insects we can study in spiders the – free observable – secondary male genital organs very well. – In Cretaceous ambers 100% of the spider genera are extinct. (*Ariadna* may be the only exception, see the paper no. 5 on Cretaceous spiders in this volume and p. 39).

On “Faunas connecting fossils”: The “Early Tertiary European amber forest(s)” existed probably for more than ten or even fifteen million years – mainly within the Eocene and in the Early Oligocene – in wide regions of Europe; see WUNDERLICH (2004). This “forest” was surely not a unit but split up in space and probably in time. Examples for such regions which were separated from the Northern (“Baltic”) part may have been the Bitterfeld and the Ukrainean Rovno areas; there is no distinct gap between these spider faunas which are preserved in amber, see below.

Exist certain spider taxa which were common to these three spider faunas? Unfortunately we still know much less about the Rovno fauna than about the other two ones. If we compare the already known spider fauna from Rovno – WUNDERLICH (2004: 1822), and the Theridiidae in this volume – to the common taxa of Bitterfeld and the Baltic region – WUNDERLICH (2004: 247) –, we find members of the following suprageneric taxa which are extinct (*) or are extinct in Europe today: Archaeidae, Cocalodinae (Salticidae), Cyatholipidae (still questionable in Rovno amber), *Mizaliinae (Oecobiidae), Synotaxidae and *Sosybiini (Trochanteriidae). Of main interest in this respect are common extinct genera and species – especially species – which are frequent and easy to determine. In contrast to “leading fossils” – which are short-living in a geological sense – I call such species – which are common to certain areas in the same geological period – “faunas connecting fossils”. They are widely distributed like “leading fossils” but they usually cannot be assigned to a special stratum and to an exact age, and – in contrast to leading fossils – at least some of them existed for a longer geological period.

As such “faunas connecting fossils” – which are common to the three areas in question – I identified already few species: *Acrometa cristata* PETRUNKEVITCH 1942 (Synotyxidae), *Pseudoteutana stigmatosa* (KOCH & BERENDT 1854) (Theridiidae), and *Adorator hispidus* (KOCH & BERENDT 1854) (Zodariidae) (the determination of the last two is still not quite sure in Rovno amber). Further “aspirants” in this respect – which have to be prooved in the future – are *Ablator triguttatus* (KOCH & BERENDT 1854) (Corinnidae), *Archaea paradoxa* (KOCH & BERENDT 1854) (Archaeidae), *Eohahnia succini* PETRUNKEVITCH 1958, *Eomatachia latifrons* PETRUNKEVITCH 1942 (Zoropsidae s.l.), *Gorgopsina frenata* (KOCH & BERENDT 1854), *Mysmena groehni* WUNDERLICH 2004 (Anapidae s. l.: Mysmeninae) and *Orchestina baltica* PETRUNKEVITCH 1942 (Oonopidae) as well as members of the genera *Balticoroma* WUNDERLICH 2004 (Anapidae: Comarominae), *Eoarchaea* FORSTER & PLATNICK 1984 (Archaeidae), *Mizalia* KOCH & BERENDT 1854 (Oecobiidae), *Sosybius* KOCH & BERENDT 1854 (Trochanteriidae) and *Succinero* WUNDERLICH 2004 (Mimetidae). Due to material from Rovno amber which I studied recently I now add the theridiid genera *Clya* KOCH & BERENDT 1854, and *Eomysmena* PETRUNKEVITCH 1942. I am still waiting for a proof of the genus *Custodela* PETRUNKEVITCH 1942 (Linyphiidae) in Rovno amber.

Biogeography: Changes of ranges in certain araneoid families

As a result of my study on fossil spiders it became clear that the range of several spider families of the superfamily Araneoidea – e. g. Cyatholipidae and Synotaxidae – shrunk during the Tertiary. These families had a wide (worldwide?) range in the Early Tertiary (the Eocene) but they are almost completely restricted to the Southern Hemisphere today. This shrinking of their range was caused in my opinion by the cooling at the Eocene/Oligocene boundary as well as by the competition by members of the Linyphiidae and especially the Theridiidae, see WUNDERLICH (2004: 227ff). The recolonization of Europe after the Oligocene cooling by the Cyatholipidae and the Synotaxidae was probably prevented by the diversification of the Linyphiidae and the Theridiidae. The today's ranges of the families Cyatholipidae and Synotaxidae are remarkable: The Australian Region is the only Region where both families occur together (as in the Eocene of Europe) but they exclude each other in South Africa – where only Cyatholipidae are known – and in South America – where only Synotaxidae exists –, see WUNDERLICH (2004: Figs. p. 238). The reason for the absence of these families on whole continents is unknown, and their former and today's distribution is not in concordance with a gondwanaland origin of these taxa. Within the Archaeidae exists a similar situation: The subfamilies Archaeinae and Mecysmaucheniinae both occur in the Australian Region, but outside of Australia exists the Mecysmaucheniinae today only in South America and the Archaeinae only in the Aethiopean Region (South Africa and Madagascar). In the Cretraceous existed both in Eurasia.

Remarks on the Bitterfeld deposit of the Baltic amber and on the Rovno amber from the Ukraine (see also above)

Bitterfeld deposit: On a probably independent Bitterfeld amber forest within the large Eocene European amber forest area: See the discussion by WUNDERLICH (2004: 246–249). – I now add findings on two genera of the family Theridiidae in which I found differences between the fauna of the Bitterfeld deposit and the non-Bitterfeld – mainly Kaliningrad (Koenigsberg) deposits –; (1) in the genus *Euryopis* MENGE 1868: Four specimens (two species) of the genus *Euryopis* originate from the Bitterfeld deposit, and only two specimens were collected in the Kaliningrad region although I studied about twenty times more spider specimens from the Kaliningrad region than from the Bitterfeld deposit. – Getting three times similar cases – as accidents? – it seems likely to me that both faunas are not quite completely identical. – (2) About half of the known specimens of *Episinus longimanus* (KOCH & BERENDT 1854) were collected in the Kaliningrad region, and the remainings at the Bitterfeld deposit.

Notes:

(1) If we compare the extant spiders faunas of northern Germany and southern Germany north of the Alps (a distance of about 700 km) we find – besides distinct quantitative differences – about 20% differences in the composition of the species.

(2) According to different authors the Bitterfeld amber was transported by water from a south-west direction to the Bitterfeld deposit. If this amber had a "scandinavian" origin – and the Kaliningrad region has been a former deposit – waters would have transported this fossil resin at first from the north-east direction to a depsit south-west of Bitterfeld and than in a north-east direction to a single and very restricted area at Bitterfeld. These ways of transport appear rather unlikely to me.

Rovno amber: Among ca. 60 specimens (13 families, a dozen identified species) of spiders I found 4 species which are unknown from Baltic (incl. Bitterfeld) amber (about 7% of the specimens), see WUNDERLICH (2004: 1821–1829) (recently I studied about 20 specimens more than in 2004). This quite unusual high percentage of unknown species may indicate the former existence of a – partly? – separated Rovno area of the Early Tertiary European amber forest(s). The differences between the Rovno and the Northern European amber faunas appear more distinct than the differences between the Bitterfeld and the Northern European amber faunas; but far more material is needed for sure conclusions in this matter. The distance between the Eocene Ukrainean and the Northern European amber forests is only slightly larger than the distance between northernmost and southernmost Germany.

Diversifications during the Cretaceous and Tertiary; gaps in the spider fauna of the Baltic amber forest as well as on geological old and young higher (supra-generic) taxa

> "The number of genera and species at the time of the <Baltic> amber forest was probably not less than today, ...". (Translation by the present author).
>
> A. MENGE (1856: 32)

Comment: This conclusion was most probably correct; it was published already one and a half centuries ago (!), three years earlier than DARWINs "Origin of Species".

Diversifications of taxa of the family Theridiidae and other araneomorph taxa during the Palaeocene and the Eocene

Numerous genera of the spider family Theridiidae – which I take here as example – are known from the Early Tertiary but not from the Cretaceous up to now. So the era(s) of their diversification(s) in the late Cretaceous or the earliest Tertiary is (are) unsure. Furthermore most other members of the superfamily Araneoidea including the families which are strongly related to the Theridiidae – Cyatholipidae, Nesticidae and Synotaxidae – are unknown from the Cretaceous.
According (e.g.) to the numerous species of the genus *Episinus* (Theridiidae) which are preserved in Baltic amber – 23 described species and several undescribed species; more than two third of the number of species which are known today worldwide –, a pronounced diversification of the Episinae happened in the Early Tertiary.

Similar diversifications occured within other subfamilies of the Theridiidae, e.g. in the Hadrotarsinae (*Lasaeola*) and Asageninae (*Clya*), as well as in several other spider families of the Baltic amber forest, e.g. certain Linyphiidae (the genus *Custodela*), Anapidae s. l., Synotaxidae and Salticidae, see WUNDERLICH (2004). Such radiations and diversifications – may be connected with the Cretaceous-Tertiary (K–T) boundary extinction events (see below), and may have happened "very fast" (in the geological sense): Within only about twenty million years between the K–T events and the existence of the Baltic – and other Early Tertiary (Eocene) European – amber forest(s). This speculation is quite unsure because of the absence of surely identified spiders of the Upper Cretaceous and the Palaeocene. Do to the new findings in fossil spiders THE ERAS OF THE UPPER CRETACEOUS AND THE PALAEOCENE SEEMS TO BE THE MOST IMPORTANT ERAS OF THE DIVERSIFICATION OF THE HIGHER ("MODERN") ARANEOMORPH SPIDERS LIKE ARANEOIDEA AND SALTICIDAE.

Proof of several diversifications within the same taxon – two examples

(1) The genus *Orchestina* s. l. (Oonopidae: Orchestininae, see below) – is diverse today, and at least two subgenera which are related to the nominate subgenus were dwellers of the Eocene European amber forests. The genera of the subfamily Orchestininae are still not well studied. This subfamily is much older than (e. g.) the subfamilies of the Theridiidae: it is known already e. g. from the Cretaceous of Burmese, Canadian and Alava (Spain) ambers. Taxa of this subfamily radiated apparently several times, e. g. (a) probably in the Jurassic (there is no proof), (b) in the Lower Cretaceous, (c) in the Early Tertiary (Eocene) during the existence of the Baltic amber forest, and (d) in the Late Tertiary. Its genera before and after the K–T events are different.

(2) According to my investigation the theridiid subfamily Asageninae (Theridiidae) diversified at least two times, (a) firstly latest in the Early Tertiary – 8 genera are known from the Eocene Baltic amber (a Cretaceous proof is absent), – and (b) after the existence of the Baltic amber forest, probably in the Oligocene: About 8 genera exist today which all are different from the genera of the Baltic amber forest. Similar are the findings in the theridiid subfamily Episinae.

Diversifications in various suprageneric taxa, faunal gaps, "young" and "old" taxa

Among the suprageneric taxa of derived spiders (Araneomorpha) which are frequent, diverse or even dominating within their families today – they are usually present in Europe and existed already in the Miocene Neotropic Dominican amber ca. 22 million years ago – exist several taxa which are completely absent in the Baltic amber (ca. 40–50 million years ago) or are very rare:

Taxon	**Baltic amber**	**extant, Europe**	**Dominican amber**
Oecobiidae: Oecobiini	–	+	+
Araneidae: Araneinae	very rare	+	+
Tetragnathidae: T'-inae	–	+	+
Linyphiidae: Erigoninae	–	+	–
" : Micronetinae	very rare	+	+
Theridiidae: Theridiinae	very rare or absent	+	+
Theridiidae: Argyrodinae	most probably absent	+	+
Dictynidae: Dictynini	–	+	+
Lycosidae	–	+	–?
Philodromidae	absent (or very rare?)	+	+?
Thomisidae: Derived subfamilies like Thomisinae	absent or very rare	+	+
Salticidae: Derived subfamilies like Salticinae	most probably absent	+	+

In summary: The diversification of these higher taxa – and PROBABLY EVEN THE ORIGIN of some of these taxa – happened at least in Europe apparently in a geological young era not before the Oligocene, probably not before/during ca. 40 and 20 million years.

Only about seven (sub)families of advanced entelegyne spiders which are most rich in species worldwide today – Araneidae: Araneinae, Gnaphosidae: Gnaphosinae, Linyphiidae: Erigoninae, Lycosidae, Theridiidae: Theridiinae, Thomisidae: Thomisinae (and strongly related subfamilies) and Salticidae: Salticinae (and strongly related "subfamilies") – represent only 5 to 7% of the 100 to 120 extant families of spiders but they evolved far more than 50% of the extant species of spiders:

"old" taxa	**"young" – "late" diversified taxa**
Certain Araneidae	Araneinae and related subfamilies
Linyphiinae	Erigoninae
	Gnaphosidae: Gnaphosinae
	Lyosidae
Salticidae: Cocalodinae	Salticinae and related subfamilies
Theridiidae other than Theridiinae	Theridiinae
Thomisidae: Stephanopinae (and related subfamilies?)	Dietinae and Thomisinae

According to the absence or strong rarity of these taxa of the Eocene Baltic amber their most conspicuous diversifications happened not in the Cretaceous or the Early Tertiary (Palaeocene, Eocene) but in the Tertiary, during the Oligocene and/or following that period. Apparently the geological "young" – or "late" radiated – taxa displaced the geological old taxa at least in Europe at that period(s). This very surprising finding has to support in further studies. See the paper no. 5 on Cretaceous spiders in this volume.

Remark on the family Gnaphosidae: The mainly ground-living members of this family are quite rare in Baltic amber (CJW), and are still not closely determined; a closer study an more material are needed.

Remark on four families of the superfamily Araneoidea which were frequent or diverse in the Early Tertiary (partly tropical) Baltic amber forest: (a) The mainly tropical Anapidae s. l. is quite rare in (the not tropical) Europe today, and (b) the – also mainly tropical – Synotaxidae and Cyatholipidae have become completely extinct in Europe during the Tertiary; they were apparently replaced mainly here by the advanced Theridiinae. The Nesticidae were more diverse on generic level in the European Eocene than today in Europe, where most species are restricted to caves (e. g. *Carpathonesticus* LEHTINEN & SAARISTO 1980).

Why happened the diversification of several "modern" and diverse taxa apparently exactly in this period, the OLIGOCENE? What was different to the previous Eocene Period? – The end of the Mesozoic era (65 million years ago) – and similar the Early Tertiary Palaeocene and Eocene) – were characterized by a very warm climate. According to various authors – see WEITSCHAT & WICHARD (2002) – a "cooling period" took place at the border of Eocene/Oligocene about 40 million years ago. At that time – caused by this cooling – the subtropical "Early Tertiary European amber forests" disappeared and the mass production of amber stopped. "Towards the end of the Eocene plants and animals attempted to retreat, and subtropical-tropical organisms disappeared from higher paleolatitudes." This led to a dramatic mass extinction in this region, and organisms could now invade from other regions. The changes of the climate, and the fauna and the flora as well within few million (?) years must have had dramatic effects to the spider fauna, too: Numerous species disappeared/ became extinct, see the examples below. So most probably members of almost all of the *EXTANT* genera of the taxa in question diversified – some probably even originated – only during the last 35 or 40 million years; altogether there should be a very high number of such spider genera. Among these are diverse extant genera as *Oecobius* (Oecobiidae), *Tetragnatha* (Tetragnathidae), *Araneus* (Araneidae), *Achaearanea* s. l. and *Theridion* s. l. (Theridiidae), *Agyneta* s. l., *Erigone*, *Lepthyphantes* s. l. and *Linyphia* (Linyphiidae), which all are unknown from the Early Tertiary. It is remarkable that genera like *Erigone* and *Lepthyphantes* s. l. as well as several species-groups of the other genera are today most diverse in the Northern Hemisphere. – "Old" extant spider genera of the Baltic amber forest: See WUNDERLICH (2004: 210–221) and below (Theridiidae). Some of such "old" genera or strongly related genera – e.g. *Segestria* (Segestriidae), *Orchestina* s. l. (with the subgenus *Baltorchestina*) (Oonopidae), *Lasaeola* (Theridiidae) and *Episinus* (Theridiidae) – survived, and are today at least as diverse as they have already been in the Early Tertiary. *Orchestina*, *Episinus* and *Lasaeola* are cosmopolitical and mainly tropical in their today's distribution.

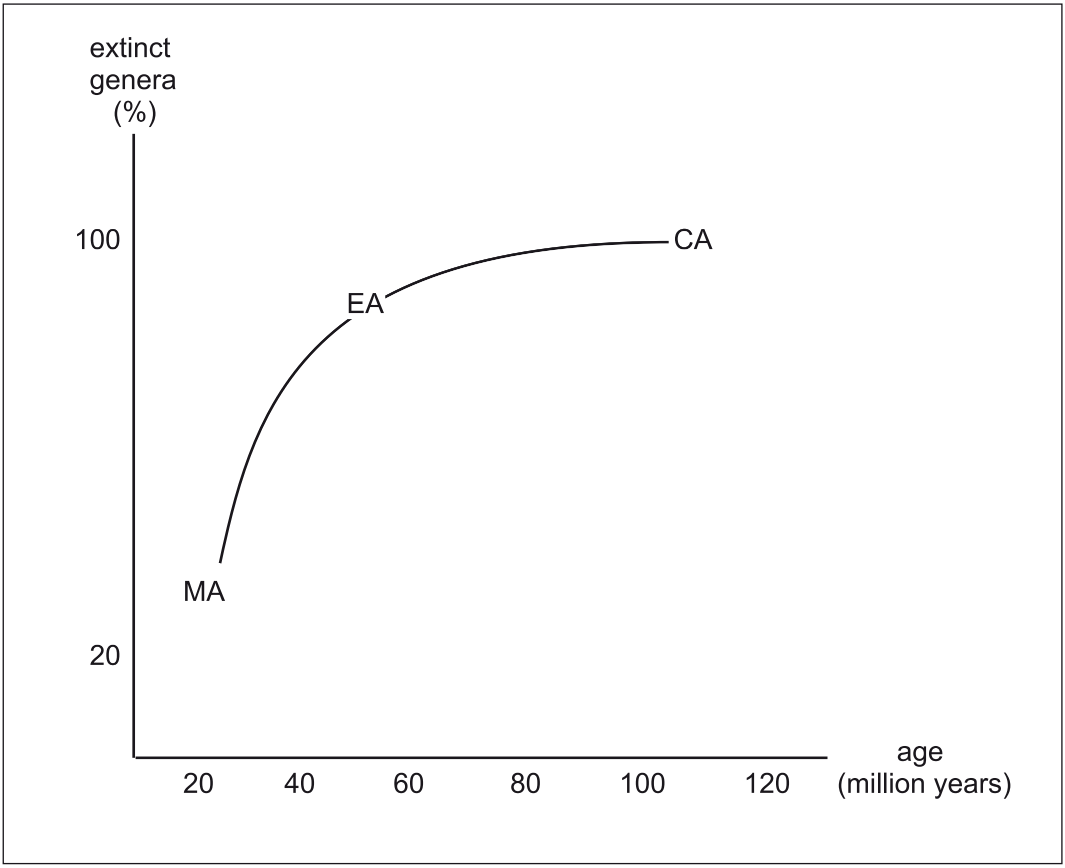
A difference in two families of the superfamily Araneoidea – which **BOTH** are very diverse today (in Europe, too) – is of great interest in this respect: In the European Eocene the family Theridiidae was about as diverse as today, but far more diverse than the family Linyphiidae. What is the explanation for this difference? Linyphiidae has its main distribution in moderate climates but Theridiidae in warmer – even tropical – climates. Were the members of these families differently adapted already in the Eocene? In this case the "Oligocene cooling" did concern both families in different ways: Most theridiid taxa became extinct, new taxa "appeared", and numerous linyphiid taxa could invade this area and diversify or could even originate in the Oligocene (and in the Miocene). Extinctions – see the next paragraph – and diversifications are linked.

The reason for the extreme **RARITY** – or even the absence – of certain members of the RTA-clade: The family Philodromidae in the Baltic amber – most of their members occur in higher strata of the vegetation – is unknown. The Philodromidae – and probably the Sparassidae as well – may have replaced the Sosybiini (Trochanteriidae). The absence of Lycosidae in the Eocene ambers – as well as derived Salticidae (absent or extremely rare?) and derived Thomisidae (extremely rare) – is enigmatic: Although members of these taxa prefer "open biotopes" and – Lycosidae and most Thomisidae – furthermore prefer habitats of the ground, numerous aeronautic spiderlings of the Thomisidae have been caught in the fossil resin (at least juveniles of these taxa are common aeronauts, and due to their conspicuous eye position juvenile specimen of Lycosidae and Salticidae cannot be mistaken). Gramineae is a relatively young taxon (it diversified late), and thus open grassy habitats were rare within the Early Tertiary European (amber) forests. The diversification of the Lycosidae and the Thomisidae may have been strongly connected with the diversification of the Gramineae (and "open" biotopes). – Reasons for the rarity of the Tetragnathidae: See paper no. 2 below.

Extinctions of higher spider taxa and the results of the Cretaceous-Tertiary extinction events (See also above: Diversifications)

Most conclusions in this respect are unsure because only little is known about the number of prae-Tertiary spider genera; most taxa have been published from Miocene spiders in Dominican amber and from Eocene spiders in Baltic amber, see e.g. WUNDERLICH (1988, 2004)).

According to PENNEY et al. (2003) spiders suffered no decline at the family level during the mass extinction of the Cretaceous-Tertiary events, but I strongly doubt this conclusion; see the paper on Cretaceous spiders in this volume. The strange spider family Lagonomegopidae ESKOV & WUNDERLICH 1995 (photo 90) had a wide range at least in the Northern Hemisphere (Cretaceous amber fossils from the Southern Hemisphere are unknown) in the Lower and Mid Cretaceous, and did – due to our today's knowledge – not survive the Cretaceous-Tertiary extinction event (and probably not the Mid Cretaceous). Because of the absence of huge already studied material of fossil spiders from the Upper Cretaceous and the Early Tertiary (Paleocene) we do not know the exact point of time of the extinction of the Lagonomegopidae. There is a greater number of further extinct spider families of the Cretaceous besides the Lagonomegopidae, see the paper no. 5 on Cretaceous spiders in this volume.



Tab. above: Percentage of extinct araneomorph spider genera which are preserved
in Miocene Dominican amber (MA) (age ca. 20 million years): 33%,
in Eocene European ambers (EA) (age ca. 40–50 million years): 90%,
in Lower and Mid Cretaceous ambers (CA) (age ca. 80–140 million years): Most probably 100% already 80 or 100 million years ago.

Several other spider families – Baltsuccinidae WUNDERLICH 2004, Ephalmatoridae PETRUNKEVITCH 1950, Insecutoridae PETRUNKEVITCH 1942 (they may be part of the Pisauridae), Protheridiidae WUNDERLICH 2004 and Spatiatoridae PETRUNKEVITCH 1942 – survived probably the Cretaceous-Tertiary extinction events only as relict taxa, and so far known today – with the exception of the Protheridiidae – only as single genera up to the Early Tertiary within the Eocene European amber forests, although we also do not know the exact point of the time of their extinction. (On subfamily and tribus level several other higher taxa have to add to this list, e.g. the Mizaliinae of the Oecobiidae, Spinitharini of the Theridiidae, the Miraraneinae of the Araneidae, and the Sosybiini of the Trochanteriidae).

The rates of extinction is enormous in certain families, and vary strongly; the rate is frequently higher in advanced families; for example 90% in the Theridiidae like the average in Baltic amber, 100% in the Cyatholipidae, the Linyphiidae, the Salticidae, and the Synotaxidae; almost 100% of the genera of the diverse family Dictynidae s. l. in Eocene Baltic amber – 16 genera –, and in Miocene Dominican amber – 4 genera – as well (!) are extinct (only *Mastigusa* survived from the Eocene). The genera of both kinds of amber are completely different. The reasons for this high rate of extinction are unknown. In the old family Segestriidae only one Eocene genus (of three genera) is extinct.

TAXONOMY

How discoveries of fossil taxa may change the rank of higher taxa

Two examples; see also the next paragraph.

(a) The family Oecobiidae

Traditionally – up to 34 years ago, see BAUM (1974) – the well known members of the spider family Oecobiidae used to be put in the former "suborder Cribellata": *Oecobius* (within the family Oecobiidae), respectively in the former "suborder Ecribellata": *Uroctea* (within the family Urocteidae). The ecribellate extinct Eocene taxon Mizaliindae (*) – which initiated and stimulated my investigation of this group of spiders – was regarded as a further family of its own but has been ranked down to the subfamiliar rank of the Oecobiidae by WUNDERLICH (2004). Recently I tried for the first time to arrange the extant and fossil suprageneric taxa of the Oecobiidae to sister groups – see WUNDERLICH (2004: 824ff, 835) – with the Cretaceous Lebanoecobiinae being the sister group to all other taxa of this family, Mizaliinae as sister group to all extant taxa, and Uroecobiinae (including the former Uroecobiinae and Urocteaninae) as the sister group to the Oecobiinae (including Oecobiini and Urocteini sensu BAUM as tribus now). Consequently I downgraded Uroecobiinae, Urocteaninae, Oecobiinae and Urocteinae to tribus level. So – within half a century – Oecobiidae and Urocteidae were united (ranked down) finally from different former "classical" suborders to a single family, and downgraded from family to tribus rank. The downgrading was mainly based on a comparison of their genital structures. (Of course we have to keep in our mind that the status (rank) of higher taxa is purely subjective, see the paper no. 13 in this volume).

(*) The Eocene genus *Mizalia* MENGE 1856 and the Cretaceous genus *Zamilia* n. gen., see the paper no. 5 on Cretaceous spiders in this volume.

(b) The family Theridiidae

After the discovery of various fossil theridiid taxa in Baltic amber probably the reverse – an UPGRADING of suprageneric taxa – may be ingenious in the family Theridiidae (see below, the paper no. 3 in this volume): New taxa – tribus or even a subfamily – are created within the subfamilies Asageninae, Episinae as well as around *Kochiura* and *Anelosimus*.

Remark: My idea of the upgrading and resurrecting of (sub)genera within the Theridiidae: Asageninae was caused mainly by findings in fossil Eocene taxa, see below.

Remark on resurrected (resurr.) (= "revived") genera

Several genera of the family Theridiidae were synonymized by LEVI, see LEVI & LEVI (1962) – and are resurrected ("revived") by the present author. OKUMA (1994) used the term "revive" in respect to give the genus *Moneta* O. PICKARD-CAMBRIDGE 1870 again the rank of a genus of its own from the synonymy with *Episinus* LATREILLE 1809. The term "resurrect" for such proceeding is quite different from a revalidation or a new combination. (Species of a resurrected genus MAY BE newly combined).

How different subjective concepts of the taxonomical range of genera may influence conclusions on fossil and extant spiders

Examples from the theridiid subfamily Asageninae and the family Archaeidae s. l.
See also *Orchestina* SIMON (Oonopidae: Orchestininae), and the paper no. 13, "Differing views on the taxonomy of spider (Araneae) families..." in this volume.

(1) Theridiidae: After my revision of extant and fossil genera of the Asageninae I distinguish altogether at least 16 genera of this subfamily, at least 8 (and several subgenera) are extant, and the same number (of 8) is extinct; not a single genus survived the Early Tertiary Period of the Eocene European amber forests. The conclusions on the (really?) extinct genera may be the subjective opinion of the present author but the results of the intensive investigation – mainly based on the male genital structures – of the fossil taxa strongly indicate that my conclusions are correct.
If we regard the genus *Steatoda* in the wide sense of LEVI & LEVI (1962) – including e. g. the extinct genus *Pseudoteutana* n. gen. – *Steatoda* would be present in the Early Tertiary Baltic amber forest and would have to date back to the Eocene. Contrarily to this opinion I regard *Pseudoteutana* as a genus of its own. I suppose a "young" (and second) diversification of the genera of the subfamily Asageninae in the Oligocene and/or Miocene, which was caused by the "Oligocene cooling" in which the present-day genera originated, see above, the paragraph "Diversifications during the Oligocene..." and below, the theridiid subfamily Asageninae, paper no. 3 of this volume.

(2) Archaeidae: (a) If the family Archaeidae is regarded in a wide sense – including Mysmaucheniidae having the rank of a subfamily only – it exists in South America, too; if Archaeidae is regarded in a strict sense it is absent in South America. – (b) If *Eriauchenius grimaldii* (PENNEY 2003) (sub *Afrarchaea*) from Cretaceous Burmese amber would really be a member of the African genus *Eriauchenius*, this genus would have to date back to the Cretaceous, and its biogeographical range would include both hemispheres. But – according to my investigation which are mainly based on a comparison of the male genital structures – *grimaldii* is **NOT** a member of *Eriauchenius,* and I place it in the new genus *Burmesarchaea* in the paper no. 5 of this volume. This placement is **NOT** a matter of opinion – both genera are clearly distinct. Thus there is no proof that *Eriauchenius* (= *Afrarchaea*) is a "long-living" genus, and it is restricted – at least today – to the Southern Hemisphere (contra PENNEY (2003).

Remarks on the species-concept in palaeontology

Palaeontologists describe "morphospecies", "palaeospecies" or even "hypothetical palaeospecies", but never "biospecies". Remains of fossils in Cretaceous and in Eocene Baltic amber are – to our present-day knowledge – too old for a proof by genetic methods. Especially in variable fossil species we can not be sure about the number of related species or the existence of subspecies or of chronospecies/chronoclines, we do not know the intraspecific variability, and – contrarily – very similar specimens may be members of different – "cryptic" – species; see the remarks below in this volume (the family Theridiidae, especially the genera *Clya*, *Episinus*, *Hirsutipalpus* and *Lasaeola*). The Eocene European amber forests existed for 10–15 (or far more) million years but we do not know how long a peculiar species was surviving; so an intraspecific variability may be not an intrapopular variability but may reflect the existence of intraspecific taxa. Furthermore there existed different parts of these forests, the "classical"

“Scandinavian” Baltic amber forest of Northern Europe (which has produced the amber of the Kaliningrad = Königsberg deposits), the German Bitterfeld forest, the Ukranean forsest(s) (e. g. Rovno), and the most oldest forest of the Paris Basin in France (which may be Palaeocene).

I distinguish provisionally the numerous morphospecies of *Clya* KOCH & BERENDT 1854 by the number of loops of their emboli – from 1 1/4 to more than 4 loops, photos 162, 168, 171, 175–177, 179, 184) – but there are transitions and no clear gaps between the “hypothetical palaeospecies”. So one may conclude that some or even most specimens are simply members of a single long-living chronospecies which outlived several/numerous million years, and my conclusions may be nothing else than speculations. To be more sure in my conclusions I compared the embolic loops of the extinct genus *Clya* mainly with the situation in the extant genus *Latrodectus* WALCKENAER of the same subfamily but this comparison is only a very restricted help. See the paper no. 3 of this volume.

A second problem is that several spider species are based on juveniles or on not clear differences in their genital organs; frequently only parts of their genital structures are recognizible in the fossils; see the remarks below (e. g. the families Borboropactidae, Spatiatoridae and Theridiidae).

Finally: (a) Most often the conspecific second sex – usually the female – is unknown. How many synonyms may be hidden behind congeneric species which are known solely from the male or from the female sex? (b) The genital structures of peculiar specimens may be deformed by heating, are only seemingly differing from other specimens and so it may miss-lead a describing author, including the present one.

BEITR. ARANEOL., 5 (2008)

DESCRIPTIONS OF FOSSIL SPIDER (ARANEAE) TAXA MAINLY IN BALTIC AMBER, AS WELL AS ON CERTAIN RELATED EXTANT TAXA

JOERG WUNDERLICH, D–69493 Hirschberg.

Abstract: The following taxa are treated in this paper:

(a) Fossil spiders: *Anameta*, A. *kuntneri* **n. sp**., Anametini **n**. **trib**. (Tetragnathidae), *Ariadna*, *A. copalis* **n. sp**., *A. ovalis* **n. sp**., *A. parva* **n. sp**. (Segestriidae), Ariadninae, *Baltleucauge gillespiae* **n. gen. n. sp**. (Tetragnathidae), Baltleucaugini **n. trib**. (Tetragnathidae), *Baltorchestina* **n. subgen**. of *Orchestina* (Oonopidae: Orchestininae), Baltsuccinidae, *Baltsuccinus*, *Burmorchestina pulcher* **n. gen. n. sp**. (Oonopidae), *Canadaorchestina* **n. gen**. (Oonopidae), Chelicerini **n. trib**. and *Chelicerinus* **n. gen**. (Synotaxidae?), *Chrysometata*, *Cyclosoma*, Diphyinae, *Eochorizopes szeklinskii* **n. gen**. **n. sp**. (Araneidae), *Eopimoa* **n. subgen**. (subgenus of *Pimoa*, Pimoidae), *Ero*, *Fictotama*, *Gallorchestina* **n. subgen**. (Oonopidae), Hersiliidae, Linyphiidae, *Macryphantes*, Metinae (Tetragnathidae), Mimetidae, *Neotama*, *Orchestina* (*Baltorchestina*): *bitterfedensis* **n. sp**., *brevis* **n. sp**., *multisetae* **n. sp**., *perfecta* **n. sp**., *rectangulata* **n. sp**., *sternalis* **n. sp**.: Orchestininae **n. subfam**. (Oonopidae), *Palaeosegestria* (?= *Ariadna*), *Pimoa longiscapus* **n. sp**. and *P. obruens* **n. sp**. (Pimoidae), *Praetermeta maculosa* **n. sp**. (Tetragnathidae), *Praetermeta* WUNDERLICH 2004 is down-graded from the genus to the subgenus level of *Meta* (**n. stat**.), Protheridiidae, *Pumiliopimoa parma* **n. gen**. **n. sp**., Pumiliopimoidae **n. fam**., Pumiliopimoini **n. trib**., *Spatiator caulis* **n. sp**. (Spatiatoridae), *Succinero*, Synotaxidae, Tetragnathidae.

(b) Extant spiders: *Ferchestina*, Hersiliidae, Ipaini **n. stat**., tribus of the Linyphiidae: Micronetinae (downgraded from Ipainae SAARISTO 2007), Linyphiidae, “linyphioid branch”, *Louisfagea*, *Merianmeta* **n. subgen**. of *Meta*, *Meta*, Metabini **n. trib**. (Tetragnathidae), *Metabus*, *Metellina* (downgraded to subgenus rank of *Meta*), Metinae (Tetragnathidae), Microsynotaxini **n. trib.**, *Microsynotaxus calliope and insolens* **n. gen. n. sp.** (Synotaxidae), Mimetidae, *Nanoa*, Nanoini **n. trib**. (Pumiliopimoidae), *Ne-*

otama, *Nipponmeta* **n. subgen**. of *Meta* (Tetragnathidae), *Orchestina dalmasi* **n. sp**., Orchestininae (Oonopidae), *Pimoa*, Pimoidae, Pumiliopimoidae **n. fam**., *Sinometa* **n. subgen**. of *Meta* (Tetragnathidae), Sinopimoidae, Stemonyphantinae, *Stridulameta* **n. subgen**. of *Meta* (Tetragnathidae), Synotaxidae, Tetragnathidae, *Weintrauboa*.

Key words (see also the abstract): Araneae, Eocene, fossils, new taxa, spiders, taxonomy.

In this paper I describe and revise numerous higher and lower taxa of fossil and extant spiders of several araneomorph spider families of the superfamilies Dysderoidea, Archaeoidea, Oecobioidea and Araneoidea except Theridiidae (see the paper no. 3 in this volume); members of the RTA-clade: See the paper no. 4 in this volume.
The relationships of certain fossil and extant taxa which are reported in this paper are of peculiar interest. Most fossil taxa are reported from the Eocene Baltic amber forest; a single genus – *Burmochestina* n. gen. (Oonopidae: Orchestininae) – is reported from the Mid Cretaceous Burmese amber.

Family SEGESTRIIDAE SIMON 1893

Remark: The subfamily status was elevated to family status by PETRUNKEVITCH 1933 but the author of this taxon is SIMON.

Two of three Eocene genera of this family survived up to now: *Ariadna* SAVIGNY & AUDOUIN 1827 and *Segestria* LATREILLE 1804; *Vetsegestria* WUNDERLICH 2004 is extinct. This is a relatively high quota of surviving genera of the Baltic amber forest: 66%, compared with only ca. 10% of the spider genera in Baltic amber in average.

Subfamily Ariadninae WUNDERLICH 2004

Genera: *Ariadna* AUDOUIN 1826 (Eocene to extant, but probably already Cretaceous, see the paper on Cretaceous spiders in this volume), as well as probably the Cretaceous genus *Palaeosegestria* PENNEY 2004 (?= *Ariadna*, see below).

Remarks: (1) Species and specimens of *Ariadna* in Baltic amber are much rarer than species and specimens of *Segestria* which may be the younger and more advanced genus. – (2) The anterior male leg was still unmodified in the Cretaceous and Early Tertiary taxa in contrast to most extant species of *Ariadna*; so this sexual dimorphism evolved probably not before the Oligocene from a (really a single?) peculiar species, in which only a weak sexual dimorphism existed, see WUNDERLICH (1988).

Relationships: Seven differences between Ariadninae and Segestriinae SIMON 1893 were listed by WUNDERLICH (2004: 658). The differences of the labium are not constant within the subfamilies and thus this character has to delete. I now add two further differences between the two subfamilies:

(a) (questionable): According to MARPLES (1967: 221) epiandrous gland spigots are absent in an *Ariadna* sp. indet.. A comparison with further species is needed.

(b) The position of the (posterior) median eyes is most often different in both subfamilies; this difference has already been known by SIMON (1893: 319), and was overlooked by BEATTY (1970: 455) and by WUNDERLICH (2004: 568):
In extant and in fossil Ariadninae the position of the median eyes – although variable – is usually between the posterior lateral eyes (fig. 4) (*) up (rarely) to the middle between anterior and posterior lateral eyes as in *Ariadna parva* n. sp. (photo 130, fig. 5), *A. arthuri* PETRUNKEVITCH 1926 (extant), and *Palaeosegestria lutzzii* PENNEY 2003 (Cretaceous; see the remark below). In the Segestriinae the position of the median eyes is anteriorly, between the anterior lateral eyes in the genus *Segestria.* I do not know a single exception.

Remark on *Palaeosegestria* PENNEY 2004 (see the fig. 7 in the paper no. 5 on Cretaceous spiders in this volume): In this Cretaceous genus the position of the oval posterior median eyes is between the anterior and posterior lateral eyes like in certain members of the genus *Ariadna*, and – according to the short fang and cymbium as well as the subspherical bulbus – it appears not unlikely to me that *Palaeosegestria* is a member of the Ariadninae; therefore I do not want to exclude that it is strongly related to *Ariadna*.

Discussion: The loss of the anterior median eyes happened latest 140 million years ago in the Lower Cretaceous, it existed already in the Cretaceous subfamily Microsegestriinae WUNDERLICH 2004 (Libanon) as well as in *Palaeosegestria* PENNEY 2004 (USA, New Jersey), see above. This loss of the anterior median eyes – in the unknown basal branch of the Segestriidae – caused an eye position similar to fig. 4 (most members of *Ariadna*). After this loss the posterior median eyes shifted in the Segestriinae to a position between the anterior median eyes in *Segestria*, see WUNDERLICH (2004: 668, fif. 2k), but the eyes moved only to a position between the anterior and posterior lateral eyes in *Vetsegestria*, see WUNDERLICH (2004: 667, fig. 2f). Contrarily in most Ariadninae the position of the median eyes remained in their plesiomorphic posterior position (fig. 4); in the evolution of species of this subfamily the posterior median eyes

---

(*) Apparently this is the plesiomorphic position of the family Segestriidae; in these spiders the posterior median eyes have not yet shifted to an anterior position; see WUNDERLICH (2004: 651, fig. above on the right).

shifted foreward to a position between the anterior and the posterior lateral eyes (fig. 5) (probably several times independently), but never up to a position between the anterior median eyes as in most Segestriinae (*Segestria*) (fig. 5).

In certain extant and fossil Ariadninae the posterior median eyes possess an oval shape, e. g. in probably all of the Eocene species in Baltic amber (figs. 4–5), in *Palaeosegestria* (Cretaceous), and in the extant species *Ariadna kisanganensis* BENOIT 1974.

***Ariadna* AUDOUIN 1826**

In contrast to *Segestria* LATREILLE 1804 and *Vetsegestria* WUNDERLICH 2004 members of *Ariadna* are very rare in Baltic amber; I know only four specimens. In most species of *Ariadna* the shape of the median eyes is circular but in three fossil species in Baltic amber (figs. 4–5) as well as in the extant *A. kisanganensis* BENOIT 1974 the shape of the median eyes is oval. Also in *Palaeosegestria* the shape of the posterior median eyes is oval, see above.

BEATTY (1970) reported the body length in extant specimens of *Ariadna* as 4 to 16 mm in the American species; *Ariadna copalis* n. sp. is 2.6 mm long (case of dwarfism), the body length of the fossil species in Baltic amber is 2.4 (*A. parva* n. sp.) up to ca. 1 cm; *A. parva* may be the smallest known species of the genus. Probably there was a general pressure of selection to larger spiders during the Tertiary, and most of the smallest species became extinct. We have to keep in our mind that large spiders are only rarely captured by the fossil resins, although I know few fossil specimens of *Sosybius* (Trochanteriidae) in Baltic amber which have a body length of more than 2 cm.

Key to the species of *Ariadna* in Baltic amber (♂):

Remarks: (1) See the ♀ of *Ariadna* sp. indet. below. (2) As known from extant spiders the number of leg bristles is variable in most species.

1 Body length about 2.4 mm, position of the oval median eyes more anteriorly (fig. 5). Pedipalpus (figs. 6–7): Tibia only slightly thickened, about as long as patella and cymbium, embolus only fairly bent. . . . . parva

\- Body length ca. 4.7–5 mm, position of the median eyes unknown or more posteriorly (fig. 4). Pedipalpus (figs. 1–3): Tibia strongly thickened, distinctly longer than patella and cymbium, tip of the embolus bent in a right angle. 2

2(1) Cymbium with a distinct retrolatera-distal depression (figs. 2–3). Position of the median eyes as in fig. 5. . . . . <u>*ovalis*</u>

- Cymbium without a depression (fig.1). Position of the median eyes unknown. . . . . <u>*defuncta*</u>

Ariadna defuncta WUNDERLICH 2004 (fig. 1)

Only the male holotype of this fossil species in Baltic amber is known, its body length is 4.7 mm. Because of the position its eys are difficult to recognize. Recently the amber piece of the holotype has been cut in different ways by H. GRABENHORST, the owner of the holotype. According to H. GRABENHORST, person. commun., the holotype will be given to the GPIUH. The shape of the median eyes may be circular or oval in this specimen, their position is almost between the posterior median eyes but not in a “typical segestriid position” as previously noted by me; see WUNDERLICH (2004: 660). The piece of amber was reworked, the left pedipalpus is better visible than before, see WUNDERLICH (2004: 667, fig. 2d), the existence of a femoral bristle is unsure, the cymbium is not inclined, and the embolus is strongly bent distally, a bubble is preserved at its tip (fig. 1). – Relationships: See the key.

***Ariadna ovalis* n. sp.** (photo 129, figs. 2–3)

Material: Holotypus ♂ in Baltic amber, F1911/BB/AR/CJW.

Preservation and syninclusions: The spider is well and almost completely preserved in a yellow piece of amber which was slightly heated; the ventral side is partly thickly covered with a white emulsion, the right legs I and II are lost beyond their coxa by autotomy, distal parts of the left legs I and II are cut off. A layer in the amber hinders the view of the right anterior side of the spider. A thin longer leg of an insect and some stellate hairs are preserved in the same piece of amber.

Diagnosis (♂; ♀ unknown): Pedipalpus (fig. 1–2): Oval posterior median eyes in a more posterior position, almost between the posterior lateral eyes. Pedipalpus (fig. 2 –3): Tibia long and distinctly thickened, cymbium with a distinct retrolateral-distal depression, embolus bent in a right angle near its end.

Description (♂):
Measurements (in mm): Body length 5.0, prosoma: Length 2.6, width 1.9; femur I 2.2, leg II: patella 0.9, tibia ca. 2.2, leg IV: Femur 1.8, tibia 1.45, metatarsus 1.4, tarsus 0.75.
Colour mainly silvery, opisthosoma medium grey.

Prosoma 1.37 times longer than wide, anteriorly not abruptly smaller, fairly low, fine rugose, hairs short, fovea a very indistinct depression, eyes as in *A*. sp. indet. (fig. 4). The mouth parts and the sternum are hidden. – Legs fairly long, order I/II/IV/III, leg I unmodified, tibia I distinctly longer than IV. Bristles: Most femora with 3–4 dorsally, IV bears 6, patellae none, tibia I ventrally 2 pairs and an apical pair (laterals are hidden), metatarsus I with a ventral pair, a single ventral one near the middle and a ventral-apical pair. Trichobothria not studied, paired tarsal claws with long teeth. – Opisthosoma 1.5 times longer than wide, with dorsal and lateral furrows, dorsal hairs short, ventral parts are hidden. – Pedipalpus (figs. 2–3; see the diagnosis): Femur bent, prodistally with a strong bristle.

Relationships: See the key. The shape of the embolus is as in *A. defuncta* but the shape of the cymbium is different.

Distribution: Eocene Baltic amber forest.

***Ariadna* sp. indet**. (photo 131, fig. 4)

Material: 1♀ in Baltic amber, F1405/BB/AR/CJW.

Remark: I previously supposed this female as being probably a member of an undescribed subfamily; see WUNDERLICH (2004: 657).

Preservation and syninclusions: The spider is almost completely preserved, only the tips of the left tarsi I and II are cut off, bubbles exist e. g. on the prosoma and dorsally of the left patella and tibia IV; the ventral side is hidden by a layer of the amber. All legs except the right leg IV are directed foreward. A juvenile member of the family Scytodidae, body length 2 mm, is preserved right behind the holotype, two larger particles of insect’s excrement, a tiny Diptera: Nematocera and some stellate hairs are preserved behind the spider.

Description (♀):
Measurements (in mm): Body length 4.7, prosomal length 2.6, tibia I 1.7.
Prosoma abruptly narrow anteriorly, eye field (fig. 4) narrow, posterior median eyes oval, their position slightly in front of the posterior lateral eyes. Tibia I bears 4, metatarsus I 3 pairs of ventral bristles, prolateral bristles are absent.

Relationships: In *A. ovalis* n. sp. the eye position is quite similar but the prosoma is not abruptly narrowed anteriorly. *A. parva* n. sp. is distinctly smaller. In *A. defuncta* the chaetotaxy is different.

Distribution: Eocene Baltic amber forest.

Ariadna parva **n. sp** (photo 130, figs. 5–7)

Material: Holotypus ♂ in Baltic amber, F1465/BB/AR/CJW.

Preservation and syninclusions: The spider is almost completely and well preserved in a small piece of yellow amber which apparently was slightly heated, only a dorsal-apical part of the right tibia I is broken off; parts of the ventral side are covered with a white emulsion. Few stellate hairs and a tiny insect larva are preserved in the same piece of amber.

Diagnosis (♂; ♀ unknown): Body length only 2.4 mm; oval median eyes (fig. 5) in a more anterior position. Pedipalpus (figs. 6–7): Tibia only very slightly thickened, only about as long as patella and cymbium, embolus long and fairly bent.

Description (♂):
Measurements (in mm): Body length 2.4, prosoma: Length 1.1, width 0.8; leg I: Femur 0.75, patella 0.3, tibia 0.7, metatarsus 0.5, tarsus 0.33, tibia IV 0.7.
Colour: Prosoma medium brown, legs light brown, opisthosoma yellow brown.
Prosoma (photo) 1.38 times longer than wide, fine rugose, low, dorsal hairs fairly long, fovea apparently absent. The oval posterior median eyes (fig. 5) are more in an anterior position. Clypeus short, chelicerae protruding, hairy anteriorly. Mouth parts hidden, the sternum separates the coxae IV by their diameter. – Legs fairly short, order I/II/IV/III, leg I unmodified, hairs indistinct, tibia I and IV equal in length. Bristles thin: Femora dorsally 1/1 on II–IV, additional distal bristles may exist, I–II bear an additional distal-prodorsal bristle, tibiae I–II bear 2 ventral pairs and distal ones, metatarsi I–II bear 2 ventral pairs and at least a single prolateral one. The paired tarsal claws bear long teeth, trichobothria were not studied. – Opisthosoma almost two times longer than wide, with dorsal and lateral folds, dorsally scarcely covered with short hairs. Most spinnerets are hidden. – Pedipalpus (figs. 6–7, see above), bristles of the articles are absent.

Relationships: Smallest known species of this genus in Baltic amber; see the key.

Distribution: Eocene Baltic amber forest.

Description of a subrecent species in copal from Madagascar:

Ariadna copalis n. sp. (photo 128, figs 7a–7d)

Material: Holotypus ♂ in copal, bought by the present author in June 2007 from a dealer in England (Lyme Regis). According to the dealer the spider is preserved in copal from N-Madagascar, but I do not want to exclude with certainty the origin from Columbia from which several pieces were present, too, in the collection of the dealer.

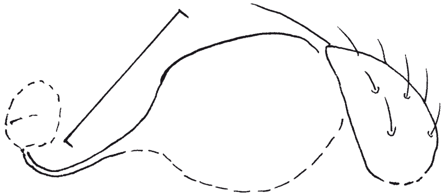
Preservation and syninclusions: The spider is well and completely preserved in a yellow piece of copal which is up to 3 cm long, fairly hard, and contains numerous tiny bubbles. The opisthosoma is injured (depressed anteriorly), some gas/air is preserved within some femora. A pair of spiders: Theridiidae and a juvenile Araneae indet., several Acari and insects (e. g. Collembola, Diptera, Hymenoptera, Psocoptera, two half Coleoptera, 1/2 small Trichoptera) are enclosed in the same piece of copal. Some gas bubbles are preserved directly behind the spinnerets.

Diagnosis (♂; ♀ unknown): Body length only 2.6 mm, eyes as in fig. 7a), leg bristles small, femora and patellae bristle-less, tibia I unmodified, bearing 2 pairs of ventral bristles besides apicals (fig. 7b), metatarsus I with a single pair of ventral bristles.

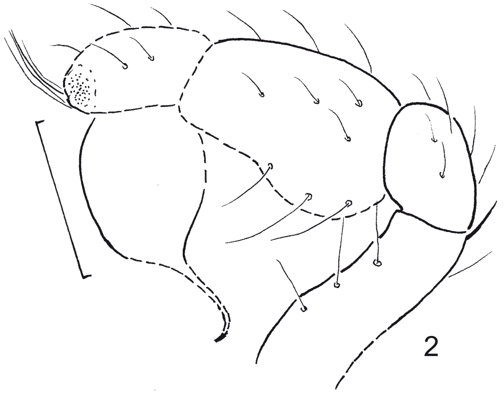
Description (♂):
Measurements (in mm): Body length 2.6, prosoma: Length 1.25, width 0.82; leg I: Femur 1.05, patella 0.35, tibia 0.85, metatarsus 0.75, tarsus 0.35.
Colour: Prosoma medium brown, legs light brown, opisthosoma yellow grey-brown.
Prosoma 1 1/2 times longer than wide, almost smooth, fovea fairly short, six eyes in a position as in fig. 7a), basal cheliceral articles fairly small, other mouth parts hidden. – Legs fairly long and slender, bristles small (see the diagnosis), tibia I (fig. 7b) bears 2 pairs of ventral bristles, 3 retrolaterals and apicals (the prolateral side is hidden). Position of the long trichobothrium on metatarsus I in 0.45. Metatarsi and the thickened tarsi bear a ventral pseudoscopula. Paired tarsal claws long and toothed, unpaired claws small. – Opisthosoma oval, slightly deformed. – Pedipalpus (figs. 7c–d): Femur slender, patella short, tibia thick, cymbium short and blunt, bulbus almost spherical, embolus fairly long and bent, sperm reservoir large.

Relationships: *Ariadna hintzei* WUNDERLICH 2004 in copal from Madagascar is distinctly larger (prosomal length 2.4 mm), the eye position is different, metatarsus I bears 3 pairs of ventral bristles, the cymbium is longer.

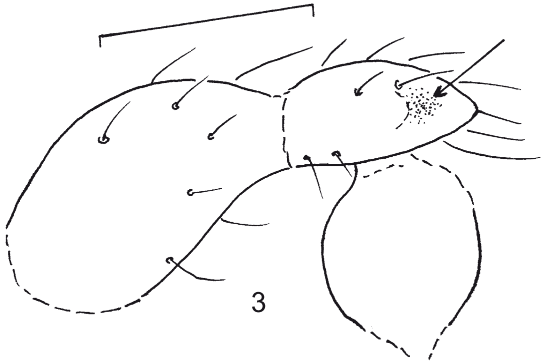
Distribution: Most probably N-Madagascar (see above).



1

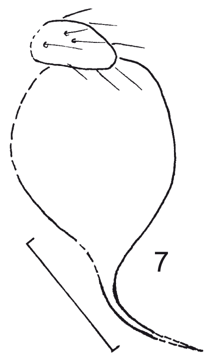


2

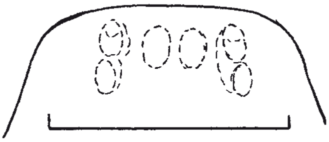


3

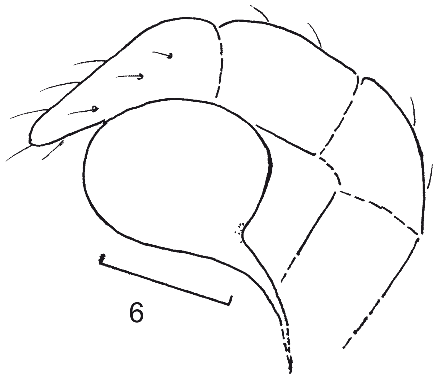
4



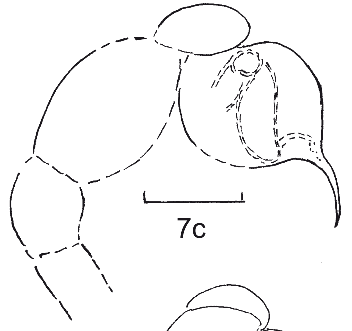
7



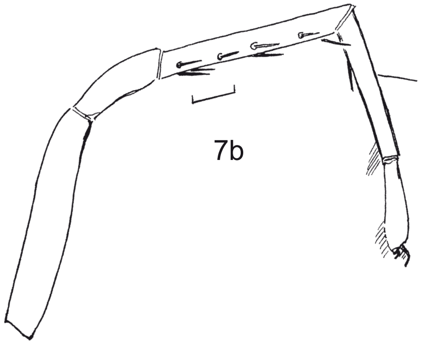
5



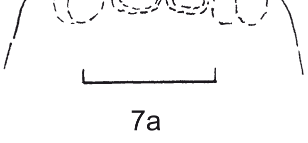
6



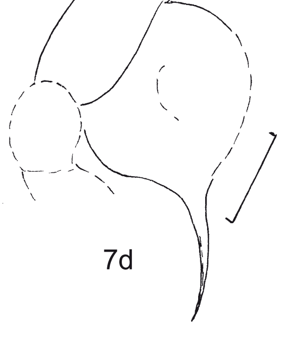
7c



7b



7a



7d

Fig. 1: Ariadna defuncta WUNDERLICH 2004, ♂ holotypus, retrolateral aspect of the l. pedipalpus. Note the bubble at the tip of the embolus; scale bar = 0.2 mm;

figs. 2–3: Ariadna ovalis **n. sp**., ♂ holotypus; 2) retrolateral aspect of the l. pedipalpus; 3) retrolateral aspect of the r. pedipalpus. The embolus is hidden by a white emulsion; the arrow points to the cymbial depression; scale bar = 0.5;

fig. 4: Ariadna sp. indet., ♀, dorsal aspect of the anterior part of the prosoma; scale bar = 0.5;

figs. 5–7: Ariadna parva **n. sp**., ♂ holotypus; 5) dorsal aspect of the anterior part of the prosoma; the eyes are partly covered with a white emulsions; 6) retrolateral aspect of the l. pedipalpus; 7) dorsal aspect of cymbium and bulbus of the r. pedipalpus; scale bar = 0.5 in fig. 5, 0.2 in figs. 6–7;

figs. 7a–7d: Ariadna copalis **n. sp**., ♂ holotypus; 7a) position of the eyes which are covered with bubbles; 7b) retrolateral aspect of the r. leg I; 7c) prolateral aspect of the l. pedipalpus; 7d) r. pedipalpus, retrodorsal-basal aspect of patella and tibia and retroventral aspect of bulbus and embolus; scale bar = 0.2.

ON EXTANT AND FOSSIL (EOCENE AND CRETACEOUS) TAXA OF THE SUBFAMILY ORCHESTININAE (ARANEAE: OONOPIDAE) (Photos 66–70, 132–138).

The tiny spiders of this subfamily – see e. g. DALMAS (1916), SAARISTO (2001), WUNDERLICH (1981, 2004) – were frequently overlooked. Their shape is fairly uniformly but certain structures – e. g. of their genitalia – are quite diverse, and their study is just at the beginning. Orchestininae is – in the geological sense – one of the oldest suprageneric araneomorph taxa besides the Ariadninae of the Segestriidae, and probably the Archaeinae of the Archaeidae which had the greatest known longevity. These taxa are already known from the Lower Cretaceous; Archaeinae probably already from the Jurassic.

Most of the material is kept in the Senckenberg Museum Frankfurt a. M. (SMF) and in the Geological-Palaeontological Museum of the University Hamburg (GPMUH); if not otherwise noted the material is still kept in the collection of J. WUNDERLICH (CJW), and will probably be given to the SMF in the future.

Groups/subfamilies of the family Oonopidae: SAARISTO (2001) distinguished six "genus groups" within the Oonopidae; four of them possess at least a partly armoured opisthosoma; the "*Oonops* group" and the "*Orchestina* group" (= Orchestininae) have a soft opisthosoma (but at least in some females of *Orchestina* and strongly related genera the epigaster may be distinctly sclerotized). In my opinion all these "groups" have to regard as subfamilies, and their relationships remind me on the conditions in the five or six subfamilies of the Anapidae s. l. (superfamily Araneoidea).
According to their diverse somatical and genitalic structures I regard the taxa Oonopidae, Oonopinae and *Orchestina* as quite "heterogeneous", and they have to split up; SAARISTO & MARUSIK (2004) already worked in this sense, and pointed out the urgent need of a revision of the diverse genus *Orchestina*.

The subfamily **ORCHESTININAE** CHAMBERLIN & IVIE 1942

Orchestina group of the Oonopidae sensu SAARISTO & MARUSIK (2004: 310).
Photos 66–70, 132–138, figs. 1–51.

The tiny specimens of the subfamily Orchestininae – I introduce here the popular names "Jumping Dwarf Six-eyed Spiders" and in German: "Springende Zwerg-Sechsaugenspinnen" – are easily recognizable by the "segestriid" position of their six eyes (photos 132f, fig. 1) – rarely exist eight eyes as an atavism, see WUNDERLICH (2004: 690, 697, fig. 8d) –, and the enlarged femora of their posterior legs which are jumping legs (photos, fig. 2). Only two genera – the type genus *Orchestina* SIMON 1882 (extant and fossil) and *Ferchestina* SAARISTO & MARUSIK (2004) (extant) – have been described within this subfamily, see DALMAS (1916).
In this paper I describe an extant new species of *Orchestina*, the extinct Eocene new subgenus *Baltorchestina* n. gen. of the genus *Orchestina* with five fossil new species in Baltic amber, the extinct new subgenus *Gallorchestina* of the genus *Orchestina* in lowermost Eocene French amber, the extinct Cretaceous *Burmorchestina* n. gen. with *B. pulcher* n. sp., and the extinct Cretaceous *Canadaorchestina* n. gen.

Diagnosis: FEMORA OF THE POSTERIOR LEGS – which are jumping legs – DISTINCTLY THICKENED (photos 132f, figs. 2, 36) (distinctly thicker than the remaining femora), six eyes in a "SEGESTRID" POSITION (fig. 1), thoracal part distinctly RAISED or domed (figs. 4, 34). ♂-pedipalpus (figs. 7, 45): SCLEROTIZED SEMINAL DUCTS of the bulbus (*) distinct.

(*) Recognized as an important taxonomic character by Y. MARUSIK, person. commun..

Further characters: Basal cheliceral articles, labium and gnathocoxae: See below. Leg bristles absent or only few apical metatarsal bristles existing which stand out from their article and are usually indistinct. Dorsal opisthosomal scutum absent, epigaster sclerotized in some taxa. The colulus may be a wide plate (fig. 32a), and bears a pair of hairs at least in certain species. ♂: Gnathocoxae usually very long and divided longitudinally in the distal half (figs. 6, 13, 16) (sexual dimorphism; divided gnathocoxae are unknown in the Cretaceous taxa which are usually not well preserved). Articles of the ♂-pedipalpus usually thickened, rarely slender (in the Cretaceous taxa).

Remarks: Male gnathocoxae (figs. 6, 13) which are divided longitudinally exist also in other Oonopidae. This peculiar structure was already documented by SAARISTO & MARUSIK (2004); there exists a scinny medial part and a retrolateral part which is usually sclerotized (*Ferchestina* SAARISTO & MARUSIK 2004: See below). – The combination of three characters: Distinctly thickened posterior femora, a “segestriid” eye position, and a raised prosoma is unique within the superfamily Dysderoidea as well all other spiders. “Segestriid” eye position: See WUNDERLICH (2004: 650–651). (Additional) anterior median eyes may be present in several species of *Orchestina* as an atavism, see DALMAS (1916), WUNDERLICH (2004: 690, 697: Fig. 8d).

Description: Ecribellate tiny spiders, body length usually 0.8–2 mm, colour of prosoma and legs usually yellow to orange, rarely exist gray darkenings. Clypeus distinctly obliquely protruding (figs. 1, 4–5) at least in the extant, subrecent and Tertiary spiders (short and vertical in the Cretaceous *Burmorchestina* n. gen.), thoracal fissure absent, basal cheliceral articles slender, fairly diverging distally, and **CONCAVE** anteriorly (fig. 4), cheliceral furrows toothless. Labium free, slightly to distinctly longer than wide and usually incised (figs. 3, 44, 47), but rhomboid in *Ferchestina* (fig. 49), and straight in ?*Orchestina madagascariensis* WUNDERLICH 2004 (fig. 33); it bears long bristles in a variable number and position: Usually exists an apical pair (figs. 3, 13, 21, 44) (apical bristles may be broken off, fig. 47), and in *Ferchestina* (see below) such bristles may be absent; in the subrecent ?*Orchestina madagascariensis* (fig. 33) from Madagascar exists a single subbasal bristle, see below. Gnathocoxae usually divided longitudinally in the male sex at least in the distal part (figs. 6, 13), serrula present. Legs: Autotomy between coxa and trochanter (frequent in fossil specimens), bristles reduced in number – they are completely absent in *Burmorchestina* – and in size, short ones are usually present apically on the metatarsi (at least on IV, *Orchestina*, fig. 2). Tarsal trichobothria absent, all metatarsi bear a single and very long trichobothrium in the distal half (figs. 2, 37–38); its usual position is in 0.6-0.9. Their position may be quite different on anterior and posterior legs, see *Orchestina* below. Paired tarsal claws biserially dentate (MARUSIK in litt.) like in other Oonopidae (erroneously reported as uniserially dentate by DALMAS (1916: 216), the retrolateral row is lost in few oonopids, see below (“relationships”); unpaired tarsal claw and claw of the ♀-pedipalpus absent like in other Oonopidae, onychium well developed. In females of some taxa the epigaster is stronger sclerotized. Lungs strongly reduced. The anterior position of the posterior tracheal stigmata – just behind the epigastral furrow – have been compared with the stigmata of the Dysderidae by DALMAS (1916: 217); its position is the same as in other Oonopidae as well as in (e. g.) Orsolobidae and Segestriidae. Colulus variable, small to tiny or wide (fig. 32a), bearing hairs (a pair of long hairs in *O. pavesii*). ♂-pedipalpus (figs. 7, 18–19, 22–24, 39, 43, 45): Most articles usually thickened but slender in *Burmeorchestina*, bulbus simple, pear-shaped or almost globular, more slender in *Burmorchestina*, embolus undivided or divided, in some species with a ventral apophysis or apophyses; the term “psembolus” sensu SAARISTO is superfluous in my opinion. Capture web absent as in other Oonopidae.

Sexual dimorphism: Males are smaller than females (the prosoma is fairly smaller), their posterior femora are relatively thicker (stouter), their gnathocoxae are divided in the distal half (figs. 3, 6, 10, 13, 21, 33), and their labium bears usually a pair of apical bristles (figs. 10, 13) (*Ferchestina* (fig. 49) is reported as an exception but see below). In certain extant species the male chelicerae bear an anterior-basal hook or the prosoma bears a dorsal hook (fig. 48); see FAGE (1916).

Type genus: *Orchestina* SIMON 1882.

Further (sub-)genera: *Baltorchestina* n. subgen. of *Orchestina* (Eocene Baltic amber), *Burmorchestina* n. gen. (Cretaceous), *Canadaorchestina* n. gen. (Cretaceous of North America), *Ferchestina* SAARISTO & MARUSIK 2004 (extant, Russia), *Gallorchestina* n. subgen. of *Orchestina* (Eocene French amber),
Remark: Extant species like *Orchestina dentifera* SIMON, *O. madagascariensis* WUNDERLICH 2004, *O. saltabunda* SIMON and *O. tubulifera* SIMON may be members of undescribed genera. See below and the remark of SAARISTO (2001: 354); a worldwide revision is needed.

Relationships: The combination of posterior jumping legs, a “segetriid” eye position, probably the existence of apical labial bristles, and the raised prosoma of the Orchestininae is unknown in the related subfamilies. According to the presence of an onychium, the strong reduction or even loss of the lungs, the absence of an unpaired tarsal claw as well as a claw of the ♀-pedipalpus the Oonopinae s. str. is most related, in which the labium is not modified as in most Orchestininae, and sclerotized sperm ducts of the tegulum are absent. Only in *Sulsula* SIMON 1882 – a true member of the Oonopinae? – the eye position is similar to the Orchestininae; in *Sulsula* femur IV is not or only slightly thickened. In the Oonopinae the shape of the prosoma is different to the Orchestininae; an autapomorphy of the Oonopinae is unknown to me. – In the Orsolobidae exists a similar eye position as in the Orchestininae but – in addition to the different diagnostic characters of the Orchestininae which are given above – the tarsal organ is raised, the prosoma is not distinctly raised, a claw of the ♀-pedipalpus exists; the paired tasal claws are biserially dentate as in most Oonopidae (at least the retrolateral row of dents is lost in some Oonopidae like *Dysderina* and probably in *Anophthalmoonops*, too, see FORSTER & PLATNICK (1985: 218); the retrolateral row is reduced in some Orchestininae).
CONVERGENCES: DALMAS (1916: 203–204) pointed out that the members of *Orchestina* – regarded in the wide sense of this author – possess certain characters of the Dysderidae (shape of the labium, position of the anterior tracheal stigmata), as well as of the Ochyroceratidae, the Pholcidae (an anterior outgrowth of the male chelicerae in some taxa) and the Segestriidae (the position of the eyes); I may add the Tetrablemmidae in this connection (in males of some members exist a dorsal prosomal outgrowth as in *Ferchestina* SAARISTO & MARUSIK 2004). Eye position, clypeus – and partly the chaetotaxy and the shape of clypeus and labium (compare e. g. *Burmorchestina* and Theotiminae DEELEMAN-REINHOLD 1995) – are similar to certain Ochyroceratidae in which an unpaired tarsal claw and a large colulus exist in contrast to the Orchestininae, and the basal cheliceral articles are not concave anteriorly; furthermore Ochyroceratidae are web-dwellers. In members of the family Leptonetidae exist an unpaired tarsal claw, and members of this family are web-dwellers like the

Ochyroceratidae; their chelicerae are particular, and the usual positions of their six eyes is unique among spiders, see WUNDERLICH (2004: 718, figs. 13b, c).

Prey, parasites and mating behaviour: See WUNDERLICH (1981) and (2004: 694). With the holotype of *Burmorchestina pulcher* n. gen. n. sp. a small Diptera: Nematocera is preserved which may have been a prey of the spider, see photo 66.

Ecology: Orchestininae specimens are hunting spiders which build no capture web. I collected specimens of *Orchestina* on the ground (under stones, in detritus and litter), under bark, and on bushes and trees as well, e. g. *O. pavesii* (SIMON) at all these habitats on the Canary Islands and other species in SE-Asia. The high frequency of Orchestininae in amber and copal – up to 20% of the specimens (in Baltic amber), see also below: *Burmorchestina* – indicates their presence and frequency in higher strata of the vegetation already in the Tertiary and the Cretaceous. – SAARISTO (2001: 309) reports Oonopidae as nocturnal but according to their high frequency in amber at least most of the fossil spiders of the subgenus *Baltorchestina* have been active at daytime when they have easily been captured by the resin which was less liquid at night. In Malaysia I observed a pair of *Orchestina* in copula in the afternoon which was discovered under the bark of a tree.

The pronounced GEOLOGICAL LONGEVITY (see below) and TAXONOMICAL DIVERSITY may be strongly influenced by the existence of the special jumping (escape) behaviour of all members of this subfamily and their ecological diversity. I observed specimens of *Orchestina* jumping more that ten times of their body length.
Remark on the jumping behaviour: It is very rare among haplogyne spiders in contrast to entelegyne hunting spiders of the RTA-clade – e. g. Clubionidae, Lycosidae, Oxyopidae, Pisauridae, Salticidae, and Zoridae s. l. – in which it is quite frequent.

Today’s distribution: Cosmopolitical, mainly tropical and subtropical. (There are fewer records from the Southern Hemisphere which is much lesser studied than the Northern Hemisphere).

Fossil distribution/records: Cretaceous: Ambers from North America (USA: New Jersey, Canada: Alberta, *Canadaorchestina*, see below, Burma (Myanmar, *Burmorchestina* n. gen., see below), China, see WUNDERLICH (2004: 1862), and N-Spain (taxon?; see WUNDERLICH (2004: 227, 1862, 1869)); still no report for Lebanese and Jordanian ambers. Tertiary ambers: Eocene: Kaliningrad/Samland, Bitterfeld, Ukraine (Rovno) (subgenera *Baltorchestina* of *Orchestina*, and most probably *Orchestina*); Miocene: Mexico (Chiapas) (subgenus *Orchestina*), Hispaniola (Dominican Republic) (subgenus *Orchestina*); Quaternary (extant and subrecent) (*Orchestina* and probably undescribed genera): Copal from Columbia, Japan, Kenya (copal or amber?), and Madagascar; *Ferchestina* from Russia. – No other subfamily of araneomorph spiders – with the rare probable exceptions of the Archaeidae: Archaeinae and the Segestriidae: Ariadninae – is known to have such a wide distribution which is combined with such a longevity, reaching from the Lower Cretaceous up to now, a spun of time of about 135 million years (Archaeinae even more).

Ferchestina SAARISTO & MARUSIK 2004 (figs. 45–46)

2004 *Ferchestina* SAARISTO & MARUSIK, Arthropoda Selecta, 13 (1–2): 51–54.

Diagnosis: Labium rhomboid and – so far known to me – without apical bristles (fig. 46); ♂: Prosoma (fig. 45) with a dorsal outgrowth, basal cheliceral articles with a proapical outgrowth, gnathocoxae probably – according to the original description – undivided. Further characters: Pedipalpal tibia quite voluminous, embolus pointed.

Relationships: In other genera of the Orchestininae a dorsal outgrowth of the male prosoma is absent, a similar outgrowth of the ♂-chelicerae is absent, too, the labium has not a rhomboid shape and bears usually paired apical bristles.

Type species: *Ferchestina storozhenkoi* SAARISTO & MARUSIK 2004 (the only known species of the genus).

Distribution: Russia.

Orchestina SIMON 1882

See the revision of extant species by DALMAS (1916). Photos 132–138, figs. 1–33

Diagnosis: The ♂-labium (fig. 3) bears apical bristles in a converging position (but see fig. 33), position of the metatarsal trichobothria I–II and III–IV quite different, ♂-pedipalpus (e. g. figs. 7, 19) with a thick bulbus which is broadly attached to the cymbium, and at least one of the articles is thickened; a short conductor (outgrowth of the embolus) exists in certain species.

Further characters: Clypeus long and widely protruding (fig. 4), gnathocoxae divided longitudinally (fig. 6), apical metatarsal bristles (in all taxa?) present.

Type species: *Schoenobates pavesii* SIMON 1882.

Intrageneric divisions: There are at least two subgenera: *Baltorchestina* n. subgen. and *Orchestina*. – According to unusual somatic structures and their emboli certain extant species like *Orchestina dentifera* SIMON, *O. saltabunda* SIMON and *O. tubulifera* SIMON may be members of undescribed subgenera or even genera of their own, see the remark of SAARISTO (2001: 354). – In the subrecent ?*Orchestina madagascariensis* WUNDERLICH 2004 the labium is not incised apically (like in *Ferchestina*) and apical bristles of the labium are most probably absent (fig. 33); this species may be the member of a species-group or subgenus of its own, too. – In the extant *Orchestina dalmasi* n. sp. the sperm duct of the bulbus is coilled in an unusual length.

Relationships: See *Ferchestina* and the remarks of SAARISTO (2001: 354). – In *Burmorchestina* n. gen. the metatarsi are bristle-less, the position of the metatarsal trichobothria I–IV is rather similar, all articles of the ♂-pedipalpus are slender, the bulbus is long and slender, and attached to the cymbium in a short area only; the fine structure of the gnathocoxae is unknown. – In *Canadaorchestina* n. gen. (figs. 50A–B) the metatarsi are probably bristle-less (metatarsal bristles are not noted by PENNEY in the original description of the generotype), the pedipalpal articles are slender, the embolus is thick, and a large conductor is present; nothing is known about the existence of apical bristles of the labium and the structure of the gnathocoxae.

Distribution: Extant (cosmopolitical) and Tertiary.

***Orchestina (Orchestina) dalmasi* n. sp.** (figs. 4–8)

Derivatio nominis: The spider is named after M. DALMAS, who published an important revision of the extant members of *Orchestina* SIMON 1882.

Material: East Malaysia, Besut, under a stone, holotype ♂, JW leg. in VIII, R6/AR/CJW; SMF.

Remark: Most legs and bristles of the holotype are lost, only the posterior pair and the left leg III are still present.

Diagnosis (♂; ♀ unknown): Body length only 0.8 mm. Depigmented yellow spiders without black rings around the eyes. Pedipalpus (figs. 7–8): Femur not thickened, tibia very thick, sperm ducts strongly coiled, distal half of the bulbus thick, embolus short.

Description (♂):
Measurements (in mm): Body length 0.8, prosoma: length 0.45, width 0.36; leg IV: Femur 0.41 (0.13 thick), tibia 0.28, metatarsus 0.32, tarsus 0.18.
Colour pale yellow, black rings around the eyes are absent.
Prosoma (figs. 4–6): Eyes large, in a wide field, basal cheliceral articles fairly slender, labium longer than wide, gnathocoxae very long, divided longitudinally in the distal half, the lateral part fairly sclerotized, the medial part almost white. The sternum separates coxae IV by almost their diameter. Legs (most legs are missing) slender but femur IV strongly thickened; position of the trichobothrium on metatarsus IV in 0.6. Opisthosoma oval. Pedipalpus: See above; the short embolus is stronger sclerotized.

Relationships: The ♂-pedipalpus is similar to *O. manicata* SIMON 1893 from Sri Lanka; according to DALMAS (1916) the embolus is pointed in *manicata* and the body length of the male is 1.1–1.3 mm.

Distribution: East Malaysia.

REMARKONASUBRECENTSPECIESINCOPALFROMMADAGASCAR

In one of the subrecent/subfossil males of *Orchestina madagascariensis* WUNDERLICH 2004 – the paratype c, F1120/CJW – the labium is well preserved and well visible; apical bristles are not recognizable and probably absent in this specimen and species; it exists only a single short labial bristle in the basal half (fig. 32). Because of the unusual structure of the labium I do not want to exclude that *madagascariensis* may be the member of an undescribed subgenus or even genus; an extant male in a good condition is needed for a definitive conclusion.

ORCHESTININAE IN EOCENE BALTIC AMBER

***Baltorchestina* n. subgen. of *Orchestina* SIMON**

Diagnosis: ♂-labium with long apical bristles in a DIVERGING position (figs. 10, 13, 21) (unfortunately these bristles are hidden in most fossils).

Further characters: Clypeus long and strongly protruding, ♂-gnathocoxae divided longitudinally (fig. 13), apical metatarsal bristles present at least on leg IV, colulus wide (fig. 32a) (so in all species?).

Type species: *Orchestina* (*Baltorchestina*) *perfecta* n. sp. – Further species: The fossil spiders which were described by WUNDERLICH (1981) as *Orchestina* SIMON in Baltic amber are transferred here to the subgenus *Baltorchestina* n. gen. (e. g. *crassipatellaris, crassitibialis, cochlembolus* and *tuberosa*); although I do not want to exclude with certainty that some of these species may be members of the subgenus *Orchestina* or of subgenera of their own.

Intrageneric division: According mainly to the structures of the embolus – but probably to the chaetotaxy and the trichobothriotaxy, too – there are several species-groups. – See the remarks above on the intrageneric division of *Orchestina* SIMON.

Relationships: In the extant – and probably Eocene – subgenus *Orchestina* SIMON 1882 the clypeus bears usually thinner long hairs (a pair of strong clypeal hairs exist in the extant *O. pilifera* DALMAS 1916 which may be convergently evolved) and the ♂-labium bears apical bristles in a CONVERGING position (fig. 3) (I did not find exceptions). Probably in contrast to the members of *Orchestina* both parts of the gnathocoxae may be well sclerotized in *Baltorchestina* (the grade of sclerotization is difficult to recognize in the fossils spiders). – In *Ferchestina* the shape of prosoma and labium are quite different, see above. – In *Burmorchestina* the position of the bristles of the labium is straight/parallel (fig. 44), and the pedipalpal articles are slender.

Distribution: Eocene Baltic amber forest.

Orchestina (Baltorchestina) cochlembolus WUNDERLICH 1981 (fig. 9)

Material (males in Baltic amber): Holotypus and paratypus GPIUH typ. cat. nos. 2522 and 2522a; 1♂ from the Bitterfeld deposit F1873/BB/AR/CJW.

The three males possess 5 pairs of clypeal hairs but their number may be higher in other specimens. The holotype and the paratype were heated, the fairly deformed embolus of the holotype has a bipartite tip, its patella is slightly larger than shown in fig. 14a) which was given by WUNDERLICH (1981), the length of the pedipalpal tibia is 0.18 mm. In the paratype are the emboli and their ventral apophyses fairly deformed (fig. 9).

Distribution: Eocene Baltic amber forest, incl. the Bitterfeld deposit.

Orchestina (Baltorchestina) crassipatellaris WUNDERLICH 1981

Material: 1♂ 1♀ in the same piece of Baltic amber, F1865/BB/AR/CJW.

The female of this species was unknown. It is situated just behind the male in the fossil resin and is partly – the opisthosoma completely – covered with a white emulsion. Measurements (in mm): Body length 1.5, prosomal length 0.53, tibia IV 0.65 (hight 0.18), the clypeus bears 4 pairs of long and bristle-shaped hairs; position of the metatarsal trichobothrium: I in 0.92, III in 0.67, IV in ca. 0.63. – Position of the metatarsal trichobothrium of male F1865: II in 0.94, IV in ca. 0.63 (of the holotype in 0.65).

Orchestina (Baltorchestina) crassitibialis WUNDERLICH 1981 (figs. 10–12)

Material: 3♂ in Baltic amber, F508, F1861 and F1862/BB/AR/CJW.

Remark: I regard these males as most probably conspecific with the holotype; the shape of their embolus may appear quite distinct in different positions (figs. 11–12).
The labium in the male F508 is almost as wide as long (fig. 10) and bears a pair of api-

cal bristles in a narrow and diverging position. The embolus (figs. 11–12) possesses a ventral outgrowth and is apically divided (not recognizable in all specimens and only in certain positions). See *B. rectangulata* n. sp.

Orchestina (Baltorchestina) ?***furca*** WUNDERLICH 1981 (photos 136–137, figs. 13–15)

Material: 3♂ in Baltic amber, F509, F1871 and F1872/BB/AR/CJW.

In the male F1871 the shape of the distal part of the embolus is different in both pedipalpi (figs. 14–15) and slightly different from the holotype of *furca*, see WUNDERLICH (1981: Fig. 15). Therefore I regard this specimen as only probably conspecific with *furca*. This piece of amber was not or only slightly heated. – In the male F509 the labium is well recognizable but the division of the gnathocoxae is not well observable (fig. 13). Relationships: See *B. bitterfeldensis* n. sp. below.

Orchestina (Baltorchestina) imperialis WUNDERLICH 1981 (fig. 16)

Material: 1♂ in Baltic amber, F1863/BB/AR/CJW.

Because of its slightly deformation in this male is the bipartition of the gnathocoxae well recognizable (fig. 16). – See *B. brevis* n. sp. below.

Descriptions of new species in Baltic amber

Orchestina (Baltorchestina) brevis **n. subgen. n. sp**. (photo 135, figs. 17–20)

Material: 4♂ in Baltic amber; holotypus F1866/BB/AR/CJW, paratypes F1867–1869/BB/AR/CJW; the paratypes are deposited in the SMF. – For a comparison: 7♂ of *O.* (*B*). *imperialis* WUNDERLICH 1981, F492, F503, F1858, F1863 and F1864/BB/AR/CJW; F1868 and F1869 from the Bitterfeld deposit.

Preservation and syninclusions: The holotype is well and almost completely preserved, in a piece of amber which was not heated; the right tarsus IV and the tip of the left tarsus IV are cut off, a white emulsion covers ventral parts of the opisthosoma, a bubble covers the anterior-ventral part of the left side of the opisthosoma. – Paratype F1867 is fairly well preserved; the piece of amber has a hole which was made by man, body and legs of the spider are surrounded and partly hidden by fissures. A Diptera: Nematocera and numerous stellate hairs are preserved in the same piece of amber. – Paratype 1868 is well preserved in the piece of amber which was heated; the right legs I and IV are lost by autotomy beyond the coxa, a large divided bubble is situated at the right side of the spider. A fly and a midge are preserved in different layers as well as a spider's thread which bears tiny scales of an insect and some stellate hairs. – Paratype F1869 is completely and only fairly well preserved in a piece of amber which was heated; fissures surround the body; few spider's threads and some stellate hairs are also preserved.

Diagnosis (♂; ♀ unknown): Small and short-legged spiders, prosomal length 0.55–0.65 mm, tibia I 0.33–0.4 mm long; clypeus with only two pairs of short and bristle-shaped hairs (fig.17), which are only 0.03–0.05 mm long. Pedipalpus (figs. 18–20): Femur fairly slender, tibia fairly thick, embolus long, slender and bent in an almost right angle in the distal part.

Description (♂):
Measurements (in mm): Body length 1.05 (holotype) – 1.15, prosomal length 0.55 (holotype) –0.65, width 0.45–ca. 0.5; legs: Holotype: Tibia I 0.33, femur IV 0.48 (0.15 high); tibia I 0.33–ca. 0.4; tibia of the pedipalpus 0.19 long, 0.11 high.
Colour mainly yellow brown, prosoma mainly medium (partly dark) brown in heated specimens.
Prosoma (fig. 17) 1.22–1.28 times longer than wide. 6 large eyes, clypeus obliquely protruding, bearing two pairs of short, bristle-shaped hairs which are only 0.33–0.05 mm long (holotype, paratype F1867; missing in the heated specimens from the Bitterfeld deposit), dorsally with long bristle-shaped hairs, thoracal area fairly raised, thoracal fissure absent. Basal cheliceral articles slender, most parts of labium and gnathocoxae hidden, the sternum separates the coxae IV by ca. their diameter. – Legs short, femur IV strongly thickened, metatarsi with apical bristles and a long trichobothrium, their position on I–II in 0.9–0.93, on IV in ca. 0.7. – Opisthosoma oval, soft, dorsally with long and more or less erect hairs. – Pedipalpus (figs. 18-20): Femur fairly slender, patella fairly small, tibia fairly thickened, embolus long, in the distal part thin and bent almost in a right angle.

Relationships: *O. (B.) imperialis* WUNDERLICH 1981 may be most related, its clypeus bears also only two pairs of long hairs and the structures of the male pedipalpus are similar, but *imperialis* is larger and long-legged, its prosomal length is 0.68–0.75 mm, the length of its tibia I is 0.6–0.7 mm, the clypeal hairs are 0.09–0.12 mm long (the position of the metatarsal trichobothria is identical).

Distribution: Eocene Baltic amber forest incl. the Bitterfeld deposit.

***Orchestina (Baltorchestina) multisetae* n. subgen. n. sp.** (figs. 21–24)

Material: Holotypus ♂ in Baltic amber and a separated piece of amber, F 1874/BB/AR/CJW.

Preservation and syninclusions: The spider is fairly well preserved in a piece of amber which was slightly heated, the pedipalpi are well recognizable, the left leg IV and the right legs except I are missing by autotomy beyond the coxa, mainly the left side of the prosoma and the left pedipalpus are covered with a white emulsion. Stellate hairs and two Diptera: Nematocera are preserved in the same piece of amber.

Diagnosis (♂; ♀ unknown): Clypeus with numerous (ca. 10 pairs) of long and bristle-shaped hairs similar to fig. 25. Pedipalpus (figs. 22–24) with thick articles, embolus long (see below).

Description (♂):
Measurements (in mm): Body length 1.2, prosomal length ca. 0.6; leg I: Tibia 0.45, metatarsus 0.42, tarsus 0.17, femur IV 0.16 high; pedipalpus: Femur 0.19 (0.12 high), patella 0.17 (0.15 heigh), tibia ca. 0.3 (0.18 high), bulbus with embolus 0.36.
Colour: Prosoma and legs medium brown, opisthosoma yellow brown.
Prosoma (fig. 21) (parts are hidden) and legs – as far as recognizable – quite similar to *O. perfecta*. Gnathocoxae long, partly hidden, labium longer than wide, with longer apical bristles which are widely separated. Coxae IV separated by their diameter by the sternum. – Opisthosoma oval, covered with long hairs; epigaster apparently stronger sclerotized. – Pedipalpus (figs. 22–24) with thick articles, patella almost globular, bulbus pear-shaped, embolus long, with a ventral apophysis (both apparently fairly deformed by heating), divided distally.

Relationships: In *O. (B). perfecta* n. sp. – in which also numerous clypeal hairs exist, see figs. 25–30 –, the ventral outgrowth of the embolus is longer and more slender and in a more basal position. – I do not want to exclude that the small male F1859/CJW – *O. (B)*. sp. indet. – may be conspecific with *multisetae*.

Distribution: Eocene Baltic amber forest.

***Orchestina (Baltorchestina) perfecta* n. subgen. n. sp**. (photos 132–134, figs. 25–30)

Material: Holotypus ♂ in Baltic amber, F1860/BB/AR/CJW.

Preservation and syninclusions: The spider is very well preserved in a small yellow piece of amber which was slightly heated; few – mainly ventral – parts of the spider are covered with a white emulsion, the left legs I and IV are missing beyond the coxa by autotomy, the left tarsus and the distal part of the left metatarsus IV are cut off, two stellate hairs are preserved in the same piece of amber.

Diagnosis (♂; ♀ unknown): Clypeus with ca. 10 pairs of long and bristle-shaped hairs (fig. 25); pedipalpus (figs. 26–30): Femur thick, bulbus long, embolus with a ventral-basal outgrowth, divided in its distal third.

Description (♂):
Measurements (in mm): Body length 1.35, prosoma: Length 0.62, width 0.56; leg I: Femur 0.65, patella 0.2, tibia 0.47; leg II: Metatarsus 0.5, tarsus 0.22; femur IV: Length ca. 0.66, height 0.16; pedipalpus: Femur length 0.2, width 0.125, patella length 0.18, width 0.15 (the tibia is partly hidden).
Colour: Prosoma and legs light brown, opisthosoma yellow brown.
Prosoma (fig. 25) 1/10 longer than wide, with long dorsal hairs and ca. 10 pairs of long clypeal hairs. Six eyes, the medians largest and contiguous. Chelicerae and gnathocoxae hidden, labium slightly longer than wide, apically with a pair of long and diverging bristles as in *multisetae* n. sp. The sternum divides the coxae IV by slightly more than their diameter. – Legs fairly long, with thin apical metatarsal bristles; position of the metatarsal I trichobothrium near the end of the article. – Opisthosoma oval, covered with long dorsal hairs. – Pedipalpus (figs. 26–30): Patella and tibia thick, embolus with a ventral-basal outgrowth, divided in the distal third; a sclerotized tegular sperm duct exists but is badly preserved and is not drawn.

Relationships: See *O. (B). multisetae* n. sp. in which also numerous clypeal hairs exist as well as in *B*. sp. indet., F1859/BB/ARCJW. In *O. (B). cochlembolus* WUNDERLICH 1981 exists a lower number of clypeal hairs.

Distribution: Eocene Baltic amber forest.

Orchestina (Baltorchestina) rectangulata **n. subgen. n. sp**. (fig. 31)

Material: Holotypus ♂ in Baltic amber, F1875/BB/AR/CJW.

Preservation and syninclusions: The spider is well preserved in a small yellow piece of amber; the left legs I and II are missing beyond the coxa by autotomy, the retrolateral half of the right tibia IV and a retrolateral part of the right pedipalpal tibia are cut off, parts of the right anterior and ventral sides of the body are covered with a white emulsion. A tiny hair-shaped structure is preserved left above the spider.

Diagnosis (♂; ♀ unknown): three pairs of long clypeal hairs. Pedipalpus (fig. 31): Patella and tibia distinctly thickened but femur fairly slender; distal part of the embolus slender, undivided, bent ventrally almost in a right angle and ventrally with a larger outgrowth.

Description (♂):
Measurements (in mm): Body length 1.25, prosoma: Length 0.5, width almost 0.5; femur I 0.48, femur IV 0.65 (height 0.16), tibia IV 0.38; pedipalpus: Tibia: Length 0.3, height 0.19, bulbus hight 0.22.
Colour: Prosoma and legs light to medium brown, opisthosoma yellow brown.
Prosoma with long dorsal hairs and 6 large eyes; the clypeus bears 3 pairs of long hairs; mouth parts hidden. – Legs only fairly long, femur IV strongly thickened, apical bristles present on all metatarsi, metatarsus IV with 3 longer apical bristles. Position of the metatarsal trichobothrium: 0.9 on I, 0.65 on IV. – Opisthosoma oval, with long dorsal hairs. – Pedipalpus: See above.

Relationships: In *O. (B.) crassitibialis* WUNDERLICH 1981 the tibia of the male pedipalpus is distinctly thicker (ca. 0.3 mm high), and the shape of the embolus is different (figs. 11–12).

Distribution: Eocene Baltic amber forest.

Orchestina (Baltorchestina) bitterfeldensis **n. subgen. n. sp**. (fig. 32)

Material: Holotypus ♂ in Baltic amber from the Bitterfeld deposit, GPIUH, coll. H. GRABENHORST no. AR-167.

Preservation and syninclusions: The spider is preserved in a thin and strongly bent piece of amber which was heated; body and legs are darkened, the right legs III and IV are lost beyond their coxa by autotomy; the dorsal side of the body is hidden, parts of the ventral side are covered with a white emulsion. – Two Diptera, a tiny Hymenoptera, particles of detritus as well as stellate hairs (two below the spider) are preserved in the same piece of amber.

Diagnosis (♂; ♀ unknown): Pedipalpus (fig. 32): Articles fairly thickened, embolus straight and divided (the clypeal hairs are unknown).

Description (♂):
Measurements (in mm): Body length ca. 1.1, opisthosoma: Length 0.6, height 0.45; leg I: Femur 0.52, patella 0.11, tibia 0.4, metatarsus 0.37, tarsus 0.21; leg IV: tibia 0.37, femur: Length 0.45, height 0.13.
Colour dark brown (darkened by heating).
Prosoma: Most parts are hidden; the sternum separates the coxae IV by their diameter. – Legs slender but femur IV strongly thickened; distinct bristles absent, position of the long trichobothria: I in 0.93, IV in ca. 0.62. – Opisthosoma oval, covered with fairly long hairs. – Pedipalpus: See above.

Relationships: See *O. (B.) sternalis* n. sp.. In *O.* (*B). furca* WUNDERLICH 1981 the embolus is divided, too, but it is bent distally to the femur.

Distribution: Eocene Baltic amber forest, the Bitterfeld deposit.

Orchestina (Baltorchestina) sternalis n. subgen. n. sp. (photo 138, figs. 32a–b)

Material: Holotypus ♂ in Eocene Baltic amber, F1935/BB/AR/CJW.

Preservation and syninclusions: The spider is well (the colulus excellently) and almost completely preserved in a larger yellow piece of amber which was slightly heated; the right leg I is missing beyond the coxa by autotomy. Fissures exist around the spider, few dorsal parts are covered with a white emulsion, few stellate hairs are present.

Diagnosis (♂; ♀ unknown): ♂-pedipalpus (fig. 32b): Femur and patella slender, tibia thick, embolus fairly long, slightly bent, with a conductor in a ventral position.

Description (♂):
Measurements (in mm): Body length 1.05, prosoma: length 0.5, width 0.45; leg I: Femur 0.46, patella 0.15, tibia 0.41, metatarsus 0.4, tarsus 0.25, tibia II 0.4, tibia III 0.25, tibia IV 0.32, femur IV 0.49, its width 0.14; width of the pedipalpal tibia 0.14.
Colour: Prosoma and legs light brown, opisthosoma yellow grey.
Prosoma high, with long dorsal hairs, clypeus with 4 pairs of hairs in a row and a single additional hair on the right side. Six eyes, anterior laterals largest, the medians separated by almost their radius. Labium as wide as long, apically with a pair of longer and strongly diverging pair of hairs. The gnathocoxae are partly covered with a white emulsion, the sternum is wide posteriorly (and partly covered here with an emulsion), separating the coxae IV by more than their diameter. – Legs only fairly long, femur IV strongly thickened. All metatarsi bear a single or a pair (the posteriors) of short apical bristles. Position of the metatarsal trichobothria 0.9 on III, 0.76 on IV, unknown on I and II. – Opisthosoma oval, covered with long hairs; colulus a wide plate which bears a pair of long hairs (fig. 32a). – Pedipalpus (fig. 32b): Femur and patella slender, tibia thick, embolus shorter than the bulbus, fairly slender, ventrally bearing a conductor which is distinctly shorter than the embolus and widened apically.

Relationships: In *O. (B.) bitterfeldensis* n. sp. femur and patella of the ♂-pedipalpus are fairly small, too, and the tibia is thickened, but the embolus is relatively shorter and a ventral conductor is absent.

Distribution: Eocene Baltic amber forest.

Orchestininae in Eocene French amber

Gallorchestina n. subgen. of *Orchestina* SIMON

Diagnosis (♂; ♀ unknown): Leg bristles absent (or rubbed off in the two type specimens?); pedipalpus (fig. 51): articles fairly thick, cymbium dorsally strongly setose, bulbus thick, tip of the embolus bifid.

Type species (by monotypy): *Orchestina parisiensis* PENNEY 2007.

Relationships: Due to the thick articles of the ♂-pedipalpus and the thick bulbus I regard *parisiensis* as a member of the genus *Orchestina* SIMON; in contrast to the nominate subgenus and the subgenus *Baltorchestina* are leg bristles – according to PENNEY – absent and the cymbium is dorsally strongly setose. A bifid tip of the embolus evolved in several taxa of the Orchestininae apparently convergently; leg bristles are most probably also absent in *Burmorchestina* n. gen..

Distribution: French amber forest from the Paris Basin, most probably Lowermost Eocene. Due to the complete absence of members of the family Salticidae in this kind of amber – see PENNEY (2007) – there may be some doubt about the age of this fossil resin which originated probably already in the Palaeocene.

Orchestininae in Cretaceous amber from Burma

Up to now no fossil taxon of this subfamily has been described/named from the Cretaceous Burmese amber which may be about 100 million years old.

***Burmorchestina* n. gen.** (photos 66–70)

Diagnosis: Leg bristles most probably completely absent, clypeus (fig. 34) not protruding, short, and in a vertical position, labium (fig. 44) with paired apical bristle-shaped hairs in a parallel position (fig. 44); pedipalpus (figs. 39–43, 45-46) with slender articles, a slender and elongated bulbus which is in a short area attached to the cymbium, as well as a long, thin and undivided embolus. See the description of the questionable ♀ of *B. pulcher* below.

Further characters: Tiny spiders; see the diagnosis of the subfamily Orchestininae. The – deformed – prosoma may really be strongly raised in the thoracal part. Not so strong differences in the position of the metatarsal trichobothria I–IV.

Type species (by monotypy): *Burmorchestina pulcher* n. sp.

Relationships: In the remaining genera of the Orchestininae – at least in the extant and Tertiary taxa – the clypeus is long and protruding (unknown in *Canadaorchestina*), the apical labial bristles and the metatarsal trichobothria (in *Orchestina*) have a different position (unknown in *Canadaorchestina*). At least a single article of the male pedipalpus is thickened in *Orchestina*, the bulbus is thick, pear-shaped or almost globular in *Canadaorchestina* and *Orchestina*, and broadly attached to the cymbium. – Convergences in some structures to certain Ochyroceratidae: See above: Relationships of the Orchestininae.

Remarks on ecology and frequency: (1) A small midge (Diptera: Nematocera) is preserved just behind the holotype of *Burmorchestina pulcher* n. sp., see the photo; this midge – which right complex eye is distinctly depressed – may well have been the potential prey of the spider. A Diptera: Nematocera has already been reported as a probable prey of a fossil member of the Orchestininae – a male *Orchestina* sp. indet. in Baltic amber –, see WUNDERLICH (2004: 101). – (2) The posterior jumping legs indicate that spiders of *Burmorchestina* were hunting spiders which built no capture web. Thin threads which are preserved near some spiders may be remains of draglines. – (3) I found ca. 20% specimens of *Burmorchestina* within numerous juvenile and adult spider specimens in Burmite. The high relative frequency and the high percentage of adult specimens of *Burmorchestina* indicate that members of this genus were dwellers of higher strata of the vegetation, probably including the bark of the amber producing trees similar to certain extant spiders of the same subfamily. (For a comparison: Within a collection of unselected spiders in Baltic amber from the Bitterfeld deposit (coll. H. GRABENHORST) I found 21% (15 of 72 specimens) of the genus *Orchestina* SIMON, subgenus *Baltorchestina*).

Distribution: Cretaceous Burmese amber from Myanmar.

***Burmorchestina pulcher* n. gen. n. sp.** (photos 66–69, figs. 33–43)

2000 *Orchestina* sp. indet., – Penney, Palaeontology, 43 (2): 244 (paratype of *B. pulcher* from the BMNH).

Material: 4♂ in Burmese amber from Myanmar; holotypus F1908/BU/AR/CJW, paratypes: F1880/BUR/AR/CJW; BMNH no. 20210; OSU B-A-1-4. – Remark: Indet. spiders of *Burmorchestina* (see below) may be conspecific.

Preservation and syninclusions: Holotype: The spider is excellently and completely preserved in a light yellow-orange piece of amber which was probably only slightly heated/compressed; only few leg articles – especially the right tibia III are laterally depressed, and the right femur III is thickened by natural lateral pressing. Few thin spider's threads are preserved, e. g. a short one is running from the left legs of the spider in direction to the midge (Diptera: Nematocera), body length 0.8 mm, which is preserved just behind the spider (photo), and which could well have been a potential prey of the spider. The midge is slightly deformed, its right eye is strongly depressed. Paratype F1880: The spider is fairly well preserved in a small piece of amber which apparently was heated in a natural way. It has been hidden by layers of the amber; therefore I put the piece in benzylium benzoicum. After few minutes the layers became more indistinct, and the eye lenses became more distinct. The spider's legs are almost complete but the right patella I as well as the dorsal parts of pro- and opisthosoma (fig. 33) are cut off within the amber, and the genital area is injured. A larger bubble is preserved within the opisthosoma in front of the spinnerets which are slightly deformed, a tiny bubble is preserved on the tip of the labium. – The paratype of the BMNH is fairly well preserved in a piece of amber which was heated; its eyes are deformed; the dorsal parts of prosoma, opisthosoma as well as 3 patellae are cut off within the amber, a bubble is preserved within prosoma and opisthosoma. A tiny Diptera, some stellate hairs and questionable parts of Lichenes are preserved in the same piece of amber. – The paratype of the OSU is well and almost completely preserved in a small clear yellow piece of amber; only the right leg IV is lost beyond the coxa by autotomy.

Diagnosis (♂; ♀ probably unknown; see the indet. ♀ below): Clypeus with two pairs of strong hairs (as well as a shorter medial hair), embolus long and bent ventrally in a right angle (figs. 39–42); see also the diagnosis of the genus.

Remark: The strong differences of the position of the metatarsal trichobothria in the holotype – in which the structures of the pedipalpus are best recognizable – and the paratypes indicate taxonomical differences which are probably not reflected by differences of the bulbi and emboli (note that bulbi and emboli are not observable in exact the same position in the four males and the probably not conspecific males).

Description (♂):
Measurements (in mm): Body length 0.9–1.0, prosoma: Length ~0.4–0.5, width 0.35–0.46 (paratype BMNH); leg I: Femur ca. 0.4, patella 0.14, tibia 0.35, metatarsus 0.4 (0.34 in the paratype from the BMNH), tarsus 0.18, tibia III 0.25, leg IV: Femur 0.5 (0.4 in the ♂ of the OSU) (height ca. 0.15, 0.12 in the ♂ of the OSU), patella 0.16, tibia 0.35, metatarsus 0.42 (0.35 in the ♂ of the OSU), tarsus 0.2.
Colour: Prosoma and legs light brown, opisthosoma light yellow brown.
Prosoma (figs. 34, 44) fine rugose, strongly raised posteriorly and with long dorsal hairs; six eyes (they bear emulsions) with the medians largest; clypeus short and almost vertical, with a pair of bristle-shaped hairs and a single median one. Basal cheliceral articles slender, diverging distally, concave anteriorly; fangs fairly long and slender. Labium free, longer than wide, apical bristle-shaped hairs apparently in a straight/parallel position. Most parts of the long gnathocoxae are hidden. Coxae IV – they are deformed by heating – separated by the sternum by ca. 1 1/2 of their diameter. – Legs (figs. 36–38) fairly long and slender, order IV/I/II/III, femur IV strongly thickened, tarsi relatively long, onychium present, bristles and unpaired tarsal claws absent. Metatar-

sal trichobothria long, their position quite variable: In 0.87–0.91 on metatarsus I–IV in the holotype, 0.9 on I in the paratype of the OSU, but in 0.75 on I and IV of paratype F1880, and 0.75 on IV in the paratype of the BMNH, ca. 0.88 on III in paratype F1880, and ca. 0.85 on III of the paratype of the BMNH. – Opisthosoma (figs. 34–35) oval, covered with short hairs; spinnerets long, deformed, the medians quite slender, ca. 8 times longer than wide, colulus probably small. – Pedipalpus (figs. 39–43, 45–46) with slender articles, cymbium longer than wide, bulbus long and slender, inserting in about the middle of the cymbium, basally thicker, sperm duct in a dorsal position; embolus long, thin and bent ventrally in about a right angle.

Relationships: I do not want to exclude that the male of *Burmorchestina* sp. indet. may be conspecific, see below.

Distribution: Cretaceous Burmese amber forest.

***Burmorchestina ?pulcher* n. sp.** (photo 70)

Material (in Burmese amber from Myanmar): 2♂ 2♀; 1♀ OSU no. B-A-1-14; 1♀ F2018/BU/AR/CJW; 1♂ F2019/BU/AR/CJW; 1♂ F1909/BU/AR/CJW.

OSU: The female spider is fairly well and completely preserved, distinctly deformed. In the same piece of amber are preserved (a) a probably adult ♀ of the spider superfamily Dysderoidea indet. and (b) a Diptera: Nematocera.
Measurements (in mm): Body length 1.05, prosoma: Length 0.55, width 0.45; femur I < 0.45, femur IV: Length ~ 0.55, width ~ 0.1, metatarsus IV 0.37.
The clypeus is not protruding, the epigaster is not sclerotized, lung covers are not recognizable. Position of the metatarsal trichobothria: I in 0.92, IV in 0.81.
Although the deformed legs – quite variable in length? – are longer than in the males of *B. pulcher* I do not want to exclude the conspecifity with *pulcher*.

F1909/CJW: The male spider is strongly deformed, the right leg II is missing by autotomy beyond the coxa, the pedipalpal structures are not exactly recognizable, the body length is 0.95 mm, the labium (fig. 47) is apically strongly incised and bears apparently no apical bristles but a pair of long bristle-shaped hairs near the middle. Position of the metatarsal trichobothria: ca. 0.85 on I, 0.9 on IV. The bulbus is slender, the embolus is long, thin and strongly bent.
The position of the metatarsal trichobothria is similar to the paratypes of *B. pulcher* n. sp.; the male in question may be conspecific.

F2018/CJW: The female spider is darkened and distinctly deformed by natural heating and pressure. Its body length is about 1.5 mm. Some articles of the right legs are cut off within the amber at two layers, the eyes are badly preserved, the femora IV are strongly thickened, the position of the trichobothrium on metatarsus IV is in 0.8.

F2019/CJW: The male spider is – including its pedipalpi – strongly deformed apparently by decomposition, its body length may have been about 1 mm; it is completely preserved. Dorsally on the opisthosoma are numerous thin hyphae growing. The spider has probably been the prey of an arthropod.

Orchestininae in Cretaceous ambers from North America

Canadaorchestina n. gen.

Diagnosis (♂; ♀ unknown): Metatarsi probably bristle-less; pedipalpus (figs. 47A–B): Articles slender, bulbus thick, broadly attached to the cymbium, embolus thick, accompaned by a large conductor.

Further characters: Position of the trichobothrium on metatarsus I in ca. 0.85, body length 1.1 mm. Shape and structures of clypeus and labium are unknown.

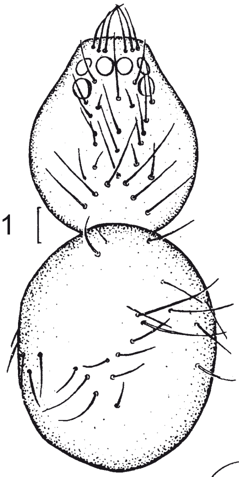
Type species by monotypy: *Orchestina albertensis* PENNEY 2006.

Relationships: Slender articles of the ♂-pedipalpus exist in *Burmorchestina* n. gen. too, but its bulbus is slender and is attached to the cymbium only in a short area, its embolus is thin, and a conductor is absent. In the Orchestininae indet. from New Jersey (see below) the pedipalpal articles are slender, too, and this taxon may me congeneric. In *Orchestina* SIMON (Eocene to extant) at least a single pedipalpal article is thickened and a large conductor is usually absent (but see *Baltorchestina cochlembolus* WUNDERLICH 1981 (fig. 9)).

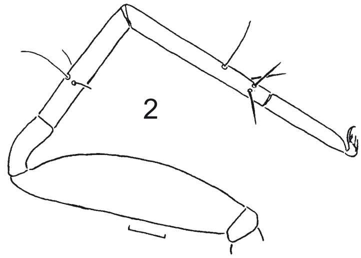
Distribution: Cretaceous amber forests of North America, of Canada and probably of New Jersey (see below).

Orchestininae indet. in Cretaceous amber from New Jersey

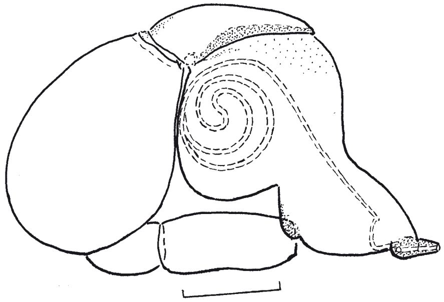
The photo of a specimen was published by GRIMALDI (2000: Fig. 42 d), a male was described by PENNEY (2004) as *Orchestina* sp. indet., in which – according to PENNEY – important taxonomic structures (the mouth parts and the tip of the embolus) are not visible. Leg bristles are absent, the position of the trichobothrium on metatarsus I is near the end of the article, the pedipalpal articles are – according to PENNEY (2004: Fig. 1) – rather slender, the bulbus is thick. Due to these characters this specimen may well be a member of *Canadaorchestina*, see above.



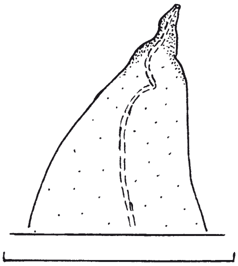
1



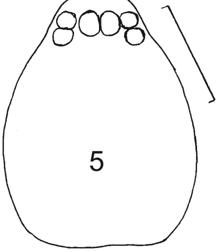
2



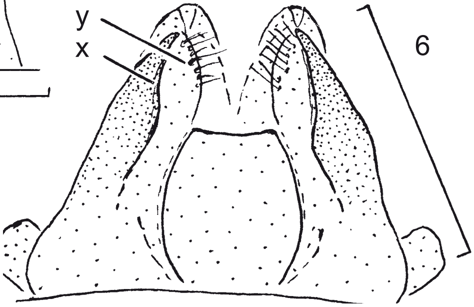
7



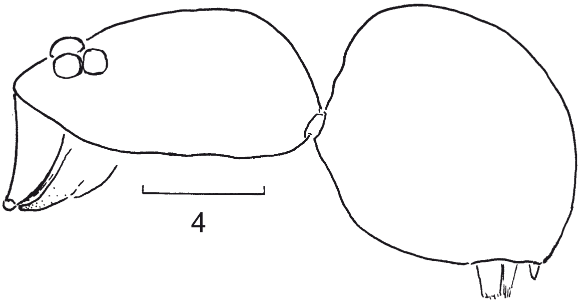
8



5



6



4

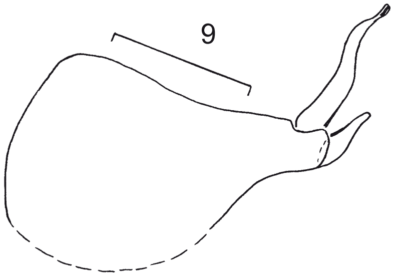
3

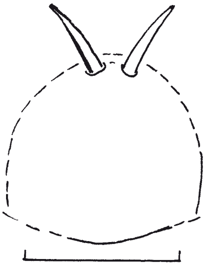
Fig. 1) Orchestina (Baltorchestina) crassiembolus WUNDERLICH 1918, ♂, holotype, dorsal aspect of the body (some hairs are cut off or not drawn); scale bar = 0.1 mm;

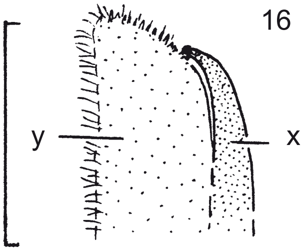
fig. 2) Orchestina (Baltorchestina) sp. indet., ♀, prolateral aspect of the l. leg IV with trichobothria and apical metatarsal bristles; scale bar = 0.1;

figs. 3) Orchestina pavesii (SIMON 1873) (extant, Lanzarote, Canary Islands, CJW), labium; scale bar = 0.1;

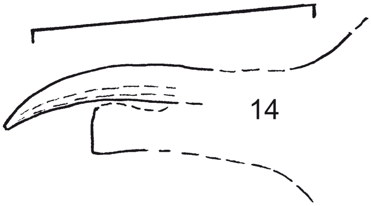
figs. 4–8: Orchestina dalmasi **n. sp.**, extant (Malaysia), ♂; 4) lateral aspect of the body; hairs are rubbed off; 5) dorsal aspect of the prosoma; hairs are rubbed off; 6) mouth parts; X = distinctly sclerotized part of the r. gnathocoxa, Y = scinny part of the gnathocoxa; 7) prolateral aspect of the l. pedipalpus; 8) distal part of the l. embolus, dorsal aspect; scale bar = 0.2 in figs. 4–5, 0.1 in figs. 6–8;

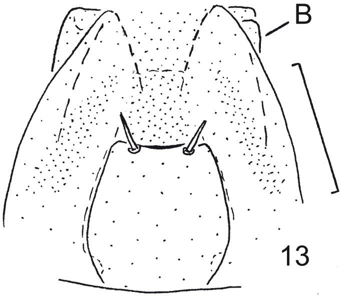

9


10

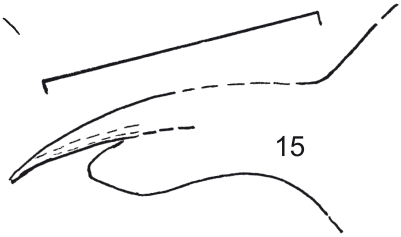


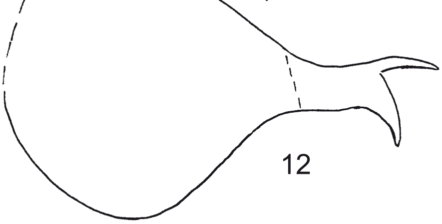
16


14



13


15


12

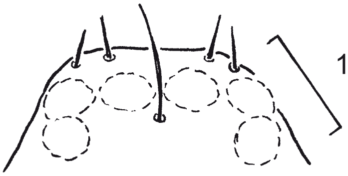

11

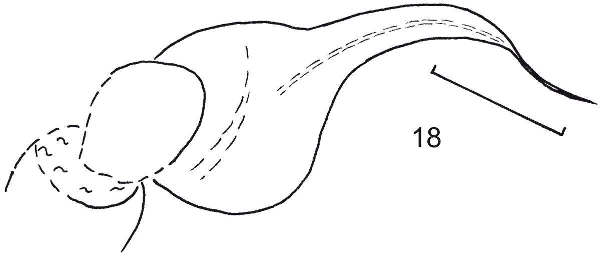
fig. 9) Orchestina (Baltorchestina) cochlembolus WUNDERLICH 1981, ♂, paratype, retrolateral aspect of the r. bulbus with embolus (fairly heated); scale bar = 0.1;

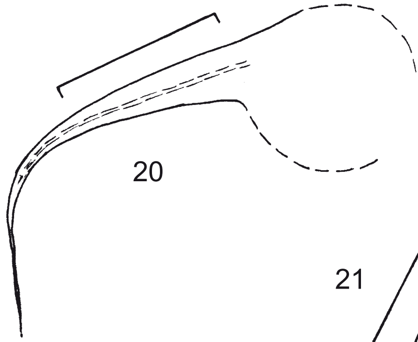
figs. 10–12: Orchestina (Baltorchestina) crassitibialis WUNDERLICH 1981, ♂; 10) F508/CJW; labium; 11) F1861/CJW, retrolateral and slightly apical aspect of the l. pedipalpus. Note the divided embolus and the embolic apophysis; 12) F1862/CJW, retrolateral aspect of the r. bulbus and embolus; scale bar = 0.1;

figs. 13–15: Orchestina (Baltorchestina) ?furca WUNDERLICH 1981, ♂; 13) F509/BB/AR/CJW, ventral aspect of the mouth parts (an emulsion covers the medial part). Note the paired apical bristles on the labium. The division of the gnathocoxae is well visible in this specimen (B = basal article of the l. chelicera); 14–15: F1871/CJW; 14) retrolateral aspect of the l. embolus (a thin covering emulsion is not drawn); 15) prolateral aspect of the r. embolus (a covering thin emulsion is not drawn); scale bar = 0.1;

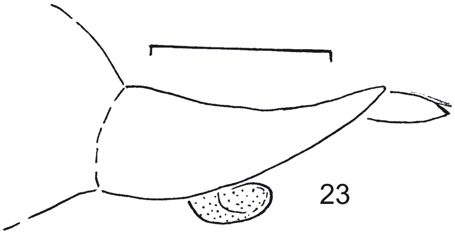
fig. 16) Orchestina (Baltorchestina) imperialis WUNDERLICH 1981, ♂, ventral aspect of the distal part of the l. gnathocoxa which is slightly deformed by heating (X = distinctly sclerotized, Y = less sclerotized (medial) part; scale bar = 0.1;

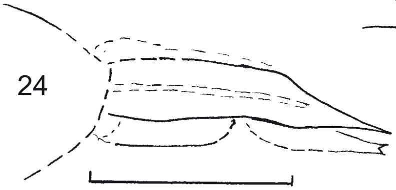

17

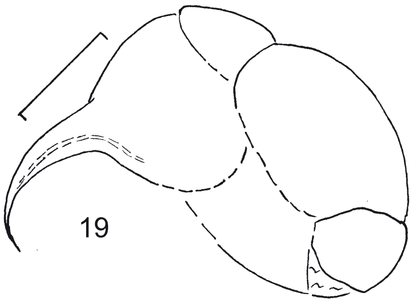

18

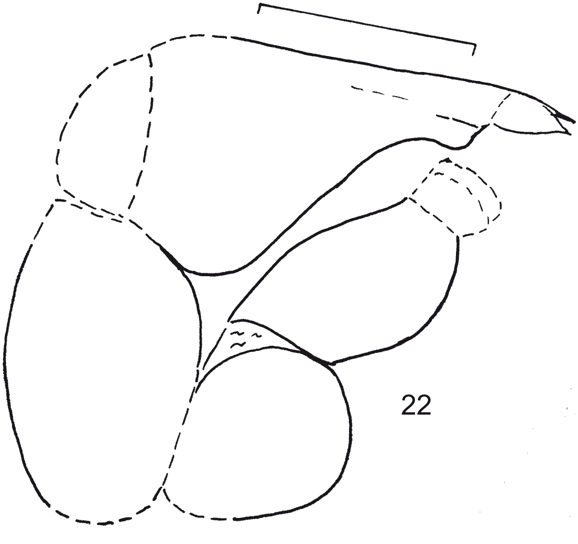

20


21


23

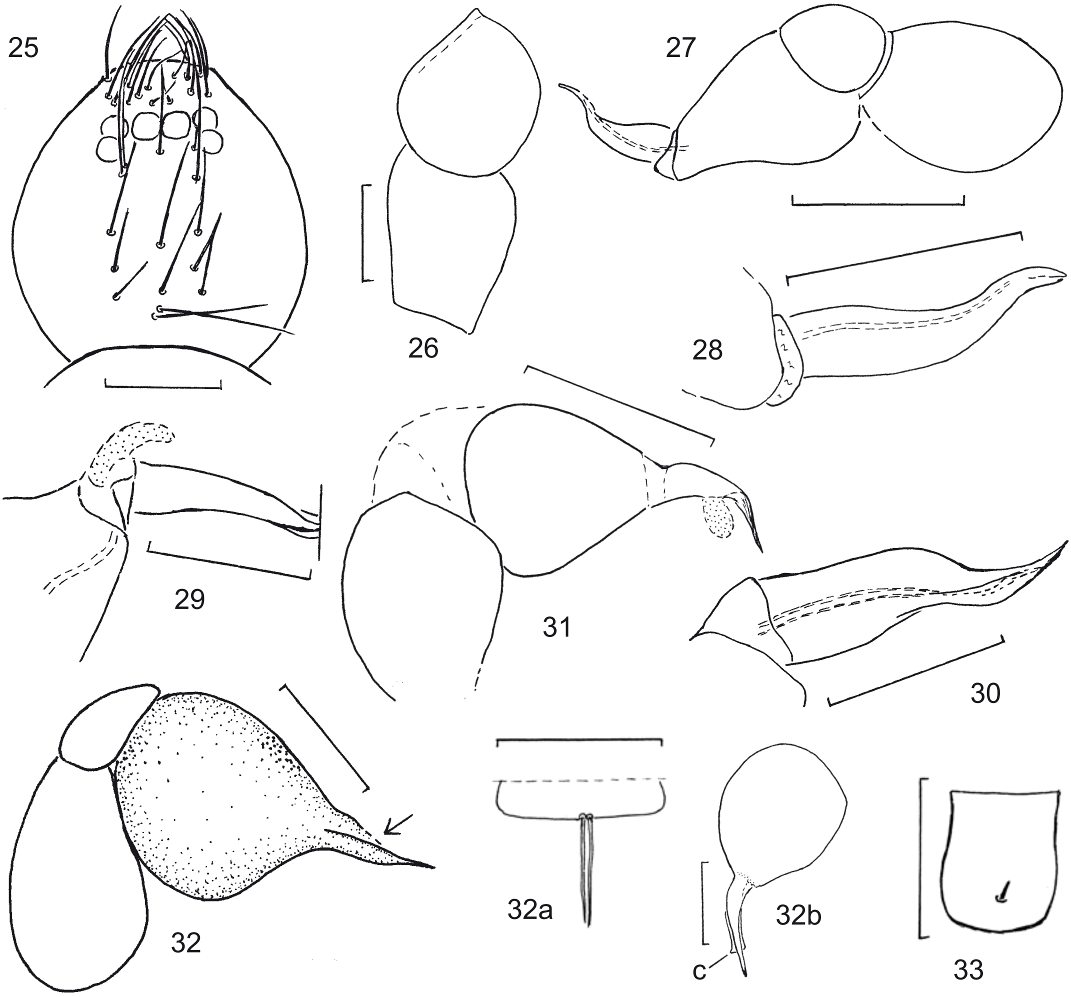

24


19


22

figs. 17–20: ***Orchestina (Baltorchestina) brevis* n. subgen. n. sp.**, ♂; 17–18: Holotype, 17) dorsal aspect of the anterior part of the prosoma; 18) retrolateral aspect of the r. pedipalpus; 19–20: Paratype F1867; 19) retrolateral aspect of the l. pedipalpus. The distal part of the embolus turned prolaterally; see the next figure; 20) ventral aspect of the l. bulbus with embolus; scale bar = 0.1;

figs. 21–24: ***Orchestina (Baltorchestina) multisetae* n. subgen. n. sp.**, ♂; 21) labium; 22) retrolateral aspect of the r. pedipalpus; 23) retrolateral aspect of the r. embolus; 24) prolateral aspect of the l. embolus; scale bar = 0.2 in fig. 22), 0.1 in the remaining figs;

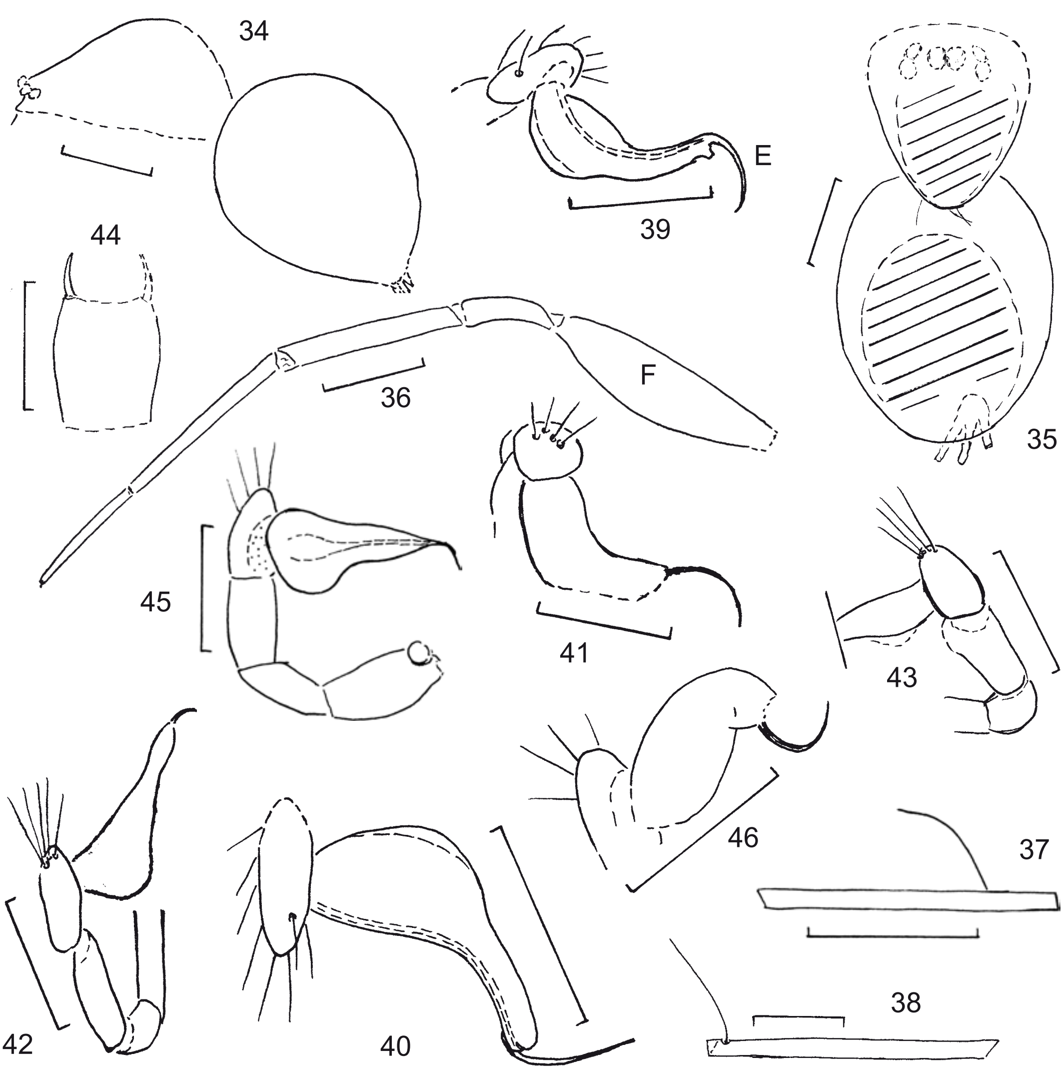


figs. 25–30: ***Orchestina (Baltorchestina) perfecta* n. subgen. n. sp., ♂**; 25) dorsal aspect of the prosoma (few hairs are not recognizable); 26) dorsal aspect of femur and patella of the r. pedipalpus; 27) retrolateral aspect of the l. pedipalpus; 28) retrolateral aspect of the r. embolus; 29) retrolateral and slightly ventral aspect of the r. embolus (its tip is hidden). Note the ventral embolic outgrowth; 30) prodorsal aspect of the l. embolus; scale bar = 0.2 in fig. 25 and 27), 0.1 in the remaining figs.;

fig. 31) ***Orchestina (Baltorchestina) rectangulata* n. subgen. n. sp.**, ♂, retrolateral aspect of the r. pedipalpus; scale bar = 0.2;

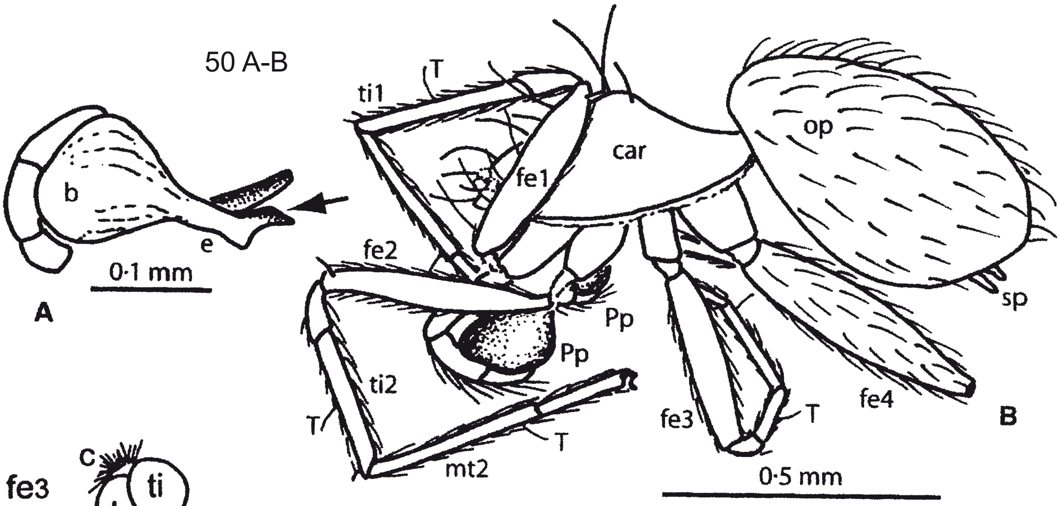
fig. 32) ***Orchestina (Baltorchestina) bitterfeldensis* n. subgen. n. sp**., ♂ (holotypus), retrolateral aspect of the r. pedipalpus. The arrow points to an area which is hidden by a tiny bubble.

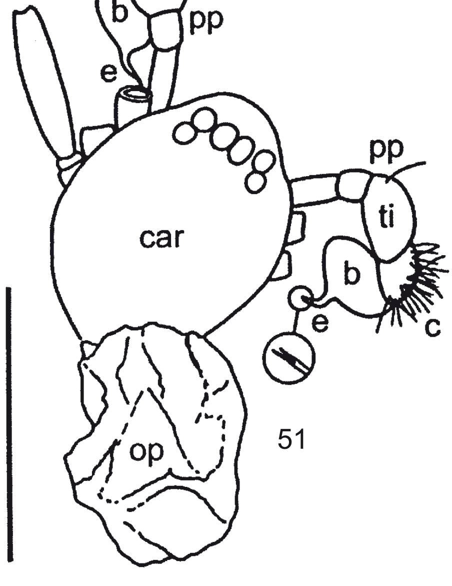
fig. 33) ?Orchestina madagascariensis WUNDERLICH 2004, ♂ (paratype c), labium, ventral aspect, slightly from the right side; scale bar = 0.1;



figs. 34–46: ***Burmorchestina pulcher*** **n. gen. n. sp.**, ♂; holotype figs. 34, 38–40, paratype (F1880/CJW) figs. 35–37, 41, paratype BMNH 20210, figs. 42–43, paratype OSU no. B-A-1-4, figs. 44–46; 34) outline of the body, lateral aspect; 35) dorsal and slightly anterior aspect of the body. Parts of pro- and opisthosoma are cut off within the amber. The exact position of the eye lenses are difficult to recognize; fig. 36) prolateral aspect of the r. leg IV (F = thickened femur); 37) prolateral and slightly basal aspect of the l. metatarsus IV with its long trichobothrium in the distal half; 38) prolateral aspect of the r. metatarsus I with its long apical trichobothrium; 39–40) retrolateral aspect of cymbium and bulbus of the r. and l. pedipalpus (E = embolus); 41) retrodorsal aspect of the deformed r. cymbium and bulbus; 42–43) prodorsal aspects of the l. pedipalpus with deformed bulbus and of the r. pedipalpus in which the embolus is hidden; 44) labium, ventral aspect and slightly from the right side, left parts are hidden; 45) retrolateral aspect of the r. pedipalpus (the articles are slightly deformed); 46) prodistal aspect of the l. bulbus and cymbium; scale bar = 0.05 in fig. 44, 0.2 in figs. 34–37, 0.1 in figs. 38–43, 45–46;

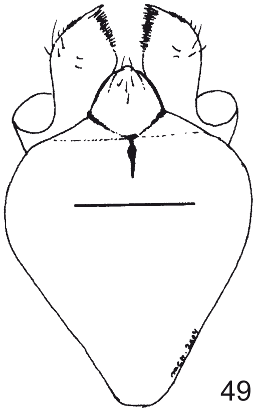
50 A-B



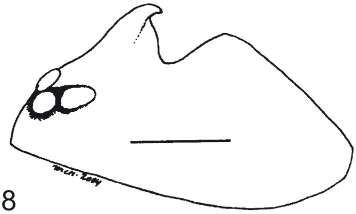


51

47



49



48

fig. 47) ***Burmorchestina*** ?***pulcher*** **n. gen. n. sp**., ♂ (F1909/CJW), deformed and incomplete labium, ventral-right and slightly apical aspect; scale bar = 0.05;

figs. 48–49: *Ferchestina storozhenkoi* SAARISTO & MARUSIK 2004, ♂; 48) lateral aspect of the prosoma; 49) ventral aspect of labium, gnathocoxae and sternum; scale bar = 0.2. Taken from SAARISTO & MARUSIK (2004: Figs. 3 and 6);

figs. 50 A–B: *Canadaorchestina albertensis* (PENNEY 2006) (**n. gen**.), ♂; A) pedipalpus, B) lateral aspect of the spider. Taken from PENNEY (2006: Figs. 1 A–B; sub *Orchestina albertensis*);

fig. 51: *Orchestina* (*Gallorchestina*) *parisiensis* PENNEY 2007 (**n. subgen**.), ♂, dorsal aspect of the holotype; scale bar = 0.5. Taken from PENNEY (2007: Fig. 1B).

FAMILY SPATIATORIDAE in Baltic amber

The previously monotypic extinct family Spatiatoridae was revised by WUNDERLICH (2004: 767–768), a second species – *Spatiator martensi* WUNDERLICH 2006 was added to the type species – *S. praeceps* PETRUNKEVITCH 1942 – in Baltic amber. The original description of *praeceps* was based on a female. Males can only provisonally be regarded as conspecific, see the discussion by WUNDERLICH (2006: 315). One of those males, which bulbus structures are well preserved and well observable in the ventral position, is described below as *S. caulis* n. sp.

***Spatiator caulis* n. sp**. (fig. 1)

2004 *Spatiator* sp. indet. (*praeceps*), – WUNDERLICH, Beitr. Araneol., 3: 768, 806–807, figs. 51, 56, photo 84.
2006 *Spatiator praeceps*, – WUNDERLICH, Zootaxa, 1325: 315, fig. 4.

Material: Holotypus ♂ and a thin piece of Baltic amber which has split up, GZUG BST 06174 (old no. B16126).

Preservation and syninclusions: The spider is very well and almost completely preserved in a thin piece of amber which apparently recently has been broken in two parts (split up); therefore the ventral parts of the spider's posterior coxae are lost now. Few parts of body and legs are covered with a white emulsion, ventral parts of the bulbi are partly covered with bubbles and emulsions. The distal part of the left tarsus II is cut off. Parts of a tiny Diptera are preserved left behind the spider at the margin of the piece of amber as well as two longer legs of a spider (Araneoidea: ?Theridiidae) closely behind the holotype; few stellate hairs exist, too.

Diagnosis (♂; ♀ unknown): Embolus long and in close contact to the long conductor (fig. 1).

Description (♂):
Measurements (in mm): Body length 3.8, prosoma: Length 2.0, width ca. 1.25; leg I: Femur 1.5, patella 0.85, tibia 1.3, metatarsus 0.83, tibia II 1.2, tibia III 0.82, tibia IV 1.5.
Colour mainly medium brown.
Body and legs – see WUNDERLICH (2004: 807, photo 84 – like in *Spatiator martensi* WUNDERLICH 2006; the tarsi are slightly thickened, the tarsal claws are short. Pedi-

palpus (fig. 1): Patella short, tibia fiarly thickened, bearing a thin prolateral bristle, embolus long and almost straight, distally partly enclosed by along and blunt conductor.

Relationships: In *S. martensi* WUNDERLICH 2006 the embolus is shorter and its tip is distinctly separated from the tip of the short conductor (fig. 2). *S. praeceps* is probably a separate species. There may be more undescribed species of *Spatiator* in Baltic amber.

Distribution: Eocene Baltic amber forest.

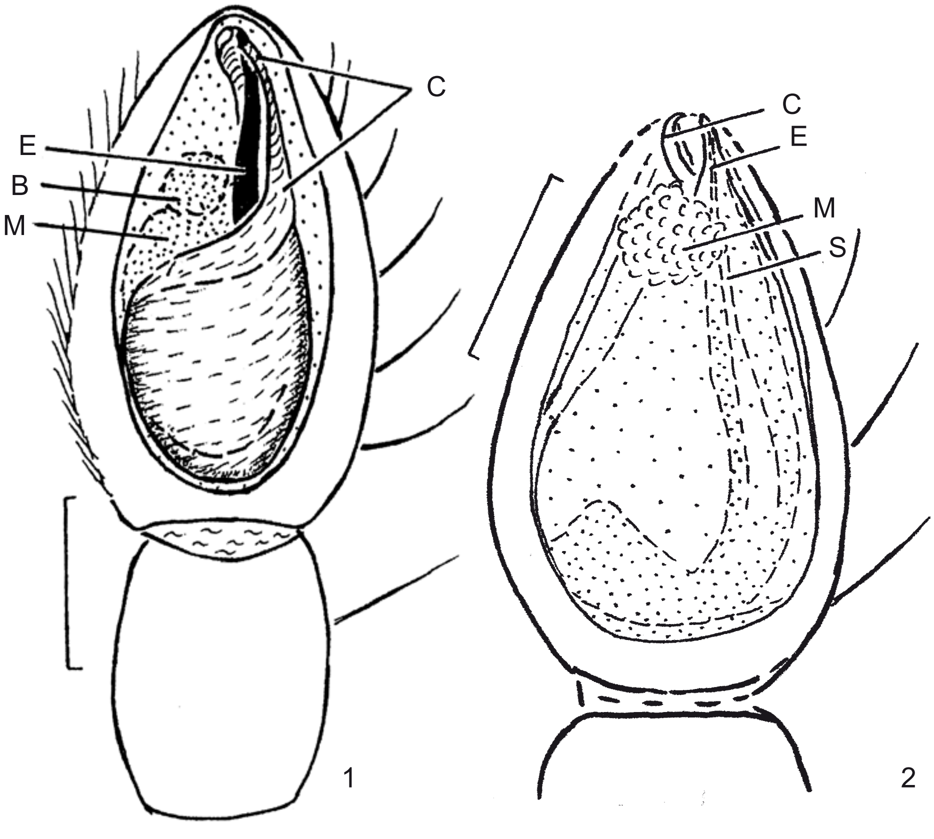


Fig. 1) *Spatiator caulis* **n. sp.**, ♂, ventral aspect of the r. pedipalpus.
Fig. 2) *Spatiator martensi* WUNDERLICH 2006, ♂, ventral aspect of the r. pedipalpus. – Scale bars 0.2 mm. B = bubble, C = conductor, E = embolus, M = emulsion, S = sperm duct

FAMILY HERSILIIDAE in Dominican amber

Regarding the neotropical genera PENNEY (2006: 901) noted erroneously that "Wunderlich (1988, 2004) synonymized all of Petrunkevitch's fossil hersiliid genera with *Neotama*." But I (2004: 816) really synonymized the extant genus *Neotama* BEAHR & BAEHR 1993, and the extinct genera in Tertiary Dominican amber *Perturbator* PETRUNKEVITCH 1971, *Priscotama* PETRUNKEVITCH 1971, and *Prototama* PETRUNKEVITCH 1971 with the extinct genus *Fictotama* PETRUNKEVITCH 1963 in Tertiary Mexican amber (!). PENNEY considered *Fictotama* and *Perturbator* as nomina dubia because of the bad condition of the type material, but their type species have to revise again more closely in my opinion.

Recently RHEIMS & BRESCOVIT (2004) created three new neotropical hersiliid genera: *Iviraiva, Yabisi* and *Ypypuera*; unfortunately these authors did not consider the four nominal fossil Miocene neotropical genera. At least one of these fossil genera may well be a junior synonym of *Fictotama*. A revision is prepared by the present author incl. a well preserved male in Dominican amber of the coll. of A. BEIGEL.

FAMILY TETRAGNATHIDAE, with descriptions of new fossil and extant taxa, and remarks on the Guizygiellinae and the Zygiellidae (photos 140–148)

Taxonomy and systematics, diagnostic characters: A revised diagnosis of the diverse family Tetragnathidae, and a revision of its subfamilies including the extinct taxa are needed, see WUNDERLICH (2004: 902ff) who gave a list of selected characters p. 905. – Members of the Tetragnathidae possess large basal cheliceral articles (fig. 1) and long ventral sensory hairs mainly of the anterior tibia and metatarsus (fig. 5); the number of leg bristles is lower than in most Araneidae and Zygiellidae: Ventral bristles on tibia and metatarsus I–II are only rarely present, and the bristles are not thick like in most Araneidae. From the Eocene fossil taxa one may conclude that a long clypeus is a ancient/plesiomorphic character of the Tetragnathidae. In the Tetragnathidae exists furthermore a tendency to widely spaced anterior and posterior lateral eyes (e. g. in *Diphya* and *Anameta*, fig. 1) and – in derived taxa – to a separate (intersegmental) or almost free paracymbium, which is frequently large and branched. An apical pedipalpal tibial apophysis (or several apophyses) and a dorsally modified cymbium (usually a cymbial "horn") exist probably basicly in males of this family (cymbial "horns" are absent in the Tetragnathinae, which may be the most advanced tetragnathid subfamily, but such “horns” exist in almost all of the Eocene taxa in Baltic amber). An epigyneal scapus and a median apophysis are probably basicly absent in the Tetragnathidae; a median apophysis – or a similar sclerite – exists in *Anameta* WUNDERLICH 2004 (fig. 6), and is present in some (!) members of the related Zygiellidae (Chrysometinae have probably to be excluded from this family). The hub of the capture web is (secondarily) free. In the resting position the legs I and II are usually stretched foreward and legs III and IV backward.

Remark on the relationships. Tetragnathidae is regarded by WUNDERLICH (2004) as sister family to Zygiellidae SIMON 1929 (= Guizygiellinae ZHU et al. 2003 according to WUNDERLICH (2004)). Guizygiellinae is regarded as subfamily of the Tetragnathidae by ZHU et al., and *Zygiella* is regarded as a member of the Tetragnathidae by LEVI and other authors. But in *Guizygiella* ZHU et al. 2003 diagnostic characters of the Tetragnathidae (see above) are absent, a fairly expressed sexual size dimorphism (smaller males) exists in contrast to the Tetragnathidae and Zygiellidae. The eye field of *Guizygiella* is wider than in the Zygiellidae. Recently PETER JÄGER (person. commun.) observed in Laos the absence of a free sector in the capture web of members of *Guizygiella*. According to this absence – as well as the wider eye field and the paired pedipalpal patellar bristle in contrast to *Zygiella* and related genera – I regard now *Guizygiella* as a taxon of the family Araneidae (**n. relat**.), which evolved a peculiar colour pattern convergently to *Zygiella*.

Fossil taxa and their extant relatives: The Eocene fossils of the family Tetragnathidae in Baltic amber were revised by WUNDERLICH (2004): 5 genera of probably 3 subfamilies: Diphyinae (most taxa, but the relationships of some genera – e. g. *Anameta* – are quite unsure), Leucauginae (*Baltleucauge* n. gen.) and Metinae (*Meta* s. l.: Subgenus *Praetermeta*). Almost all genera are extinct but *Meta* C. L. KOCH 1836 s. l. survived with its down-ranked subgenus *Praetermeta* WUNDERLICH 2004 (n. stat.).
In this paper I add to my previous paper (2004): (1) the extinct new tribus Anametini (type genus *Anameta* WUNDERLICH 2004), with *Anameta kuntneri* n. sp., which I regard as a questionable member of the Diphyinae, and in which – in contrast to most other Tetragnathidae except the extinct genus *Priscometa* PETRUNKEVITCH 1958 – a quite long clypeus exists (fig. 1), (2) new taxa of the Leucauginae: Baltleucaugini n. trib. with *Baltleucauge gillespiae* n. gen. n. sp., – the only known Eocene Tetragnathidae in which femoral trichobothria exist, figs. 10–11 –, (3) new taxa of the Metinae: (a) four new extant subgenera of *Meta* s. l. with the fossil species *Meta (Praetermeta) maculosa* n. sp., and (b) the new tribus Metabini which includes the extant genus *Metabus* O. PICKARD-CAMBRIDGE 1899 and probably the extinct genus *Chrysometata* WUNDERLICH 2004.
Questionable tetragnathid taxa from the Cretaceous: See (a) the paper no. 5 on Cretaceous spiders in amber in this volume. (b) *Macryphantes* SELDEN 1990 – see WUNDERLICH (2004: 854) – may be a member of an undescribed family. Ventral tarsal bristles as in *Macryphantes* within the ecribellate branch of the Araneoidea are also known to me in extinct members of the Protheridiidae: Protheridiinae WUNDERLICH 2004 which I know from Cretaceous (questionable) and from Eocene ambers.

Remarks on cymbial modifications/cuspules and stridulatory organs: There is a "tendency" to evolve modified dorsal cymbial structures, e. g. bristles in Metinae and related genera: Cuspules/spines e. g. in *Chrysometata* WUNDERLICH 2004 (figs. 22–23), *Metabus* and *Sancus* as well as different and peculiar kinds of stridulatory organs within this subfamily (and in certain taxa which are probably related):

(a) *Meta (Stridulameta) stridulans* WUNDERLICH 1987 and *M. (Stridulameta) shenae* ZHU 2003: Retrolateral cheliceral files in connection with a prolateral edge of the pedipalpal femur in both sexes,
(b) *Meta (Merianmeta) merianae* (SCOPOLI 1763): Stridulatory files on the retrodorsal branch of the paracymbium (figs. 18, 19a–b) (a sure counterpart is unknown),
(c) *Zygiometella perlongipes* (O. PICKARD-CAMBRIDGE 1872) – its relationships are unclear –: A retrolateral cheliceral border in connection with a prolateral field of tibial spines on the male pedipalpus.
Stridulatory organs in other tetragnathid subfamilies are unknown to me.

Biogeography and relationships of the fossils: Most fossil Tetragnathidae in Baltic amber are probably members of the mainly tropical Diphyinae, some are Metinae; *Baltleucauge* is the only fossil genus of the Leucauginae. Close relationships of these taxa are unsure. Taxa of the almost pantropical Diphyinae and Leucauginae do not occur in Europe today. – Taxa of the Metinae are present in Europe: (a) members of the extinct subgenus *Praetermeta* of *Meta* s. l. (Metini) are strongly related to extant species; (b) the extinct genus *Chrysometata* (probably Metabini) may be related to the South American genus *Metabus*. – A striking faunal gap: The absence of members of the subfamily Tetragnathinae in the Baltic amber – although they are frequent today, their distribution is cosmopolitan, and fossils of this subfamily are knowm from the Miocene Dominican amber forest, see WUNDERLICH (1988) – is probably a result of the relatively late origin of this subfamily.

Ecology and reasons for the rarity of Eocene fossils: (1) The extreme rarity of members of most tetragnathid species in Baltic amber may indicate that most of these spiders did not live in the inner part of the Baltic amber forest, but probably in sunny habitats outside the forest, at its margin or in particular areas. Most extant species of *Meta* s. l. occur outside forests as probably did members the extinct subgenus *Praetermeta* from which I found only two specimens. – Most Tetragnathidae in Baltic amber are probably members of the subfamily Diphyinae which prefer a tropical climate (as do members of Leucauginae), but the climate of the Baltic amber was mainly subtropical, which may partly explain the rarity of these fossils. Contrarily several members of the Metinae occur in moderate or subtropical climates but they are rare in Baltic amber because they usually avoid forests (except *Merianmeta* and the cave spiders of *Meta*). – (2) Most Tetragnathidae are large(r) spiders which could surely not easily be captured by the sticky Eocene resin. The same is true for most Metinae. Thus some more – unknown – members of larger species of these subfamilies may well have existed in the Eocene Baltic amber forest.

Subfamily DIPHYINAE (?): ANAMETINI n. trib.

Diagnosis (♂; ♀ unknown): Clypeus almost as long as the field of the median eyes (fig. 1), anterior and posterior lateral eyes widely spaced (fig. 1). Pedipalpus (figs. 2–3, 6–8): Cymbium with a "denticulate" dorsal process (DCP; previously called by me "CDP" as in Pimoidae, see WUNDERLICH (2004: 941, fig. 2)), and a retrolateral process/horn (CH), paracymbium a large, and – at least partly – free sclerite, excavate prolaterally, terminal apophysis apparently present (hidden by a bubble in the type species), embolus long, in a distal position and in close (not coiled) contact with a long conductor.

Further characters: Posterior eye row recurved, chelicerae long, lateral stridulatory files absent, legs with numerous long bristles, femoral trichobothria absent, tibia and metatarsus I with long ventral hairs, pedipalpal tibia unmodified, without outgrowth, pedipalpal femur with a ventral-apical hump (fig. 6).

Type genus: *Anameta* WUNDERLICH 2004 (the only known genus of the tribus).

Relationships: According to the large chelicerae, the long ventral hairs of the anterior tibiae and metatarsi as well as the distal position of the embolus and its close contact to the embolus I regard *Anameta* as a member of the family Tetragnathidae although a small tegular apophysis – a questionable “median” apophysis – may be present. The long clypeus and the shape of the paracymbium are quite unusual within the Tetragnathidae, cymbial denticles are rare. A long clypeus and widely spaced lateral eyes exist also in *Diphya*, a long clypeus in *Priscometa*, too, widely spaced lateral eyes within the Tetragnathinae as well as in the Aziliinae and the Dolichognathinae, too – see WUNDERLICH (2004: 906) – in which the genital structures are quite different. According to the strongly reduced anterior median eyes, the different shape of the chelicerae and the paracymbium, the large tegulum as well as the absence of cymbial cusps/denticles and a (questionable) terminal apophysis the genus *Diphya* and the Diphyinae – in which *Anameta* originally provisorically was included by the present author – are probably related. Prosoma, chelicerae, eyes, and the structures of the male pedipalpus are different in Aziliinae and Dolichognathinae. – Cymbial cusps/denticles are widely distributed within the Araneoidea; they exist e. g. in *Pimoa* (see Pimoidae below), *Sintula* (Linyphiidae) as well as in *Metabus* and *Chrysometata* (Tetragnathidae), in which the lateral eyes are not widely spaced, and the structures of the male palpus are quite different. – In the Eocene Baltsuccinidae WUNDERLICH 2004 are the lateral eyes not widely spaced and the structures of the pedipalpus are different, e. g. cymbial outgrowths and denticles are absent although a part of the paracymbium is similar. – The position of the eyes and certain structures of the male pedipalpus – as a dorsal-basal depression of the cymbium (which is smaller in *Anameta*) – are similar to *Dianleucauge* SONG & ZHU 1994 from China (sub Metinae) by ZHU MINGSHENG et al. (2003) and is probably most related to *Diphya*), but the clypeus is short in *Dianleucauge* and the shape of the paracymbium is quite different. – The position of the eyes of the Anametini is similar to the extant genus *Zygiometella* WUNDERLICH 1994 from the Near East which relationships are unsure (it may berelated to the Metinae); in *Zy-*

giometella a unique stridulatory cheliceral-pedipalpal organ exists, the clypeus is short, outgrowths and denticles of the cymbium are absent, and the structure of the paracymbium is quite different. – Anametini may be a basal branch of the Tetragnathidae, an Eocene relict in which probable remains of a median apophysis are still existing (but this structure is more likely a terminal apophysis), and is probably most related to – or a member of – the Diphyinae, which may be not monophylelic. *Diphya* NICOLET 1849 – regarded as a member of the Metinae (!) by ZHU MINGSHENG et al. (2003) – as well as probably few related genera may represent the tribus Diphyini; a revision of these taxa is urgently needed. – The long clypeus and the large and dentate male chelicerae are similar in the fossil genus *Chelicerinus* n. gen. (a questionable member of the family Synotaxidae, see below), in which a wide pedipalpal tibia exist, and long ventral leg hairs as well as femoral and metatarsal bristles are absent.

Distribution: Eocene Baltic amber forest incl. the Bitterfeld deposit.

Anameta WUNDERLICH 2004

Diagnosis, **relationships** and **distribution**: See above and WUNDERLICH (2004: 911–912). Remarks: (1) Parts of the bulbi of the type species are hidden by an emulsion, and therefore the questionable terminal apophysis was not observable in the only known specimen of the generotype, *Anameta distenda* WUNDERLICH 2004 (figs. 1–3) but it is visible in the new species. – (2) I may add here to the diagnosis of the genus – according to *A. kuntneri* n. sp. – that the metatarsus II bears a pair of dorsal-basal bristles and the pedipalpal femur bears a ventral-apical hump (fig. 6). – (3) I regard *Anameta* as a questionable member of the Diphyinae. (4) Members of this genus occured in the Eocene Baltic amber forest (*A. kuntneri* n. sp.), and is also known from the Bitterfeld deposit (*A. distenda* WUNDERLICH 2004).

***Anameta kuntneri* n. sp.** (photos 145–146, figs. 4–8)

Derivatio nominis: This species is dedicated to MATJAZ KUNTNER, who revised – and is still revising – mainly genera of the families Araneidae/Nephilinae, and Tetragnathidae.

Material: Holotypus ♂ in Baltic amber, F1891/BB/AR/CJW.

Preservation and syninclusions: The spider is excellently and almost completely preserved in a yellow piece of amber which was not heated; only the apical part of the right femur I and the basal part of the right patella I as well as the apical part of the right tibia IV are (retro)dorsally cut off. Anterior parts of the prosoma are partly covered with a white emulsion. A short part of a dragline runs backward from the left anterior spinneret, branched spider's threads are preserved below the left tarsus and metatarsus IV. – 1/2 tiny incomplete and deformed winged insect, some stellate hairs and air bag pollen grains are preserved in the same piece of amber, an air bubble is situated right of the right bulbus.

Ecology: The simultaneous presence of stellate hairs (most probably originating from Fagaceae) and air bag pollen grains (probably originating from Pinaceae) – which both are preserved with the spider – indicate that the spider existed in a mixed forest.

Diagnosis (♂; ♀ unknown): Pedipalpus (figs. 4–8): Cymbium with a long retrodorsal "horn", the dorsal denticulate cymbial process (DCP) bears 2–3 cusps and 2 thick bristles.

Description (♂):
Measurements (in mm): Body length 3.5, prosomal length 1.5, length of the basal cheliceral articles 0.8; leg I: Femur 1.8, patella 0.65, tibia 1.8, metatarsus 1.9, tarsus 0.9, tibia IV 0.95.
Colour: prosoma and legs medium brown, opisthosoma yellow brown, legs not annulated.
Prosoma wide, covered with few short hairs, fovea very large. Eyes (fig. 4) of the posterior row large, anterior median eyes smallest, posterior row recurved, anterior and posterior eyes spaced by ca. a diameter of the anterior eyes, posterior median eyes separated by ca. one of their diameter. Clypeus long and concave, similar to *A. distenda* WUNDERLICH 2004 (fig. 1). Basal cheliceral articles slender, longer than the hight of the prosoma, slightly diverging distally (similar to fig. 1), lateral files and condylus absent, teeth of the furrows hidden, fangs long. Gnathocoxae wide and parallel, labium free, rebordered, slightly wider than long. Sternum fairly longer than wide, separating coxae IV by less than their diameter. – Legs long and hairy, order I/II/IV/III, I distinctly longest, III distinctly shortest, long ventral sensory hairs exist mainly on tibia and metatarsus I–II (fig. 5). Tibia I and II are fairly bent (photo). Bristles numerous, on femora, patellae, tibiae and metatarsi; femora with a distal-lateral pair (one of the bristles may be absent on II), proapical bristles may exist, I–II bear a single, III–IV 2 dorsal bristles. Patellae with 2 dorsal bristles, the basal one small. Tibiae with dorsal and lateral bristles but ventral ones absent; I bears 2 dorsal, 3 prolateral and 2 retrolateral ones. Metatarsus I bears 5 dorsal and lateral bristles. Position of the metatarsal I–II trichobothrium in 0.17. Paired tarsal claws toothed, unpaired claws long and bent in a right angle. – Opisthosoma (photo) oval, scarcely covered with short hairs, with 2 pairs of dorsal sigillae; position of the small tracheal spiracle near to the stout anterior spinnerets; the fairly large colulus bears 5 small hairs. – Pedipalpus (figs. 6–8): Femur with a ventral-apical hump, patella short, with a single thin dorsal bristle on a hump, tibia also short, with 8 long and thin dorsal bristles, 6 of these in a distal row. Cymbium retrolaterally with an erect horn-shaped apophysis (CH), dorsally with a "denticulate" outgrowth (DCP) which bears 2–3 cusps and 2 spines. Paracymbium large, directed ventrally and pointed at the tip, most probably not a free sclerite but fused basally, with a deep anterior excavation, bearing long hairs which are directed foreward, dorsally with an outgrowth. Tegulum large. A tegular apophysis near the base of the embolus

may be a small “terminal apophysis”. Embolus long, its distal two third lying in a large conductor.

Relationships: The single other known congeneric species – *A. distenda* WUNDERLICH 2004 – originates from the Bitterfeld deposit; it has a very short horn-shaped apophysis which bears a cusp, the higher DCP bears 4 cusps and additionally a basal one.

Distribution: Eocene Baltic amber forest.

Subfamily LEUCAUGINAE: BALTLEUCAUGINI n. trib.

Diagnosis (♂; ♀ unknown): Anterior and posterior lateral eyes widely spaced as in *Anameta* (fig. 1), all femora bear 4–6 trichobothria in two irregular rows in the basal half (fig. 10) (probably only a single row on femur IV, fig. 11). Pedipalpus (figs. 12–14): Cymbium without a distinct dorsal horn but with a hairy dorsal-basal depression, paracymbium bipartite, apparently fused to the cymbium, bulbus flat, embolus long and thin, in a retrolateral position near the cymbial margin.

Further characters: Clypeus only as long as 1 1/2 diameters of the anterior median eyes (fig. 9), posterior eye row recurved, labium not rebordered.

Remark: The hairy cymbial depression may have had a function in the courtship behaviour, and I do not want to exclude that a sexual stimulating secretion – a pheromone? – has been produced in this depression (remains of such a secretion are not recognizable).

Type genus by monotypy: *Baltleucauge* n. gen..

Relationships: According to the femoral trichobothria in two rows and the unmodified male chelicerae I regard *Baltleucauge* as a taxon of the subfamily Leucauginae. In other – the extant – members of the Leucauginae the anterior and posterior lateral eyes are not widely spaced, the cymbium bears usually a dorsal “horn”, a hairy cymbial depression is absent, and the position of the embolus is quite different; their opisthosoma is frequently raised above the spinnerets. – The Cretaceous genus *Macryphantes* SELDEN 1990 may be a taxon of an undescribed family, see WUNDERLICH (2004: 854) and above. In *Macryphantes* exist femoral trichobothria and a paracymbium similar to *Baltleucauge* but the leg bristles are stout, tarsal bristles are present similar to the Uloboridae and the extinct Protheridiinae WUNDERLICH 2004, and the embolus has a quite different position.

Distribution: Eocene Baltic amber forest.

***Baltleucauge* n. gen.**

Diagnosis, relationships and distribution: See the tribus Baltleucaugini.

Type species by monotypy: *Baltleucauge gillespiae* n. sp.

***Baltleucauge gillespiae* n. gen. n. sp.** (photo 148, figs. 9–14)

Derivatio nominis: The species is dedicated to ROSIE GILLESPI in California, who worked for many years intensively on extant Tetragnathidae.

Material: Holotypus ♂ in Baltic amber, F1017/BB/AR/CJW.

Preservation and syninclusions: The spider is well preserved in a yellow piece of amber which was not heated; parts as sternum and opisthosoma are covered with a thin white emulsion, the prosoma is posteriorly distinctly injured (depressed), the left leg III is complete but other legs are partly cut off, e. g. both anterior legs near the tip of their femora; both femora I and the left tibia II have "rings" from oxidation. Some thin spider's threads, few stellate hairs and 2 2/2 Diptera: Nematocera as well as legs of Diptera are preserved in the same piece of amber.

Diagnosis (♂; ♀ unknown): See above.

Description (♂):
Measurements (in mm): Body length 4.0, prosomal length 1.8, opisthosomal length 2.6; leg II: Femur 4.0, metatarsus ca. 3.3, tarsus III 0.7.
Colour light brown.
Prosoma (fig. 9) wide and fairly low, with a furrow between the cephalic and the thoracal part, covered with short hairs, fovea well developed. 8 large eyes similar to *Anameta* (fig. 1), anterior medians smallest, separated by less than their diameter, posterior row recurved, posterior median eyes separated by ca. their diameter, anterior and posterior lateral eyes separated by ca. their diameter. Basal cheliceral articles large, anterior margin of the furrow with at least 2 large teeth, fangs long, labium wider than long, not rebordered. Sternum small elongated between the coxae IV. – Legs (figs. 10–11) long, I distinctly largest, III distinctly shortest; with longer hairs e. g. ventrally on tibia I–II and metatarsus II. Trichobothria with tiny bothria (diameter ca. 0.015 mm); femora: Usually two irregular rows of 4–6 in a dorsal-basal position (on IV only a single row). Metatarsal trichobothria unknown. Bristles long and thin, on femora, patellae, tibiae and metatarsi; femur I bears 1 dorsally in the basal half, 1 retrolaterally in the middle, and ca. 5 dorsal-lateral ones in the distal half; tibia III with 1 dorsally in the basal half and 1 prolaterally

in the distal half, metatarsus III bears 1 dorsal and 1 prolateral bristle near its base. Paired tarsal claws with a long and several short teeth, unpaired claw long and bent in a right angle. Accessory tarsal hairs are present. – Opisthosoma (photo) long oval, covered with very short hairs, colulus large and hairy, spinnerets stout. – Pedipalpus (figs. 12–14; see above): Femur long and slender, patella with a dorsal bristle, tibia long, with ca. 5 trichobothria.

Relationships and distribution: See above.

Subfamily METINAE SIMON 1894

Subfamily name: The name Metidae SIMON 1894 (sub Meteae) is seemingly praeoccupied in Copepoda by Metidae BOECK 1872, based on *Metis* PHILIPPI 1843, and therefore Metinae should be praeoccupied as well (the genus name *Meta* C. L. KOCH 1836 is not praeocupied). According to O. KRAUS (person. commun. in IV 2008) the word “metis” exists in two different meanings, and the genitive “metidis” (gr. “metidos”) corresponds to the more commonly used word “metis”. In Copepoda the family name “Metididae” should therefore be used instead of “Metidae”, and “Metidae” in Araneae would not be praeoccupied.

Diagnosis (*): Presence of long dorsal cymbial bristles (fig. 17) (except in the extinct subgenus *Praetermeta*), a large and two-partite paracymbium (figs. 16–18), which consists of (a) a hairy, weakly sclerotized (yellow) and undivided ventral branch as well as (b) of a smooth, more sclerotized (brown) and usually divided retrolateral branch. Base of the embolus with an outgrowth (existing in *Metellina* as well).

Further characters and variability (see also the genus *Meta* s. l.): Male chelicerae not distinctly modified, the posterior margin of the furrow bears usually 2–3 large teeth in the smaller species but more often 4 teeth in larger species of *Merianmeta*, *Meta* s. str., *Stridulameta* (this character is intraspecifically variable!), femoral trichobothria absent, anterior and posterior lateral eyes close together, tibia of the male pedipalpus with one or several apical apophysis/apophyses including a conical dorsal one (figs. 15–16, 21), cymbium in some taxa – e. g. in the subgnera *Metellina* and *Stridulameta* – retrobasally with tiny bristles or spines (fig. 17), dorsal cymbial outgrowth absent (but see the subgenus *Sinometa*), conductor not wrapping the embolus (except in the subgenus *Metellina*), a fairly sclerotized ♀-genital field ("epigyne") may be present, PROBABLY “semientelegyne” condition sensu WIEHLE (1967).

(*) Remarks: A diagnosis depends on the taxa which are included. The exact number of taxa which have to include in the Metellininae is unsure; some are regarded as questionable members. Therefore I’ll give here a provisional and strict diagnosis of the Metinae which is based on the type genus and *Meta* s. l.. – Metinae in the wide traditional sense, see e. g. ZHU MINGSHENG (2003)) may be a polyphyletic or paraphyletic taxon.

Relationships: Tetragnathinae is PROBABLY most related, see WUNDERLICH (2004: 906); in Tetragnathinae bear the femora trichobothria, the male chelicerae are modified, very large, diverging and bearing frequently additional anterior and/or lateral teeth in the distal half, and the conductor wraps/encloses the embolus.

Type tribus: Metini SIMON 1894. Type genus: *Meta* C. L. KOCH 1836, which may be the only sure genus of this tribus and subfamily, see the next paragraph:

Relationships; related, probably related and misplaced taxa: Related – probably con-subfamiliar and sister group to the Metini – might be the Metabunini n. trib. which includes *Metabus* O. PICKARD-CAMBRIDGE 1899 (extant), and probably *Chrysometata* WUNDERLICH 2004 (extinct), see below. – Furthermore related may be the extant genera *Nanometa* SIMON 1908, *Nanningia* ZHU et al. 1997, *Metlaucauge* LEVI 1980, *Sancus* TULLGREN 1910 (= *Leucognatha* WUNDERLICH 1992) and *Zygiometella* WUNDERLICH 1995. – See also above: Diphyinae: Anametini, and other extinct genera of questionable Diphyinae. – *Chrysometa* SIMON 1895 has been regarded as a member of the Metinae by LEVI (1986); it may – more likely not – be related to *Zygiella* F. O. PICKARD-CAMBRIDGE 1902, see WUNDERLICH (2004). – *Metleucauge* and *Sancus* have elongated articles of the male pedipalpus; their structures of the bulbus are fairly similar to *Meta*; (*Metleucauge* possesses a ventral spur of the pedipalpal trochanter). Both genera may be closely related to each other although KUNTNER & ALVAREZ-PADILLA (2006) regard *Sancus* as sister group to *Tetragnatha* + *Pachygnatha* in which the femora bear trichobothria in contrast to *Sancus* and *Metleucauge*. – *Zygiometella* WUNDERLICH 1995 has been regarded as a questionable taxon of the Metinae but due to its genital structures its relationships appear quite unsure. – Remark: Taxa of even different families have been listed sub Metinae, e. g. *Metella* FAGE 1831 (= *Pimoa*) (Pimoidae) and Linyphiidae sub *Meta* sensu BARRION & LITSINGER (1995), see below.

Distribution: At least (mainly) the Northern Hemisphere but probably cosmopolitical.

Tribus and genera of extant and extinct (*) Metinae, the Metabini has probably to exclude:

Metini:
Meta C. L. KOCH 1836 s. l., with 8 subgenera incl. (*) *Praetermeta* WUNDERLICH 2004.

Metabini:
Metabus O. PICKARD-CAMBRIDGE 1899 and probably (*) *Chrysometata* WUNDERLICH 2004, see below.

(1) The tribus METINI

Diagnosis: Tibia of the male pedipalpus shorter than the cymbium, cymbial cuspules and protruding terminal apophysis absent, paracymbium composed of two different branches.

Distribution and remark on the name: See above: Metinae.

Type genus: *Meta* C. L. KOCH 1836 (s. l.). – Remarks: A splitting of the genus *Meta* s. l. – see the subgenera below – may be a matter of opinion. *Metellina* was regarded as synonymous with *Meta* by WUNDERLICH (1987: 127). If *Metellina* is regarded as a genus of its own we consequently would have 8 different genera within the Metini.

Remark: The taxa of the Metinae of the Australian Region are not included in this study.

Relationships: See Metabini below.

Meta C. L. KOCH 1836 **s. l**.: Diagnosis, relationships and distribution are identical with the Metini. The type species is *Meta fusca* LATREILLE 1805 (= *Meta menardi* LATREILLE 1804).

Subgenera of *Meta* s. l.: In the present paper I regard the genus *Meta* C. L. KOCH 1836 in a wide sense, comprising 8 subgenera, but the subgenera may be regarded – this is a matter of opinion – only as species-groups or even as genera of their own; see *Merianmeta* below. *Metellina* and the fossil genus *Praetermeta* WUNDERLICH 2004 (which is downgraded here from genus rank) are – according to their copulatory organs – so strongly related that I regard them as subgenera of *Meta* (**n. stat**.). *Meta stridulans* WUNDERLICH 1992 and *Meta shenae* ZHU et al. 2003 build – according to the structures of their male pedipalpi and based on their unique cheliceral stridulatory organ – as subgenus of its own: *Stridulameta* **n. subgen**. *M. merianae* (SCOPOLI 1763) has unique paracymbial files which I – according to their structure – regard as stridulatory files, and it is regarded here as the single member of the subgenus *Merianmeta* **n. subgen**. (from *Metellina*). MARUSIK & KOPONEN (1992) could still not know the diverse *Meta*-species which were described by ZHU et al. (2003) from China and the fossil genus *Praetermeta* WUNDERLICH 2004; they differentiated *Meta* and *Metellina* by several characters as the body shape, *Metellina* 4–8 mm, but *M. merianae* has a body length of up to 12 mm; see the key to the subgenera below. Several characters, e.g. of the diverse SE-Asian species – like the grade of sclerotization of the paracymbium, the position and the shape of the conductor and the hidden embolus – led me to a splitting of *Meta*. – *Menosira* CHICUNI 1955 from SE-Asia is – according to its figured copulatory organs – so strongly related to the taxa which are mentioned above, that I grade it down to subgenus rank (**n. stat**.) of *Meta* s. l.. Finally I create the subgenus *Sinometa* **n. subgen**. from China.

Evolution: It seems likely to me that – within *Meta* s. l. – the strength of sclerotization of certain pedipalpal structures depends simply on the size of (the members of) a species, with stronger sclerotization in larger species; and – furthermore – it is conspicuous that the largest and strongest pigmented spiders are cave-dwelling species (the subgenus *Meta*). I suppose (1) that in the extinct subgenus *Praetermeta* strong dorsal-distal cymbial bristles and tiny dorsal-basal spines as in fig. 17 are STILL absent, and (2) that in the extant subgenus *Meta* an advanced pattern exists, and it evolved latest: Compared with the free-living and relatively small members of the Eocene subgenus *Praetermeta* the species of *Meta* s. str. are cave-dwellers, their body is larger, and their paracymbium is stronger sclerotized. If this is true the subgenus *Meta* s. str. evolved latest, and we find within the genus *Meta* s. l. AN INCREASING LENGHT OF THE BODY (similar to "Cope's rule" in mammals): From the Eocene subgenus *Praetermeta* (about 6 mm) along the extant subgenus *Merianmeta* (7.5–12 mm) to the extant subgenus *Meta* (8–17 mm), although this is only a supposion because we do not know of the (non-)existence of other Eocene species of *Meta* s. l. than those of *Praetermeta*. According to its habitat (in dark and humid localities as well as in caves), its body length (7.5–12 mm), and its fairly dark body colour the extant *Meta* (*Merianmeta*) *merianae* is the model of a link (a relalively young branch of) between the extinct subgenus *Praetermeta* – which is similar to the extant subgenus *Metellina* – and the extant subgenus *Meta* s. str.. *Stridulameta* may be – according to its disjunct kind of distribution (Madeira and China each a single species) – a relict taxon.

Distribution: Mainly – or only? – the Northern Hemisphere. Two species of the extinct subgenus *Praetermeta* WUNDERLICH 2004 of the Baltic amber forest are the only taxa which are known from fossils, see below.

Key to the subgenera of *Meta* s. l. of the Northern Hemisphere:

Remark: Only *Praetermeta* is known from fossils.

1 Chelicerae with lateral stridulatory files in both sexes (weaker developed in the female); pedipalpal femur with a prolateral edge. – Extant, Madaira (*stridulans*) and China (*shenae*). . . . . Stridulameta

- No such stridulatory organ. 2

2(1) Anterior metatarsi and cymbium bristle-less. ♂-pedipalpus: Figs. 15–16; ♀ unknown. – Extinct, Eocene Baltic amber. . . . . .Praetermeta

- Anterior metatarsi with a single or several bristle(s), cymbium with bristles (fig. 17). The ♂-pedipalpus of *Praetermeta* is similar to *Metellina*, in which the cymbium bears a field of tiny bristles/spines (fig. 17). – Extant 3

3(2) Posterior median eyes spaced by their radius or less. Opisthosoma with shallow lateral lobes. Tip of the embolus screw-shaped.– SE-Asia (*nigrodorsata*)..*Nipponmeta*

- Posterior median eyes spaced by about their diameter. Opisthosoma without lateral lobes (quite indistinct "humps" exist in some females of *Metellina*). Tip of the embolus not screw-shaped. 4

4(3) Opisthosoma dorsally with a distinct light longitudinal band. – SE-Asia. 5

- Opisthosoma usually without such a band. SE-Asia and Holarctic. 6

5(4) Fangs very thick (fig. 20). Cymbium basally strongly widened, with a dorsal hump (fig. 21). Epigyne with a hairy and weakly sclerotized "scape" (*qianshunensis*) . . . . *Sinometa*

- Fangs of normal size. Cymbium basally not widened, without a dorsal hump. Epigyne with a strongly sclerotized scape (*ornata*) . . . . *Menosira*

6(4) Paracymbium (figs. 18–19): Retrodorsal (smooth) branch slender and with a field of stridulatory files as well as connected to the hairy retroventral branch by a transparent area. Bristles on metatarsus I, cheliceral teeth, body length, and usually the colour of the body are like in *Meta* s. str. In shaddowy habitats and the entrances of caves. – Europe (*merianae*). . . . . *Merianmeta*

- Paracymbium without such files nor a transparent connection, similar to fig. 16. – Widely distributed on the Northern Hemisphere. 7

7(6) Usually light coloured spiders, ventral bristles of metatarsus I near the middle usually absent. Cheliceral furrow: 3 (rarely 2) teeth of the posterior margin. Retrodorsal (smooth) branch of the paracymbium weakly sclerotized and with a distinct medial outgrowth which points to the hairy retroventral branch, similar to x in fig. 16; the wide(r) conductor covers the embolus completely. ♀: Position of the introducing epigynal openings ventrally. Body length most often less than 10 mm. Not cave spiders but prefering open biotopes . . . . *Metellina*

- Darker coloured spiders, metatarsus I ventrally near the middle usually with 1–2 bristles. Cheliceral furrow: 4 (rarely 3) teeth of the posterior margin. No distinct outgrowth of the retrodorsal paracymbial branch which is always large, strongly sclerotized and stands out from the retroventral paracymbial branch in a right angle. Embolus **ONLY BASALLY** covered by the more slender conductor. ♀: Position of the introducing openings posteriorly. Largest spiders of *Meta* s. l. besides *Merianmeta* and *Stridulameta*, body length 8–17 mm. Cave spiders. . . . .*Meta* (s. str.)

The extant and extinct subgenera/species groups of *Meta* s. l., and description of the fossil *Meta* (*Praetermeta*) *maculosa* n. sp.

Remarks on species which were/are transferred from *Meta* s. l.: *barretti* KULCZYNSKI 1899, *minima* DENIS 1953 and *reticuloides* YAGINUMA 1958 = *Metellina*; *baywanga* BARRION & LITSINGER 1995 and *tiniktirika* BARRION & LITSINGER 1995 (according to their genital organs and kind of autotomy) = Linyphiidae: Linyphiinae, *melanicruciata* SAITO 1939 = *Enoplognatha m*. (**n. comb**.) regarding to the large tooth of the anterior cheliceral margins (♂) and the structures of the ♂-pedipalpus.

Meta C. L. KOCH 1836) s. str. (= *menardi* species-group)

Archicybaeus GERTSCH 1933 is considered a junior synonym of *Meta* s. str., see LEHTINEN (1967: 217).

Diagnosis: Darker coloured spiders, metatarsus I ventrally near the middle usually with 1–2 bristles, embolus only partly – basally – covered by the more slender conductor, retrodorsal paracymbial branch large, strongly sclerotized, and standing out in a right angle. ♀: Position of the introducing openings posteriorly. Large, strongly pigmented cave spiders, body length 8–17 mm (*M. bourneti*).

Further characters: Retromargin of the cheliceral furrow usually with 4 (rarely 3) teeth, Opisthosoma almost as high as long.

Relationships: See the key. The cheliceral teeth are like in *Merianmeta* and similar to *Metellina*.

Type species: *Meta fusca* WALCKENAER (now *Meta menardi*).

Further species (see MARUSIK & KOPONEN (1992)): *M. bourneti* SIMON 1922, *doloff* LEVI 1980, *japonica* TANIKAWA 1993, *manchurica* MARUSIK & KOPONEN 1992, *menardi* LATREILLE 1804 and *ovalis* GERTSCH 1933 (= *americana* MARUSIK & KOPONEN 1992).

Distribution: Holarctic.

Metellina CHAMBERLIN & IVIE 1941 (= *curtisi* species-group of *Meta* s. l.)

Diagnosis: Lighter coloured, smaller and free-living spiders, body length most often less than 10 mm. Cymbium basally with a field of tiny spines (F in fig. 17), retrodorsal (smooth) branch of the paracymbium weakly sclerotized and with a distinct – more distinct than in *Meta* – outgrowth which points to the hairy retroventral branch, similar to x in fig. 16; the wide conductor covers the embolus completely. ♀: Position of the introducing epigyneal openings ventrally.
Further characters: Cheliceral retromargin usually with 3 (rarely 2) teeth, opisthosoma slightly flattened, indistinct "humps" may exist, see *Nipponmeta*.

Relationships: See the key, *Meta*, *Nipponmeta* and and *Praetermeta*.

Type species: *Metellina curtisi* (MCCOOK 1893).

Further species: *barretti* KULCZYNSKI 1899, *mengei* BLACKWALL 1869, *mimetoides* CHAMBERLIN & IVIE 1941, *minima* DENIS 1953, *orientalis* SPASSKY 1932) (?= *kirgisica* BAKHVALOV 1974), *reticuloides* YAGINUMA 1958, and *segmentata* CLERCK 1757.

Distribution: Holarktic.

***Merianmeta* n. subgen**. (= *merianae* species-group of *Meta* s. l.) (photo 140, figs. 18–19a, b).

Diagnosis: Fairly dark coloured spiders. Paracymbium (figs. photo 140, 19a–b): Retrodorsal (smooth) branch slender and with a field of stridulatory files as well as connected to the hairy retroventral branch by a transparent area.
Further characters: See the key above. The spiders prefer shaddowish biotopes.

Remark: The paracymbial files are very similar to retrolateral cheliceral stridulatory files in linyphiid spiders, and are therefore here regarded as stridulatory files, too. A sure counterpart to these files is unknown, but I do not want to exclude that an anterior clypeal processes (fig. 18) may possess this function (a paracymbial field of files rubbing probably against the clypeal process of the opposite side).

Relationships: See the key. The cheliceral teeth are as in *Meta* s. str.

Type species (by monotypy): *Meta merianae* (SCOPOLI 1763).

Distribution: Europe.

Menosira CHIKUNI 1955 (subgenus of *Meta*, **n. stat**., downgraded from genus rank) (= *ornata* species-group)

Diagnosis: Opisthosoma dorsally with a longitudinal white band. The wide conductor covers only a large basal part of the embolus. The epigyne has a strongly sclerotized medial part.

Relationships: See the key.

Type species (by monotypy): *Menosira ornata* CHIKUNI 1955.

Distribution: SE-Asia.

***Nipponmeta* n. subgen**. (= *nigrodorsalis* species-group of *Meta* s. l.)

Diagnosis: Posterior median eyes separated by about their radius or less, field of the median eyes wider behind than in front, opisthosoma with shallow lateral lobes, outgrowth of the embolus apically screw-shaped.

Relationships: In the remaining subgenera are opisthosomal lobes absent (quite indistinct "humps" exist in some females of *Metellina*), and the posterior median eyes are usually spaced by about their diameter (not in *Praetermeta*).

Type species (by monotypy): *Meta nigrodorsalis* TANAKAWA 1994.

Distribution: SE-Asia.

Praetermeta WUNDERLICH 2004 (= *velans* species-group of *Meta* s. l.) (subgenus of *Meta*, **n. stat**.; downgraded from genus rank)

Revised diagnosis (♂; ♀ unknown): Anterior metatarsi bristle-less, anterior median eyes most probably spaced by only their radius, opisthosoma long and narrow (photo 141), 1.7 times longer than wide (*maculosa*). ♂-pedipalpus (figs. 15–16): Cymbial bristles absent, slender part of the embolus hidden in the ventral aspect.

Relationships: *Metellina* may be most related; in *Metellina* the anterior metatarsi bear bristles and the opisthosoma is at most 1.5 times longer than wide. In *Nipponmeta* are the posterior median eyes also spaced by only their radius.

Type species: *Meta* (*Praetermeta*) *velans* WUNDERLICH 2004. (Further species: *M.* (*P.) maculosa* n. sp., see below).

Distribution: Eocene Baltic amber forest.

Meta (***Praetermeta***) ***maculosa*** **n. sp**. (photos 141–142, figs. 15–16)

Material: Holotypus ♂ in Baltic amber, F1367/BB/AR/CJW.

Preservation and syninclusions: The spider is not well and only incompletely preserved in a piece of amber which was heated and put in benzylium benzoicum for a short time, but the structures of the right pedipalpus are excellently preserved (photo, figs. 15–16). The ventral side of body and legs is – partly thickly – covered with a white emulsion, the left pedipalpus, too; the dorsal side of the body has changed to a spotted surface by the use of the benzylium. Several leg articles are cut off, e. g. the left legs I and II through the end of their femur and the left legs III and IV through their patella. The right fang is spread off. – Stellate hairs are absent.

Diagnosis (♂; ♀ unknown): Anterior-distal cheliceral tooth absent; the medial outgrowth of the smooth retrodorsal paracymbial branch does not reach the hairy retroventral branch (fig. 16).

Description (♂):
Measurements (in mm): Body length 5.8, prosoma: Length 2.7, width ca. 2.2, opisthosoma: Length ca. 2.9, width 1.7; leg III: Femur ca. 2.8, patella ca. 1.3, tibia III 1.7.
Prosoma defect, eyes large to fairly large, posterior row procurved, posterior median eyes large and spaced probably by only their radius. The large basal cheliceral articles bear few large teeth on the promargon of the furrow, but no anterior-distal tooth. The fang is long, mouth parts and sternum are hidden. – Legs long and hairy, probably very similar to *M. velans*; bristles long, femora 2 dorsally and 2 lateral pairs in the distal quarter, tibia IV 1 dorsally in the distal half, 3 retrolaterally, and 2 prolaterally; metatarsus IV bears at least 4 bristles. Position of the metatarsal trichobothria unknown. – Opisthosoma ca. 1.7 times longer than wide, covered with short hairs. Spinnerets stout, colulus fairly large, triangular. – Pedipalpus (figs. 15–16): Patella short, with 2 thin dorsal bristles, tibia longer than wide, with at least 4 trichobothria, longer hairs, and a bristle-shaped hair at the base of the conique apical process. Cymbium without dorsal process, paracymbium with a long, hairy and undivided retroventral branch and a divided smooth retrodorsal branch which has a medial process. Conductor fairly wide; the distal (slender) part of the embolus is hidden.

Relationships: In *Meta* (*Praetermeta*) *velans* (WUNDERLICH 2004) (**n. comb**.) the ♂-chelicerae baer an anterior-distal tooth, and the medial outgrowth of the smooth retrodorsal paracymbial branch overlaps the hairy retroventral paracymbial branch.

Distribution: Eocene Baltic amber forest.

***Sinometa* n. subgen**. (= *qianshanensis* species-group) (Figs. 20–21)

Diagnosis: Fangs very thick (fig. 20). Cymbium basally strongly widened, with a dorsal hump (fig. 21). Epigyne with a hairy and weakly sclerotized scape.

Relationships: See the key.

Type species (by monotypy): *Meta qianshunensis* ZHU & ZHU 1983.

Distribution: China.

***Stridulameta* n. subgen**. (= *stridulans* species-group)

Diagnosis: The chelicerae bear retrolateral stridulatory files in both sexes (they are weaker developed in the female), and the pedipalpal femur bears a prolateral edge, see WUNDERLICH (1987: 130, figs. 353–359).
Further character: Larger and light pigmented spiders. The pedipalpal tibia bears an apical retroventral apophysis.

Relationships: See the key. The depression of the "epigyne" is similar to *Metellina*, the tegular loops of the sperm duct are similar to the subgenus *Meta*, as well as the embolus, which is only partly hidden by the conductor. *Stridulameta* has morphologically an "connecting" position between both subgenera.

Type species: *Meta stridulans* WUNDERLICH 1992. (Further species: *Meta shenae* ZHU et al. 2003).

Distribution: Madeira and China. With respect to its disjunct distribution *Stridulameta* is apparently a relict taxon.

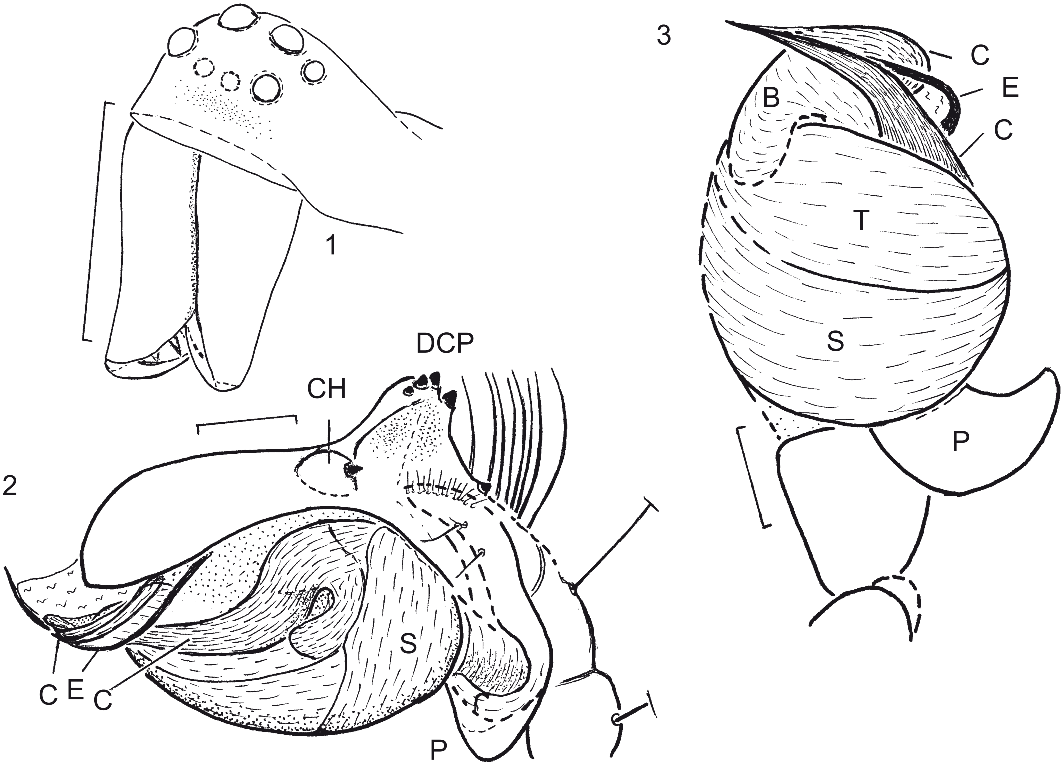
(2) The tribus METABINI n. trib.

Diagnosis: ♂-pedipalpus (figs. 22–23): Tibia longer than the cymbium, cymbium/ paracymbium undivided, with dorsal cuspules in the basal half, terminal apophysis widely protruding apically.

Type genus: *Metabus* O. PICKARD-CAMBRIDGE 1899. Further genus (regarded as related with hesitation only): The fossil genus *Chrysometata* WUNDERLICH 2004 in Baltic amber (trasferred from Zygiellidae this way) (**n. quest. relat**.) (*).

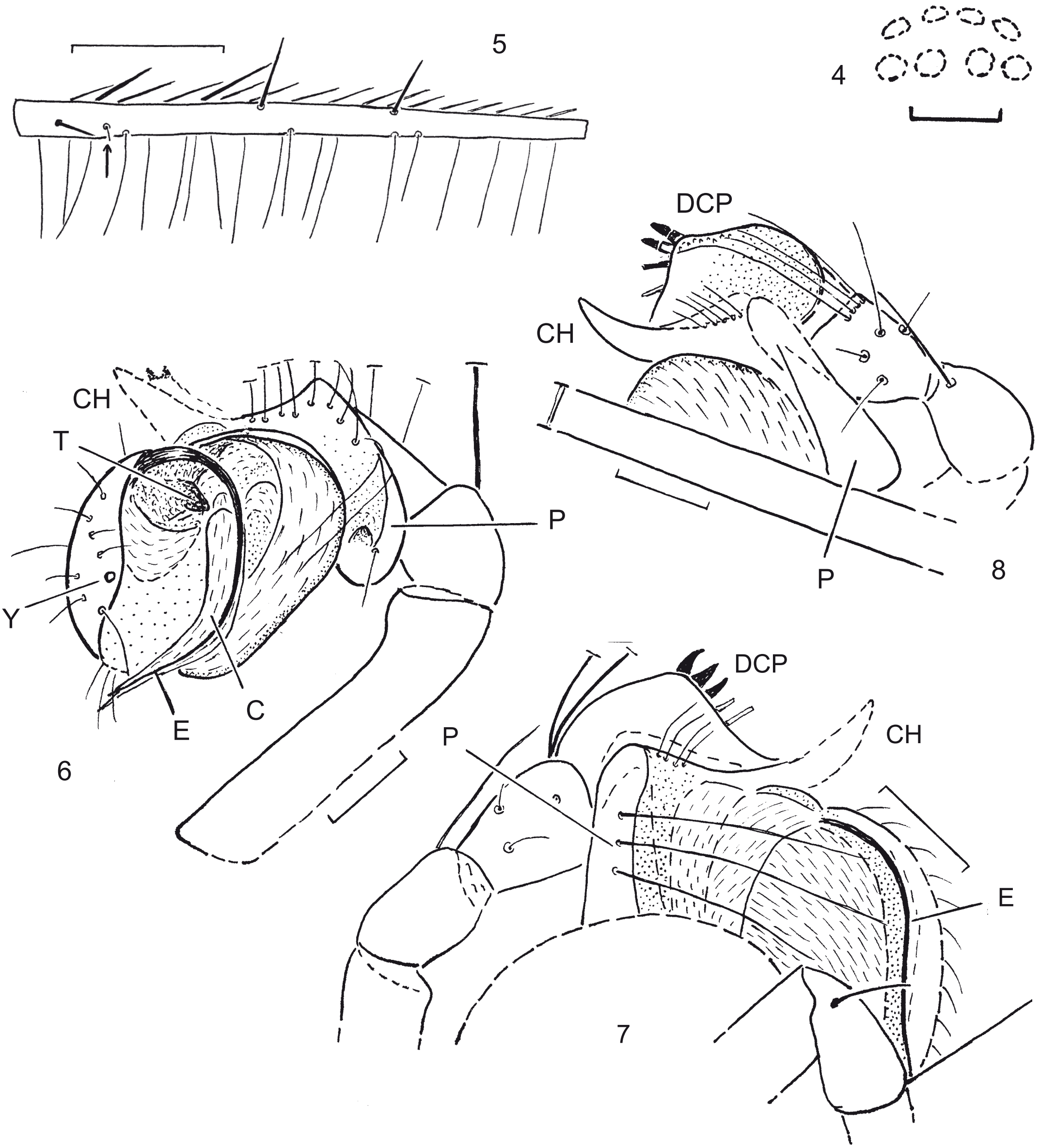
Relationships: In the probably related Metini the pedipalpal tibia is shorter than the cymbium, cymbial cuspules and a protruding terminal apophysis are absent, strong cymbial bristles are basicly present, the paracymbium is composed of two different branches, and a protruding terminal apophysis of the bulbus is absent.

Distribution: Extant: South America: *Metabus*; probably fossil: Eocene Baltic amber forest: *Chrysometata* (relationships unsure)

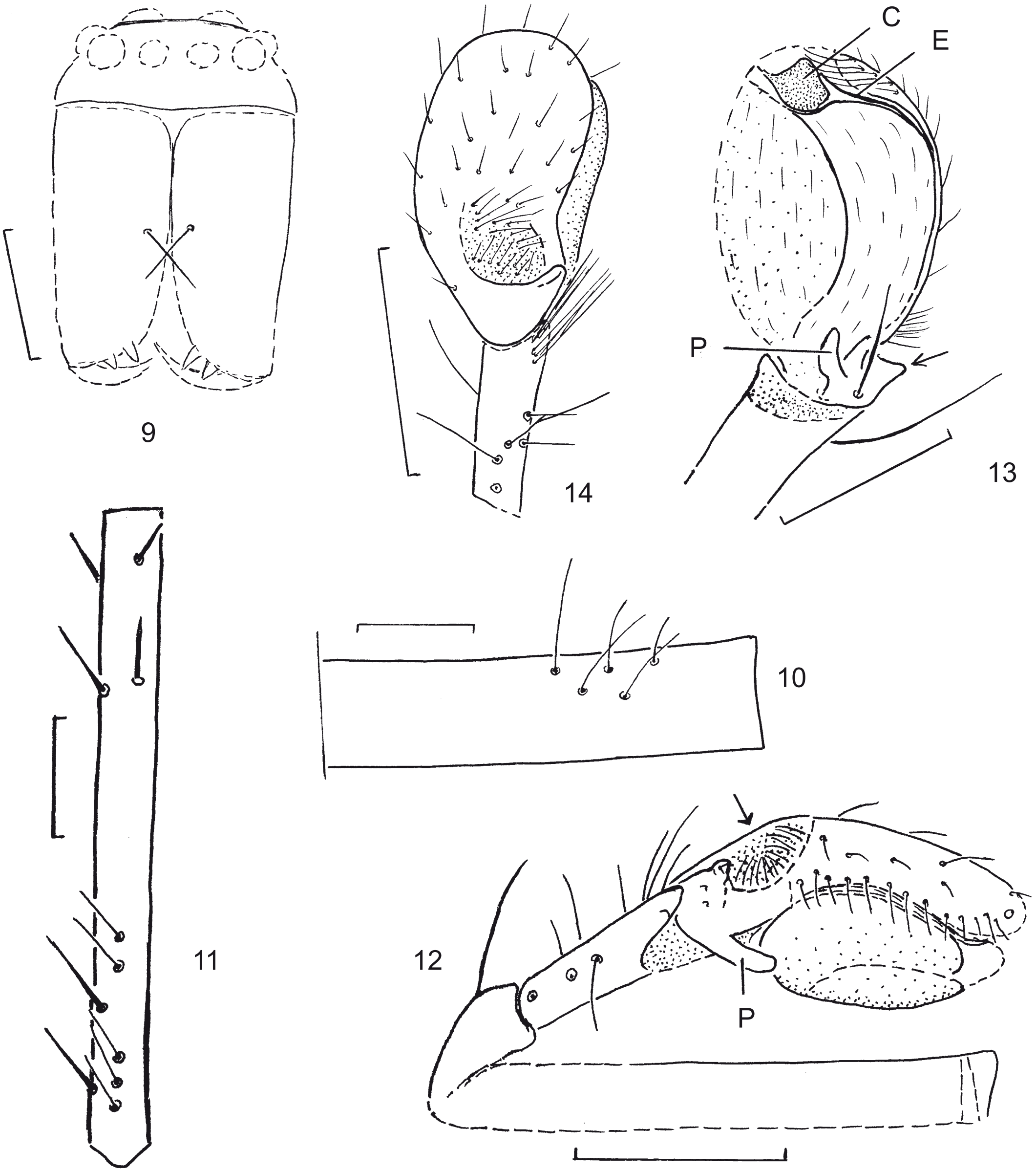


Figs. 1–3: *Anameta distenda* WUNDERLICH 2004, ♂; 1) anterior-left aspect of the prosoma; 2) retrolateral and slightly apical aspect of the l. pedipalpus; 3) ventral aspect of the l. pedipalpus; B = bubble, C = conductor, CH = cymbial hook, DCP = dorsal cymbial process, E = embolus, P = paracymbium, S = subtegulum, T = tegulum. Scale bar = 1.0 in fig. 1, 0.2 in figs. 2–3;

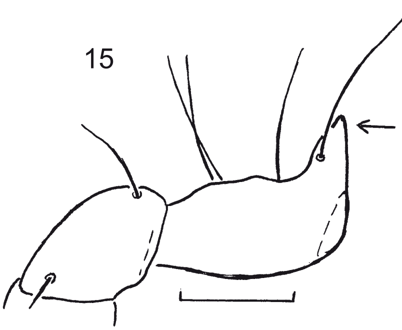
(*) In the only known species of *Chrysometata* – *C. palaearctica* WUNDERLICH 2004 – exists dorsal-basal cymbial cuspules (figs. 22–23) similar to *Metabus*, including a basal row of about a dozen “teeth” in a “comb” (fig. 22), which were overlooked by me in 2004, and which are absent in *Metabus*. I will not exclude that *Chrysometata* and *Metabus* are not strongly related and the existence of cymbial cuspules is nothing else than a convergence.

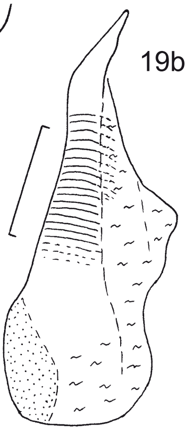


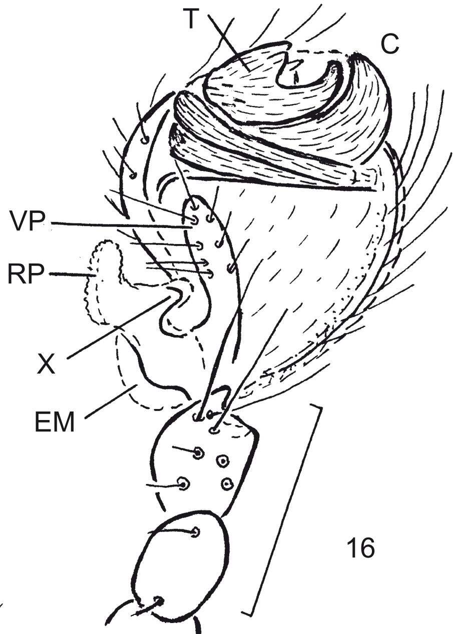
figs. 4–8: ***Anameta kuntneri* n. sp.,** ♂; 4) dorsal aspect of the eyes (because of white emulsions the exact position of the yes is hidden); 5) retrodorsal aspect of the r. metatarsus I. Note the short trichobothrium (arrow), 5 long bristles which are more or less erect, strong prolateral hairs as well as long and thin retroventral sensory hairs (other hairs are not drawn); 6) retroapical aspect of the l. pedipalpus (only few hairs are drawn); 7) retrolateral and slightly ventral aspect of the r. pedipalpus which partly is hidden by a bubble and a leg patella; 8) retrolateral and slightly basal aspect of the l. pedipalpus (ventral parts are hidden, only few hairs are drawn); C = conductor, DCP = dorsal cymbial process, CH = cymbial hook, E = embolus, P = paracymbium, T ?= terminal apophysis, Y = tarsal organ of the cymbium, remaining abbreviations as in figs. 1–3; scale bar = 0.5 in figs. 4–5, 0.2 in the remaining figs;

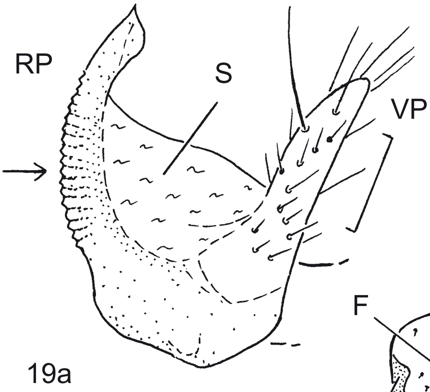


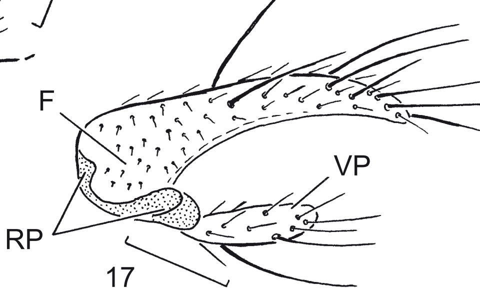
figs. 9–14: ***Baltleucauge gillespiae* n. gen. n. sp.**, ♂; 9) anterior aspect of the prosoma (parts are hidden by a white emulsion); 10) retrodorsal aspect of the basal part of the l. femur I. Note the two irregular rows of erect trichobothria (normal hairs are not drawn); 11) prodorsal aspect of the l. femur IV. Note the 5 trichobothria in a single row; 12) retrolateral aspect of the r. pedipalpus. The arrow points to the hairy dorsal depression of the cymbium (HDC). The conductor is hidden. (Only few hairs are drawn); 13) ventral aspect of the l. pedipalpus. The arrow points to the dorsal outgrowth at the base of the cymbial depression. Parts of the bulbus are hidden; 14) dorsal aspect of the r. pedipalpus; C = conductor, E = embolus, P = paracymbium; scale bar = 0.5;

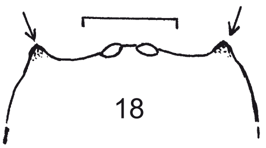

15


19b


16


19a


17

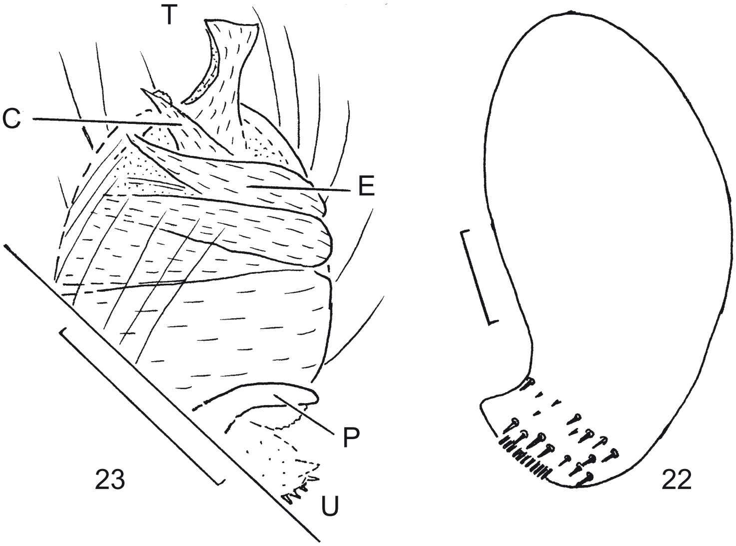

18

figs. 15–16: ***Meta*** (***Praetermeta***) ***maculosa* n. sp.**, ♂; 15) prolateral aspect of the l. pedipalpal patella and tibia. The arrow points to the apical-dorsal tibial outgrowth; 16) dorsal aspect of the r. pedipalpal patella and tibia with paracymbium, cymbium and bulbus twisted to almost the ventral aspect; C = conductor, EM = emulsion, RP = retrolateral branch of the paracymbium, T = terminal apophysis, VP = ventral branch of the paracymbium, X = medial outgrowth of the retrolateral paracymbial branch which points to the ventral paracymbial branch; scale bar = 0.2 and 0.5;

fig. 17) Meta (Metellina) minima DENIS 1953, ♂, retrolateral aspect of the r. cymbium; F = field of tiny spines, RP, VP = retrolateral and ventral branches of the paracymbium; scale bar = 0.2;

figs. 18–19b: Meta (Merianmeta) merianae (SCOPOLI 1763), ♂; 18) dorsal aspect of the anterior part of the prosoma with the anterior median eyes and the paired anterior-lateral clypeal processes (arrows); 19a) retrolateral aspect of the r. cymbium. The arrow points to the questionable stridulatory files; 19b) dorsal aspect of the r. dorsal cymbial branch. Note the field of questionable stridulatory files; RP, VP = retrolateral and ventral cymbial branches, S = scinny area; scale bar = 0.2;

figs. 20–21: <u>*Meta*</u> (<u>*Sinometa*</u>) <u>*qianshanensis*</u> ZHU & ZHU 2003, ♂; 20) posterior aspect of the l. chelicera; 21) prolateral aspect of the l. pedipalpus; no scale bar; taken from ZHU & ZHU (2003: Figs. 28 B, F);



figs. 22–23: <u>*Chrysometata palaearctica*</u> WUNDERLICH 2004, ♂ holotypus; 22) dorsal aspect of the l. cymbium with cusps. Hairs are not drawn; 23) ventral aspect of the l. pedipalpus. Only few hairs are drawn; the probasal part is hidden by a leg; C = questionable conductor, E = questionable embolus, P = paracymbium, T = terminal apophysis, U = cymbial cuspules; scale bar = 0.2.

FAMILY ARANEIDAE: Subfamily ARANEINAE?

Members of this subfamily are rare in Baltic amber (the subfamiliar relationships of the fossils are unsure), see WUNDERLICH (2004: 978–984). The reason for their rarity may be the larger body size of most adult Araneinae.
Spiders which are treated below possess an opisthosoma which is strongly elongated beyond the spinnerets (photos 149–153, figs. 4, 8). An elongated opisthosoma exists in certain fossil spiders which are preserved in Baltic amber; it is known to me from fossil members of the superfamily Araneoidea: Besides Araneidae (*Cyclosoma* and *Eochorizopes*) it exists in most Cyatholipidae, some Synotaxida as well as in few tiny Anapidae s. l.: Mysmeninae – see WUNDERLICH (2004) – and in very few Theridiidae

(*Caudasinus* n. gen.). In the araneid spiders of the genera *Cyclosoma* and *Eochorizopes* exist a very short clypeus (photo, fig. 2) in contrast to the taxa of the remaining families in which the clyeus is much longer.

***Eochorizopes* n. gen.**

Diagnosis (based on inadult specimens): Opisthosoma (photos, fig. 5) long and strongly elongated beyond the spinnerets (probably in connection with a kind of camouflage), cephalic part raised and separated from the thoracal part, small eyes in a wide field (photos, fig. 1), leg bristles long and thin, male chelicerae modified (fig. 2).

Further characters: No distinct condylus, labium slightly wider than long (fig. 3), femoral bristles present, METATARSAL BRISTLES ABSENT, opisthosoma soft and blunt posteriorly, tarsi distinctly shorter than metatarsi, posterior spinnerets with three long and slender spigots (fig. 7).

Type species (by monotypy): *Eochorizomma szeklinskiae* n. sp.

Relationships: The short clypeus and the position of the eyes of *Eochorizopes* are quite similar to certain members of the Araneidae, mainly to *Chorizopes* O. PICKARD-CAMBRIDGE 1870 (SE-Asia) but – e. g. in *Chorizopes* sp. indet. from Laos, SMF 56401 – the leg bristles are thicker and exist at least on the posterior metatarsi, humps exist posteriorly on the opisthosoma and the labium is wide and triangular. The early Eocene *Eochorizopes* is probably related to the ancestor of *Chorizopes* and possesses still femoral bristles as well as a hook-less opisthosoma. An adult male of *Eochorizopes* is needed for closer conclusions. – Relationships to fossil taxa: In *Cyclosoma* PETRUNKEVITCH 1958 – see below – the opisthosoma is also elongated beyond the spinnerets but the eye field is compact, the eyes are large and the tarsi are much longer compared with the metatarsi. In the remaining araneid genera in Baltic amber the opisthosoma is not elongated and the metatarsi bear at least a single bristle, see WUNDERLICH (2004).

Distribution: Eocene Baltic amber forest.

***Eochorizopes szeklinskiae* n. gen. n. sp.** (photos 149–153, fig. 1–7)

Derivatio nominis and acknowledgements: It is a pleasure to me to name this species after ELKE SZEKLINSKI from the island Baltrum, who kindly gave the paratype of the new species from her private collection to the GPI of the University of Hamburg (Dr. W. WEITSCHAT). – I also thank CARSTEN GRÖHN (Hamburg) who recognized the unusual opisthosomal shape of the paratype and asked me for a determination and description of this specimen.

Material (in Baltic amber): Holotype juv. ♂, F1879/BB/AR/CJW; paratype ?subad. ♀, GPIUH no. 4407.

Preservation and syninclusions: The holotype is well but incompletely preserved, most parts of its dorsal side are covered with a white emulsion, the dorsal half of the right pedipalpal tarsus as well as most leg tarsi and metatarsi are cut off, the ventral side of the right tarsus I and the left tarsus III are preserved, spinnerets, colulus and anal tubercle are excellently preserved (see the photos). A dragline originates from the left anterior spinneret, and remains of two stellate hairs are situated left of the spider's opisthosoma. – The paratype is completely and well preserved in a piece of amber which is 3.8 cm long and was slightly heated; parts of the ventral side are covered with a white emulsion, the legs are bent under the body, a bubble is preserved under the right pedipalpal tarsus. A tiny mite, a tiny leg of an insect (Diptera?), a tiny stellate hair and numerous small particles of detritus are preserved in the same piece of amber.

Remarks: According to the similar body shape, the position of the eyes, and the chaetotaxy I regard both type specimens as most probably conspecific. I do not want to exclude that the female paratype is subadult, it may be younger, most parts of the genital area are hidden, a scapus is absent. According to the shape of its only slightly thickened pedipalpi the male may have been at least two moultings before being adult. As an adult specimen its body length should probably have been more than five or even eight millimeters. If a distinct sexual size dimorphism exists, the length of the adult female should have been ten millimeters or more.

Diagnosis: See the diagnosis of the genus. Position of the metatarsal I trichobothrium in 0.26 (juv. male).

Description:
Measurements (in mm): ?Subad. female: Body length 6.5, prosoma: Length 2.1, width 1.6, opisthosoma: Length 4.4, width 1.9, hight ca. 1.5; leg I: Femur ca. 1.6, metatarsus ca. 1.3, tarsus ca. 0.5, leg IV: Femur ca. 1.8, tibia 1.2, metatarsus 1.35, tarsus 0.65. – Juv. male: Body length 3.2, prosomal length 1.2; leg I: Femur 1.2, patella 0.5, tibia 0.8, metatarsus 0.85, femur III 0.8, femur IV 1.1; pedipalpal tarsus: Length 0.46, width 0.14.
Colour: Prosoma and legs medium brown, opisthosoma light brown.
Prosoma (figs. 1–3) long, wide anteriorly, cephalic part distinctly bulging and clearly separated from the thoracal part by a furrow; 8 small eyes in a wide field, posterior row almost straight, posterior median eyes close together, field of the median eyes longer than wide, clypeus very short, basal cheliceral articles fairly stout, excavated medially and with a medial-distal hump in the juv. male, a distinct condylus is absent. Fangs stout in the juv. male, hidden in the juv. female. Labium free, in the juv. male 1.35 times wider than long, gnathocoxae stout. Sternum 1.2 times longer than wide, slightly elongated between coxae IV. Pedipalpus slender in the juv. female and with a large dentate tarsal

claw, fairly thickened in the juv. male (photo), with a long and slender tarsal claw which is only slightly bent and most probably smooth. – Legs (fig. 4) only fairly long, slender, hairs short and indistinct, sequence IV/I/II/III, III distinctly shortest. Bristles long and thin: Most femora bear a dorsal one in the basal half near the middle, I additionally a prolateral one in the distal half, patellae with 2 dorsal and a retrolateral bristle(s), tibiae with several bristles, female with 8 on tibia I, metatarsi bristle-less. Trichobothria absent on femora and tarsi, its position on metatarsus I in 0.26 (juv. male), short. Paired tarsal claws with long teeth, unpaired claw long. – Opisthosoma (figs. 5–7) long and slender, more slender in the larger juv. female, blunt anteriorly and posteriorly, strongly elongated beyond the spinnerets, covered with short hairs. Tracheal spiracle small, its position near the spinnerets. Colulus with 4 hairs in the juv. male, anal tubercle two-jointed, anterior spinnerets thick, posterior spinnerets with three long and slender spigots in the juv. male. Genital area of the female flat (most parts are hidden).

Relationships and distribution: See above.

Cyclosoma PETRUNKEVITCH 1958

Diagnosis (based on a small juvenile specimen, the holotype): Opisthosoma (fig. 8) long and strongly elongated beyond the spinnerets (probably in connection with a kind of camouflage), eyes large and spaced by not more than their diameter, leg bristles long and thin, tarsi about as long as metatarsi, metatarsal bristles absent.

Type species (by monotypy): *Cyclosoma succini* PETRUNKEVITCH 1958.

Relationships: Close relationships of this species which is known only quite juvenile are unknown to me; it may be a member of the Araneidae, probably of the Araneinae. WUNDERLICH (2004: 1030, 1156) discussed possible relationships to the Anapidae: Mysmeninae and the Cyatholipidae. According to PETRUNKEVITCH (1958) *Cyclosoma* is a member of the Theridiosomatidae (regarded as a subfamily of the Araneidae at that time) but in Theridiosomatidae a claw of the ♀-pedipalpus is absent (as in the Cyatholipidae), chaetotaxy and trichobothriotaxy are different. The relatively long tarsi of the rather young holotype are similar to members of most Anapidae s. l., and in some Mysmeninae the shape of the opisthosoma is similar, but their clypeus is long. In older araneid spiders are the tarsi usually much shorter than the metatarsi of young spiderlings (allometric growth). The short clypeus of *Cyclosoma* is like in almost all members of the Araneidae. – Relationships to fossil taxa: In the remaining araneid genera in Baltic amber is the opisthosoma not elongated – except in *Eochorizopes*, see above – and the metatarsi bear at least a single bristle.

Cyclosoma succini PETRUNKEVITCH 1958 (photo 154, fig. 8)

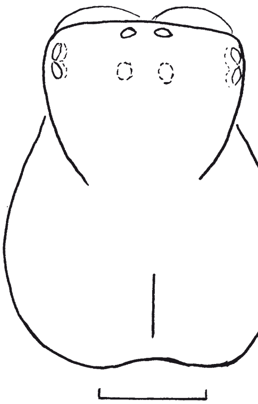
Material: Holotype juv. female, Geol. Mus. Copenhagen no. 9996.

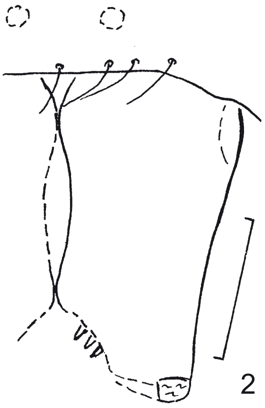
Remarks: Up to now the rather young holotype is the only known specimen of the monotypic extinct genus *Cyclosoma* PETRUNKEVITCH 1958. Parts of the spider are covered with a white emulsion. Long tarsi: See above (relationships).

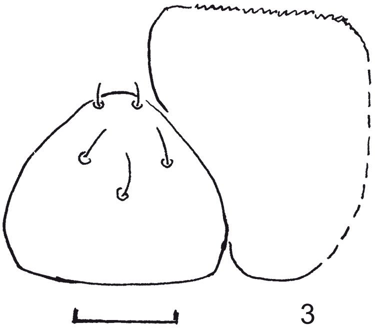
Description:
Body length 2 mm, prosoma 0.6 mm long, tibia I 0.45 mm long, clypeus relatively short, eye field fairly narrow, anterior median eyes small, the remaining eyes large and rather close together, the eyes of the posterior row are spaced by only about their diameter, cephalic part somewhat convex, thoracal part low, clypeus short, basal cheliceral articles fairly long, fangs stout, the labium is hidden. The pedipalpus has a large and smooth claw. Legs fairly slender, I longest. All patellae and tibiae bear 2 long and thin dorsal bristles; other leg bristles are apparently absent. Tarsi about as long or slightly longer than the metatarsi, unpaired tarsal claws bent in a right angle and shorter than the smooth paired claws. A comb of tarsus IV is absent. At least metatarsi I and II bear a trichobothrium, their position is in 0.24. The opisthosoma (fig. 8) is strongly elongeted beyond the spinnerets which are situated in the middle of the length, and blunt posteriorly, covered with short hairs.

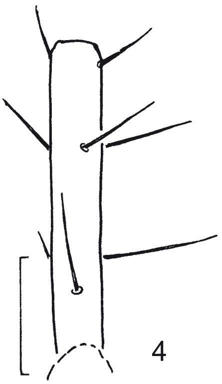
Relationships: See the genus.

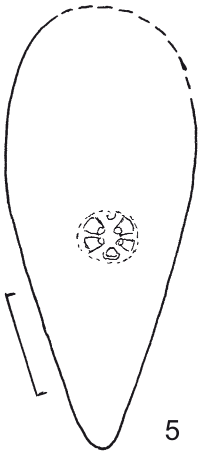
Distribution: Eocene Baltic amber forest.

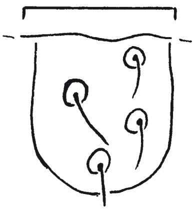


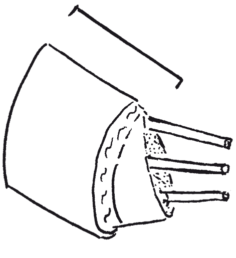


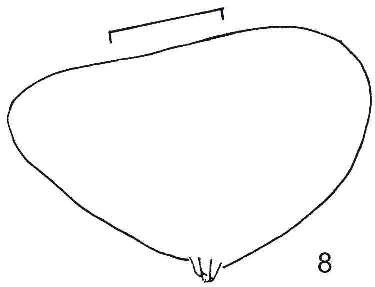












Figs. 1–7: ***Eochorizomma szeklinskiae* n. gen. n. sp**.; 1) dorsal aspect of the prosoma of the paratype, ?subad. ♀; 2) anterior aspect of the l. chelicera and anterior median eyes of the holotype, the juv. ♂ (most parts of the fangs are hidden); 3) ventral aspect of labium and l. gnathocoxa of the holotype (the most tiny hairs of the labium are not drawn); 4) dorsal aspect of the l. tibia I of the holotype; 5) ventral aspect of the opisthosoma of the paratype; 6) ventral aspect of the colulus of the holotype; 7) retroventral aspect of the r. posterior spinneret with three long spigots of the holotype (hairs are not drawn). – Scale bars = 1.0 mm in figs. 1) and 5), 0.5 in fig. 4), 0.2 in fig. 2), 0.1 in figs. 3) and 7) and 0.05 in fig. 6).

Fig. 8) ***Cyclosoma succini*** PETRUNKEVITCH 1958, juv. ♀ (holotype), outline of the opisthosoma, seen from the right side. – Scale bar = 0.5 mm.

FAMILY MIMETIDAE

MIMETINAE s. str. (= Mimetidae sensu PLATNICK (1998))

A dozen extant genera of this subfamily are known worldwide today, only two genera from Europe, *Ero* and *Mimetus*. Four mimetid genera were described by WUNDERLICH (2004: 1260–1269) from Eocene Baltic and Ukrainean (Rovno) ambers; two genera are extinct, *Ero* and *Mimetus* survived; so the portion of surviving genera is relatively high in this family.
According to DANILO HARMS (person. commun. in XII 2007) *Succinero rovnoensis* WUNDERLICH 2004 – preserved in Ukrainean amber from Rovno – is a member of the extant genus *Ero* C. L. KOCH 1837. *Ero* is one of the fairly rare (10%) Eocene genera which survived up to now. If *E. rovnoenesis* is really near to *E. cambridgei* KULCZYNSKI 1911 at least one species exists still in Europe which is well related to an Eocene species (similar to the genus *Ulesanis*, Theridiidae), see paper no. 3. The synonymy of *Succinero* WUNDERLICH 2004 (?= *Ero*) is still unclear.

FAMILY PIMOIDAE

The family Pimoidae – see WUNDERLICH (1986) – has recently been regarded as more diverse than ten or twenty years ago. The diagnosis of this family has been strongly changed by HORMIGA (2003, 2005, 2008): Besides the type *genus Pimoa* CHAMBERLIN & IVIE 1943 (three subgenera, extant and fossil in Eocene Baltic amber): the extant genera *Weintrauboa* HORMIGA 2003, *Nanoa* HORMIGA et al. 2005, and *Putaoa* HORMIGA & TU 2008 were assigned to the Pimoidae which were described from the Northern Hemisphere. I now exclude *Nanoa* from the Pimoidae; in my opininion it is a member of a different familiy, Pumiliopimoidae n. fam., see below.

Fossils: Pimoidae are known as fossils from the single genus *Pimoa*; specimens are rare in Baltic amber, and every species is represented by only a single specimen up to now. WUNDERLICH (2004: 1279f) described five fossil species of *Pimoa* in Baltic amber of the new subgenus *Eopimoa*. In the following I will add two species in the same kind of Eocene amber, and I give short remarks on an undetermined specimen which is preserved together with a part of a capture web.

Phylogeny and taxonomy

The diagnosis of the Pimoidae changed greatly within the last ten years because of the discovery of new taxa which have been included in this family. The problem is: What are the limits of this family? Which taxa have to include?

Concerning the diagnostic characters of the family: The existence of a "pimoid embolic process" (PEP, fig. 8) is apparently the most important diagnostic pimoid character, and probably the only one; it is well developed, long and filiform in *Pimoa,* reduced in *Weintrauboa* (figs. 6–7) and strongly bifurcate near the base in *Putaoa* (figs. 8–9) (**). – Selected further diagnostic characters and convergences: At least one of the articles of the anterior male leg may be modified (bent, partly thickened and/or hairy), e.g. in several members of *Pimoa* and *Weintrauboa* "pimoid cymbial sclerite" (*) (PCS, fig. 2) (which is widened distally) and cymbial cuspules (fig. 2) and frequently present. The free ("intersegmental") retrobasal paracymbium of *Putaoa* and *Weintrauboa* is fused to the cymbium in *Pimoa*. The tiny cymbial cuspules in *Weintrauboa* are placed in a different (basal) position of the cymbium – and arranged in rows – in cotrast to *Pimoa*, and may have been evolved convergently in both genera. I regard the – partly similar – modified bent anterior male metatarsi of *Weintrauboa* as having convergently evolved to the linyphiid genus *Stemonyphantes* MENGE 1866, which has quite different structures of the bulbus, and no cymbial cuspules in contrast to most Pimoidae. – *Putaoa* HORMIGA & TU 2008 may – due to reduced structures like the median apophysis (fig. 9) – be the geologically youngest genus of the Pimoidae. – The genus *Nanoa* is excluded from the Pimoidae by me, see below, the new family Pumiliopimoidae.

(*) See WUNDERLICH (2004: 1293, fig. 10) (fig. taken from HORMIGA (1994).

(**) In the subgenus *Louisfagea* of *Pimoa* evolved a PEP which is bifurcate in its distal half.

Relationships, convergences, and on the rank (status) of the taxon Pimoidae

Linyphiidae BLACKWALL 1859 is regarded as sister taxon to the Pimoidae WUNDERLICH 1986, see HORMIGA (1994), WUNDERLICH (1986); see also the paper on the "linyphioid branch" below.
Cymbial cuspules or denticles – which are modified stout spines – exist on different parts of the cymbium of the Pimoidae (frequently on a process); they may be strongly reduced or situated in rows of tiny denticles away from a process (in *Weintrauboa*) or even absent (in *Putaoa* and very few *Pimoa*). Cuspules/spines in a dorsal-basal position of the cymbium of the Pimoidae evolved convergently to the cuspules/denticles/ spines on certain outgrowths of the cymbium in quite different genera within the superfamily Araneoidea, e. g. in *Meta* C. L. KOCH 1836 (tiny ones in certain spe-

cies, fig. 17 above), *Metabus* O. PICKARD-CAMBRIDGE 1899, *Sancus* TULLGREN 1910 and the extinct genus *Anameta* WUNDERLICH 2004 (all are members of the Tetragnathidae, the relationships of *Anameta* are doubtful, see below, the "linyphioid branch"), in *Allomengea* and *Sintula* (both Linyphiidae), *Nanoa* (Pumiliopimoidae), *Spinilipus* (extinct) and *Tekella* (both Cyatholipidae). The genital structures of these genera are quite different from the Pimoidae. (**PARACYMBIAL** cuspules evolved convergently e.g. in *Gaucelmus* KEYSERLING 1884 (Nesticidae) and in the extinct genus *Acrometa* PETRUNKEVITCH 1942 (Synotaxidae)).

In the extant linyphiid genus *Allomengea* STRAND 1917 long and strong modified bristles exist on a cymbial outgrowth which are quite longer than the cuspules/denticles of the Pimoidae and are not pointed. In *A. scopigera* (GRUBE 1859) several metatarsal trichobothria – more than a single one on at least one of the metatarsi, the number is not constant on the articles – exist as in certain members of *Pimoa*. The presence of more than a single metatarsal trichobothrium is extraordinarily rare in members of the superfamily Araneoidea; these are the only cases which are known to me.

The retrobasal paracymbium in *Pimoa*, which is fused to the cymbium – corresponding to the plesiomorphic pattern of the paracymbium in the ecribellate basal branch of the Araneoidea s. l., e. g. in members of the Araneidae – may be a plesiomorphic character of the Pimoidae (*), contra HORMIGA (2003), who regarded it more likely as secondarily fused to the cymbium in *Pimoa*. The free ("intersegmantal") paracymbium may be an autapomorphy of the Linyphiidae which evolved convergently several times, e.g. in the ancestor of *Putaoa* + *Weintrauboa* within the Pimoidae, within the Tetragnathidae: Tetragnathinae, in the Nesticidae: *Nesticella* LEHTINEN & SAARISTO 1980, and in the Zygiellidae, see above. (If the speculation of HORMIGA (2003) is correct – the paracymbium of *Pimoa* being **SECONDARILY** fused to the cymbium –, it might be only a matter of opinion to regard *Pimoa* as a family of its own or only as a subfamily of the Linyphiidae).

(*) Like the fused paracymbium of the Pumiliopimoidae n. fam., and the Sinopimoidae, see below: On the "linyphioid branch" of the superfamily Araneoidea.

Simple **key** to the genera of the Pimoidae:

1 Paracymbium fused to the cymbium, cymbium usually with at least few strong cuspules (fig. 2) (*), embolus long (filiform), lateral cheliceral files exist in the extant taxa. Vulva: Introductory openings apically or distally. Widely spread in the Northern Hemisphere incl. SE-Asia, and extinct (Eocene Baltic amber forest: Subgenus *Eopimoa*, see below) . . . . *Pimoa*

- Paracymbium a free sclerite (fig. 2) (it is attached to the cymbium by a membrane which may be difficult to recognize), cymbial cuspules absent or tiny (some *Weintrauboa*) (figs. 6–7), embolus long or short (*Putaoa*), cheliceral files absent. SE-Asia, extant. 2

2(1) Pedipalpal tibia with strong bristles or even thick spines, embolus relatively short and stout (figs. 8–9). Vulva: Introductory openings laterally (**) . . . . <u>*Putaoa*</u>

- Such spines are absent, embolus long (fig. 6). Introductory openings distally . . . . <u>*Weintrauboa*</u>

(*) Cymbial cusps/denticles may exist on different parts of the cymbium in the Pimoidae; their number is strongly reduced in certain species of the subgenus *Pimoa*, and they may be apparently completely absent, e. g. in the fossil *Pimoa (Eopimoa) inopinata* WUNDERLICH 2004. The tiny cuspules in *Weitrauboa* (fig. 7) exist in a different position to *Pimoa* (they evolved probably convergently), and they are completely absent in *Putaoa*.

(**) The two known species – *huaping* and *megacantha* – are regarded as congeneric by HORMIGA & TU (2008)

<u>***Pimoa***</u> **CHAMBERLIN & IVIE 1943**

Herewith I resurrect (“revive”) the taxon *Louisfagea* BRIGNOLI 1971 (= *Metella* FAGE 1931) (**gen. resurr**.) from the synonymy with *Pimoa* to the rank of a subgenus of *Pimoa* (**n. stat**.); it has been synonymized with *Pimoa* by HORMIGA (1994) but it is different from *Pimoa* s. str., see <u>the **key** below</u> on the extant and fossil subgenera:

1 ♂♀: Lateral cheliceral stridulatory files present. Position of the metatarsal tricho-bothrium I in the distal third or numerous (7–11) trichobothria. ♂: Pimoid embolic process (PEP) not bifurcate. – Extant (not in Europe). . . . . <u>Subgenus *Pimoa*</u>

- ♂♀: Cheliceral files present. Position of the single metatarsal I trichobothrium in the medial third. ♂: PEP bifurcate, in the distal half, see HORMIGA (1994: Fig. 10). – Extant, Southern Europe . . . . <u>Subgenus *Louisfagea*</u>

- ♂♀: Cheliceral files absent. Position of the single trichobothrium on metatarsus I in the basal third. PEP not bifurcate. – Eocene Baltic amber forest. . . . . <u>Subgenus *Eopimoa*</u>

***Eopimoa* n. subgen**. of *Pimoa*

Diagnosis (♂; ♀ unknown): Cheliceral stridulatory files absent, position of the trichobothria on metatarsal I in the basal third (at least in *hormigai*). Further characters: Metatarsal trichobothria short and indistinct, metatarsus I bears a dozen bristles in the basal and distal half.

Type species: *Pimoa hormigai* WUNDERLICH 2004; Beitr. Araneol., 3: 1284, figs. 23–26. – Further species were dwellers of the Eocene Baltic amber forest, see WUNDERLICH (2004: 1283–1297), and the species which are described below.

Relationships: See the key above; the PEP is not bifurcated like in the subgenus *Pimoa*.

Distribution: Eocene Baltic amber forest.

***Pimoa (Eopimoa) obruens* n. sp**. (photo 159, figs. 1–3)

Material: Holotypus ♂ in Baltic amber, F1888/BB/AR/CJW.

Preservation and syninclusions: The spider is well and almost completely preserved, only the tips of the right tarsi I and IV are cut off, the ventral side of the prosoma is fairly covered with a white emulsion; numerous fissures exist left above the spider on a layer within the amber. – A Diptera: Nematocera and some stellate hairs are preserved in the same piece of amber, a dragline and a spider's thread in front of the left cymbium are also present.

Diagnosis (♂; ♀ unknown): Pedipalpus (figs. 1–3): Cymbial dorsal process very large, apically blunt and bearing numerous cuspules in a large depression.

Description (♂):
Measurements (in mm): Body length 2.7, prosomal length 1.3; leg I: Femur 2.6, patella 0.6, tibia 3.1, metatarsus 3.1, tarsus 1.2, tibia IV 2.0.
Colour light brown.
Prosoma with short hairs and large eyes, lateral cheliceral stridulatory files absent, fangs long. – Legs long and slender, covered with fairly short hairs. Bristles: Femora with a dorsal one in the basal half, I additionally with a prolateral one, patella 2 dorsally, tibia I–II 2 dorsally, 2 ventrally and 2 lateral pairs, metatarsus IV with 3 bristles near the middle. Position of the metatarsal III trichobothrium in 0.3; position on metatarsus II probably in 0.23. – Opisthosoma oval, covered with short hairs; spinnerets stout. – Pedipalpus (figs. 1–3) with short patella and tibia, tibia raised dorsally-distally, para-

cymbium sickle-shaped and fused to the cymbium, PCS wide distally, CDP very large, bearing numerous cuspules in a large depression, embolus hidden.

Relationships: In the related *P. (Eopimoa) multicuspuli* WUNDERLICH 2004 is the cymbial dorsal process retrolaterally more protruding, and its body length is distinctly larger, ca. 5.5 mm.

Distribution: Eocene Baltic amber forest.

***Pimoa (Eopimoa) longiscapus* n. sp.** (photo 160, fig. 2)

Material: Holotypus ♀ in Baltic amber, F1039/BB/AR/CJW.

Remark: I put the piece of amber for clearing for few seconds in benzoeacid (benzylium benzoicum).

Preservation and syninclusions: The spider is incompletely preserved, the mouth parts are covered with a white emulsion, several leg articles are cut off, only the right leg III and the left leg IV are complete. – 2 2/2 Diptera (one with a line of excrement) and few stellate hairs are preserved in the same piece of amber.

Diagnosis (♀): Length of the dorsal-apical bristle of the pedipalpal tibia 0.35 mm, patellar bristle only slightly longer (0.38 mm); scapus (fig. 4) long, more slender apically.

Description (♀):
Measurements (in mm): Body length 3.0, prosomal length 1.25, femur I more than 2 mm (the tip is cut off), leg IV: Femur 2.0, patella 0.35, tibia 1.85, metatarsus 1.85, tarsus 1.0; length of the scapus 0.75.
Colour yellow brown.
Prosoma (most parts are hidden) with a large fovea and large eyes, large chelicerae and fangs. Pedipalpi long, tarsal claw toothed, dorsal patellar bristle slightly longer than the tibial bristle (0.38 : 0.35 mm). – Legs incompletely preserved, long, with long bristles, femur I bears at least a dorsal and a prolateral one in the basal half, femur II bears 2 dorsal bristles, femur IV a single bristle in the basal half. Patellae with 2 dorsal bristles, tibia IV with 2 dorsal, 2 ventral and 2 lateral pairs, metatarsus IV bears 3 bristles in the basal third and a dorsal one near the middle. Position of the metatarsal trichobothria unknown. – Opisthosoma oval, covered with short hairs, spinnerets stout, epigynal scapus (fig. 4) long, fairly pointed and bent.

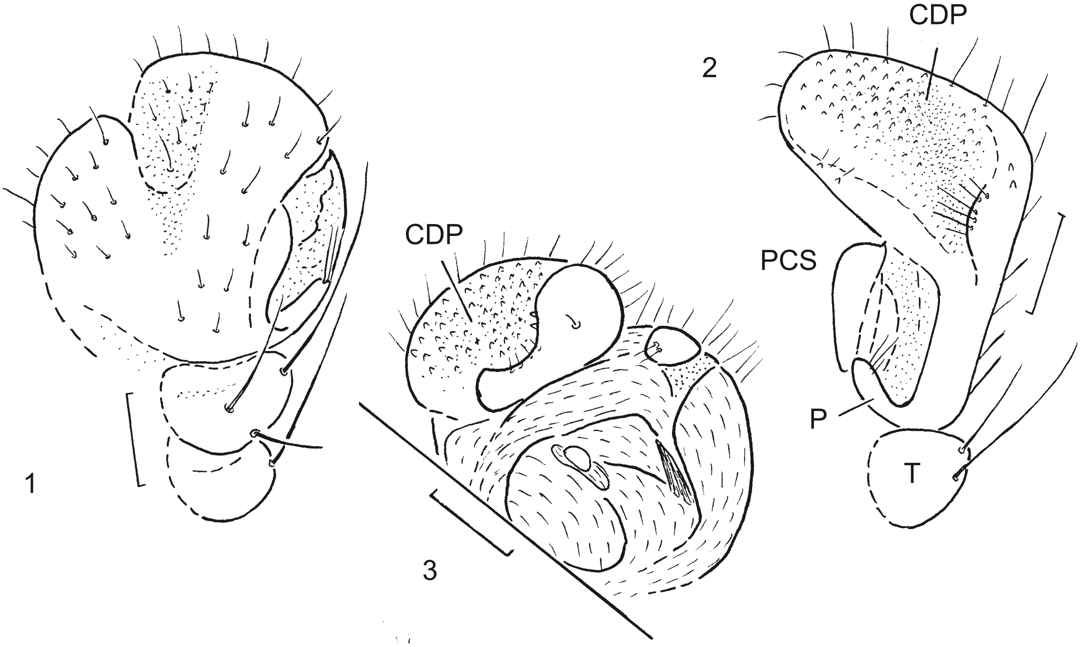
Relationships: In *P. (Eopimoa) lingula* WUNDERLICH 2004 (fig. 5) the scapus is longer (1.05 mm), apically blunter, the lateral folds are more distinct, and the apical-dorsal bristle of the pedipalpal tibia is much shorter than the patellar bristle (0.4 : 0.55).

Distribution: Eocene Baltic amber forest.

***Pimoa* (*Eopimoa*) sp. indet.**

Material: 1♂ in Baltic amber, F1018/BB/AR/CJW.

The length of the spider's prosoma is 2.8 mm, the length of tibia I is 7.5 mm, almost as long as in *P. multicuspuli* WUNDERLICH 2004.
The spider is well preserved, mainly the right side is covered with a white emulsion, the retrolateral part of the bulbus, the right coxae I and II and some other leg articles as well the tip of the opisthosoma are cut off, the structures of the bulbi are hidden or cut off. A part of a capture web is preserved in contact to the right side of the spider's body and legs; the web part is one-dimensional, irregular and branched; sticky droplets are absent.



Figs. 1–3: ***Pimoa (Eopimoa) obruens* n. sp.**, ♂; 1) dorsal aspect of the r. pedipalpus; 2) retrodistal aspect of the l. pedipalpus (ventral parts are hidden); 3) retrodorsal aspect of the r. pedipalpus (prolateral parts are hidden). CDP = cymbial dorsal process with cuspules, P = paracymbium, PCS = pimoid cymbial process, T = tibia. Scale bar = 0.2;

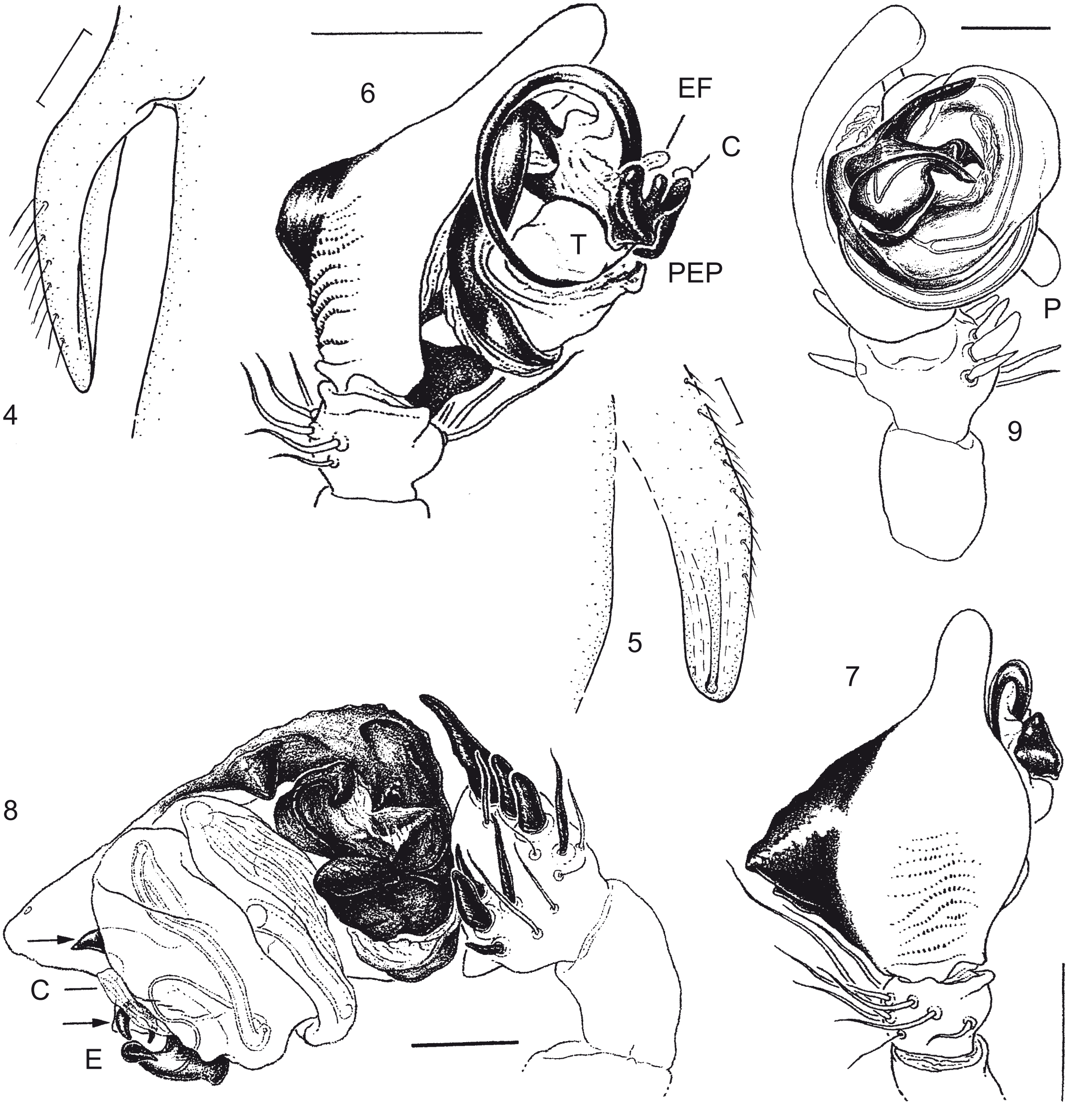


fig. 4) ***Pimoa (Eopimoa) longiscapus* n. sp**., ♀, left aspect of the scapus. Scale bar = 0.2;

fig. 5) <u>*Pimoa (Eopimoa) lingula*</u> WUNDERLICH 2004, ♀ (holotype), right aspect of the scapus (the basal-ventral part is hidden). Scale bar = 0.2;

figs. 6–7: <u>*Weintrauboa contortipes*</u> (KARSCH 1881), ♂, prolateral and dorsal aspects of the l. pedipalpus. Scale bar = 0.5. Taken from HORMIGA et al. (2003: Figs. 1D–E);

figs. 8–9: <u>*Putaoa huaping*</u> HORMIGA & TU 2008, ♂, retrolateraal and ventral aspect of the l. pedipalpus. Scale bars 0.2. The arrows in fig. 8 point to apical ends of the pimoid embolic process. Taken from HORMIGA & TU (2008).

FOSSIL AND EXTANT SPIDERS OF THE “LINYPHIOID BRANCH” OF THE SUPERFAMILY ARANEOIDEA (ARANEAE), WITH THE DESCRIPTION OF THE NEW FAMILY PUMILIOPIMOIDAE

Within the “linyphioid branch” of the superfamily Araneoidea – the Orb Weavers and their relatives – the number of families has been growing during the last years: Besides the nominate family Linyphiidae BLACKWALL 1959 the following families have been described: Pimoidae WUNDERLICH 1986 (at first as a subfamily of the Linyphiidae, see above, extant and fossil), Baltsuccinidae WUNDERLICH 2004 (extinct), and recently Sinopimoidae LI & WUNDERLICH 2008 (extant). In this paper I add a further family, the Pumiliopimoidae, which is known from Eocene Baltic amber and most probably extant as a relict taxon in North America (the genus *Nanoa*). These families – and probably few more, see below (Linyphiidae: Stemonyphantinae, the remarks (1) and (2)), – are known from the Northern Hemisphere only, with the exception of the most diverse Linyphiidae which is also known from the Southern Hemisphere. With the exception of the Linyphiidae all these families are known from one genus or two genera only, but our knowledge of tropical and fossil spiders is still limited, and there may exist further – still unknown – genera and even families of this branch.

(1) Taxa and characters of the “linyphioid branch” of the superfamily Araneoidea

From this branch we know the following – probably five – families:

(a) Baltsuccinidae WUNDERLICH 2004, only the genus *Baltsuccinus* WUNDERLICH 2004 in Eocene Baltic amber. The relationships of this family are unsure, the female and the kind of its leg autotomy are still unknown, cheliceral stridulatory files are absent;

(b) Linyphiidae BLACKWALL 1859, the most diverse family of this branch (members of the subfamily Erigoninae represent more than half of the species of the “linyphioid branch”), including the Stemonyphantinae WUNDERLICH 1986 of the Northern Hemisphere, which relationships and rank – a family of its own? – are unsure. Linyphiidae is the only family of this branch which members occur in the Northern, and in the Southern Hemisphere as well. The subfamilies Linyphiinae and Micronetinae are known from the Eocene, see WUNDERLICH (2004). Micronetinae include the Ipainae SARISTO 2008 in my opinion (*). – Remarkably Erigoninae are unknown from the Eocene; it apparently is a “young” subfamily in the geological sense;

(c) Pimoidae WUNDERLICH 1986 with a wide range in the Northern Hemisphere, holarctic, in Eurasia mainly in subtropical regions; the genera *Pimoa* CHAMBERLIN & IVIE 1943 (extant and fossil in Eocene Baltic amber, see above), *Putaoa* HORMIGA & TU 2008, and *Weintrauboa* HORMIGA 2003 (extant, SE-Asia). (*Nanoa*: See the Pumiliopimoidae at next);

(d) Pumiliopimoidae n. fam., which is known from Eocene fossils in Baltic amber (Pumiliopimoini n. trib., a single species of *Pumiliopimoa* n. gen.), and extant from North America (Nanoini n. trib., a single species of *Nanoa* HORMIGA et al. 2005, sub Pimoidae); close relationships of the family are questionable, see below.

(e) Sinopimoidae LI & WUNDERLICH 2008, only a single species of the genus *Sinopimoa* LI & WUNDERLICH 2008, extant, tropical SE-Asia. – Remark: HORMIGA (2008: 4) – without studying material – doubted the rank of this family and suggested that it may be a member of the Linyphiidae, and possibly of the Erigoninae, although he stated himself that “Unlike erigonines, *Sinopimoa* has a prolateral femoral macroseta.”. Also due to the structures of the male pedipalpus – mainly to the fused and not sickle-shaped paracymbium which stands out from the cymbium – *Sinopimoa* is doubtless not a member of the family Linyphiidae. Furthermore in most Erigoninae the tibia of the male pedipalpus bears apophyses which are absent in *Sinopimoa*, and an epigynal scape like in *Sinopimoa* is absent in most taxa of the Erigoninae.

(*) SAARISTO (2007: 38) characterized this taxon – “summarizing” the subfamiliar characters of his Ipainae – (a) by two “likely apomorphies of the entire family” (the Linyphiidae) (these are apomorphies of the Linyphiidae but plesiomorphic characters of the Ipainae!), (b) by a peculiar shape of the paracymbium: with a question mark (!), (c) by a “filiform embolus” – this is also known from other taxa of the Micronetinae like *Centrophantes* MILLER & POLENEC 1975, and (d) by “a movable epigyne (not in all genera)” (!). In my opinion the combination of these characters may probably justify the creation of a tribus of its own – Ipaini **n. stat**. – but not of a new subfamily.

Remarks: (1) The relationships of the extinct Eocene genus *Praetheridion* WUNDERLICH 2004 (Protheridiidae: Praetheridiini WUNDERLICH 2004) are unsure; females, the kind of the leg autotomy and the existence of stridulatory files are still unknown. – (2) The relationships of the extinct Eocene genus *Anameta* WUNDERLICH 2004 – with hesitation regarded as a member of the family Tetragnathidae by the present author, see above: Anametini – are unclear, too; females, the leg autotomy, and the kind of the capture web are unknown; its cymbial cuspules are similar to cuspules of the Pimoidae.

Diagnosis of the “linyphioid branch”: The only branch of the superfamily Araneoidea – and spiders in general – in which the COMBINATION exists of (a) a “triad complex” of the spinnerets (an autapomorphic character of the ecribellate branch of the superfamily Araneoidea), (b) usually (or always?) a patella-tibia leg autotomy (the kind of the leg autotomy is unknown in the Baltsucinidae and unsure in the Pumiliopimoidae), and (c) the tendency to – or even the basical existence of – retrolateral stridulatory cheliceral files. (Such files are far more frequent in extant taxa than in extinct Eocene taxa, see the remark (1) below, and the genus *Pimoa* above. – A peculiar structure of the tail of the spermatozoa may exist furthermore.

Further characters: Ecribellate, three-clawed spiders which possess a well developed colulus. Basically existence of numerous leg bristles on femora, patellae, tibiae (laterally, too) and metatarsi (e. g. in the Pimoidae and basal Linyphiidae; lost e. g. in dwarf species of the Erigoninae, strongly reduced in the Pumiliopimoidae and Sinopimoidae). Clypeus long in almost all taxa, at least as long as the length of the field of the median eyes. Opisthosomal scuta exist in small/tiny spiders of the Pumiliopimoidae (at least on the epigaster) and in certain members of the Linyphiidae: Erigoninae. Retroapical tibial apophyses of the ♂-pedipalpus – similar to (e. g.) members of the RTA-clade and numerous taxa of the Tetragnathidae – exist in most taxa of the very diverse Erigoninae (extant). Retrobasal paracymbium usually well developed (see remark 2 below), epigynal scapus most often existing and well developed (except in most dwarf spiders like Linyphiidae: Erigoninae and several Micronetinae).

Remarks: (1) In my opinion the lateral stridulatory files of the chelicerae are BASICLY ABSENT in the "linyphioid branch" (not an apomorphic family character); they EVOLVED AND THEY WERE LOST AGAIN in several taxa of the Linyphiidae. These files are absent in the extinct Eocene Baltsuccinidae, in all Pimoidae except the extant members of *Pimoa*, in the Pumiliopimoidae (Eocene and extant taxa), as well as in basal Linyphiidae like certain members of the Linyphiinae, and in females of the subfamily Stemonyphantinae. So such files may have originated only late in the geological sense, and evolved convergently three times: (a) in the Linyphiidae, (b) in certain ("young") Pimoidae (in extant members of *Pimoa*), and (c) in the Sinopimoidae. – (2) The paracymbium is basically fused to the cymbium; a free (movable) paracymbium exists in almost all members of the Linyphiidae, evolved convergently in the ancestor of *Putaoa* + *Weintrauboa* of the Pimoidae, and evolved – as a third convergence – in the Baltsuccinidae (its relationships are unsure, the structure of its paracymbium is quite peculiar). – (3) Determination: Especially certain taxa of the family Synotaxidae may be mistaken as members of the "linyphioid branch", e. g. as Pumiliopimoidae; but in the Synotaxidae dorsal femoral and lateral tibial bristles of leg I are absent, and the leg autotomy exists between coxa and trochanter.

The **relationships** of the "linyphioid branch" are not quite sure. The structures of cymbium and paracymbium may indicate that the Tetragnathidae are most related; the paracymbium is a free (movable) sclerite in certain groups of both taxa similar to the family Zygiellidae which is strongly related to the Araneidae or an araneid subfamily only. The extinct Eocene genus *Anameta* (?Tetragnathidae: Anametini, see above) possesses a mixture of more tetragnathid characters (e. g. the structures of the bulbus) and more linyphioid characters (e. g. the long clypeus, which exists in basal Tetragnathidae as well). – According to the long clypeus and the irregular (not orb-shaped) capture web the "bristle-less femur clade" of the Araneoidea may be the sister group to the "linyphioid branch" than the Tetragnathidae. In the "bristle-less femur clade" femoral, metatarsal and lateral tibial bristles are lost. – Remarkably both branches – which were frequent already in the Eocene – are unknown from the (at least the Lower and Middle) Cretaceous, in contrast to the orb-weaving Araneoidea families Araneidae and Zygiellidae.

The number and the relationships of the families WITHIN the "linyphioid branch" are also unclear (see above); we are far away from knowing a sufficient cladogram of the families; especially the relationships of the Baltsuccinidae, the Pumiliopimoidae, and the Sinopimoidae are doubtful.

Distribution: Cosmopolitical.

Key to the extinct and extant families of the "linyphioid branch":

Remarks: Linyphiidae is the only linyphioid family which is known from both Hemispheres, the remaining families are known from the Northern Hemisphere only. The tropical Sinopimoidae is the only family which is not known from fossils, Baltsuccinidae is completely extinct. – See also the remarks above, especially on the extinct family Protheridiidae (*Praetheridion*), and on the extinct genus *Anameta* (Anametini, questionableTetragnathidae) which are not included in this key.

1 Numerous leg bristles, body length (♂) 3.5–4.2 mm, retrolateral cheliceral files absent,CYMBIUMNARROW,PARACYMBIUMWITHTWOQUITEDIFFERENTBRANCHES, the distal branch close/parallel to cymbium and bulbus, structures of the bulbus very complicated, embolus very long, see WUNDERLICH (2004: 1147, figs. 3f). – ♀ unknown. – Extinct, Eocene Baltic amber forest, only the genus *Baltsuccinus* . . . . Baltsuccinidae

- Combination of characters – especially the paracymbium – different; few or numerous leg bristles, body length quite variable, cheliceral files present or absent, paracymbium frequently standing out from the cymbium, distally close to the bulbus only in the Linyphiidae; fossil and extant. 2

2(1) Body length 3–12 mm, numerous leg bristles (on femora and metatarsi, too), retrolateral cheliceral stridulatory files usually absent but existing in extant members of *Pimoa*, epigynal scapus present, ♂-pedipalpus with a simple paracymbium which is fused to the cymbium in *Pimoa* but a free sclerite in *Putaoa* and *Weitrauboa*, CYMBIUM WITH CUSPULES/DENTICLES in almost all species (absent in *Putaoa*), and a particular outgrowth (absent in *Putaoa*), embolus always with a "PIMOID EMBOLIC PROCESS" (see the family Pimoidae above), ♂-leg I modified (thickened, bent or hairy) in several extant species. – Fossil in Eocene Baltic amber (*Pimoa*) and extant in the Northern Hemisphere: *Pimoa*, *Weintrauboa* and *Putaoa*. . . . . Pimoidae

- Body length and leg bristles variable (*), retrolateral cheliceral files present (Sinopimoidae, most Linyphiidae) or absent (Pumiliopimoidae, few Linyphiidae), epigynal scapus present or absent, paracymbium simple or complicated, cymbium not modified or modified in a different way, CUSPULES in almost all species ABSENT (present in few Linyphiidae), embolic process absent or different, ♂-leg I rarely modified (e. g. in members of the Stemonyphantinae (Linyphiidae)). – Fossil and extant 3

3(2) Retrolateral cheliceral files absent, body length about 1.4–2 mm, the opisthosoma bears scuta (in *Nanoa* and *Pumiliopimoa* on the epigaster, in *Pumiliopimoa* anteriorly-dorsally, too, see the photos 156–157), PARACYMBIUM FUSED to the cymbium, two- or three-partite (figs. 4, 9–11), embolus very long and basally hidden by the cymbium (figs. 3–4, 11–13), the epigyne (*Nanoa*, fig. 5) bears a scapus. – Fossil in Eocene Baltic amber (*Pumiliopimoa*, in which the body shape is similar to certain Cyatholipidae) and extant in N-America (*Nanoa*) . . . . Pumiliopimoidae

- Retrolateral cheliceral files present, body length 1.2–1.3 mm, opisthosoma soft, pedipalpal tibia with a powerful erect retrobasal outgrowth (fig. 1a) (**), PARACYMBIUM FUSED to the cymbium, undivided, long and pointed, weakly sclerotized (fig. 1b), prosoma with a characteristic colour: Yellow with a pair of wide brown longitudinal bands in the type species. Bulbus without strongly sclerotized sclerites, basally with a large tegular outgrowth (fig. 1b), epigyne distinctly protruding. – Extant, tropical SE-Asia. Only *Sinopimoa* . . . . .Sinopimoidae

- Retrolateral cheliceral files – see WUNDERLICH (2004: 1355, fig. 2) – existing in almost all taxa, body length quite variable (*), opisthosoma most often soft but scutate in numerous members of the Erigoninae, PARACYMBIUM stronger sclerotized and (almost) hairless, in almost all species A FREE (MOVABLE) SCLERITE and u- or sickle-shaped, the distal part close/parallel to cymbium and bulbus, see WUNDERLICH (2004: 1358, fig. 20); existence of a suprategulum. – Fossils: The subfamilies Linyphiinae as well as (rare) Micronetinae (but not Stemonyphantinae and Erigoninae) in Eocene ambers; extant very diverse in both Hemispheres . . . . Linyphiidae

---

(*) The body length is more than 3 mm only in various Linyphiidae. Some Linyphiidae: Erigoninae are less than 1 mm long and their legs may be bristle-less (Eocene Erigoninae are unknown).

(**) A large erect tibial outgrowth of the ♂-pedipalpus exists also in *Megalepthyphantes* of the Linyphiidae.

(2) Description of a new family of the superfamily Araneoidea:

PUMILIOPIMOIDAE n. fam. (Photos 156–158,, figs. 2–13)

Derivatio nominis: See *Pumiliopimoa* n. gen.

Diagnosis: Few thin leg bristles (few dorsal tibial ones, prolateral bristles on tibia I and bristles on femur I exist in *Pumiliopimoa* (Pumiliopimoini) (figs. 7–8) but are absent in *Nanoa* (Nanoini), metatarsal bristles absent) (*), lateral cheliceral stridulatory files absent, epigaster sclerotized, epigyne (*Nanoa*, fig. 5) with a long scapus, ♂-pedipalpus (figs. 3–4, 9–13): Tibia plate-shaped elongated with an edge dorsally-apically, paracymbium fused to the cymbium and two- or three-partite, bulbus simple, with one or two short tegular apophyses – which were called “median apophysis” and “conductor” in *Nanoa* by HORMIGA et al. (2005) –, and a very long embolus which describes at least one circle, and is hidden by the cymbium in its basal part in which it bears a skinny seam.

Further characters: Body length about 1.4–2.0 mm, fovea present or absent (*Nanoa*), labium free in both genera (fig. 2), legs rather stout, sequence of the dorsal tibial bristles 2/2/1/1 in *Pumiliopimoa* (*). Claw of the ♀-pedipalpus present in *Nanoa* (unknown in *Pumiliopimoa*), lung covers/epigaster sclerotized, a dorsal-anterior opisthosomal scutum (photo) exists in *Pumiliopimoa* but is absent in *Nanoa*. The LEG AUTOTOMY is unknown in *Pumiliopimoa*; in *Nanoa* it is published as being between patella and tibia, but in a photo taken by D. BUCKLE (via e-mail) a posterior leg is absent beyond the coxa (!) in a male of *Nanoa enana*.

Relationships: According to the existence of femoral bristles, the kind of autotomy – PROBABLY between patella and tibia in *Nanoa* (but see above!); in *Pumiliopimoa* the leg autotomy is unknown (!) –, the long clypeus, and the structures of the copulatory organs – e. g. the existence of a retrobasal paracymbium and a scape of the epigyne in *Nanoa* – the family Pumiliopimoidae is a member of the superfamily Araneoidea, and apparently of the “linyphioid branch” (see its diagnosis above). In certain Linyphiidae the shape of the paracymbium is somewhat similar but it is a free sclerite (*) (similar to the pimoid genera *Putaoa* and *Weintrauboa* HORMIGA 2003), cheliceral stridulatory

---

(*) Pumiliopimoidae possesses – most probably as a result of dwarfism – the lowest number of leg bristles within the “linyphioid branch” besides numerous members of the Linyphiidae: Erigoninae, very few members of the Linyphiinae, and the Sinopimoidae. Very few dorsal tibial bristles exist in *Nanoa*; according to G. HORMIGA exists only a single bristle in the female dorsally on tibia IV (I suppose that dorsal bristles on the other tibiae may have been rubbed off). A single dorsal FEMORAL and a lateral tibial bristle existed still in the Eocene genus *Pumiliopimoa* but they are absent in the extant genus *Nanoa*.

files (most often) and a suprategulum exist. In the tiny Sinopimoidae LI & WUNDERLICH 2008 stridulatory files exist, and the structures of the copulatory organs are completely different, the fused paracymbium is undivided, the pedipalpal tibia bears a large outgrowth (fig. 1). The Pimoidae are larger spiders – body length 3 1/2–12 mm –, the ♂-leg I is frequently modified, the fused paracymbium is unmodified and undivided, cymbial cuspules, a "cymbial process", and a "pimoid cymbial sclerite" exist frequently, a "pimoid embolic process" is always present, see (e.g.) HORMIGA (2003) and above. Pumiliopimoidae are apparently more related to the Pimoidae than to the Linyphiidae in which more complicated structures of the bulbus with an embolic division exist. According to HORMIGA & TU (2008) *Nanoa* is the sister group to *Pimoa* but in my opinion the conformation of the structures of the bulbus and the absence of an embolic process in *Nanoa* exclude close relationships of both taxa; see the following remarks.

Remarks: (1) The simple structures of the bulbus of the Pumiliopimodae represent the most primitive – and in my opinion plesiomorphic – condition within the “linyphioid branch” (besides the reduced structures in certain dwarf members of the family Linyphiidae). The sickle-shaped pracymbium reminds on the paracymbium of most Linyphiidae but is fused to the cymbium in contrast to the Linyphiidae. – (2) It is not quite clear to me if the absence of cheliceral files in the Pumiliopimoidae is a basic character of the “linyphioid branch” or a loss. – (3) With respect to the terms of the sclerites of the ♂-pedipalpus of *Nanoa* sensu HORMIGA et al. (2005): In my opinion it is not correct to homologize the parts of the paracymbium of the Pumiliopimoidae with the “cymbial denticulate process” and the “pimoid cymbial sclerite” of the Pimoidae. I regard the “pimoid cymbial sclerite” of *Nanoa* as part of the (two-partite) paracymbium and the “cymbial process” as nothing else than an outgrowth of the cymbium which bears a strong bristle (not cuspules!). Such an outgrowth evolved numerous times convergently within the “linyphioid branch”, see above (Pimoidae). – (4) The structures of cymbium, paracymbium and bulbus in the Pumiliopimodae are similar to these structures in certain members of the Cyatholipidae and Synotaxidae in which a leg autotomy between coxa and trochanter exists, femoral as well es lateral tibial bristles are absent, and additional derived familiar characters exist.

(*) In the Stemonyphantinae the paracymbium is – probably secondarily – partly fused to the cymbium.

Type tribus: Pumiliopimoini n. trib. (extinct, monotypic). Further tribus: Nanoini n. trib. (extant, monotypic); transfered here from the Pimoidae (**n. relat**.).

Natural history: Specimens of *Nanoa enana* were primarily collected using pit falls in mixed conifer forests in mountain areas, about 1000–1500m above NN, “in late-successional old growth forest litter”. The Baltic amber forest was a mixed forest; the producer of the Baltic amber were conifers. The rarity of the fossil spiders of *Pumiliopimoa parma* (three specimens within more than 100 000 specimens in Baltic amber) indicate that spiders of this genus also were ground-dwelling animals, and – like their extant relatives – not dwellers of higher strata of the vegetation. They may have reached higher strata as aeronauts (or) by accident. I do not want to exclude that the members of *Pumiliopimoa* were “mountain spiders” similar to the Pimoidae; this feature would also explain their rarity in the Baltic amber. The existence of a capture web of these spiders is unknown in the extant spiders but remains of a questionable capture web are preserved with the holotype of the fossil *Pumiliopimoa parma*.

Distribution: Eocene Baltic amber forest (*Pumiliopimoa*) and extant North America, USA, (California and Oregon) (*Nanoa*). – If my conclusions regarding the relationships of *Nanoa* are correct, Pumiliopimoidae is a relict family which had a much wider range in the Eocene than today, and survived only in the wilderness of forests in North America. – A similar disjunct distribution in spiders is known from the family Plectreuridae: An extant genus occurs in Central and North America, a related extinct genus is known from the Eocene Baltic amber forest, see above and WUNDERLICH (2004: 670ff). See also the genera of the Comarominae (Anapidae s. l.), WUNDERLICH (2004: 1034ff).

(a) PUMILIOPIMOINI n. trib.

Diagnosis (♂; ♀ unknown): Opisthosoma with an anterior-dorsal scutum (photo), ♂-pedipalpus (figs. 9–13): Paracymbium complicated, three-partite, with a bristle between its branches (fig. 9) (distal branch of the paracymbium blunt, the basal branch pointed). – Further characters like the chaetotaxy: See the family diagnosis. The spiders are 1.6–1.9 mm long.

Type genus (by monotypy): *Pumiliopimoa* n. gen.

Relationships: According to the reduced leg bristles, the existence of a – dorsal or ventral (epigastral) – opisthosomal scutum, and the structures of the ♂-pedipalpus – a divided paracymbium, the existence of at least one small tegular apophysis and a very long embolus which is basally hidden by the cymbium and bears a scinny seam – the monotypic genus *Nanoa* HORMIGA et al. 2005 (Nanoaini n. trib.) (extant, N-America) seems to me most probably related – confamiliar – to *Pumiliopimoa*. Members of both genera are tiny spiders which possess rather stout legs. In *Nanoa* (figs. 2–5) the anterior part of the prosoma is more abruptly narrow, a fovea is absent, femoral and lateral tibial bristles are absent (!), a dorsal opisthosomal scutum is absent (the epigaster is sclerotized), a stridulatory organ exists between spines of the coxae IV and the lung covers (fig. 2), and the cymbium possesses a retrodistal outgrowth which bears a powerful bristle, the paracymbium is simpler, only two-partite, its basal brach is blunt and its distal branch is pointed, and it bears no bristle between its branches; the tip of the embolus is widened in *Nanoa* (its tip is unknown in *Pumiliopimoa*).

Distribution: Eocene Baltic amber forest.

***Pumiliopimoa* n. gen**. (figs. 6–13)

Derivatio nominis: Pumilio (lat.) means tiny, *Pimoa* is the nominate genus of the Pimoidae which may be related to the Pumiliopimoidae.

The gender of the name is feminine.

Type species (by monotypy): *Pumiliopimoa parma* n. sp.

Diagnosis, relationships and **distribution**: See above.

***Pumiliopimoa parma* n. gen. n. sp**. (photos 156–158, figs. 6–13)

Material: 3♂ in Eocene Baltic amber, holotype and two separated pieces of amber, F1091/BB/AR/CJW, paratypes: F1090/BB/AR/CJW and F2025/BB/AR/CJW with a separated piece of amber.

Preservation and syninclusions: The holotype is completely preserved, covered with a white emulsion which is thicker ventrally. The piece of amber was heated, a larger disc-shaped structure (caused by heating) is in contact to the left side of the spider (another one is situated in front below the spider), remains of a tiny arthropod exists in the larger pice which was separated by me; excrements of insects as well as stellate hairs are preserved, and two divided threads of spider's silk (droplets are absent) – a part of a capture web? – are running through the piece of amber, and are in contact with articles of the right legs III and IV of the spider. – The paratype F1090 is well and completely preserved, lying on a layer within the amber which partly hide the ventral side of the spider, a white emulsion is absent, stellate hairs are absent, too. – The paratype 2025 is completely and fairly well preserved, the left-ventral part of the prosoma, most left leg articles, the left pedipalpus and few dorsal parts of the right pedipalpus are cut off. A white emulsion covers parts of the opisthosoma and legs, the prosoma is partly darkened by heating, a large gas bubble covers the sternum, stellate hairs exist, remains of a Trichoptera are preserved in the piece of amber which has been separated by me.

Diagnosis (♂; ♀ unknown): See above.

Remark: In the paratype F2025 an opisthosomal scutum is not recognizable and the basal branch shape of the paracymbium is fairly different from the remaining specimens; I regard these differences as most likely caused by heating of the piece of amber in which this spider is embedded by a dealer of inclusions.

Description (♂):
Measurements (in mm): Body length 1.6–1.9 (holotype), prosoma: Length 0.77–0.9, width 0.68–0.74; leg I (paratype F1090): Femur 0.72 (hight 0.17), patella 0.22, tibia 0.6, metatarsus 0.5, tarsus 0.35, tibia II 0.55, tibia III 0.43, tibia IV 0.6.
Colour: prosoma, legs and opisthosomal scutum dark brown, opisthosoma light grey-brown.
Prosoma (photo, fig. 6) oval, anteriorly not abruptly narrow, profile rather convex, almost smooth, fovea well developed, eyes small, posterior row straight, field of the anterior median eyes not protruding, posterior median eyes separated by slightly more than their diameter, clypeus longer than the field of the median eyes, basal cheliceral articles of medium length, retrolateral files absent, fangs slender, the anterior marging of the cheliceral furrow bears few teeth, labium free, wider than long, gnathocoxae thick, serrula present, sternum almost as wide as long, smooth, gnathocoxae IV separated by 3/4 of their diameter. – Legs (photos, figs. 7–8) rather stout, order probably I/IV/II/III, III distinctly shortest, hairs indistinct, bearing only few and thin bristles, sequence of the dorsal tibial bristles 2/2/1/1, tibia I additionally with a prolateral bristle in the distal half, femora: Only I bears a dorsal and a prolateral one in the distal half, the patellae bear 2 thin dorsal bristles, the metatarsi none. Metatarsi I–III bear a long trichobothrium, its position on II (paratype F2025) in 0.37. Three tarsal claws which are well developed. – Opisthosoma (photo) oval, covered with short hairs, epigaster and lung covers sclerotized, dorsally anteriorly with a short and wide scutum (it is not recognizable in the paratype F2025), tracheal spiracle apparently small, in a position near the spinnerets which are short (most spinnerets are hidden by a white emulsion). – ♂-pedipalpus (figs. 9–13): Articles slender, patella short, bearing a thin dorsal bristle in the distal half, tibia longer than wide, plate-shaped apically and lying on the cymbium, bearing a long and thin bristle in the distal half and at least one trichobothrium, paracymbium – its shape varies strongly in slightly different positions! – large and complicated, at least three-partite, with a strong bristle between the branches; tegulum bearing a large blunt outgrowth, additionally with a small ("median") apophysis, and probably a conductor. Embolus very long, describing more than two circles, basally hidden by the cymbium and here with a scinny seam (so far observable).

Relationships: See above.

Distribution: Eocene Baltic amber forest.

(b) NANOINI n. trib. (figs. 2–5)

Diagnosis: Existence of a stridulatory organ consisting of spines of the coxae IV and files of the covers of the lungs (fig. 2), ♂-pedipalpus (figs. 3–4): Cymbium retrodistally with an outgrowth (called "cymbial process" by HORMIGA et al. (2005)) which bears a powerful bristle, distal branch of the paracymbium (called "pimoid cymbial sclerite" by these authors) pointed, the basal branch blunt. Two sclerites of the tegulum were called "potential homologues of the araneid conductor and median apophysis" by HORMIGA et al. (2005: 252) but see below (relationships). ♀: Epigyne (fig. 5) with a long and slender scapus.

Further characters: Tiny spiders, body length 1.42–1.65 mm, few leg bristles only, see the family above; embolus very long; see also the diagnosis of the family. The kind of the leg autotomy may be between patella and tibia, but in a photo taken by D. BUCKLE a male shows the loss of a posterior leg beyond the coxa (!).

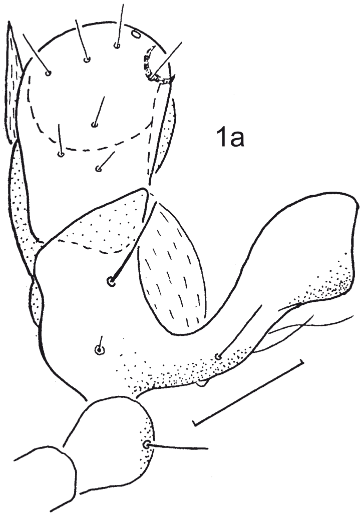
Type genus (by monotypy): *Nanoa* HORMIGA et al. 2005. (A single species: *Nanoa enana* HORMIGA et al. 2005).

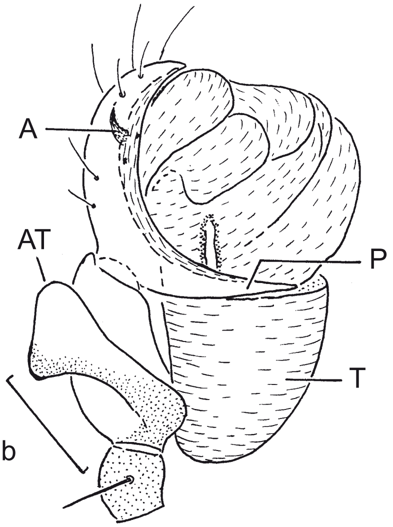
Relationships: Pumiliopimoini seems most related, see above. – In the Nanoini a (divided) retrobasal paracymbium exists which is fused to the cymbium. This kind of a paracymbium is an autapomorphy of the ecribellate branch of the Araneoidea s. l. in which the Nanoini fits well. The fused paracymbium – a plesiomorphic character of *Nanoa* (and the Pimoidae as well in my opinion) – is designated as synAPOMORPHY (!) of *Nanoa* and *Pimoa* by HORMIGA et al. (2005: 252). – If one reads carefully this paper, these authors (which one?) regards *Nanoa* – apparently presupposedly (!) – as a member of the family Pimoidae, and subsequently – as a result of their cladistic analysis – as the sister group to *Pimoa* CHAMBERLIN & IVIE 1943 – a quite remarkable proceeding and method!
I strongly disagree with the homologization of certain structures of the ♂-pedipalpus of *Nanoa* with pimoid structures which are published by HORMIGA et al.. In *Nanoa* – as in the related extinct genus *Pumiliopimoa* n. gen., see above – all the typical structures of the Pimoidae are absent: Cymbial cuspules, a distally widened pimoid cymbial process and a pimoid embolic process (“lost” according to HORMIGA et al (2005: 252)). All known Pimoidae – of the genera *Pimoa*, *Putaoa* and *Weintrauboa* – are distinctly larger spiders than *Nanoa*. In my opinion the “pimoid cymbial process” of *Nanoa* sensu HORMIGA et al. (2005) is nothing else than the anterior branch of the paracymbium, and the strong bristle of the cymbium – called “the single cymbial cuspule” by these authors (2005: 252) – is quite different to the pimoid cymbial cuspules (see the notes on cymbial bristles and cuspules above , the chapter on the Pimoidae), and is simply a powerful bristle (*). – *Nanoa* does not fit in any of the extant spider families but seems well related to the extant genus *Pumiliopimoa*. Due to the characters of *Nanoa* as well as – compared to the Pimoidae – the strongly reduced size and number of leg bristles, the existence of opisthosomal scuta, and the configuration of the sclerites of the male pedipalpus – the presence of a divided paracymbium and the absence of pimoid sclerites – I transfer it herewith from the Pimoidae to the Pumiliopimoidae n. fam.: Nanoini n. trib. (**n. relat**.).

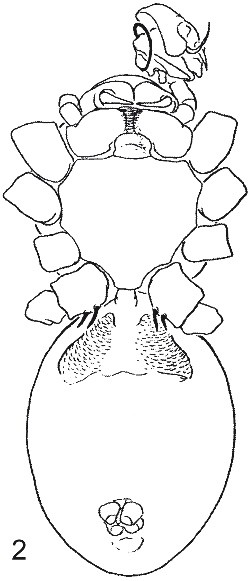
(*) A thickened cymbial bristle exists e. g. in the fossil genus *Dubiosynotaxus* WUNDERLICH 2004 of the family Synotaxidae, as well as in the genera *Spinilipus* WUNDERLICH 1993 (extinct), *Tekella* URQUHART 1894 (extant, New Zealand) of the Cyatholipidae; both families are strongly related to each other, and are members of the “bristle-less femur clade”. A stridulatory organ – of a different kind but similar to *Nanoa* – between coxae IV and opisthosoma exists in the fossil taxon *Succinitaxus brevis* WUNDERLICH 2004 (Synotaxidae) and – quite similar – in various members of the Linyphiidae: Erigoninae.

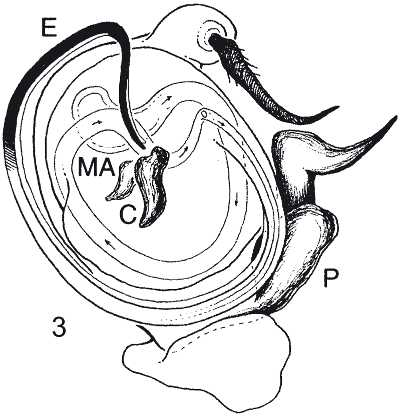
Natural history (see above): The spiders are dwellers of the mountain wilderness between ca. 1000 and 1500m.

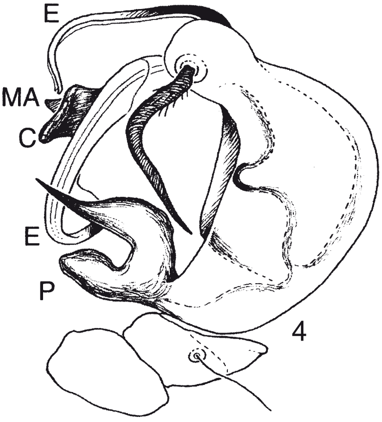
Distribution: North America, USA (California and Oregon).











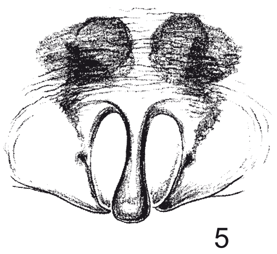
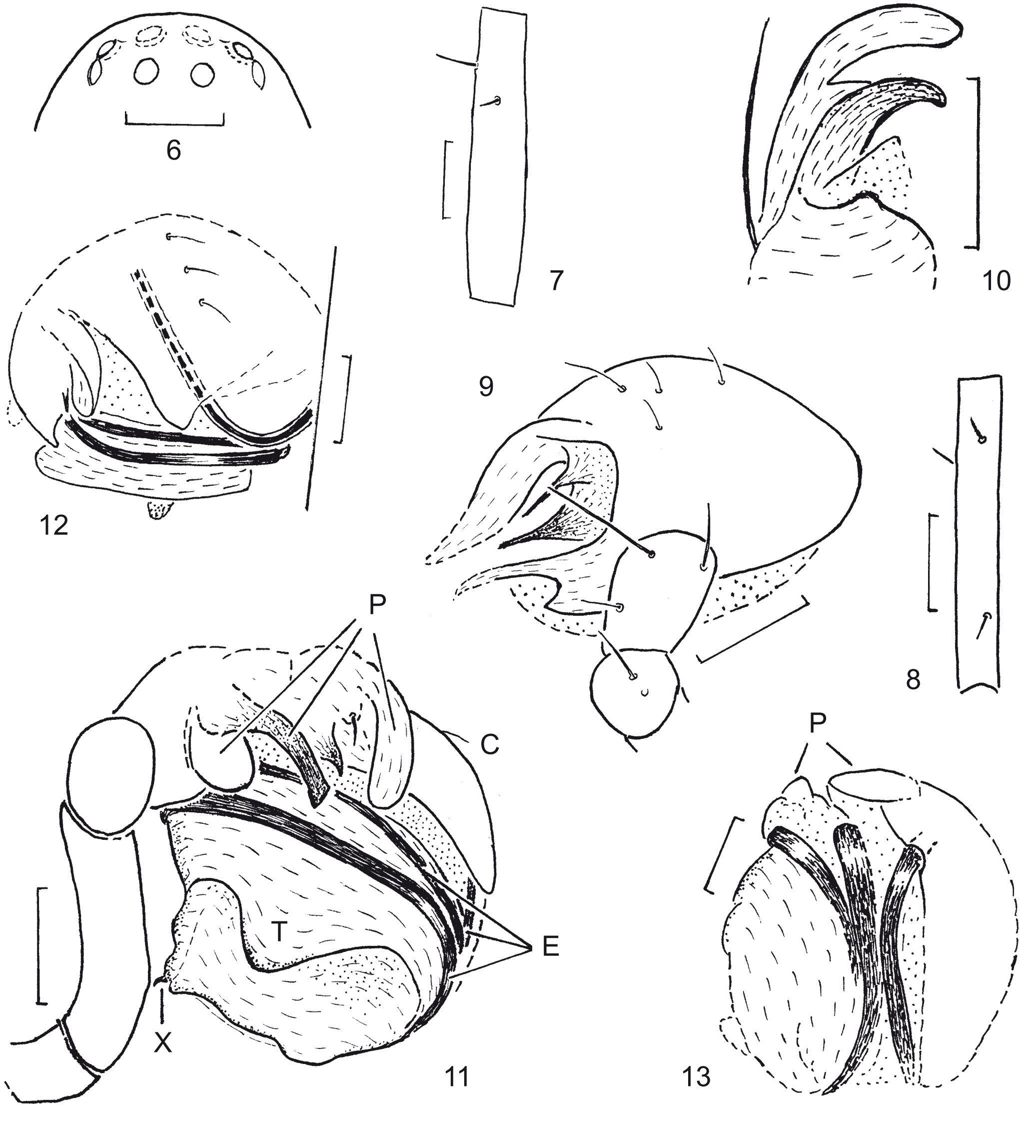


Fig. 1a–b) Sinopimoa bicolor LI & WUNDERLICH 2008 (Sinopimoidae), extant, China, ♂; dorsal and retrolateral aspects of the r. pedipalpus. Note the large tibial outgrowth; A = sclerotized edge of the retromarginal pit of the cymbium, AT = apophysis of the tibia, P = paracymbium, T = tegular apophysis; scale bar = 0.1 mm;

figs. 2–5: Nanoa enana HORMIGA et al. 2005 (Pumiliopimoidae n. fam., n. relat.), extant, USA; 2–4) ♂, 2) ventral aspect of body and l. pedipalpus; note the stridulatory organ between the lung covers and spines of the coxae IV; 3–4) ventral and retrolateral aspect of the l. pedipalpus; note the powerful cymbial bristle; 5) ♀, ventral aspect of the epigyne; C = conductor, E = embolus, MA = median apophysis, P = paracymbium which is regarded here as two-partite (u-shaped); no scale bars; taken from HORMIGA et al. (2005);



figs. 6–13: ***Pumiliopimoa parma* n. gen. n. sp.** (Pumiliopimoidae **n. fam.**), ♂, extinct, in Eocene Baltic amber; 6) dorsal aspect of the eyes (holotype); 7) dorsal aspect of the r. femur I (holotype); 8) dorsal aspect of the r. tibia I (holotype); 9) dorsal aspect of the l. pedipalpus (distal parts of the paracymbium are hidden) (paratype F1090); 10) retrobasal aspect of the paracymbium of the r. pedipalpus (paratype F1090); 11) retrolateral and retroventral (cymbium and bulbus) aspect of the r. pedipalpus. The structures are slightly deformed. Tibia and cymbium are dorsally partly cut off (paratype F2025); 12) apical aspect of the l. pedipalpus. Parts are hidden or cut off (paratype F2025); 13) retrodistal aspect of the r. pedipalpus; parts are hidden by a white emulsion (holotype); C = cymbium, E = embolus, P = paracymbium, T = outgrowth of the tegulum; X = "median apophysis" and questionable conductor nearby; scale bars = 0.2 in figs. 6–8, 0.1 in the remaining figs.

DESCRIPTIONS OF A CRYPTIC FOSSIL AND AN ENIGMATIC EXTANT GENUS OF THE FAMILY SYNOTAXIDAE

The fossil Synotaxidae in Baltic amber were revised by WUNDERLICH (2004). In the present paper I add a further taxon in Baltic amber – of the Chelicerini n. trib. –, and I describe the extant monotypic new tribus Microsynotaxini from Australia.

The intrafamiliar relationships of the higher taxa of the Synotaxidae were shortly discussed by WUNDERLICH (2004: 1192). The family is probably not monophyletic; a revision is needed, especially of the taxa of the Australian Region; the relationships of the extinct subfamily Acrometinae WUNDERLICH 1979 are unclear, see WUNDERLICH (2004: 1195).

(a) CHELICERINI n. trib. in Eocene Baltic amber

Diagnosis (♂; ♀ unknown): Prosoma (fig. 1, photo 155) fairly low, chelicerae (fig. 1) large, with anterior depressions, a basal-lateral bulge, and large teeth on the anterior marging of their furrows, colulus (fig. 3) small, with a single hair. Pedipalpus (figs. 4–7): Tibia very wide, bearing long marginal hairs, bulbus with a long outgrowth which is partly lying on the cymbium, embolus long, describing several loops.

Further characters: Clypeus (fig. 1) long, legs (photo, fig. 2) long and slender, without long ventral hairs, only patellae and tibiae bear bristles, sequence of the long tibial bristles 2/2/1/2, comb of tarsus IV absent, leg autotomy between coxa and trochanter, paracymbium unknown.

Type genus (by monotypy): *Chelicerinus* n. gen.

The **relationships** are quite unsure: The chaetotaxy, the long clypeus, and the wide pedipalpal tibia which bears long marginal hairs are like in the family Theridiidae and in some Synotaxidae, but the shape of the large chelicerae, the absence of prosomal stridulatory files and of a tarsal comb IV are not frequent in the Theridiidae; a comb of tarsus IV is absent in members of the Synotaxidae. Unfortunately shape and position of the paracymbium are not surely known in the Chelicerini. The shape of the strong chelicerae reminds on the conditions in theTetragnathidae, and a long clypeus exists in

few questionable Tetragnathidae like *Anameta* WUNDERLICH 2004, but femoral and metatarsal bristles as well as long ventral leg hairs exist usually in Tetragnathidae, and the structures of the male pedipalpus are different.
Chelicerini does not fit in any of the theridiid subfamilies. In the Nesticidae bears the colulus a pair of hairs instead of a single hair. I regard Chelicerini as a questionable taxon of the family Synotaxidae which relationships are quite unsure; it may be the member of a subfamily of its own.

Distribution: Eocene Baltic amber forest, Bitterfeld deposit.

***Chelicerinus* n. gen.**

The gender of the name is masculine.

Diagnosis (♂; ♀ unknown) and **relationships**: See the tribus.

Type species (by monotypy): *Chelicerinus abnormis* n. sp.

Distribution: Eocene Baltic amber forest, the Bitterfeld deposit.

***Chelicerinus abnormis* n. gen. n. sp.** (photo 155, fig. 1–7)

Material: Holotypus ♂ in Baltic amber from the Bitterfeld deposit, F1414/BB/AR/CJW.

Preservation and syninclusions: The spider is partly well but incompletely preserved in a piece of amber which was most probably heated, a white emulsion is absent. Both anterior legs and the right leg II are lost beyond the coxa by autotomy, several leg articles are cut off, the right legs III and IV and the left legs II and III are almost complete. Both parts of the pedipalpal tibiae and cymbiae are cut off. A double dragline is running backwards from the anterior spinnerets in a loop to the right tarsus IV. Bubbles are present on the right side on the prosoma and under the opisthosoma; stellate hairs, particles of detritus and small parts of bark as well as a long and thin hair-shaped particle are preserved in the same piece of amber.

Diagnosis (♂; ♀ unknown; see above): Chelicerae as in fig. 1, pedipalpus as in figs. 4–7.

Description (♂):
Measurements (in mm): Body length 3.8, prosoma: Length ca. 1.8, height above coxa I ca. 0.6; leg II: Femur ca. 3.0, patella 0.5, leg IV: Femur 2.1, patella ca. 0.55, tibia 2.0, metatarsus 2.15, tarsus 1.1, pedipalpal femur ca. 0.9.
Colour: Prosoma and legs medium brown, opisthosoma light brown, dorsally brown darkened by heating.
Prosoma (photo 155, fig. 1) fairly low, with a large and deep fovea and short dorsal hairs, posterior files absent, clypeus long and protruding ventrally, eye field wide, not raised, bearing a pair of tiny hairs; eyes fairly small, posterior medians smallest, clypeus long and concave. Basal cheliceral articles large and parallel, lateral files absent, basal-lateral bulging, with anterior depressions near the base and in the middle; anterior margin of the furrow with a large and two-partite tooth and a smaller tooth in a more distal position, fangs long. – Legs (the first pair is lost) long and slender, hairs of normal length, long ventral hairs absent. Only patellae and tibiae bear bristles, tibial bristles long, their sequence 2/2/1/2 (fig. 2). Metatarsal trichobothria indistinct, comb of tarsus IV absent, ventral hairs short, tarsal claws short. – Opisthosoma egg-shaped, longer than wide and high, covered with short indistinct hairs; colulus (fig. 3) small, bearing a single short hair, tracheal spiracle indistinct. – Pedipalpus: See above. A slender structure may be the paracymbium. The structures of the bulbus are partly hidden and hard to recognize; the embolus is very long and describes several loops.

Relationships: See above.

Distribution: Eocene Baltic amber forest, the Bitterfeld deposit.

(b) MICROSYNOTAXINI n. trib. from Australia (extant)

Diagnosis: Tiny spiders (body length about 1 mm) with very large eyes (figs. 8–9), stridulatory organs absent, thin bristles exist on patellae and tibiae, colulus and spigots of spinnerets reduced; ♂-pedipalpus (figs. 10–12, 15–17) with a divided retrobasal paracymbium which is fused to the cymbium, bulbus with a medial and a terminal apophysis, and a thin embolus in a circular position. Epigyne/vulva (figs. 13–14) without a scape, with large receptacula seminis and short ducts of the vulva.

Type genus (by monotypy): *Microsynotaxus* n. gen.

Relationships: According to its characters – e. g. the small tracheal spiracle, the structure of the paracymbium, and the configuration of the structures of the bulbus – Microsynotaxini is most likely a member of the Synotaxidae (s. l.). The tribus does apparently not fit in one of the known synotaxid subfamilies, and thus it probably may even be regarded as a subfamily of its own. C. GRISWOLD (he studied the material about 10 years ago) and R. R. FORSTER (in litt. 1997) were not sure about the relationships of this taxon. Related genera are probably known from the Eocene Baltic amber forest, see below: Relationships of the genus *Microsynotaxus*.

Distribution: Australia.

***Microsynotaxus* n. gen**.

Diagnosis (see the tribus): Prosoma (fig. 8) dorsally strongly convex, basal part of the embolus hidden (fig. 11), epigyne a wide and weakly sclerotized plate, inserting openings apparently at the posterior margin.

Type species: *Microsynotaxus insolens* n. sp.

Relationships: According to the structures of their bulbus probably certain Eocene genera of the Baltic amber forest are related: In *Dubiosynotaxus* WUNDERLICH 2004 tibial bristles are absent, and the tarsi are longer than the metatarsi; in *Succinitaxus* WUNDERLICH 2004 the opisthosoma is slightly bulging above the spinnerets, a sclerotized epigaster and a coxal-epigastral stridulatory organ are present.

Distribution: Australia.

***Microsynotaxus insolens* n. gen. n. sp**. (figs. 8–14)

Material (most spiders are kept in the Queensland Museum Brisbane, QM): Australia, Queensland; 1. Kroombit Tops Dawes Range, 45 km SSW Calliope, open forest, 2♂1♀ V. E. DAVIES leg. 9.–19. XII. 1983; holotype ♂, 1♀ paratype QM no. 20416; 1♂ paratype MNHN; Krombit Tops (Lower Dry K.), open forest, "beating", 2♂ paratypes, V. E. DAVIES & J. GALLON leg. 9.–19. XII. 1983, QM no. S 20413 and S 20417; 2. Mt. Glorious State Forest, subtropical rain forest, *Argyrodendron actinophyllum*, 1♂ paratype, Y. BASSERT leg. 26. IX. 1987, QM no. S5333, 1♂ paratype, Y. BASSERT leg. 18. I. (no. S5102) SMF.

Diagnosis: ♂: Pedipalpus (figs. 10–12) with an undivided conductor and an embolus in an oval/wide position. ♀: Epigyne (fig. 13) a wide, weakly sclerotized plate, the vulva structures are well visible. Vulva (fig. 14) with large receptacula and short duct, position of the inserting openings apparently at the posterior margin.

Description:
Measurements (in mm): ♂: Body length 1.0–1.1, prosoma: Length 0.47, width 0.46; leg I: Femur 0.5, patella 0.18, tibia 0.4, metatarsus 0.29, tarsus 0.21, tibia II 0.37, tibia III 0.21, tibia IV 0.35; ♀: Prosoma: Length 0.5, width 0.49, tibia I 0.42, tibia IV 0.35.
Colour: Prosoma yellow to grey brown, marginally and partly dorsally more or less darkened, legs yellow, trochantera I–II, metatarsi ventrally and tibiae ventrally-basally, medially and distally with black spots, patella IV basally-ventrally and femur IV ventrally-distally black. Opisthosoma yellow and grey, dorsally with a wide, saddle-shaped white band. – Prosoma (figs. 8–9) as wide as long, without a fovea. Eyes large and close together, posterior row recurved. Clypeus long, chelicerae of medium size, promargin of the furrow with a small denticle. Labium almost two times wider than long, with a seam to the sternum, distally strongly rebordered, coxae IV separated by 1.5 times of their diameter. – Legs short and slender, with short hairs and 1/1 small dorsal bristles on the patellae and 1 dorsal bristle on the tibiae in their basal half, their length 1 1/4 diameters of the tibiae. Position of the long trichobothrium of metatarsus I in 0.85, metatarsus IV without trichobothrium. Metatarsus I slightly bent. – Opisthosoma (fig. 8) wide and almost egg-shaped, colulus tiny, tracheal spiracle fairly small and near to the spinnerets. Anterior spinnerets stout. Spigots (thanks to the investigation of C. GRISWOLD): There appears to be no cylindrical gland spigots (CY) on the median spinnerets; only two aciniform gland spigots and a single posterior minor ampullate gland spigot. The PLS spinning field is still simpler: 5 mesal AC and a large median spigot. There is no sign of the araneoid triplet of 2 aggregate gland spigots and a flagelliform gland spigot, and the position of the one large spigot suggests that it may be a CY. The mesal CY is absent, as in the Cyatholipidae and other Synotaxidae. – ♂-pedipalpus (figs. 10–12): Patella slightly longer than wide, distally with a small bristle, tibia prodorsally elongated, with a dorsal trichobothrium; structures of the bulbus: See the diagnosis.

Relationships: In *M. calliope* n. sp. the paracymbium is smaller and its shape is different, the conductor is slightly smaller and distinctly divided, the position of the distal (free visible) part of the embolus is circular.

Distribution: Australia, Queensland.

***Microsynotaxus calliope* n. gen. n. sp.** (figs. 15–17)

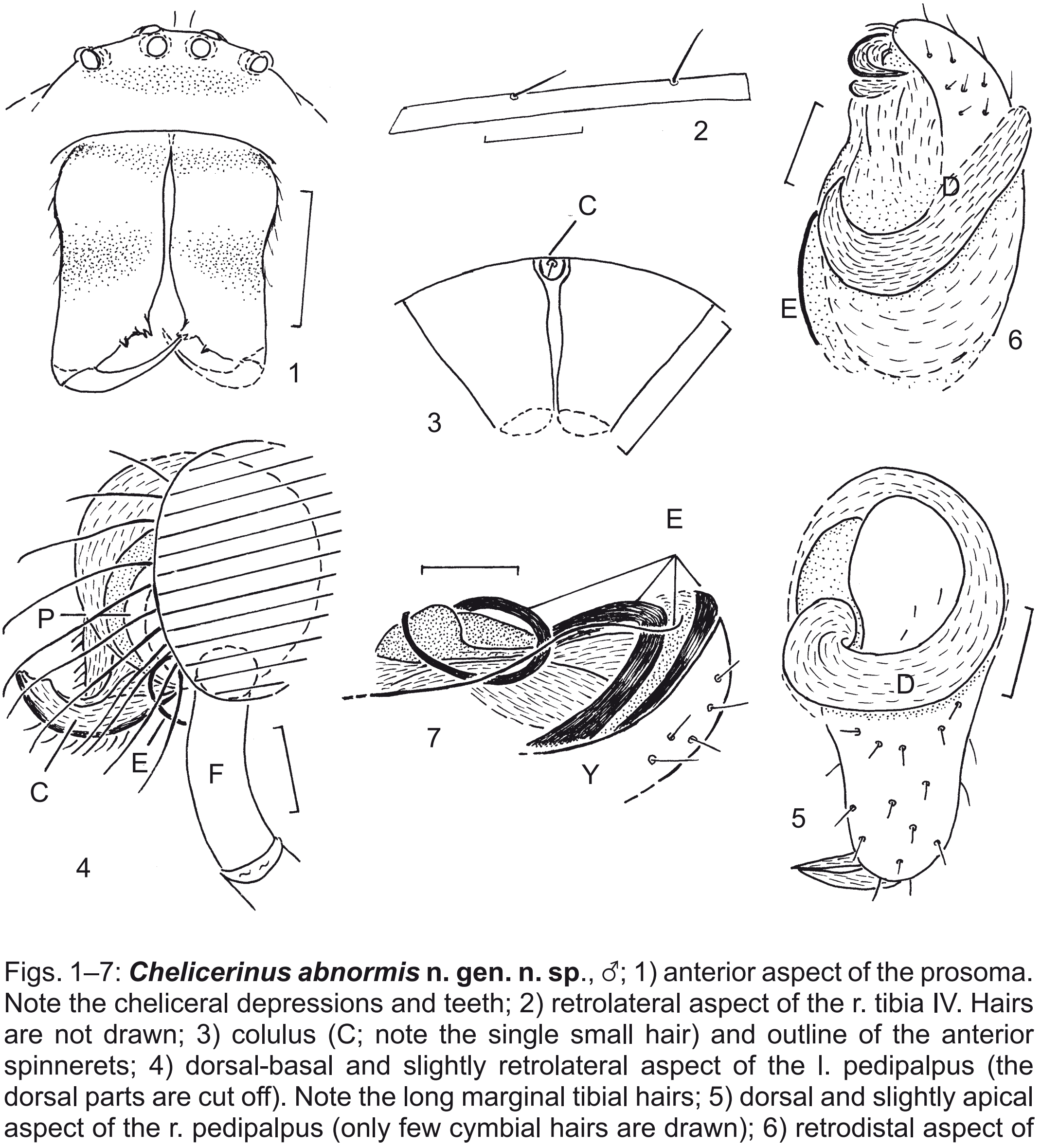
Material (kept in the Queensland Museum Brisbane): Australia, Queensland, Kroombit Tops, Dawes Range, 45 km SSW Calliope, open forest; ♂ holotype V. E. DAVIES & J. GALLON leg. 9.–19. XII. 1983 together with *M. insolens*, QM no. 20416a (ex no. 20416).

Diagnosis (♂; ♀ unknown): ♂-pedipalpus (figs. 15–17) with a distinctly divided conductor and a circular position of the embolus.

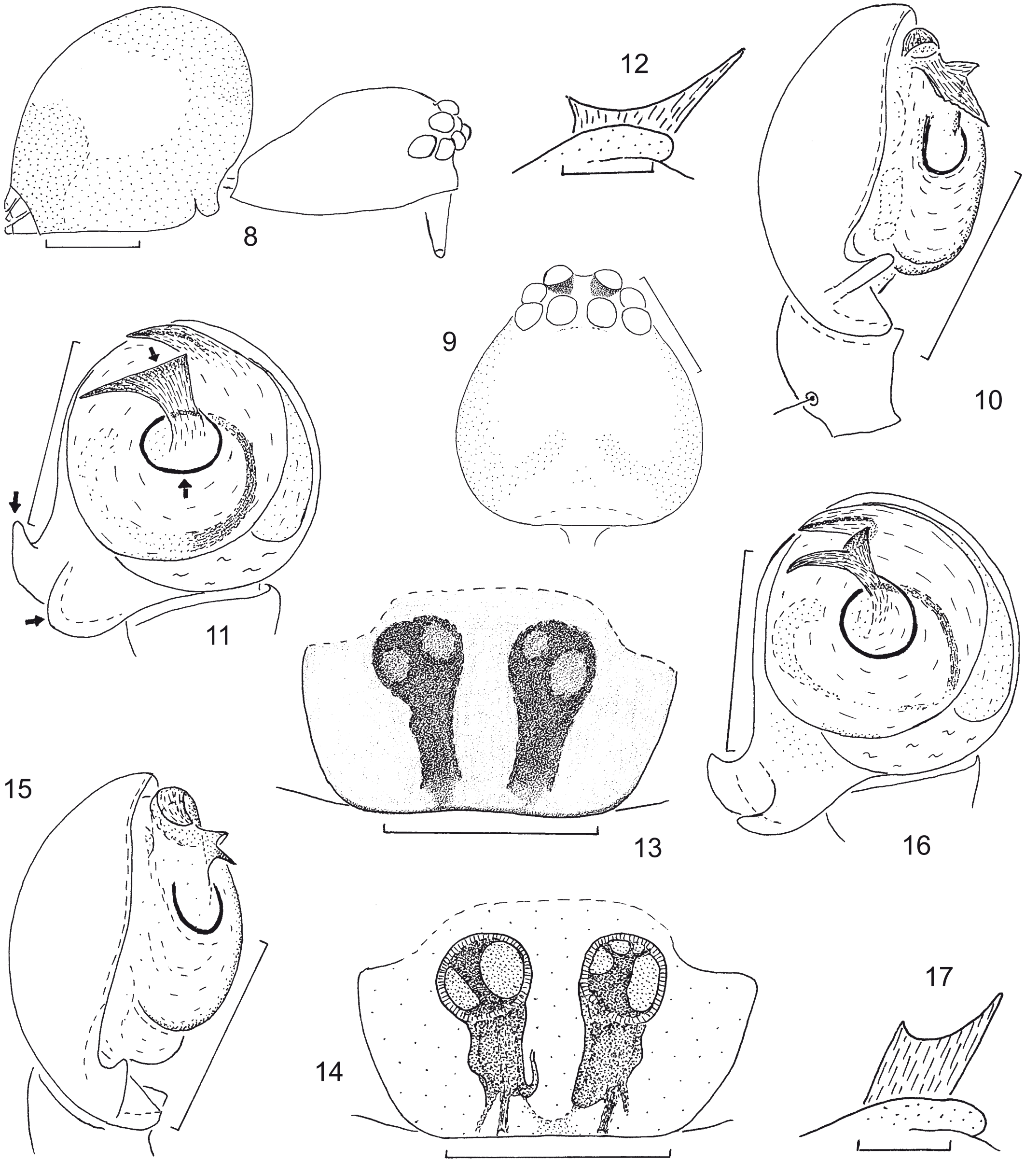
Description: Measurements, body and legs as in *M. insolens* n. sp., see above.

Relationships: See *M. insolens* n. sp.

Distribution: Australia, Queensland.



Figs. 1–7: ***Chelicerinus abnormis* n. gen. n. sp.**, ♂; 1) anterior aspect of the prosoma. Note the cheliceral depressions and teeth; 2) retrolateral aspect of the r. tibia IV. Hairs are not drawn; 3) colulus (C; note the single small hair) and outline of the anterior spinnerets; 4) dorsal-basal and slightly retrolateral aspect of the l. pedipalpus (the dorsal parts are cut off). Note the long marginal tibial hairs; 5) dorsal and slightly apical aspect of the r. pedipalpus (only few cymbial hairs are drawn); 6) retrodistal aspect of the l. pedipalpus; 7) proventral aspect of certain bulbus structures of the l. pedipalpus (other structures are hidden) near the tip of the r. chelicera. C ?= conductor, D = dorsal outgrowth of the bulbus which lies on the cymbium; E = embolus, F = femur, P ?= paracymbium, Y = cymbium. Scale bars = 0.5 mm in figs. 1–2, 0.2 in the remaining figs.;



Figs. 8–14: ***Microsynotaxus insolens* n. gen. n. sp**.; 8) ♂, lateral aspect of the body; 9) dorsal aspect of the ♂-prosoma; 10) retrolateral aspect of the r. ♂-pedipalpus; 11) ventral aspect of the r. ♂-pedipalpus; 12) apical aspect of the conductor of the r. ♂-pedipalpus; 13–14) epigyne and dorsal aspect of the vulva. Scale bars = 0.2 in figs. 8–9, 0.03 in fig. 12, 0.1 in the remaining figs.;

figs. 15–17: ***Microsynotaxus calliope* n. gen. n. sp**., ♂; 15–16) retrolateral aspect of the r. pedipalpus; 17) apical aspect of the conductor of the r. pedipalpus. Scale bars = 0.03 in fig. 17, 0.1 in the remaining figs.;

REFERENCES, cited (mainly recent papers are listed; see the references with the paper on the Theridiidae in this volume, and N. I. PLATNICK (1981–1998): Advances in Spider Taxonomy, as well as The World Spider Catalog (2007) via the internet.

HORMIGA, G. (1994): A Revision and Cladistic Analysis of the Spider Family Pimoidae (Araneoidea: Araneae). -- Smithsonian contrib. Zool., 549: 1–104.

-- (2003): *Weintrauboa*, a new genus of pimoid spiders from Japan and adjacent islands, with comments on the monophyly and diagnosis of the family Pimoidae and the genus *Pimoa* (Araneoidea, Araneae). -- Zool. J. Linnean Soc., 139: 261–281.

-- (2008): On the spider genus *Weintrauboa* (Araneae, Pimoidae), with a description of a new species from China and comments on its phylogenetic relationships. -- Zootaxa, 1814: 1–20.

HORMIGA, G., EBERHARDT, W. G. & CODDINGTON, J. A. (1995): Web-construction Behaviour in Australian *Phonognatha* and the Phylogeny of Nephiline and Tetragnathid Spiders (Araneae: Tetragnathidae). -- Aust. J. Zool., 43: 313–364.

HORMIGA, G., BUCKLE, D. J. & SCHARFF, N. (2005): *Nanoa*, an enigmatic new genus of pimoid spiders from western North America (Pimoidae, Araneae). -- Zool. J. Linnean Soc., 145: 249–262.

HORMIGA, G. & TU, L. (2008): On *Putaoa*, a new genus of the spider family Pimoidae (Araneae) from China, with a cladistic test of its monophyly and phylogenetic placement. -- Zotaxa, 1792: 1–21.

KUNTNER, M. (2006): Phylogenetic systematics of the Gondwanan nephilid spider lineage Clitaetrinae (Araneae, Nephilidae). -- Zoologica Scripta, 35 (1): 19–62).

KUNTNER, M. & ALVAREZ-PADILLA, F. (2006): Systematics of the Afro-Macaronesian spider genus *Sancus* (Araneae, Tetragnathidae). -- J. Arachnology, 34: 113.125.

LEVI, H. W. (1980): The Orb-Weaver Genus *Mecynogea*, the Subfamily Metinae and the Genera *Pachygnatha*, *Glenognatha* and *Azilia* of the Subfamily Tetragnathinae North of Mexico (Araneae: Araneidae). -- Bull. Mus. Comp. Zool. Harvard Univ., 149 (1): 1–75.

-- (1986): The Neotropical Orb-weaver Genera *Chrysometa* and *Homalometa* (Araneae: Tetragnathidae). -- Bull. Mus. Comp. Zool. Harvard Univ., 151 (3): 91–215.

LI, S. & WUNDERLICH, J. (2008): Sinopimoidae, a new spider family from China (Arachnida, Araneae). -- Acta Zootaxonomica Sinica, 33 (1): 1–6.

LI, S. & XU, X. (2007): Taxononomic study of the Spider family Pimoidae (Arachnidae: Araneae) from China. -- Zool. Studies, 46 (4): 483–502.

MARUSIK, Y. M. & KOPONEN, S. (1992): A *review* of Meta (Araneae, Tetragnathidae), with description of two new species. -- J. Arachnol., 20: 137–143.

PENNEY, D. (2004): New spiders in Upper Cretaceous amber from New Jersey in the American Museum of Natural History (Arthropoda: Araneae). -- Palaeontology, 47 (2): 367–375.

-- (2006): Tertiary neotropical Hersiliidae (Arthropoda, Araneae) with new combinations for the extant fauna and comments on historical biogeography of the family. -- Palaeontology, 49 (4): 899–906.

-- (2007): A new fossil oonopid spider in lowermost Eocene amber from the Paris Basin, with comments on the fossil assemblage. -- African Invertebrates, 48 (1): 71–75.

RHEIMS, C. A. & BRESCOVIT, A. D. (2004): Revision and cladistic analysis of the spider family Hersiliidae (Arachnida, Araneae) with emphasis on Neotropical and Nearctic species. -- Insect Syst. & Evol. (Group 4), 35 (2): 189–239.

SAARISTO, M. I. (2007): A new subfamily of linyphiid spiders based on a new genus created for the *keyserlingi*-group of the genus *Lepthyphantes* (Aranei: Linyphiidae). -- Arthropoda Selecta, 16 (1): 33–42.

SAARISTO, M. I. & MARUSIK, Y. M. (2004): *Ferchestina*, a new genus of oonopid spiders from Russian Far East (Aranei: Oonopidae). -- Arthropoda Selecta, 13 (1–2): 51–54.

TANIKAWA, A. (1993): A new species of the genus *Meta* (Araneae: Tetragnathidae) from Japan. -- Acta Aracnol., 42 (2): 97–101.

-- (1994): A New Species of the Spider Genus *Meta* C. L. KOCH, 1836 (Araneae: Tetragnathidae) from Japan. -- Acta Arachnol., 43 (1): 65–69.

TULLGREN, A. (1902): Spiders coll. in the Aysen Valley. -- Bih. Svensk. Vet. Ak. Handl., 28 (4;1): 1–77.

ULRICH, H. (2003): How recent are the Empedoidea of Baltic amber? -- Studia dipterologica, 10 (1): 321–327.

WUNDERLICH, J. (1981): Fossile Zwerg-Sechsaugenspinnen (Oonopidae) der Gattung *Orchestina* SIMON, 1882 im Bernstein, mit Anmerkungen zur Sexual-Biologie (Arachnida: Araneae). -- Mitt. Geol.-Paläont. Inst. Univ. Hamburg, 51: 83–113.

-- (1995): Description of the new genus *Calcarsynotaxus* from Australia (Arachnida: Araneae: Synotaxidae). -- Beitr. Araneol., 4: 539–542.

-- (2004): Spiders in Amber and Copal. -- Beitr. Araneol., 3 (A, B): 1–1908). Publishing House J. Wunderlich, 69493 Hirschberg, Germany.

-- (2006): *Spatiator martensi* n. sp., a second species of the extinct spider family Spatiatoridae in Eocene Baltic amber (Araneae). -- Zootaxa, 1325: 313–318.

ZHU MINGSHENG, SONG DAXIANG & ZHANG JUNXIA (2003): Tetragnathidae (Arachnida: Araneae). -- In: Fauna Sinica, Invertebrata vol. 35: 1–402, 16 tab.. Beijing, China.

BEITR. ARANEOL., 5 (2008)

ON EXTANT AND FOSSIL (EOCENE) EUROPEAN COMB-FOOTED SPIDERS (ARANEAE: THERIDIIDAE), WITH NOTES ON THEIR SUBFAMILIES, AND WITH DESCRIPTIONS OF NEW TAXA

JOERG WUNDERLICH, D-69493 Hirschberg.

Abstract: The fossil and – mainly supraspecific extant European – taxa of the Comb-footed spiders (Araneae: Theridiidae) are dealt with. From the Eocene European amber forests – from the Baltic area, from the Bitterfeld and from the Ukrainean deposits – members of 7 families, 30 genera and about 100 species are reported, 24 new genera and 78 new species are described, the genera *Euryopis* and *Ulesanis* are reported for the first time. Theridiidae – and questionable Theridiinae – are reported from the Eocene but it are unknown from the Cretaceous. The **new subfamily** Anelosiminae and **four new tribus** – the extinct Spinitharini (Episinae), as well as the extant Achaearanini, Echinotheridiini (both Theridiinae), and Magnopholcommatini (questionable Pholcommatinae) – are described. The subfamilies Enoplognathinae, and Phoroncidiinae as well as the names Asageninae (not Latrodectinae) and Episinae (not Spintharinae) are accepted/resurrected. A new species of the genus *Argyrodes* s. l. (Argyrodinae) in copal of Columbia is described. Five new extant theridiinae genera (*Achaeridion, Anatolidion, Canalidion, Heterotheridion, Ohlertidion*), and a single new species are described from the Palaearctic, a new genus (*Pycnoepisinus*) and species from Africa, and a new genus (*Monetoculus*) and species from Malaysia (both Episinae). *Takayus* YOSHIDA 2001 is reported from Europe. *Marianana* GEORGESCU 1989 (extant, Europe) is regarded as a junior synonym of *Theonoe* SIMON 1881 (**n. syn**.). Keys are given to the identification of Eocene and extant European genera of the Theridiidae, and their subfamilies worldwide. Questions regarding the biogeography, ecology, phylogeny, and taxonomy – mainly convergences, the taxonomical value and the variability of the colulus and the paracymbium – of the family Theridiidae are discussed.

Key words (see also the key words at the beginning of this volume): Achaearanini, amber, Anelosiminae, Araneae, Asageninae, Baltic amber, biodiversity, Bitterfeld deposit, body size, colulus, Cretaceous, Dipoeninae, Echinotheridiini, Enoplognathinae, Eocene, Episinae, Europe, extinctions, fossils, healing events, identification keys, K-T boundary events, Latrodectinae, leg amputations, Magnopholcommatini, new taxa, paracymbium, Pholcommatinae, Phoroncidiinae, plug Rovno amber, spiders, Spintharinae, Spini-tharini, subspecies, superspecies, tendency, Theridiidae, Theridiinae, Theridulini, trend, Ukrainean amber.

Contents of this paper, method and **material**. Contents: See the first part of this volume, and the index below. – Material of the coll. M. KUTSCHER (from Bitterfeld) is now stored in the MGG. A part of the type material of the CJW has already been deposited in the SMF. – Method: The variability of peculiar structures – like the colulus and the paracymbium – within the subfamilies and certain genera were usually studied IN A SUFFICIENT NUMBER of taxa. The CHAETOTAXY and the TRICHOBOTHRIOTAXY were not ignored, and FOSSILS are included in the study on the theridiid phylogeny. Taxinomical important structures are checked for convergences.

INTRODUCTION

In my previous investigations of spiders in Baltic amber I left open a treatment of the most diverse family Theridiidae, see WUNDERLICH (2004: 1245–1247). I now complete the previous investigation of spider families in Baltic amber in adding and revising fossil theridiid taxa in Eocene European – Baltic, Bitterfeld, Ukrainean – ambers. Included are the revisions and new descriptions of various extant taxa – especially of palaearctic Asageninae and Theridiinae –, remarks on and keys to the theridiid subfamilies, – and two new species in copal from Columbia and Madagascar, as well as findings on phylogeny, ecology and behaviour; see below and above, the chapter "Frozen behaviour". Keys are given to the identification of Eocene and extant European theridiid genera. The extant west-palaearctic genera of the subfamily Theridiinae are treated in a chapter of its own at the end of this paper.
TAXONOMY AND PHYLOGENY: Certain fossil taxa of the Theridiidae – e. g. members of the subfamily Asageninae – in Baltic amber gave me important hints to the theridiid phylogeny and intrafamiliar relationships. Unfortunately (a) the work of ARCHER (1947, 1950) has never been critically revised; several genera which were created by this author were ignored or erroneously/overhasty synonymized by certain authors; the important paper of LEVI & LEVI (1962) blocked for long time revisions on superspecific theridid taxa because the revision of theridiid genera was seemingly already finished, (b) the chaetotaxonomy and the trichobothriotaxy were ignored by previous authors, and (c) the variability of the paracymbium and of the colulus within a given taxon has been studied only superficially and IN TOO FEW TAXA.
The FAUNAS: Today Theridiidae is the most diverse spider family besides Linyphiidae and Salticidae; according to PLATNICK (2004) 2209 species in 80 genera are known. It is in concordance with the personal experience of the present author as well as of H.W. LEVI and C. DEELEMAN (person. commun.) that a huge number – probably

thousands of theridiid species and numerous genera, mainly from tropical rain forests – are still undescribed. From the West-Palaearctic Region I know about 40 genera (5 are described in this paper for the first time). From Europe we know today far more than 200 theridiid species (and additionally a certain number of dubious species).

Fossils and biodiversity: Theridiidae is the most diverse spider family – and one of the most diverse arthropod families – in Eocene ambers; the 30 theridiid genera which are now known from this period are probably only an incomplete section of the real number of genera which existed in the Eocene European forests (*). Only about 25 true theridiid species from 6 genera – *Clya* (extinct), *Eomysmena* (extinct), *Episinus, Euryopis, Lasaeola* s. l. and *Pseudoteutana* n. gen. – have been described from Baltic amber previously; in this paper I add 24 new genera and 78 new species from 7 subfamilies; now 30 genera and about 100 species (some are dubious) are known from this kind of amber; see below: "Historical biogeography". The Eocene Theridiidae in Baltic amber are now probably studied in more detail than the extant Palaearctic taxa.

It was of great interest to compare in detail the Early Tertiary (Palaeogene: Eocene) theridiid fauna with the extant European theridiid fauna: On the generic level both faunas turned out to be almost completely different: About 90% of the fossil genera are extinct, only 4 genera survived: *Episinus, Euryopis, Lasaeola* and *Ulesanis*. I found only few/slight differences between the Baltic, Bitterfeld and Rovno theridiid amber faunas (**). Specimens of the subfamily Asageninae are most frequent in Baltic amber.

(*) The "point of saturation" in the known theridiid taxa of the Baltic amber forest has not been reached as can be concluded from fossil material: (a) Among large lots – some hundred adult males each – which I studied during the last two years – I selected most often at least one undescribed species, (b) about half of the theridiid species in Baltic amber are known from a single specimen only.

(**) It is highly remarkable that sure pre-Tertiary – and even pre-Eocene – reports of the family Theridiidae are (still?) completely unknown; previous – Cretaceous – reports are misidentifications, see the paper no. 5 on Cretaceous spiders in this volume.

Frequency and number of Eocene species: See below.

Morphology and behaviour of extant taxa: See the very informative introduction to the family Theridiidae by KNOFLACH & PFALLER (2004: 111–160). With respect to several morphological characters the Theridiidae possesses one of the most pronounced diversity within the superfamily Araneoidea, e. g. regarding the size of the body – less than one millimeter in some Pholcommatinae and Phoroncidiinae up to more than one centimeter in certain Asageninae and worm-shaped members of the Argyrodinae – the colour, the shape of the body, the existence/absence as well as the size and the hairs of the colulus, furthermore the type and the position of the paracymbium, see below. The kind of the capture web is quite variable, too; it may be reduced (Episininae), and it may be usually completely absent (Hadrotarsidae, several Argyrodinae). Within the superfamily Araneoidea exists a comparable variability of some of these characters in the diverse families Anapidae s. l., Araneidae, and Linyphiidae.

Remarks on evolution, competition, changes in the diversity, and biogeographical pattern in geological periods (see also below, on the phylogeny)

Biogeography (see also below, the subfamilies).

In contrast to certain families – like Linyphiidae and Salticidae – most of the theridiid subfamilies were already derived and diverse in the Eocene, but the today's most diverse subfamily – Theridiinae – was rare or even absent in the European Eocene (*). Members of the probably most ancestral theridiid branch, the subfamily Asageninae, which possesses the most plesiomorphic characters, were already frequent in the Northern Hemisphere in the Eocene European amber forests. (Most of the remaining subfamilies have a mainly tropical distribution and are more frequent in the Southern Hemisphere). So it seems not unlikely that the origin of the Asageninae – similar apparently Enoplognathinae and Pholcommatinae – has been in the Northern Hemisphere. A similar situation exists in the family pair Linyphiidae/Pimoidae; Pimoidae is the more ancestral branch, and is restricted – at least today – to the Northern Hemisphere, see WUNDERLICH (2004). See also the pair of the family Theridiidae and the more ancestral family Nesticidae which is also distributed mainly in the Northern Hemisphere as well as the pair Araneidae and the probably more ancestral Zygiellidae: The latter is almost restricted to the Northern Hemisphere. The question is: Has Laurasia been the area of the origin of the ANCESTRAL partners of the family pairs in question? At least some of these taxa (Araneidae, Zygiellidae) – and their sister groups – may have originated during the Cretaceous diversification of the angiosperms in Laurasia.

(*) This subfamily may be an example for an – in the geological sense – young branch (it probably originated in the tropics).

Today Theridiidae – especially the subfamily Theridiinae – is one of the most diverse spider (sub)families in the tropics all over the world. In the – mainly subtropical – Eocene Baltic amber forest the family Theridiidae (except Theridiinae) as well as the related Synotaxidae were diverse, but today Synotaxidae are almost absent in the Northern Hemisphere (with very few exceptions of Central and North America), and are – compared with the Theridiidae – much less diverse in the tropics. According to the diverse faunas of these families in the Early Tertiary – and their similar habitats as well similar prey capture with the help of capture webs – there apparently was a conspicuous competition between them. It seems that the Theridiidae displaced more and more the – older/more ancestral? – Synotaxidae (and Cyatholipidae as well) during the Tertiary, most successfully probably especially during – as well as after – the drastic climatic cooling at the border of the Eocene and the Oligocene. The “winner” of this interfamiliar competition were clearly the Theridiidae (and the Linyphiidae as well) which displaced the Synotaxidae and the Cyatholipidae (the latter were less diverse in the Baltic amber forest than Synotaxidae) as well as the Anapidae s. l. which also were diverse during the Eocene in Europe. According to this hypothetic idea the Oligocene cooling set in motion (was the impulse for) the displacing of the families in question as well as the diversification of the Theridiidae: Theridiinae. This diversification – and “pioneering occupation” – blocked apparently a re-colonizing of the Synotaxidae – and the Cyatholipidae as well – up to now to most parts of the Northern Hemisphere, and almost all parts of the Holarctic Region.

Remarks on taxonomy and synonymy: (1) LEVI & LEVI (1962) treated in a very important and helpful taxonomical paper all theridiid genera of the world, but their lumping of numerous genera was not justified in my opinion (and the opinion of other recent authors), see below, e. g. genera of the subfamilies Asageninae and Theridiinae. I had to resurrect several genera mainly of these subfamilies, partly in the sense of previous authors like E. SIMON. I accept SUBGENERA within *Achaearanea, Argyrodes, Euryopis, Lasaeola, Selimus,* and *Steatoda* which I regard in a wide sense. – (2) Most previous authors did not consider certain characters as leg chaetotaxy and trichobothriotaxy as well as convergences and reversals, and the enormous variability of peculiar structures (e. g. of the paracymbium! See below) within certain genera and subfamilies. Furthermore the existence or absence of the colulus were partly erroneously reported (the existence of a colulus was overlooked in several taxa like *Anelosimus*, *Episinus* (fig. 379), and *Ulesanis*). – (3) The relationships of several genera are quite doubtful; examples are: (a) extant genera: *Cerocida, Latrodectus, Magnopholcomma* n. gen., *Proboscidula, Stemmops* and *Wirada*; (b) extinct genera: *Globulidion, Hirsutipalpus, Kochiuridion, Obscurpholcomma, Spinitharinus*, and *Succinura* (all are n. gen.).

Diagnosis and apomorphic characters of the family Theridiidae: Existence of: (1) Basicly and usually a ventral **comb** of serrated and bent hairs of tarsus IV (fig. 125a; see below, further characters). (2) Basicly and most often a prosomal-opisthosomal stridulatory organ (figs. 197, 405) (reduced/absent e. g. in certain members of the subfamily Hadrotarsinae). (3) The LABIUM IS NOT REBORDERED in contrast to most other Araneoidea (fig. 2). (4) A conspicuous clypeus which is most often long to very long (similar to Anapidae s. l. and Theridiosomatidae) (figs. 36, 42, 256). (5) Frequently long articles of the male pedipalpus (most often the femur). (6) A plate-shaped elongated tibia of the male pedipalpus which is widened distally and bears an oblique row of long distal hairs (photos 162f, figs. 35, 122, 143). (7) Paracymbium: A **retrobasal paracymbium** – a synapomorphic character of the ecribellate branch of the superfamily Araneoidea – **is completely absent** (has been lost) (*); on the other hand either (8a) a retrodistal-ectal paracymbium (fig. 37, 116, 443) (a basal character of the Theridiidae) or (8b) an internal and strongly sclerotized paracymbium exists; this may be hook-shaped (fig. 34) or hood-shaped (figs. 41, 49). (9) An epigynal scapus – a putative synapomorphy of the superfamily Araneoidea – is usually absent/lost (it is present e. g. in certain members of *Lasaeola*, apparently as a “formal reversal”) (**); contrarily (10) a large single epigynal pit or paired openings (photo 197, figs. 30, 156b, 245, 265, 432) exist in almost all taxa.

Further PUTATIVE APOMORPHIES of the family Theridiidae are (11) a strongly sclerotized or even armoured body and legs (photo 238) (this character has apparently been lost, one or several times, “reversals” exist), and (12) myrmecophagy (see below), with the evolution of gum-footed lines in adaptation to their main prey, the ant workers or a reduction/loss of the capture web. – (A peripheral retreat at the capture web may be an autapomorphy of the Asageninae).

(*) except in *Carniella* (in my opinion a “formal reversal”). – A retrolateral “paracymbium” about in the middle of the cymbium exists in *Moneta* (fig. 382) and *Monetoculus* n. gen. (Episinae), as

well as in *Protosteatoda* n. gen. (Asageninae); a prodistal/prolateral cymbial outgrowth exists in *Coscinida* (Hadrotarsinae) (fig. 330), and *Crustulina* (Asageninae) (fig. 40).
(**) Rarely a clavus originates at the posterior margin of the epigynal pit (in some *Kochiura* and *Anelosimus*, Anelosiminae, as well in few Theridiinae like *Echinotheridion andTidarren*).

Further theridiid characters (synapomorphic with their sister taxon, the Nesticidae, or even with the "spineless femur clade") are the absence of metatarsal and femoral bristles. (Compare the apical bristles of tibia I and prolateral bristle-shaped hairs in a row of the Spinitharini (Episinae) (fig. 23)). The basic – and most frequent – sequence of the dorsal tibial bristles is 2/2/1/2. – A trichobothrium on metatarsus IV is usually absent, usually present on III, its position is usually in the basal half of the article. – The shape of the opisthosoma is almost globular e. g. in most of the the advanced Theridiinae (which usually have a prominent epigaster in the male) but oval in the ancestral Asageninae as well as in the Enoplognathinae and Episinae (in some Episinae it is flattened as well). The hairs of the colulus: See below, the variablitity of structures. – The tarsal comb (a ventral row of serrated hairs of tarsus IV, fig. 125a) (*), an irregular capture web which has gumfooted lines as well as probably a special "theridiid tegular apophyses" are synapomorphies of Theridiidae ("Combfooted Spiders") + Nesticidae. The tarsal comb is absent or more or less modified in some theridiid taxa like Argyrodinae and certain Hadrotarsinae as well as in most fossil Nesticidae in Baltic amber. The capture web is strongly reduced in the Episinae (fig. 333) as well in most kleptoparasitic Argyrodinae and in the Hadrotarsinae; in most Argyrodinae and Hadrotarsinae a capture web is completely absent. – The cymbium is modified in the distal half, e. g. in *Achaearanea, Anelosimus*, *Coscinida, Crustulina, Echinotheridion*, several *Euryopis* s. l., *Kochiura, Latrodectus*, *Neottiura*, and *Tidarren*; see above (the paracymbium). – The ventral side of the bulbus is frequently flattened and usually directed retrolaterally (occasionally ventrally or shifted dorsally), the plate-shaped tibia and the cymbium shifted usually medially; exceptions are most Asageninae as well as some Pholcommatinae and Phoroncidiinae. – The distal part of the pedipalpus of the subadult male is usually very large, see the photo 312 (it may be similar in other families, e. g. in certain Linyphiidae). – As in most spider families the autotomy occurs usually between coxa and trochanter (photo 278), and is not rare in the fossil specimens; in extinct members of the Enoplognathinae in Baltic amber it may be absent. – Leg amputations and healing effects (e. g. the photos 1–7, 9–11, 348, figs. 261, 336) occur similar to Zodariidae and are well documented in various fossil spiders of different subfamilies like the Enoplognathinae (e. g. in *Hirsutipalpus varipes* n. gen. n. sp.), and in the Hadrotarsinae. In some fossil taxa the number of leg amputations is higher than the number of autotomized legs. Most amputations were apparently caused by ants, see the next paragraph.
Ant mimicry: See below (sexual dimorphism).
Ants is a frequent prey of the Theridiidae (photos 31–32, 35), especially of the Asageninae, Hadrotarsinae and some Episinae; fossils: See also below. (Coevolution and ants as the prey of Zodariidae and numerous taxa of other spider families: See WUNDERLICH (2004)).
Kleptoparasitism and araneophagy: See the photos 31–32 and AGNARSSON (2004: 471). Sociality – see AGNARSSON (2004: 471) – is known within some *Anelosimus* (Anelosiminae) and *Theridion* s. l. (Theridiinae). There is no sure proof of sociality in Early Tertiary spiders, but see below, the questional case in members of the genus *Ulesanis* (Phoroncidiinae), in which the number of couples in the same piece of amber is quite unusually high (similar to certain fossil Anapidae s. l.: *Balticoroma*).

The body length of Theridiidae varies usually between less than 1 mm and more than 1 cm (of fossil males between 1.2 and 3.5 mm). The smallest FOSSIL Theridiidae exists among Pholcommatinae and Phoroncidiinae; the largest are certain members of the Asageninae (e.g. *Eomysmena*) and Episinae; intraspecific variability: See *Hirsutipalpus varipes* (extinct). A strong sexual size dimorphism (female gigantism) exists in the extant genus *Latrodectus* (Asageninae) but is not known from fossil spiders.

(*) A similar comb of tarsus IV evolved PROBABLY SEPARATELY/CONVERGENTLY in Nesticidae and Theridiidae. Such a comb is also known from other superfamilies: As apomorphies of the Pholcidae (Dysderoidea s.l.) and of the Nicodamidae: Nicodaminae (Amaurobioidea?).

Subfamilies and **tribus** (provisorical arrangement): Anelosiminae, Argyrodinae, Asageninae (= Latrodectinae) (with the tribus Asagenini, Latrodectini and Protosteatodini n. trib. (extinct)), Enoplognathinae, Episinae (= Epsininae, Monetinae, Spintharinae) (with the tribus Episini and Spinitharini), Hadrotarsinae (= Dipoeninae, Euryopinae), Pholcommatinae (?Magnopholcommatini n. trib. and Pholcommatini), Phoroncidiinae and Theridiinae (which include numerous still undescribed extant tribus, and few described tribus: Achaearanini, Echinotheridiini, Theridiini, Theridulini).

Remarks on suprageneric taxa: (1) Some subfamilies are difficult to distinguish based on a single morphological character, but not if multicharacter analysis is used. Well diagnosed are the subfamilies Argyrodinae, Hadrotarsinae, and Phoroncidiinae (s. str.). Fairly well diagnosed are Anelosiminae, Asageninae and Enoplognathinae. Episinae, Theridiinae – which probably is not a monophyletic taxon –, and especially the Pholcommatinae (Magnopholcommatini may represent a subfamily of its own) are not well diagnosed. (2) Theridulini ARCHER 1950 – Theridulinae: SAARISTO (2006: 84) – may in my opinion well be a tribus of the Theridiinae. (3) Like in most other diverse families of spiders the number and the limits of certain subfamilies and tribus is dubious; AGNARSSON (2004), e.g., regarded the Enoplognathinae and – with some hesitation the Phoroncidiinae – as parts of the Pholcommatinae (s. l.); in my opinion these taxa may better be regarded as subfamilies of their own; see their diagnoses and the key to the subfamilies.

Relationships: In the Nesticidae a comb of tarsus IV and gum-footed lines of the capture web are usually present, too (it is remarkable that a comb is apparently absent in several extinct taxa of the Nesticidae of the Early Tertiary Baltic amber, see WUNDERLICH (1986)); according to CODDINGTON exists furthermore a "theridiid tegular apophyses" but – in contrast to the Theridiidae – the labium is rebordered, denticles in the cheliceral furrow, see WUNDERLICH (1986: 224: Fig. 253) (unknown in the fossil taxa), and a retrobasal paracymbium – usually large and complicated – as well as most often an epigynal scape (rarely present in the Theridiidae) exist in the Nesticidae. Furthermore the bulbus points not retrolaterally; a prosomal-opisthosomal stridulatory organ, opisthosomal scuta and a retreat are absent in all taxa of the Nesticidae (and a large colulus – which bears to my knowledge exactly two hairs – exists in all nesticid taxa). – According to ARNEDO (2004: 241) "No genetical analyses support theridiid-nesticid monophyly." (!). – In the Synotaxidae exists a retrobasal paracymbium and the labium – similar to fig. 2b – is usually rebordered to my knowledge (but not in *Synotaxus*); contra JOCQUE & DIPPENAAR-SCHOEMAN (2007: 242).

Distribution: Extant: Cosmopolitical (all subfamilies); Asageninae, Enoplognathinae and Pholcommatinae occur mainly on the Northern Hemisphere; fossil: Tertiary, e.g. Baltic, Rumanian, Ukrainean (all Eocene) and Dominican (Miocene) ambers; almost all subfamilies are present in the larger deposits of Tertiary ambers of the Early Tertiary European amber forests but Argyrodinae are not and Theridiinae are not surely known from Baltic amber (Argyrodinae are most probably completely absent in this kind of amber). Some taxa are mainly or even exclusively known from the BITTERFELD DEPOSIT (Baltic amber): Most fossil specimens of *Euryopis* MENGE (Hadrotarsinae) originate from Bitterfeld, only few from the Kaliningrad deposit and derived deposits.

Theridiid sexual dimorphisms: Body and legs of males may be stronger sclerotized than in the female sex, especially in the subfamily Asageninae. In several species of the family Theridiidae – in European ones, too – exist a sexual dimorph myrmecomorphy: The males are ant-shaped in contrast to the females, e. g. in species of *Asagena* like *meridionalis*, *Coleosoma* and some species of *Neottiura* like *herbigrada*, see WUNDERLICH (2004: 196). – Size dimorphism: As in most spiders the females are usually larger than the males; the “giant” females are much larger in members of the genus *Latrodectus* (Asageninae); the prosomal length of both sexes may be equal in members of *Enoplognatha* (Enoplognathinae), and *Steatoda* (Asageninae) or the males are even larger in these genera and their subfamilies. – The legs are usually longer and more slender in the male sex. Clasping spurs: See below.

Opisthosoma: Outgrowths exist in several genera; they are more strongly developed in the female (!) sex e. g. of *Ulesanis* L. KOCH 1872 (photos 245f, figs. 223–224) and in extant females of *Episinus* WALCKENAER 1809. In females of (e. g.) *Arctachaea*, *Coleosoma*, *Dipoena melanogaster* C. L. KOCH 1837, *Paidiscura* ARCHER 1950, and *Theridula* EMERTON 1882 the opisthosoma is – frequently distinctly – wider than in males. – In larger species – especially in species of the subfamily Asageninae – the colulus in the female sex bears usually a larger number of hairs (fig. 47); see below “variability of structures”.

Dimorphisms of the male prosoma:

(a) A strongly flattened/widened fang exists in the male sex of *Arctachaea* (fig. 499),

(b) strong dorsal furrows of the ♂-prosoma in numerous Hadrotarsinae (*Lasaeola* SIMON 1881 s.l.) (photo 275, fig.246) which are completely absent in the female sex,

(c) sexually dimorphic lobes of the male prosoma (frequently outgrowth of the clypeus, figs. below) exist – as “mating structures” – in certain members of every theridiid subfamily (probably except the Hadrotarsinae, see b): In the Argyrodinae: Very frequently in *Argyrodes* SIMON 1864 s. l. (fig. 17), in the Asageninae: *Craspedisia* SIMON 1894 and *Proboscidula* MILLER 1970 (fig. 13) (questionable Asageninae), Episinae: “Horns” in the eye region in *Episinus*, Pholcommatinae: *Carniella* THALER & STEINBERGER 1988 (fig. 19), *Globulidion* n. gen. (extinct, with a raised cephalic part., photos 224–226, figs. 7–8), and *Magnopholcomma* n. gen. (probably Pholcommatinae, fig. 21, photos 241–243), Phoroncidiinae: Protruding eye region e. g. in *Ulesanis* L. KOCH

1872 (NOT largely different from the female, figs. below), and Theridiinae: In *Cephalobares* O. PICKARD-CAMBRIDGE 1870 (with a "swollen" cephalic part), *Coleosoma* O. PICKARD-CAMBRIDGE 1882 and *Thymoites* KEYSERLING 1884 (fig. 11). Most frequent are outhgrowths within or near the eye field, especially in small or tiny spiders in which powerful secondary male genital organs exist. These outgrowths may fix a couple during copulation, and excretions of pheromone glands within hairy areas may attract the female, e. g. in *Argyrodes*, and probably in the extinct genus *Eomysmena* (Asageninae, photos 191f, figs. 3–4); the exact funtion of the outgrowth is unknown in most species.

Peculiar structures – like lobes, pits, furrows and hairy areas – of the male prosoma possess a function in the courtship and mating behaviour in spiders, see WUNDERLICH (2004: 160–172), including the production of pheromones in pits and in hairy areas which may attract females. Such lobes, pits and hairy areas evolved already in extinct Eocene members of the Combfooted Spiders (family Theridiidae), and they evolved millions of years later in a surprisingly similar way – CONVERGENTLY – in another spider family (the Linyphiidae) of the same superfamily (the Araneoidea): The advanced Dwarf Spiders (the subfamily Erigoninae). Members of this "young" subfamily are unknown from the Eocene; so all examples which are shown below concern extant spiders. (With the exceptions of an African and an American species they all occur in Europe).

From the structure and the shape of such sexually dimorphic structures in extant male linyphiid spiders – see e. g. WUNDERLICH (2004: 164, fig. 5), and the figs. below – we may conclude on the sexual behaviour of extinct theridiid spiders of the Eocene European amber forests up to 50 million years ago, which had a similar pattern (see the figs.).

In the figs. 3–22 below such pairs or triplets OF BOTH FAMILIES are grouped together in which more or less similar structures exist, which have evolved convergently, see e. g. (a) the hairy prosomal areas (figs. 3–6) in which pheromones have probably been produced; (b) the dorsal globular prosomal lobes (figs. 7–10) which may have been gripped and held by the female during copulation, see WUNDERLICH (2004: 164, fig. 5); (c) lobes, furrows and hairy areas, too, exist in the spiders which are shown in the figs. 17–18; (d) the clypeal outgrowths which are shown in the figs. 21–22 are situated in front of the anterior median eyes but their shape is different in both families. The function of these outgrowths – and the function of some others – is difficult to understand; at least some of them are used for mating.

Certain structures – compared to structures and behaviour of today's species – allow conclusions on the behaviour of extinct spiders. Parasitized spiders (photo 26) as well as spiders which are preserved as prey (photos 31f, fig. 1) – demostrate "frozen behaviour" of a world which existed 40 to 50 million years ago:

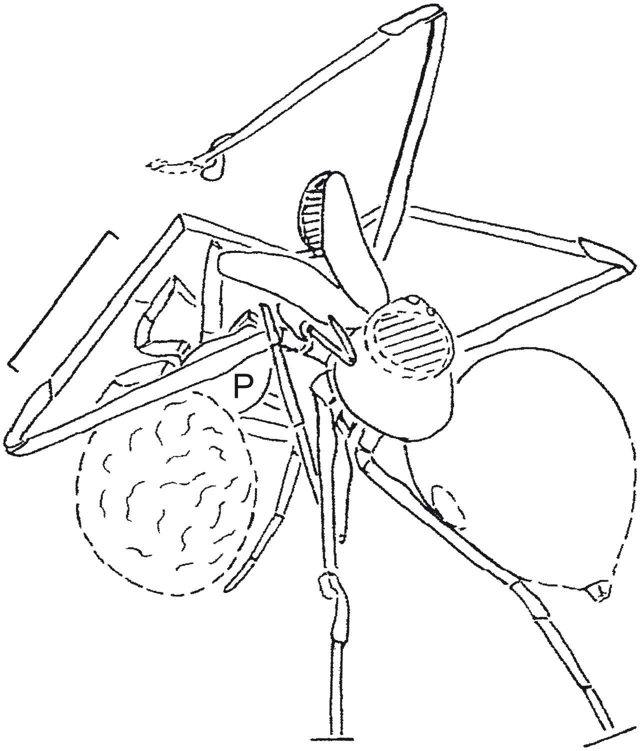
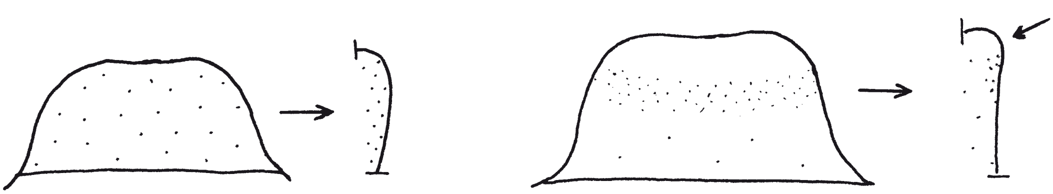
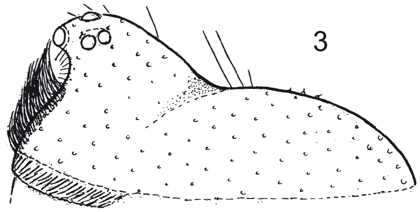


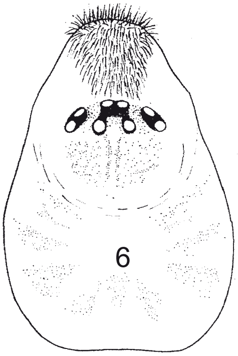
Fig. 1) A probably juvenile Combfooted Spider (Theridiidae) (P = its prosoma) as the prey of a juv. Archaeid spider (on the right side) in Baltic amber. Note the opisthosomal folds of the theridiid spider which apparently has been sucked out. The “head” of the *Archaea* is cut off. SMF (F713/CJW). Scale bar = 1 mm.



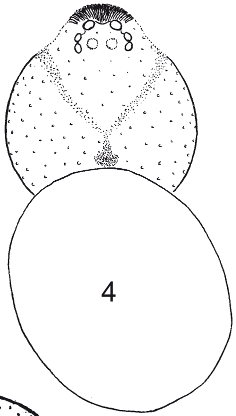
Figs. 2a–b: Ventral aspect and lateral outline (on the right side) of the labium of a theridiid and a nesticid spider in which the bulge (arrow) may be stronger developed.



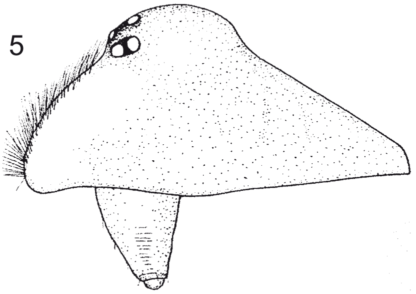
3



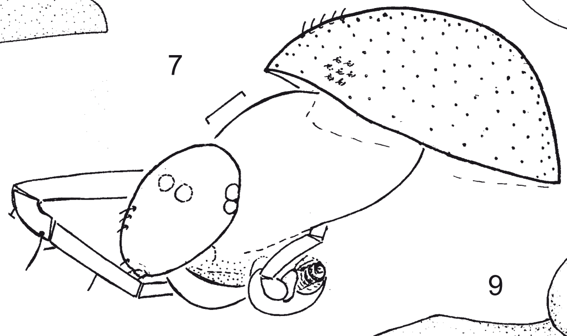
6



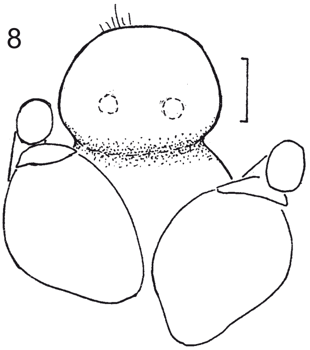
4



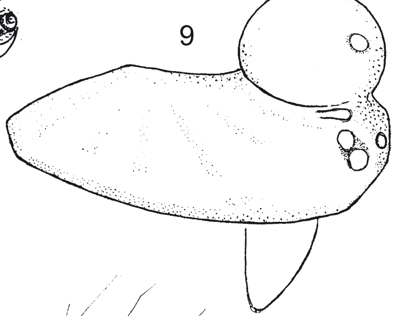
5



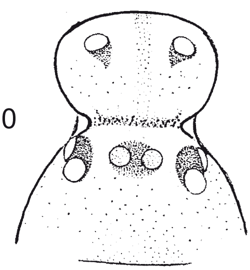
7



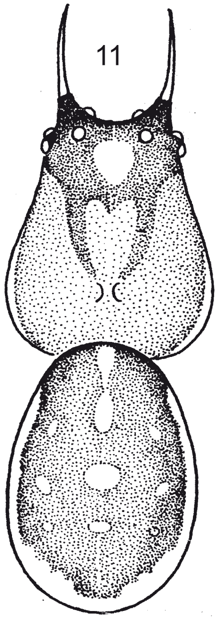
8



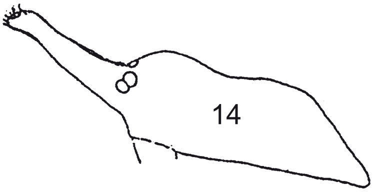
9



10

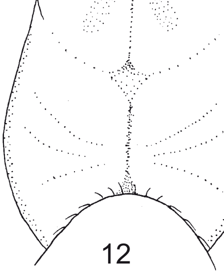


11

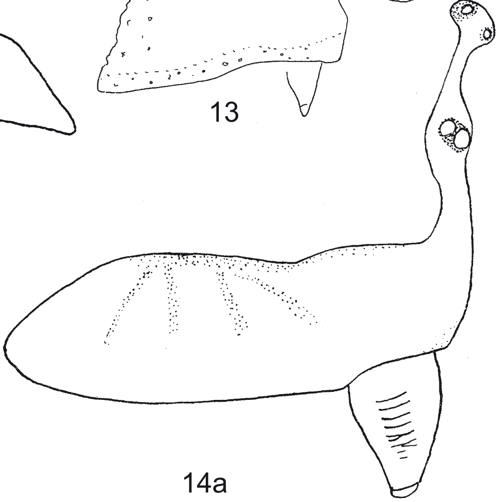


14

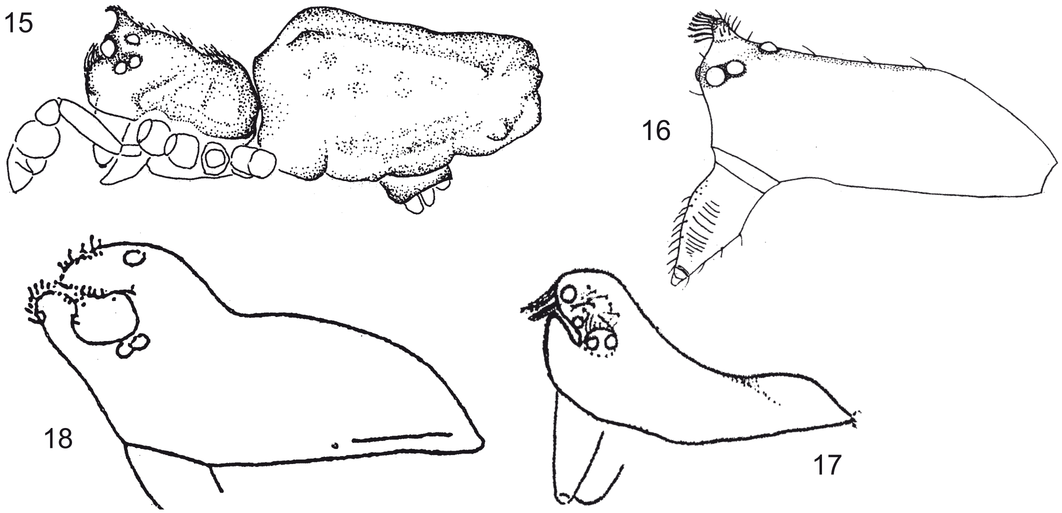
13



12



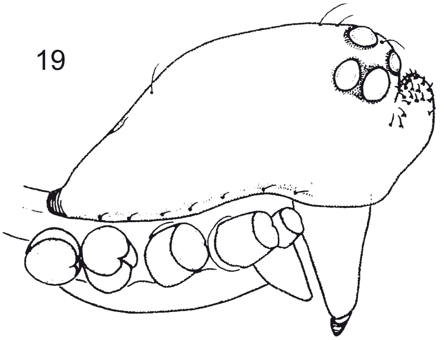
14a



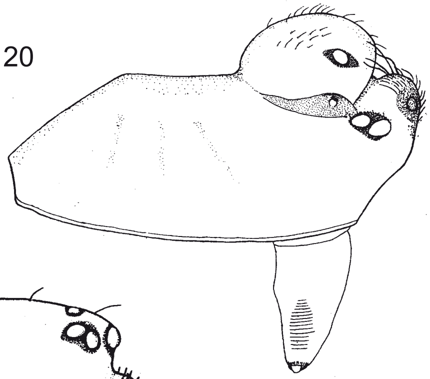
Figs. 3–22: Convergences in prosomal lobes/outgrowths of male fossil Combfooted Spiders (family Theridiidae) (figs. 3–4, 7–8, 11, 13, 15, 17, 19, 21–21a), compared with mating structures of male extant Dwarf Spiders (family Linyphiidae, subfamily Erigoninae) (the remaining figs.). Examples of convergently evolved structures in different families and in different periods: The Early Tertiary Theridiidae and the today's Linyphiidae;

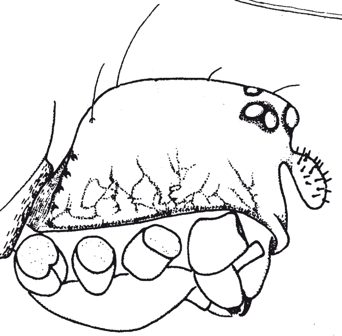
3–4) lateral and dorsal aspect of the prosoma of an undetermined species of the genus *Eomysmena* PETRUNKEVITCH (Theridiidae) in Baltic amber;
5–6) lateral and dorsal aspect of the prosoma of *Strongyliceps anderseni* HOLM 1962 (Linyphiidae) from the East African mountains. Note the field of dense hairs on the clypeus. Extant male spiders are known to produce pheromones and secretions in those fields which are attractive to females;
7–8) frontal-lateral and frontal aspect of the prosoma of *Globulidion cochlea* n. gen. n. sp. (Theridiidae) in Baltic amber;
9–10) lateral and frontal aspect of the prosoma of *Parapelecopsis nemoralis* (BLACKWALL 1841) (Linyphiidae);
11) *Thymoites wangi* ZHU 1998 (Theridiidae), dorsal aspect of the body;
12) *Panamomops mengei* SIMON 1926 (Linyphiidae), dorsal aspect of the body;
13) *Proboscidula loricata* MILLER 1970 (Theridiidae), lateral aspect of the prosoma (see fig. 21a);
14) *Savignia fronticornis* (SIMON 1884) (Linyphiidae), lateral aspect of the prosoma;
14a) *Walckenaeria acuminata* BLACKWALL 1833 (Linyphiidae), lateral aspect of the prosoma;
15) *Deelemanella borneo* YOSHIDA 2000 (Theridiidae: Argyrodinae), lateral aspect of the body;
16) *Walckenaeria corniculans* (O. PICKARD-CAMBRIDGE 1875), (Linyphiidae), lateral aspect of the body;
17) *Argyrodes crassipatellaris* WUNDERLICH 1988 (Theridiidae, extinct, in Dominican amber), lateral aspect of the prosoma;
18) *Diplocephalus crassiloba* (SIMON 1884) (Linyphiidae), lateral aspect of the prosoma;

19



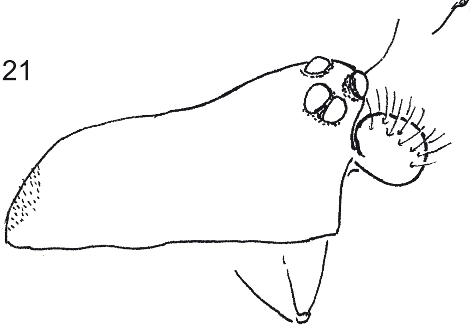
20

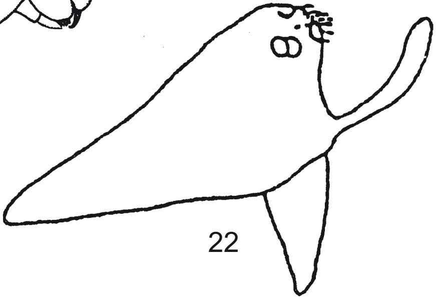




21a

21





22

19) *Carniella siam* KNOFLACH 1996 (Theridiidae), lateral aspect of the prosoma;
20) *Diplocephalus latifrons* (O. PICKARD-CAMBRIDGE 1863) (Linyphiidae), lateral aspect of the prosoma;
21) *Magnopholcomma globulus* n. gen. n. sp. (Theridiidae), lateral aspect of the prosoma;
21a) *Proboscidula milleri* KNOFLACH 1995 (Theridiidae), lateral aspect of the prosoma (see fig. 13);
22) *Scotinotylus monoceros* (SIMON 1884) (Linyphiidae), lateral aspect of the prosoma.
The body length of these spiders is 1.5 to 4 mm.
Figs. 5–6 are taken from HOLM (1962), figs. 9–10, 12, 14a, 16 and 20 from WIEHLE (1960), fig. 11 from ZHU (1998), fig. 13 from LEVI (1962), figs. 14, 18 and 22 from SIMON (1884), fig. 15 from YOSHIDA (2003), figs. 19 and 21a) from KNOFLACH (1996 and 1995).

Variability of structures (see the tab. below): A very or even extremely long clypeus exists mainly in most species of *Episinus* (Episinae), Hadrotarsinae (e. g. in *Lasaeola*), and Phoroncidiinae. – The labium: It may be fused to the sternum e. g. in certain genera of the Pholcommatinae, see this subfamily below, and in the Theridiinae, see AGNARSSON (2004: 501–502). The shape of the labium is quite different within the subfamilies; its triangular shape is NOT a synapomorphy of the Hadrotarsinae, contra

AGNARSSON (2004: 520) (*). – The colulus is very variable and completely lost together with its hairs several times convergently: In the Theridiinae as an apomorphy, in some Hadrotarsinae (e. g. in *Coscinida*), and in some (extinct) Episinae. A large colulus exists in most Asageninae – see below: "Evolutionary trends..." – and bears in larger spiders of this subfamily at least three hairs (I found up to more than ten hairs in large females of *Latrodectus* and *Steatoda* (fig. 47) (less in conspecific males), but there may be only two hairs in small or tiny Asageninae (e. g. in *Clya* and *Crustulina*). The intraspecific variability is more expressed in large species. In the extinct genus *Eomysmena* the number of these hairs varies from 3 to 5. The number of hairs of the colulus in the Asageninae increased probably in connection with the increasing body size of members of this subfamily during the Tertiary. In most theridiid taxa the colulus bears one pair of hairs (fig. 70), in certain taxa – e.g. in the Anelosiminae exist – intraspecific variable, as well – a pair of hairs or only a single hair (figs. 465–466), in *Lasaeola* and *Spinitharinus* – a single hair may exist, in fossil *Spinisinus* I did not find colular hairs, in most Enoplognathinae there are two hairs but in some species there are three hairs or only a single one (figs. 148–150). In some species of the Anelosiminae, *Euryopis* (Hadrotarsinae), and Phoronciinae (e. g. *Ulesanis*) a colulus is more or less (strongly) reduced but hairs remain.

(*) Several wrong conclusions of similar kind – e. g. on the position of the paracymbium – are drawn from the investigation of too few species within a taxon which findings are generalized overhaste. See also the following remark.

Remark: Numerous authors – e. g. AGNARSSON (2004) and/or LEVI & LEVI (1962) – noted erroneously in several genera – e. g. in *Anelosimus, Episinus*, *Pholcomma* and *Phoroncidia* s. l. – "colulus replaced by two setae" but I found – besides these hairs – a distinct colulus in most species of these genera (e. g. figs. 173, 232, 379), although the – retractile? – colulus may be sunk in as in a hole and the colular area has to dissect for a closer investigation, see below. (Formerly the existence of a colulus has already been recognized in *Anelosimus* by LEVI (1953: 410, fig. 14: "Spinnerets and colulus").

Legs: The first leg is usually the longest but in some taxa leg IV is the longest. The sequence of the dorsal tibial bristles is most often 2/2/1/2 (apparently the basic sequence in the Theridiidae and related families); in the Hadrotarsinae (see below) it may be 2/2/1/1, 1/1/1/1 or 0/0/0/0 (exceptionally 2/2/2/2). Tibial bristles are completely absent in the Argyrodinae, the Phoroncidiinae, some species of *Lasaeola* and few other taxa; their sequence may be quite variable within certain diverse genera, e.g. in *Euryopis* s. l. and *Lasaeola* s. l. or even – rarely – within the same species, in *Coscinida tibialis* (see below, Hadrotarsinae). A trichibothrium exists usually on metatarsus I–III but in few taxa – e. g. in *Carniella*, *Macaridion*, *Paidiscura, Simitidion, Theonoe,* and *Crustulina guttata* – it is absent on metatarsus III and in few genera – e. g. in *Asagena* – it exists on metatarsus IV (as a reversal?). – The unpaired tarsal claw may be longer than the paired claws, and bent in a right angle, e. g. in the subfamily Argyrodinae. – Size of the tarsal organ: See below. In *Rugathodes* and probably in *Eolyrifer* n. gen. are the teeth of the tarsal claws reduced/absent.

Body colour of the fossil spiders: In certain inclusions the original colour may be preserved if the pieces of amber were not heated. Examples are specimens of the extinct genus *Succinura* n. gen. (Pholcommatinae): Some of the spider inclusions possess a redbrown colour like most extant members of this subfamily (e. g. photo 238), other inclusions – usually heated ones – have a dark grey-brown colour of the body, and most probably the colour has been changed by heating of the amber pieces (certain specimens of the Pholcommatinae). – A red "warning colour" exists in some species of the extant genus *Latrodectus* (Asageninae).

Paracymbium: See below, and the subfamilies Asageninae, Episinae and Pholcommatinae.

The capture web of the Theridiidae (photos 39–41) is irregular (never an orbweb) and very variable. Gum-footed lines of the irregular capture web are frequent; these lines – as well as the whole capture web – may be reduced or even absent, e. g. in kleptoparasitic Argyrodinae (web reduced or even absent), in the Hadrotarsinae (web strongly reduced or – most often – completely absent) and Episininae (web reduced, H-shaped, fig. 333). In the *Theridion*-type web sensu BENJAMIN & ZSCHOKKE (2003) viscid elements are present as they are present in gum-footed lines. The *Coleosoma*-type of the capture web sensu BENJAMIN & ZSCHOKKE (2003) is a sheet web. – A retreat may be present (probably as an apomorphy of the Theridiidae in contrast to the Nesticidae): A peripheral retreat e. g. in the Asageninae, a central retreat (the *Achaearanea*-type) or a retreat is absent (it may be lost), see BENJAMIN & ZSCHOKKE (2003). Fossil theridiid females have been embedded while building their capture web (F2082/CJW and F1819/CJW), photos 40–41.

KEY TO THE FOSSIL AND EXTANT SUBFAMILIES OF THE THERIDIIDAE, with special reference to the fossil taxa in Baltic amber:

Remarks: (1) In this key I use frequently characters which may be recognizable in fossil spiders. (2) If possible: Don't use single characters but combinations of characters. (3) A colulus – as well as hairs replacing it – are completely absent in the subfamily Theridiinae, as well as in some Hadrotarsinae and in some extinct Episinae (see no. 6); its existence/absence is hard to recognize in some extant and in most fossil spiders; it may be hidden more or less by an emulsion (in fossils) or by a fold (especially in the Anelosiminae and Phoroncidiinae in which it may be retracted). (4) Further characters: See the diagnoses of the subfamilies below. Tibial bristles: See the remark 3 in the key of the Theridiinae below. (5) The diverse Episinae are divided into two tribes, see nos. 6 and 8. (6) The related families Nesticidae and Synotaxidae (but not the Cyatholipidae) are deliminated at the end of the key.

1 Dorsal tibial bristles absent (bristle-shaped hairs may be present!). Eye field strongly raised and overhanging the clypeus in both sexes (Phoroncidiinae, fig. 223) or prosoma usually with anterior outgrowth(s) in the male sex (fig. 17). Opisthosoma usually modified. Unpaired tarsal claws frequently longer than paired claws (Argyrodinae, several Phoroncidiinae). Ectal (retrodistal) position of the paracymbium (fig. 228) 2

- Dorsal tibial bristles rarely absent (e.g. in few Hadrotarsinae, *Succinura* of the Pholcommatinae), they may be indistinct. Male prosoma in some taxa with outgrowth (e. g. fig. 21, 482). Opisthosoma modified or not; unpaired tarsal claw most often distinctly shorter than the paired claws. Ectal (retrodistal) or internal position of the paracymbium 3

2(1) Opisthosoma usually long, extending beyond the spinnerets (extremely like in the photo 337; fig. 445b), and with silvery markings, soft, without hair-bearing plates, male prosoma most often with one or two anterior outgrowths (fig. 17), but body never with spines, its length usually more than 2 mm. Legs long and slender. Colulus large. Extant and Miocene Dominican amber. (A single specimen of the genus *Argyrodes* in questionable Baltic amber is most probably a fake, see the chapter on fakes above, and below). . . . . **Argyrodinae**

- Opisthosoma (figs. 221, 223, photos 245, 253) unusually voluminous, much larger than the prosoma, without silvery spots, frequently strongly overhanging the prosoma, heavily armoured, and with a large sclerotized ring around the spinnerets which hide the colulus, most often with lateral and posterior hair-bearing plates (in contrast to certain Pholcommatinae which may be similar), the tiny scuta are usually small and impressed, and/or opisthosoma with dorsal humps or spines (fig. 221). Legs stout; eye region strongly overhanging the clypeus in both sexes (fig. 223). Tiny to small spiders (body length most often 1.5–2 mm, rarely 3 mm).The shape is similar in certain Anapinae and *Praetereuryopis* (Hadrotarsinae). Extant and fossil in Baltic amber and in copal. . . . . **Phoroncidiinae**

3(1) Basal cheliceral articles unusually small (fig. 280) (*) (similar to most Phoroncidiinae), cheliceral promargin without teeth (*), fangs long and slender, prosomal stridulatory files absent. Anterior tarsi frequently thickened, and most often bearing distally-ventrally specialized hairs similar to a scopula (fig. 316). ♂: Prosoma most often very high and not rarely with deep dorsal furrows (*Lasaeola*, photo. 265, figs. 246, 256), paracymbium in an internal position. ♀: Pedipalpal claw frequently large and modified/toothed/obliquely bent, vulva in almost all species with two pairs of receptacula seminis (photo 283, fig. 302). Extant and fossil in Tertiary resins. . . . . **Hadrotarsinae**

- Basal cheliceral articles of normal size (figs. 392, 445b) or even large, rarely unusually small (fig. 371), fangs variable, promarginal cheliceral teeth and prosomal stridulatory files present or absent. ♂: Prosoma variable, low or high, a single longitudinal deep fovea may be present. Specialized hairs of the anterior tarsi absent, claw of the ♀-pedipalpus not modified. Position of the paracymbium internal or ectal. ♀: Vulva with a single pair of receptacula seminis. Extant and fossil 4

4(3) ♂-opisthosoma of several – and all known fossil – taxa covered by a large and frequently circular scutum (photos 238–239) (compare Phoroncidiinae, in which usually small or large and hair-bearing plates (scuta) exist, photo 245); if a dorsal scutum is absent in both sexes (**) – e. g. in the extant genera *Carniella* and *Theonoe* – the anterior median eyes are usually distinctly smaller than the other eyes. In several taxa the male clypeus bears an outgrowth (e. g. figs. 7–8). – Usually tiny and short-legged spiders with a body length of 1–2 mm, colour of body and legs usually red- or orange-brown, position of the paracymbium usually on the ectal cymbial margin as in the Phoroncidiinae (fig. 234) (but not in the extinct genera *Succinura* n. gen. and *Vicipholcomma* n. gen. which relationships are unsure), usually tapering similar to Enoplognathinae (no. 7). Extant and fossil in Tertiary ambers. . . . . **Pholcommatinae**

- COMBINATION of characters different: Opisthosoma dorsally most often soft; if dorsally armoured has the scutum usually an oval shape (e. g. in the fossil genus *Hirsutipalpus* (Enoplognathinae), and certain Asageninae). – Remaining characters variable; the male clypeus bears only very rarely an outgrowth (or a pair of outgrowths), e.g. in the extant genus *Thymoites* (fig. 11). Tiny to large spiders. Extant and fossil. 5

5(4) Colulus with 2 (in small spiders) up to >10 hairs (fig. 47), >3/5 hairs in male/female *Latrodectus*. Prosoma dorsally – and the sternum as well – most often rugose/wrinkled (photos 190f, 197, figs. 36, 38, 108) (similar to some of the tiny Phoroncidiinae and certain Pholcommatinae in which prosomal stridulatory files are absent or strongly reduced in contrast to the distinct files of the Asageninae, fig. 38, except the Latrodectinae), at least some articles of the anterior legs and/or of the pedipalpal femur with ventral cusps (figs. 28, 146, photos 190f) (the extant genus *Latrodectus* is one of the rare exceptions). Position of the paracymbium internal or ectal (figs. 34, 41, 37), in the fossil taxa in Baltic amber always ectal (fig. 63). Extant and fossil . . . . . . **Asageninae**

- Colulus as well as colular hairs completely absent (Theridiinae, some Episinae) or colulus present, bearing usually a pair of hairs, rarely a single or 3 hairs. Prosoma very rarely rugose, legs usually without ventral cusps (but see Anelosiminae). Position of the paracymbium variable (internal or ectal). Extant and fossil 6

6(5) Legs “spiny”: Either (usually) tibia I with strong prolateral hairs and – at least in the male – with a strong proapical bristle (photo 324, figs. 435, 437) (except in one species) or (very rarely) metatarsus I with long and strong prolateral bristles only (fig. 441). ♂-pedipalpus with short articles. Fossil in Baltic amber (see no. 8) . . . . **Episinae** part 1: The extinct tribus **Spinitharini**

- Tibia I without strong prolateral hairs or a proapical spine-shaped bristle; metatarsus I without spine-shaped bristles. ♂-pedipalpus with long or short articles. Extant and fossil 7

7(6) Colulus present and large; it bears 1–3 hairs (figs. 148–150). Posterior margin of the cheliceral furrow with few teeth or denticles. Sequence of the tibial bristles variable. ♂: Basal cheliceral articles usually quite large, with at least one large(r) promarginal tooth (figs. 156–157) (see also fig. 137, Asageninae?). Paracymbium in an RETRO-ECTAL position and spine-shaped tapering (figs. 153, 166) (similar to most Pholcommatinae). Extant and fossil in Baltic amber . . . . **Enoplognathinae**

- Colulus present, frequently distinctly reduced, in certain Anelosiminae and Episinae hidden (sunkdown), bearing 1–2 hairs. Posterior margin of the cheliceral furrow usually bearing at least a single tooth. Sequence of the tibial bristles variable. ♂: Basal cheliceral articles fairly large in some Anelosiminae. Paracymbium in an INTERNAL position (hidden within the cymbium, figs. 48, 52, 492, 540). Extant and fossil in Tertiary ambers. 8

- Colulus as well as replacing hairs COMPLETELY ABSENT. Posterior margin of the cheliceral furrow TOOTHLESS. Sequence of the tibial bristles usually 2/2/1/2, rarely less (e. g. 1/1/1/1 in *Macaridion*). ♂: Basal cheliceral articles rarely enlarged and very rarely with a large tooth on the anterior margin of the cheliceral furrow (fig. 564). Paracymbium hidden, usually hood-shaped (fig. 472), in *Tidarren* hooked. Extant, very frequent and most diverse; two questionable genera in Baltic amber . . . . **Theridiinae**

8(7) Opisthosoma usually dorsally with a wide longitudinal dark band (fig. 450; unknown in the fossils), longer than wide or wide as long, not flat, the posterior cheliceral margin bears at least two small teeth, colulus small or tiny, bearing 1–2 usually very long hairs in a distal position (figs. 465–469), sequence of the tibial bristles in extant taxa 1/1/1/1 but 2/2/1/2 in the single known fossil genus *Kochiuridion*. ♂: Ventral hairs of metatarsus and/or femur I frequently with thickened bases or with spine-shaped bristles (fig. 451). Pedipalpus (e. g. fig. 453, 460): Cymbium usually modified (e. g. elongated), embolus frequently strongly coiled; ♀: Epigyne without a large pit, frequently wide and with furrows, occasionally with a posterior outgrowth (parmula). Fossil in Baltic amber (*Kochiuridion* n. gen.) and extant (*Anelosimus*; in Europe *Kochiura* and *Selima*) . . . . **Anelosiminae**

- Opisthosoma usually without a longitudinal dorsal band, distinctly longer than wide and IN EXTANT SPECIES usually flattened (except in *Twaitesia*) as well as with humps and/or widened posteriorly (fig. 391) (oval in the fossils; photos. 301, 303), posterior cheliceral margin usually toothless, colulus usually large (it may be hidden), and with a pair of hairs (fig. 386), sequence of the tibial bristles always 2/2/1/2. ♂: Ventral hairs of metatarsus and femur I without a thickened base. Cymbium rarely modified, embolus not coiled; ♀: Epigyne with a large pit (e. g. as in fig. 381). See no. 6. Fossil and extant . . . . **Episinae** part 2: Tribus **Episini**

- – – – – – – – – – – – – – – – – – –

- Similar, comb of tarsus IV usually existing like in most Theridiidae (***), but with a large retrobasal paracymbium which usually is multisectional; prosomal stridulatory files absent. Fossil (Eocene European ambers, ****) and extant . . . family Nesticidae

- Similar, but comb of tarsus IV absent, and retrobasal paracymbium present (it may be small and is usually not multisectional but may be bipartite); posterior prosomal stridulatory files rarely present. Eocene ambers (****) and extant. . family Synotaxidae

---

(*) Rarely different : In the genus *Coscinida* SIMON 1894 (e. g.) exists exceptionally larger chelicerae (figs. 327, 428), and a promarginal cheliceral tooth may be present, but two pairs of receptacula seminis exist (fig. 332), and long legs IV; ♂-pedipalpus : Figs. 326, 329–330.

(**) The extant Australian genus *Magnopholcomma* n. gen. (Magnopholcommatini) (figs. 212–220) is not included here. Its relationships are quite unsure; some of its characters are similar, others are quite different from the “normal” tiny and frequently armoured Pholcommatinae: The body length of Magnopholcomma is 4 mm, the anterior median eyes are large, the legs are fairly long, and a dorsal opisthosomal scutum is absent.

(***) A comb of tarsus IV evolved convergently in spiders of the families Pholcidae (quite difficult to recognize in fossils), and in the Nicodamidae: Nicodaminae (fossils unknown).

(****) See WUNDERLICH (2004).

PHYLOGENETICS

See also above: “Remarks on evolution...” in the introduction, the paragraph “convergences”, and below, the subfamily Asageninae.

Origin/age of the family Theridiidae and its diversifications; co-evolution.

Unfortunately we still know little about – especially Upper – Cretaceous and about Palaeocene spiders. The geological oldest sure Theridiidae are known from the Eocene European (incl. the Baltic and Ukrainean) amber forests. According to PENNEY et al. (2003) the origin of the Theridiidae has – “theoretically” (!) – to date back to the Early Cretaceous. (Apparently this was concluded by the so-called “proof” of a fossil Linyphiidae in the Early Cretaceous (!) as a related taxon). Actually – according to WUNDERLICH (2004: 1299) – the single specimen of the supposed linyphiid spider is not a member of the Linyphiidae but most probably a member of the family Zygiellidae (Araneidae s. l.). I doubt strongly the “conclusion” of PENNEY et al. (2003) about the oldest Theridiidae. The origin of the family Theridiidae may be much later than in the Early or Middle Cretaceous; see also MARUSIK & PENNEY (2005: 202).
I suppose that the main diversification of the Theridiidae – like other ecribellate families of the Araneoidea besides the Araneidae and Zygiellidae – happened in the same geological period as the main diversification of the ants: During the Early Tertiary, the Eocene, and probably the Palaeocene. Not a single surely identified theridiid spider has been reported from the Cretaceous; see the paper no. 5 on Cretaceous spiders. I suppose that we will discover Cretaceous theridiid stem taxa and/or their sister groups which evolved theridiid characters step by step during this geological period, the Cretaceous. The fossil family Protheridiidae WUNDERLICH 2004 in Baltic amber may be related to such a stem taxon; it has been reported from Baltic amber, and recently in Early Cretaceous amber (questionable), see the paper no. 5 on Cretaceous spiders in this volume. – Regarding the subfamily Theridiinae – which is most diverse today, and known from the Miocene Dominican amber forest –: There is no evidence of an earlier diversification than during the existence of the Eocene Baltic amber forest.
Numerous extant Theridiidae feed on ants; by far ants is the most frequent prey of Eocene Theridiidae (as well as of other spider taxa in Baltic amber; see the material below, the photos 31, 32, 35, and WUNDERLICH (2004, e. g. co-evolution with ants, pp 89f, 186f and 267f). Especially members of the Hadrotarsinae – which lost their capture web – feed on ants, see e. g. CARICO (1978). Other Theridiidae like Episinae evolved special capture webs – which possess gum-footed lines – to catch worker ants. The ancestral Asageninae – as well as Phoroncidiinae and several Pholcommatinae (in the male sex) (photos 222ff) – evolved heavy sclerotizations of body and legs which may be helpful in defending aggressive ants (the extant members of the genus *Latrodectus* are exceptions; they feed e. g. on large beetles); the hardened or armoured body may be an apomorphic adaptation of the ancestral Theridiidae to their dangerous prey. Armoured body and legs are absent in the Episinae and are very rare in the advanced subfamilies of the Theridiidae: Anelosiminae, Argyrodinae, Hadrotarsinae, and Theridiinae.

SUBFAMILIES: In contrast to several other diverse spider families – like Linyphiidae and Salticidae – almost all of the main theridiid branches are reported from the Early Tertiary; Argyrodinae are most probably absent, and the proof of the Theridiinae is questionable.

Evolutionary "trends", convergences, reductions and reversals; geologigally oldest proofs of peculiar structures and behaviour

Comparing spiders of the Eocene Baltic amber forest with the Miocene Dominican amber spiders and with extant species we find several differences in morphological structures, ecology and behaviour which may reflect "evolutionary trends or tendencies" (*) (and several convergences, too); e.g. increasing of body size, reductions of the colulus (and its hairs), retromarginal cheliceral teeth and gum-footed lines of the capture web; shifting from the – ancestral – ectal retrodistal/marginal position of a weakly sclerotized paracymbium to an intracymbial (internal), strongly sclerotized and hook-shaped or hood-shaped structure:

(*) A "trend" (or "tendency") in the sense of the present author is regarded as "a line of characters" following a particular type of modulation, which is not predetermined, and can be recognized from its final stage. It is the disposition for the multiple convergent evolution of morphological structures which have a similar function (or a similar behaviour or ecological preference); see below: b–g.
(The "parallel evolution" of the orb web from a "pre-orb web" in the "Cribellate branch" and the "Ecribellate branch" of the superfamily Araneoidea I regard as a special case of convergent evolution).

(a) Shifting of the habitat/stratum preferences. Most extant members of the Asageninae live near the ground, numerous spiders occur under stones. Apparently in contrast to this ecological pattern I found numerous specimens of seven genera of this subfamily in Baltic amber; most fossil spiders possessed long or fairly long legs, and some are quite frequently preserved in the Baltic amber. From this findings I conclude (1) that numerous Asageninae were dwellers of higher strata of the vegetation (probably on bark, too) in the Early Tertiary and (2) that the preference in this subfamily shifted from higher strata to strata of litter layers on the ground during the Tertiary Period. Probably the competition of members of the diverse derived subfamily Theridiinae – which diversified in the Middle Tertiary – caused this change. – The situation may be similar in the Episinae which today outside the tropics prefer lower strata of the vegetation. In the Baltic amber the members of this subfamily were so frequent that we may conclude that several Episinae species of the Baltic amber forest were dwellers of higher strata of the vegetation. Unfortunately we still do not know Early Tertiary amber species of the family Theridiidae besides the European amber forests. – See also below: "Ecology, ethology and frequency,...". – The ancestors of the Theridiidae may have survived the K-T boundary events as dwellers on the ground, and their theridiid descendants invaded heigher strata of the vegetation.

(b) Increasing of the body size during the Tertiary and sexual dimorphism (see WUNDERLICH (2004: 261) (Araneidae, Zygiellidae) and Segestriidae (this vol., above); sexual size dimorphism: See above and below). – We do not know the largest spiders of the Baltic amber forest, only the largest spiders which have been captured by the fossil resin (body length ca. 2 cm). Large spiders could escape from the sticky resin. A comparison of spiders in Baltic amber with extant spiders shows clearly that (1) most of the extant spiders are larger than the fossils, and (2) the average of the extant spiders is distinctly larger than the average of their fossil relatives. Aparently in the Asageninae and in certain genera of other subfamilies – as *Episinus* of the Episinae (*Monetoculus* n. gen. from Malaysia is a rare exception) – the smallest members became extinct during the Tertiary. I take male Asageninae as an example:

Body length of extant Asageninae: 1.5 mm (*Crustulina*) – ca. 8 mm (e.g. *Steatoda* sp.);
body length of fossil Asageninae: 1.4 mm (*Nanosteatoda*) – 4 mm (♀ of *Eomysmena*),

Extant Asageninae are rarely only about 2 mm long, usually longer; I regard their medium size being about 4.8 mm;
fossil Asageninae in Baltic amber are most often about 2 mm long or smaller; I found their medium size being about 2.3 mm.
The average and also the maximum of the body length of the extant Asageninae are about twice the length of their fossil relatives in Baltic amber (and both are similar in other theridiid subfamilies).

Remarks: (1) Most Asageninae – except the mainly tropical Latrodectinae, which are unknown in Baltic amber – occur in temperate and subtropic regions which are similar to the clima zones of the Baltic amber. – (2) The largest fossil Asageninae may have been dwellers on the ground and were not embedded in the fossil resin because of their larger size and their habitat. Therefore CONCLUSIONS IN THIS MATTER ARE UNSURE.

PENNEY & LANGAN (2006) found 2.6 mm as the average size (length) of the body in Theridiidae of the Baltic amber forest, but I found only 2.1 mm. These authors used only the formerly described material. In former times tiny spiders were more often overlooked than today, and thus the larger size which was published by these authors is most probably simply caused by the differing selection of material. PENNEY & LANGAN found a large difference between the body size of Theridiidae in Dominican amber (1.8 mm in average) and in Baltic amber (2.6 mm), and concluded on differences of the palaeo-oecosystems and the structure of higher strata of the vegetation, but their conclusions seem quite doubtful to me if compared with my findings of a body size of only 2.1 mm in web-building Theridiidae of the Baltic amber forest. (In this statistic members of the Hadrotarsinae which are not dwellers of capture webs have to exclude). Furthermore one has to consider that the Baltic amber forest was a mixed forest of coniferous trees and deciduous trees – in which ballooning spiders most probably were easily able to moove from non resin-producing leaf-trees to resin-producing needle-trees – in contrast to the Dominican amber forest which included predominantly more open habitats. Finally dwarfism is to my knowledge – independently of the type of the ecosysteme – basicly more pronounced in tropic regions (like the area of the Dominican amber forest) than in non-tropic regions.

Latrodectus is an extant genus of the Asageninae in which a female "gigantism" evolved. Such a huge sexual size dimorphism is unknown in fossil Theridiidae (in which most members are only known from males!) as well as in other Early Tertiary spiders up to now (probably it existed in the Araneidae: Nephilinae).

The stronger sclerotization in the male sex of certain Asageninae (and the stronger denticles on their legs) – as well as the more distinct myrmecomorphy in males of the extant genus *Coleosoma* O. PICKARD-CAMBRIDGE 1882 (Theridiinae) – may be caused by the pressure of selection. Ants are more dangerous to the more vagile male spiders (during their search for females in mating periods) than to females.
(Ants were (and are) a prey of numerous Asageninae (see below, e. g. an ant as the questionable prey with a male of *Eomysmena* sp. indet., F1715/CJW).

A sexual dimorphism of the chelicerae exists within several theridiid subfamilies; in various Asageninae and Enoplognathinae (e. g.) the male – clasping – chelicerae are more or less diverging and bear one or several large(r) teeth on the promargin, e.g. in *Phylloneta*. In *Protosteatoda* n. gen. (fig. 137) (Asageninae) and in *Hirsutipalpus* n. gen. (figs 156–157) (Enoplognathinae) I suggest such a sexual dimorphism although the female is unknown; in males of the related extant and "advanced" extant genus *Enoplognatha* PAVESI (Enoplognathinae) this "tendency" leads to conspicuous enlarged and diverging male chelicerae which bear at least one large promarginal tooth in contrast to the females. – See also the sexual dimorph fangs in the extant genus *Arctachaea* which may indicate different kinds of prey in both sexes.

(c) A distally widened opisthosoma which bears humps within the genus *Episinus* (Episinae) may well be a kind of CAMOUFLAGE and is frequent in extant spiders (fig. 333), and *Theridula* (Theridiinae, fig.); colour markings including "eye spots" and outgrowths may camouflage or mask the spiders body, as well as in Miocene Episinae of the Dominican amber forest – see WUNDERLICH (1988) – but it is ABSENT in all congeneric species of the Baltic amber forest. Probably these opisthosomal patterns evolved only during the Oligocene within about twenty million years between the existence of the Baltic and the Dominican amber forests. So the knowledge of fossil taxa can complete and even change the diagnosis of extant taxa. – The existence/absence of opisthosomal humps of certain members of *Episinus* is also known from the Archaeidae: Archaeinae and the Mimetidae: Mimetinae: In several extant taxa of these subfamilies opisthosomal humps exist but in the fossils of the Baltic amber forest they were still absent (*Baltarchaea* is an exception), see WUNDERLICH (2004). – Dorsal opisthosomal humps existed already in Eocene members of the genus *Ulesanis* which are quite similar to extant relatives: There are no differences, see the figs. and the photos 245f. In the fossil species of this genus – like in extant spiders – the opisthosomal humps are – sexually dimorphic – stronger developed in the female sex.

(d) An armoured/sclerotized body with a dorsal opisthosomal scutum at least in the male is best developed in ancestral subfamilies, in Phoroncidiinae, most Pholcommatinae, and several Asageninae (see above). It was already well developed in the Eocene relatives. Such sclerotizations exist also in some fossil Enoplognathinae but are absent – lost? – in all Anelosiminae and Episinae, all extant Enoplognathinae, as well as in most members of Argyrodinae, Hadrotarsinae (but see *Praetereuryopis*!) and Theridiinae. In the extant genus *Latrodectus* (Asageninae) the body is not strongly sclerotized; in this – derived and probably geologically young – genus the sclerotizations (as well as femoral cusps) probably have been lost as reversals. A sclerotized epigaster exists in numerous taxa, a ring around the pedicel – which may bear stridulatory picks – is not rare and exists in several theridiid taxa; it was most strongly developed in the Phoroncidiinae, already in the Eocene spiders, see the photos 245f.

(e) Colulus (see also above: "Variability of structures", and below: "Intrafamiliar relationships..."): Most fossil theridiid spider species in Miocene Dominican amber and most extant theridiid spider species – e. g. members of the subfamily Theridiinae and *Coscinida* – have completely lost a colulus as well as hairs of the colulus. In contrast to that almost all (!) of the Baltic amber Theridiidae possess a hairy colulus (e. g. figs. 70, 128, 221, 459) (because of an emulsion or of its position in most fossil specimens a colulus is not or not well recognizable). In the tiny and armoured Phoroncidiinae and in some Anelosiminae a colulus is reduced; it may be sunk down, and may drop completely out of sight in the normal position or may be partly replaced by two hairs (fig. 232). – Basicly an additional third colular hair probably existed.

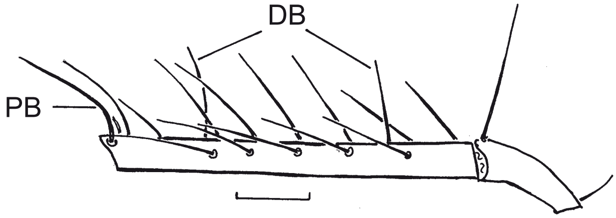
Remark on the colulus of extant taxa: LEVI & LEVI (1962) stated erroneously that several theridiid genera – e. g. *Pholcomma, Episinus* and related genera – have the colulus replaced by two hairs (setae) but according to my investigations a well developed colulus exists in these genera, and a small or tiny colulus exists also in *Anelosimus* s. l. and *Ulesanis* (fig. 232) (but not in *Coscinida*).

(f) Strong hairs and spines of the anterior legs, prey capture behaviour and clasping spines. In certain taxa of the superfamily Araneoidea s. str. the spiders watch for prey in a "sit-and-wait position" in the manner of Crab Spiders (Thomisidae), or the spiders search actively (mooving) for their prey – as do spiders of the family Mimetidae (figs. 26, 27). In such spiders strong ventral or prolateral bristles or even spines ("macrosetae") of the anterior (and second) leg(s) have been evolved IN BOTH SEXES. Strong VENTRAL bristles – usually paired – evolved in numerous families, e. g. in the Thomisidae and in males of the theridiid species *Proboscidula milleri* KNOFLACH 1995 (fig. 29; see below, questionable "clasping spines"). Strong PROLATERAL bristles evolved in the Mimetidae (fig. 26) latest in the Eocene (apparently they were lost in several taxa, see WUNDERLICH (2004: 1249ff)) and evolved sporadically in different families, e. g. in *Arkys* WALCKENAER 1837 and *Testudinaria* TASZANOWSKI 1879 (both Araneidae), see LEVI (2005), *Chthonos* CODDINGTON 1986 (Theridiosomatidae) (fig. 25), *Ophrynia* JOCQUE 1981 (Linyphiidae) (only in the male sex!), the extinct genus *Anameta* WUNDERLICH 2004 (Tetragnathidae) (females unknown), and in the Theridiidae: Episinae: Spinitharini (photo 324, figs. 23–24; probably existing in the male sex only, see below). Members of the Mimetidae – and probably of *Chthonos* and of the extint Spinitharini, too – lost their capture web.

In four fossil genera of the new described tribus Spinitharini – *Caudasinus* n. gen., *Spinisinus* n. gen., *Spinitharinus* n. gen., and *Mimetidion* n. gen. – exist strong prolateral hairs, bristles or spines, and/or a proapical spine on the anterior tibia at least in most males, figs. 23–24, photo 324 (these structures have not been found in fossil females up to now). These hairs, bristles and spines of the Spinitharini – they are unique in this position among members of the family Theridiidae although THIN long prolateral hairs of tibia I exist in several theridiid taxa as *Balticoridion* n. gen. – may well have played a role in the prey capture behaviour of the fossil spiders, similar to the Mimetidae, and these fossil spiders probably lost their capture web also in this connection convergently to members of the Mimetidae. The reduced capture web of the ancestral Episinae could well be a (prae-)disposition to a – hypothetical – complete loss of the capture web in the extinct Spinitharini. The existence of a mediograde "sit-and wait position" in certain fossils of the Spinitharini of the genera *Spinisinus* (e.g. *parvioculi*) and *Spinitharinus* (*coniectens* and *curvatus*) (see the photo 318) may be hints to the mimetidae-like method of their prey capture behaviour – and a loss of their capture web, too –, although in related other fossil spiders – as in the male of *Caudasinus* sp. indet. – the leg position is quite different: The anterior legs are stretched out foreward, see the photo 334. This was PROBABLY NOT the peculiar prey catching position in this specimen and species, but this may have been an unnatural position which was caused by its dying on a layer of the sticky resin. – Because of the probable absence of proapical spines of tibia I in the conspecific females this spines may be regarded in a quite different sense as "clasping spines" which probably helped to fix the position of a mating couple. More fossil females of this tribus are needed to confirm one of these suggestions.

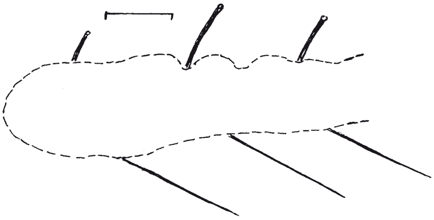
Clasping spines/spurs are rare in the Theridiidae. I regard the spines of the male leg I in *Proboscidula milleri* KNOFLACH 1995 (fig. 29) (questionable) and in *Phoroncidia ?aculeata* WESTWOOD 1835 as clasping spines, see WUNDERLICH (2004: 1851, fig. 20). A (clasping?) spine exists on metatarsus I in *Ariamnes attenuatus*, see AGNARSSON (2004: fig. 35 D). See also the extinct genus *Mimetidion* (fig. 24) (Episinae: Spinitharini). The function of the strong ventral cusps of the legs in several members of the Asageninae (already existing in the Eocene fossils, fig. 146) – besides the clasping spurs in *Asagena* (fig. 28) – is unknown to me. Because of their existence on posterior legs, too, their function as clasping structures appears not sure to me. Does males of these taxa capture another kind of prey than the females or capture their prey in a different way or mate in an unusual position?

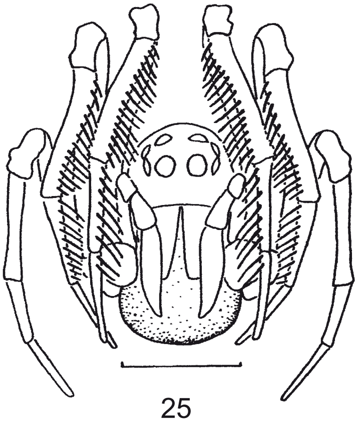
See also the metatarsal bristles in the extant genus *Anatolidion* n. gen. (Theridiinae), fig. 491.



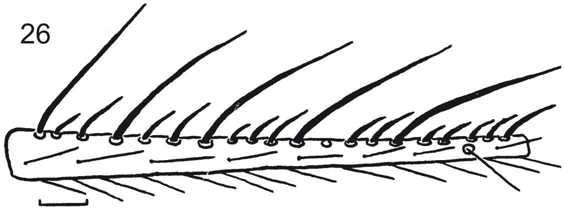
23

24

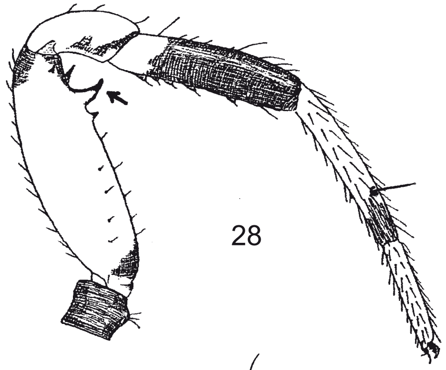




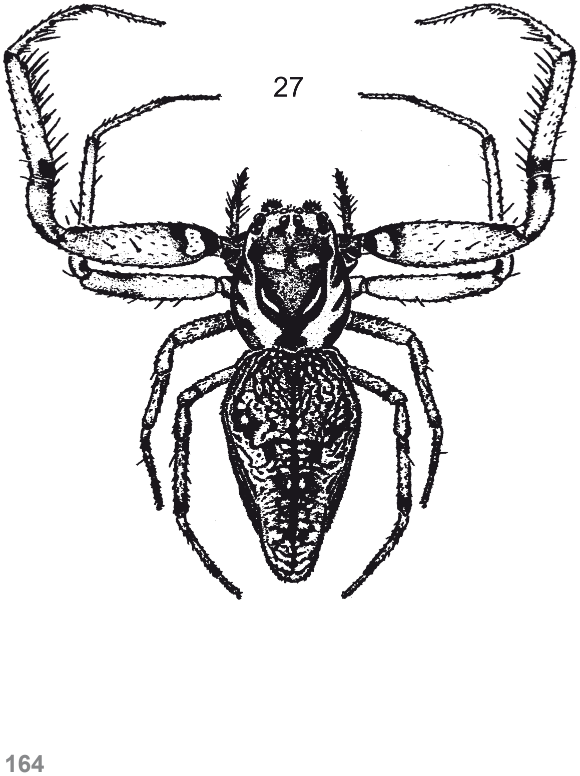
25



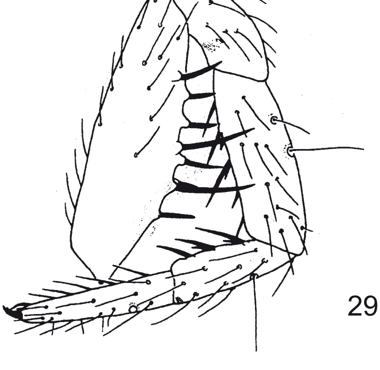
26



28



27



29

Figs. 23–29: Bristles, spines, cusps and spurs in extinct and extant taxa of the Theridiidae (figs. 23–24, 28–29), and – for a comparison – of selected other families of the superfamily Araneoidea (figs. 25–27). Most of the structures evolved convergently.
23) Prolateral aspect of the male patella and tibia I of *Spinisinus parvioculi* n. gen. n. sp. (Theridiidae: Episinae: Spinitharini, extinct) (DB = dorsal tibial bristles, PB = strong proapical tibial bristle);
24) dorsal aspect of the basal part of the r. metatarsus I of *Mimetidion furca* n. gen. n. sp. (Theridiidae: Episinae: Spinitharini, extinct). The distal parts of the strong prolateral bristles – three are drawn – are cut off with the amber material;
25) Anterior aspect of a specimen of *Chthonos pectorosa* (O. PICKARD-CAMBRIDGE 1882) (Theridiosomatidae, extant). Note the strong prolateral bristles on legs I–II; taken from CODDINGTON (1986);
26) dorsal aspect of the r. tibia I of *Ero* sp. (Mimetidae, extant and extinct);
27) dorsal aspect of a specimen of *Oarces reticulatus* (NICOLET 1849) (Mimetidae, extant); taken from PLATNICK & SHADAB (1993);
28) posterior aspect of a male right leg II (!) of *Asagena phalerata* (PANZER 1802) (Theridiidae: Asageninae, extant). Note the ventral-distal femoral spur (arrow); taken from WIEHLE (1937);
29) lateral aspect of a male leg I of *Proboscidula milleri* KNOFLACH 1995 (Theridiidae: Pholcommatinae, extant) with strong ventral bristles on femur, tibia and metatarsus; taken from KNOFLACH (1995).

(g) Pedipalpal structures. According to SAARISTO (1978) the homology of several theridiid bulbus sclerites is unsure; e. g. the "functional conductor" may have different origins in various genera; occasionally there exist two conductors like in *Ohlertidion ohlerti* (THORELL 1870). SAARISTO used the term "terminal apophysis" in a topographic sense instead of "radix" sensu LEVI & LEVI (1962). Like the "median apophysis" sensu LEVI & LEVI (1962) basicly two structures may come in consideration: One bears a sperm duct (the "locking apophysis A"), the second one is called the "locking apophysis B" by SAARISTO and LEVI in UBICK et al. (2006: 235). In fossil spiders it is even more difficult to name sclerites of the bulbus and I am unsure about my correct identification of certain sclerites; see also AGNARSSON (2004).
An elongated, circular to even spiral embolus has been evolved convergently in numerous extant taxa of almost all theridiid subfamilies (as well as of most other more diverse entelegyne spider families), and already in Eocene Theridiidae. Within extant Theridiidae this pattern is most striking in the extant genus *Latrodectus* (Latrodectinae) (fig. 46). In fossil Theridiidae I found a long and more or less circular/spiral embolus in *Episinus* (fig. 365), *Spinisinus* (fig. 401) (Episinae), *Clya* (Asageninae) (fig. 94) as well as in *Globulidion* (fig. 89), *Succinura* and *Vicipholcomma* (Pholcommatinae) (fig. 203), and *Kochiuridion* (Anelosiminae) (fig. 460). – Among spiders of the family Synotaxidae a spiral embolus has been evolved already in the Early Tertiary spiders of the Baltic amber forest, too, e.g. in the genus *Acrometa*, see WUNDERLICH (2004: 1222, fig. 3); see also certain members of the families Archaeidae, Anapidae s. l., Corinnidae, Sparassidae, Trochanteriidae and Salticidae. – The paracymbium: See above and below: Asageninae, Episinae and Pholcommatinae.
A retrolateral cymbial bristle evolved convergently within the Hadrotarsinae (some species of *Lasaeola*), and two times within the Episinae (*Moneta* and *Monetoculus* n. gen.) (figs. 382, 394).

Intrafamiliar relationships, evolution of the higher theridiid taxa, and on certain evolutionnary directions ("trends")

According to AGNARSSON (2004) HADROTARSINAE is the MOST ANCESTRAL TAXON of the Theridiidae, the sister group of the remaining theridiid taxa or even a family of its own. But – according to the absence of several typical theridiid characters (most are only PUTATIVE theridiid autapomorphies, see below), as well as the presence of several apparently DERIVED theridiid characters of this subfamily – e.g. the absence of a capture web, a prosomal-opisthosomal stridulatory organ, a retrodistal (marginal) paracymbium, the presence of very small basal cheliceral articles, two pairs of receptacula seminis, grouped flat tipped ventral setae of tarsus I, as well as modified hairs of the comb of the tarsus IV, and a modified claw of the female pedipalpus – I regard the Hadrotarsinae far more derived than the Asageninae which possesses – at least basicly – a well developed comb of tarsus IV, a stridulatory organ with conspicuous files, a large retrodistal paracymbium, and a large capture web including gum-footed lines. Fundamentally I regard reduced characters as derived. I agree with the conclusion of BENJAMIN & ZSCHOKKE (2003: 301) that "... we might consider the <web and its construction> behaviour of *Latrodectus* and *Steatoda* <Asageninae> to be the primitive condition in theridiids." (words in brackets are added by the present author). (Almost superfluous to say that from this web characters ALONE we cannot conclude that Asageninae is the most ancestral subfamily of the Theridiidae); see below: "The colulus" and the subfamily Asageninae. The part of a fossil web: See *Pseudoteutana* n. gen.

In my opinion the absence of prosomal files – as well as frequently an only weakly developed tarsal comb – of the Hadrotarsinae are simply the result of the loss of the capture web: The presence of such kind of a well developed stridulatory organ makes sense in web-building spiders in which the capture web can transfer vibrations. As the loss of the capture web is surely a derived character, the loss of the prosomal-opisthosomal stridulatory organ should logically also be a derived character in the derived Hadrotarsinae (*). The reduced colulus is another derived hadrotarsine pattern.

According to AGNARSSON (2004) the tarsal organ is small in the Asageninae (sub Latrodectinae), and in the Hadrotarsinae, but large in the remaining theridiid subfamilies. I can not confirm parts of this findings: I found the tarsal organ small in most Asageninae, indeed, its diameter is ca. 1/5 of the tarsal diameter e. g. in *Crustulina guttata.* The tarsal organ is large in certain higher theridiid taxa; it is extremely large in some Argyrodinae – see AGNARSSON (2004: Fig. 33F) – but it is only 1/5 of the tarsal diameter in *Enoplognatha nigrocincta* and 1/4 in *Episinus truncatus*. AGNARSSON (2004: 466) suggests the small tarsal organ of the Asageninae (sub Latrodectinae) as a basal pattern of the family Theridiidae but IN THE SISTER GROUP of the Theridiidae – Nesticidae – exists a large tarsal organ (!). It seems likely to me that the small tarsal organ of the Asageninae is a derived character of this subfamily, and the small tarsal organ of the Hadrotarsinae may have evolved convergently.

According to ARNEDO et al. (2004) "Hadrotarsinae is embedded within Theridiidae".

(*) The recognition of the taxonomical importance of a functional connection between – e.g. somatical, behavioural as well as ecological structures like the existence of stridulatory files and a capture web – is not a matter of computer cladistics. Regarding such connections and true directions of the evolution – the most fast (but unintelligent) computers (and their US-ers which are adapted to computering) cannot replace humans brain and phantasy.

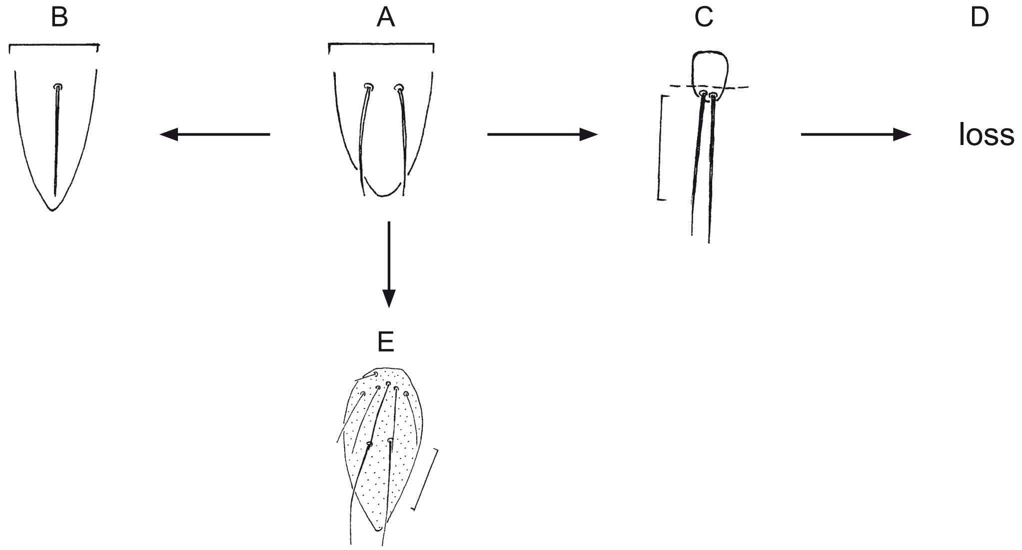
Remark: Surely the rank of a taxon – of the Hadrotarsinae or any other taxon – is NOT a matter of "less utility" – as supposed by AGNARSSON (2004: 466) – but depends on its phylogenetic relationships – and on the subjective opinion of a peculiar author.

The relationships and the ranks of some subfamilies are not definitively accepted (see also above). Examples are the Pholcommatinae and the Enoplognathinae – should both be regarded only as tribes (of the Pholcommatinae)? The sister group relationships of the Phoroncidiinae – see AGNARSSON (2004: 468), ARNEDO et al. (2004) – to the Pholcommatinae and to the Enoplognathinae as well as of the Hadrotarsinae (= Dipoeninae) to the Episinae (= Spintharinae), and of the Anelosiminae to the Theridiinae are unsure. The diagnostic characters of the Episinae are also weak; besides the reduced and special capture web I do not know a peculiar morphological diagnostic character. The rank and assemblage of the Theridiinae is not definitive, and this most diverse and derived – paraphyletic? – taxon has most probably to split up in the future. The monophyly of the Theridiinae has been confirmed by a study of genes – see ARNEDO et al. (2004) –, but still members of ONLY A DOZEN (of probably hundreds of numerous still undescribed genera) were studied/published by these authors, and thus their results are only preliminary, dubious and not definitive.

Certain morphological or behavioural characters of the Theridiidae have to discuss as ancestral or derived, plesiomorphic or apomorphic:

The colulus (see also above). According to various authors a large and hairy colulus is a basic pattern of the family Theridiidae, but the existence of three or more colular hairs as an autapomorphy of the Theridiidae may be unlikely – in my opinion it is more likely an autapomorphy of the Asageninae – whereas A PAIR of colular hairs is apparently a common ancestral/plesiomorphic character of the Theridiidae plus the Nesticidae. The – probably atavistic (!) – presence of an (additional) unpaired colular hair within some Asageninae (fig. 128), some Episinae (fig. 420), some Anelosiminae (figs. 465–467) and some Enoplognathinae (fig. 150) may be a hint that three colular hairs are an autapomorphic theridiid pattern, but I prefer to regard the existence of a pair of such hairs as a basic character of the family Theridiidae because it also exists in its putative sister group, the Nesticidae, and it is apparently connected to the body size.
The evolutionary directions of the colulus and its hairs – see the tab. below – may have been directed from a large to a small colulus which bears a single hair only, several times convergently from a basicly paired (A below) to a single hair (B), as well as – apparently several times – e. g. in the Theridiinae and in *Coscinida* – to the complete loss of the colulus and its hairs (D). Anelosimini – with their existence of 1–2 hairs on a small to tiny colulus (C, fig. 468) – seems to be the "morphological link" to its possible sister group, the Theridiinae, in which the colulus and its hairs are completely lost (D). A large colulus with more than two hairs (E, fig. 47) – which is combined with the pres-

ence of a retrodistal paracymbium (see below) as well as the presence of retromarginal cheliceral teeth – exists only in the Asageninae. I regard this combination of characters – as well as the patterns of their capture web – as strong hints that Asageninae is the most ancestral subfamily of the Theridiidae; contra AGNARSSON (2004) who regards the Hadrotarsidae as most ancestral.



Tab. above: Hypothetical model of the evolution of the colulus and its hairs in selected subfamilies of the Theridiidae.

A = basic pattern of the colulus which bears a pair of hairs: In most subfamilies, e. g. in basal and small members of the Asageninae (see E),
B = single hair e. g. in certain Enoplognathinae (in which usually a pair exists),
C = reduced colulus which bears 1–2 hair(s) e. g. in the Anelosiminae,
D = loss of the colulus and its hairs in the Theridiinae,
E = increased size of the colulus and number of its hairs e. g. in large members of the Asageninae like *Latrodectus* and *Eomysmena*.

The bulbus-cymbium lock mechanisms, paracymbia, their variability in closely related taxa, the direction of evolution, convergences and reversals: An ectal “retrodistal paracymbium” (figs. A1 below, 37, 63) is generally regarded as the most important basic autapomorphy of the family Theridiidae. An apparently homologous “internal paracymbium” sensu WUNDERLICH (1986) may be hood-shaped (e. g. fig. A3, A4 below: Asageninae) or hook-shaped (fig. A2 below); a hood-shaped paracymbium evolved several times independently, e.g., within (1) the Episinae and (2) the Asageninae. The existence of two quite different kinds of paracymbia in related genera is quite remarkable: (1) in the Episinae: A retrodistal paracymbium in *Spinitharinus* n. gen. (fig. 431) and an internal/hood-shaped paracymbium in *Spinisinus* n. gen., (2) in the Asageninae: A retrodistal (ectal) paracymbium in all of the fossil genera (figs. 63, 116, 141) and the extant genus *Craspedisia* (fig. 37) and an internal/hood-shaped paracymbium

in the extant genera (figs. A2–4 below: Asageninae) except *Craspedisia*; see also this character in the extinct genus *Balticoridion* n. gen. (questionable Theridiinae), as well as (3) in the Pholcommatinae (see below): Usually exists a retrodistal paracymbium (figs. 182–183) but it is absent in the genera *Succinura* and *Vicipholcomma* (indeed the relationships of these genera are questionable).
(1) If Spinitharinae is a true member of the Episinae the retrodistal paracymbium shifted at least two times to an internal (hook-shaped or hood-shaped) paracymbium in this subfamily. – Within the Episinae a third kind of paracymbium exists, in *Thwaitesia*: A hook-shaped internal paracymbium. A fourth (!) kind of a "paracymbial structure" within this subfamily exists in *Moneta* O. PICKARD-CAMBRIDGE 1871: A peculiar retrolateral "paracymbium" (fig. 382).
(2) In the Asageninae I found a conspicuous variability of the position and the sclerotization of the paracymbium: In all extant genera – except in *Craspedisia* – the retrodistal paracymbium has a more – e. g. in *Crustulina* and *Latrodectus* – or less internal (inside) position on the cymbium (figs. A2–4 below), according to LEVI & LEVI (1962: 59): "paracymbium hook in back of the cymbium, not on margin.". In contrast to most extant genera the paracymbial position is in ALL(!) fossil/extinct genera of the Early Tertiary Baltic amber – as well as in the extant genus *Craspedisia* – ectal, ON the cymbial margin (figs. A1 below, figs. 63, 116). Within the Asageninae the position of the (weakly sclerotized) retrodistal/ectal paracymbium shifted to an internal position (of a strongly sclerotized paracymbium), and furthermore from an internal hook-shaped (e.g. in most *Steatoda*, fig. 56, A2 below) to an internal hood-shaped type in *Asagena* (fig. 34), and in ?*Steatoda cingulata* (fig. A4 below). – Note also the variability of the paracymbium in the Pholcommatinae.
CONCLUSION: From these differences we have to conclude that in several higher Theridiidae taxa the position of the paracymbium shifted during the Eocene (and probably already earlier) from the ectal cymbial retromargin to the inner part of the cymbium. This shifting happened several times within the Asageninae, probably in a single step or twice. The enormous variability of this structure within a single subfamily – in the Episinae we have almost all known kinds of theridiid paracymbia – LIMITS FUNDAMENTALLY STRONGLY ITS TAXONOMIC VALUE.

Retromarginal cheliceral teeth exist, e.g., in Anelosiminae, Argyrodinae, some Pholcomminae, some Asageninae, few Episinae (*Moneta*) and probably very few Theri-diinae. The absence of such teeth may be an apomorphic character of the Theridiidae – with a striking number of reversals!? – or a synapomorphy of Nesticidae + Theridiidae. Contrarily – and more likely in my opinion – such teeth may well have existed basicly in the Theridiidae and were lost several times during the evolution within this family, e.g. probably as an apomorphy of the Theridiinae s. str. (with very few reversals).

The "peripheral retreat" is most probably an apomorphic character of the subfamily Asageninae, and is absent e. g. in the theridiid's sister group, the Nesticidae.

Further characters of the family Theridiidae: See AGNARSSON (2004).

In my opinion it is still impossible to present a plausible CLADOGRAM. The sequence of branchings may be as following:

Asageninae as the most basal branch which is followed by . . .
a branch (one, two or three subfamilies and branches?) of Enoplognathinae + Pholcommatinae (+ Phoroncidiinae?),
a twig of the Episinae,
a twig of the Hadrotasinae?
a twig of the Argyrodinae,
and a final branch (or two branches?) of Anelosiminae and Theridiinae.

It is remarkable that in this sequence the extant (!) members (see below: “Ecology,...”) of the basal subfamilies were/are living mainly near the ground but most of the more advanced subfamilies were/are living in higher strata of the vegetation (Phoroncidiinae is an exception – is it a more derived subfamily?).
MAY THE ECOLOGY OF THESE SPIDERS GIVE AN IMPORTANT HINT TO THEIR PHYLOGENY? This is a question of the “ecophylogeny”.

Remarks on my hypotheses of the theridiid evolution: The diversifying ants influenced – probably during the Early Tertiary – the evolution/diversification of the Theridiidae (a–c): (a) the Asageninae evolved an armoured body and legs in defending the – and preying on – ant workers latest in the Eocene; (b) the Episinae evolved – apparently in the same period – a specialized reduced capture web to catch worker ants, (c) the Hadrotarsinae evolved a special ant capture behaviour and lost their capture web; (d) the Argyrodinae evolved a kleptoparasitic behaviour and a reduced capture web; (e) in (the stem species of) the Anelosiminae + the Theridiinae the ectal paracymbium shifted to an internal position; and (f) the (stem species of the) Theridiinae lost completely the colulus and its hairs.

Surviving genera: The portion of surviving genera (the common group of extant AND Eocene taxa): Four genera of three subfamilies survived from the Eocene European amber forests: *Episinus* of the Episinae, *Lasaeola* and *Euryopis* of the Hadrotarsinae, as well as *Ulesanis* of the Phoroncidiinae. This percentage is rather small, it is only 10% of the extant European genera and 12% of the known Eocene genera. It means that – known so far – 88% of the genera in Baltic amber are extinct. The “successful” surviving genera occur in Europe, too, but they are not typical European taxa, they all possess a very wide (*Ulesanis*) or even cosmopolitical distribution.

Close relatives or even direct ancestors of extant species? Some extinct species may be related to extant species, but we only know a small part – of the unknown number – of extinct species; therefore we must be careful with conclusions in this matter. Among the Theridiidae in Baltic amber the extinct species *Ulesanis antecessor* n. sp. may well be closely related to extant species, see below: Phoroncidiinae. Certain fossil members of the diverse genera *Episinus* and *Lasaeola* may be closely related to extant European species, too, and they will probably be identified in future investigations. See also *Pseudoteutana* n. gen. (Asageninae) which may be part of the extant genus *Steatoda* in a wide sense.

Remarks on probable subspecies in the fossils: (1) According to the very similar male genital structures of STRONGLY RELATED SPECIES there may be proofs of some subspecies of fossil spiders in Baltic amber. Examples are *Lasaeola latisulci* n. sp. and *L. communis* n. sp., *Episinus appendix* n. sp. and a probably conspecific male, *E. isopteraque* n. sp. and a probably conspecific male as well as *Spinisinus splendidus* n. sp. and *S. parvioculi* n. sp. – which may be subspecies of a single species – in which a variable shape of conductor as well as tegular and median apophysis exist. See also *Succinura bellavista* n. sp. – (2) Unfortunately we do not know the intrapopular variability of genital structures in the fossil spiders: Ten males may originate from ten different populations (rarely two males are preserved in the same piece of amber – see the genera *Clya* and *Lasaeola* – and usually their bulbi are not visible or observable in the same position). Frequently it is impossible to observe the bulbi in an exact identic position; a slightly different position, or an expanded bulbus may cause different shapes of their structures. In *Clya* I found "intermediates" between different questionable morpho-species, see below (the subfamily Asageninae), and the paper "Different views of the taxonomy..." in this volume.

ECOLOGY, ETHOLOGY and FREQUENCY of the Theridiidae in Tertiary ambers

In most larger unselected collections almost every third spider in Baltic amber is a member of the family Theridiidae if we take juveniles and adults together. Fossil specimens of Theridiidae in Baltic amber – mainly members of the genera *Clya*, *Episinus* and *Lasaeola* – are even more frequent than Synotaxidae (mainly *Acrometa*) or Linyphiidae (mainly *Custodela*). All these taxa are members of the superfamily Araneoidea. Only members of the genus *Orchestina* (Oonopidae) may be more frequent in Baltic amber than members of *Acrometa*, *Clya, Custodela, Episinus* or *Lasaeola*, see WUNDERLICH (2004: 226) (the tiny Oonopidae are most often ignored or overlooked by collectors, dealers as well as of most scientific investigators of fossil spiders of former times).
Most members of the Theridiidae (Anelosiminae, Argyrodinae, Hadrotarsinae, Episinae, Phoroncidiinae, and Theridiinae) – as well as of most other representants of the superfamily Araneoidea – are mainly dwellers OF HIGHER STRATA of the vegetation. This mode of life is surely the main reason of their frequency in fossil resins, and qualify the very diverse family Theridiidae to give hints to the general diversity of spiders in the Eocene which was at least as diverse as today (clearly higher on family level).
Contrarily extant members of three theridiid subfamilies are found NEAR THE GROUND, in litter and under stones, e. g. most extant Asageninae (some live at the bark of trees), Enoplognathinae, and Pholcommatinae. Some West-Palaearctic members of *Theonoe* are microcavernicolous; *Theonoe* (= *Marianana*) *mihaili* (GEORGESCU 1989) from Rumania and *Rugathodes pico* (MERRET & ASHMOLE 1989) from the Azores are true cave spiders. – Fossils: The fossil resin captured surely mainly spiders which were dwellers of higher strata of the vegetation; but in the Eocene European ambers the members of the Anelosiminae and Theridiinae (most frequent today!) are rarely preserved (Argyrodinae were most probably absent), and Asageninae – e. g.

specimens and species of *Clya* – on the other hand are very frequent (!). From this frequency/rareness of the taxa in the Early Tertiary ambers we may probably conclude nothing about the adaptation of the Eocene Asageninae as dwellers near the ground or in higher strata because we have no fossil material which was surely captured at the ground; but with some doubt I suppose (1) that the ecological preference of the (of some?) Asageninae changed apparently during the last 40 million years – probably already during the cooling period of the Oligocene – from higher strata of the vegetation to ground-dwelling today. Furthermore we may conclude with respect to their ecology; (2) Episinae are frequent in Baltic amber; hence apparently they prefered higher strata already in the Early Tertiary as they do today; (3) Pholcommatinae: The rareness of specimens of this subfamily in Baltic amber is easily explainable by their distinct preference of habitats near the ground already in the Early Tertiary (as today), but not in higher strata from which they would have captured more frequently by the fossil resins; (4) The rareness of the Phoroncidiinae is not a surprise because members of this subfamily possess mainly a tropical distribution whereas the Eocene European amber forests included only few tropical – but mainly subtropical – regions; (5) the rareness of the fossil Anelosiminae and Theridiinae may be caused by the late diversification of these probably geologically relatively young subfamilies, and the rareness of the Anelosiminae MAY furthermore be the result of their mainly peculiar web-building on Fagaceae – but not on needle-trees like today – which produce no resin. – So the frequency/rarity of peculiar members of higher theridiid taxa has quite different reasons.

Cryptic body-shape; mimesis: Most extant and fossil members of the subfamily Phoroncidiinae – e. g. of the genera *Phoroncidia* WESTWOOD s. l. and *Ulesanis* L. KOCH, as well as (less distinct) of *Caudasinus* n. gen. of the Episinae – possess outgrowths or spines of their opisthosoma: Most extant species of *Ulesanis* have a very high opisthosoma which bears dorsal humps – stronger developed in the female sex, figs. 23–224 – like the fossils in Baltic amber (photos 245f). Other species – members of *Phoroncidia* s. str. – possess opisthosomal spines (fig. 221) similar to araneid spiders of the subfamily Gasteracanthinae. I suppose some shapes of the opisthosoma being a kind of camouflage (phytomimesis): A female spider of *Ulesanis longicymbium* n. sp., which is preserved in Baltic amber together with a part of her capture web, masked probably some threads with the help of plant particles (photo 255) similar to members of araneid spiders of the genus *Cyclosa* MENGE 1866 which possess – convergently evolved – opisthosomal outgrowths; see also *Eozorichopes* n. gen. (Araneidae). A second "evolutionary strategy" to hide the spiders body may be the dwarfism in *Ulesanis* which members have occasionally a body length of only 1 mm. This kind of a dwarf and cryptic body in theridiid spiders – see the photos 245f – can dated back now to the Early Teriary (Eocene). See also the paragraph on mimesis and the cryptic shape of the body in *Baltarchaea conica* (KOCH & BERENDT) (Archaeidae) and the spiny body of certain Thomisidae in Baltic amber, WUNDERLICH (2004: 184, photos 67, 405–408, figs. p. 1759), and the paper no. 14 on this matter in this volume. – A cryptic behaviour was probably also existing in Eocene members of the subfamily Episinae which stretched their anterior legs foreward on their reduced capture web in higher strata of the vegetation, see the photos 306–307 and fig. 333.

Sex ratio: Fossil female Theridiidae in Baltic amber are much rarer than males; the sex ratio (♂ : ♀) reaches from almost 20 : 1 in *Eomysmena* to almost 100 : 1 e. g. in

Clya. But in reality fossil females in amber are not SO rare because (1) most dealers selected more male spiders for my study, and (2) fossil females are basicly more difficult to determine to their correct genus – or even their family – and were misidentified by different authors/collectors.

Prey, leg amputations and healing events: According to my findings the ANTS WERE THE MAIN PREY OF EOCINE THERIDIIDAE – as well as of members of other spider families like Zodariidae, see WUNDERLICH (2004: 91–96), and the photos 31, 32, 35 (e. g. F657/CJW and F1677/CJW) – in the Eocene amber forests. In members of the subfamily Hadrotarsinae – which usually do not build capture webs and which feed on ants (see e. g. below the ants with *Lasaeola communis*, F1476/CJW, F1677/CJW) –, in *Clya* and *Eomysmena* of the subfamily Asageninae as well as in some Enoplognathinae, e. g. not rarely in *Hirsutipalpus* n. gen. – I found leg amputations and apparently healing events at their stumps, too. The leg amputations may have been caused mainly by ants which have powerful mandibles; the events occurred between leg articles as well as THROUGH leg articles of various regions, mainly of tibiae and metatarsi. I found autotomy (between coxa and trochanter) in fossil Hadrotarsinae and in extant Enoplognathinae (e. g. *Enoplognatha ovata*) but not in the fossils of *Hirsutipalpus*, in which leg amputations are frequent. – Healing events (see below, the genera *Clavibertus*, *Clya* (e. g. *lugubris*), *Eomysmena*, *Hirsutipalpus*, *Lasaeola*, photos 1–11, 348, and figs. below, the paper no. 11 on healing events in extant spiders (this volume), and WUNDERLICH (2004: 154–157, photo 351)): I found no remains of blood at the end of the stumps of injured legs, and the stumps are apparently "closed". Furthermore – as can be concluded from the kind of their preservation – most or even all of the injured spiders were embedded in the resin ALIVE, and the legs were not cut off within the fossil resin; therefore I regard the wounds of these stumps as "healed".
Besides the Theridiidae I found "healing events" frequently mainly in a single further spider family, the Zodariidae; see WUNDERLICH (2004: 1581), including amputations THROUGH a leg article and apparently "healing" in an extant spider. As a member of a different superfamily the Zodariidae is not related to the Theridiidae; thus leg amputations and "healing" of their stumps evolved surely convergently in these families. In both families exist an interesting concordance: Like in those theridiid taxa (e. g. *Hirsutipalpus*), in which leg amputations are not rare, a leg autotomy is also absent in the Zodariidae. On the other hand: In different fossil taxa of other families whose members feed on ants, too, I found only rarely leg amputations (e. g. in *Sosybius* sp. of the family Trochanteriidae), and leg autotomy occurs in this genus.

Questionable cannibalism (photos 29–30): A male of *Clya obscura* (KOCH & BERENDT 1854) (F1600/BB/CJW) is spun in in thin spider's threads; the opisthosoma and parts of the four anterior legs are distinctly deformed. The spider has been the prey of a spider, probably of a conspecific female, and so this may be a case of cannibalism. A similar cases are probably a male indet. of *Eomysmena* (F1696/BB/CJW) (Asageninae), and a male of *Hirsutipalpus varipes*, see below (Enoplognathinae). Photo 218.

Parasitizing Acari: I know three specimens of fossil Theridiidae which were parasitized by mite larvae: The holotype (adult male) of *Lasaeola bitterfeldensis* n. sp. (Hadrotarsinae), and two subadult males: One of *Spinitharinus* sp. indet (fig. 26, Episinae, see below), and another theridiid specimen which has not been determined to the genus level, see WUNDERLICH (2004: 119, photo 591). Most parasitizing Acari are apparently members of the family Erythraeidae, see Photo 259.

FAUNA, BIODIVERSITY

The fossil theridiid fauna which is preserved in Baltic amber is surpisingly diverse: In this paper I list members of seven or even eight of the nine theridiid subfamilies (Argyrodinae are absent, Theridiinae is questionable), see the tab. below, which includes the comparison of two other faunas and the fauna worldwide:

Taxon	**Baltic amber**	**Europe today**	**Dominican amber**	**worldwide**
subfamilies	8(?)	9	6	9
genera	30	~40	13	>>85
species	almost 100	>200	ca. 40	>>2200

Tab. above: Comparison of different theridiid faunas regarding their subfamilies, genera and species. – Newly described genera of extant European Theridiinae: See below; numerous – mainly tropical – extant genera and species are not yet described. Taxa in Dominicam amber: See PENNEY (2005) and WUNDERLICH (1988).
The “intrafamiliar index of diversity” (ratio of the numbers of genera to species) is 0.3 in the extinct Eocine Theridiidae and 0.2 in the extant Theridiidae.

From these findings – mainly only from a single forest and only from certain habitats (!) – one may conclude that the diversity of the Early Tertiary theridiid fauna in a given area was higher than today. Its composition was quite different: Asageninae, Episinae, and Pholcommatinae were more frequent, the Argyrodinae were absent within the fauna of the Eocene European amber forests, and the Theridiinae were quite rare or even absent (the reasons: See also above). One reason for the higher diversity in that period was surely the different – mainly subtropical – climate in the Eocene which results in the presence of some tropical taxa within the Baltic amber forest in contrast to the extant European taxa. Members especially of the Phoroncidiinae (and less distinct of the Episinae, which were frequent in the Eocene European amber forests) – prefer (today) a tropical climate.

Subfamily	in Baltic amber	extant worldwide	ratio
Asageninae	8	>7?	1.0?
Enoplognathinae	3	3	1.0
Pholcommatinae	7?	>6	1.0
Episinae	5	7	0.7
Phoroncidiinae	1	>3?	0.3?
Hadrotarsinae	3	14?	ca. 0.2?
Argyrodinae	0	>7	
Anelosiminae	1	several	0.3?
Theridiinae	2?	>>50 (>100?)	0.04(-0.02)?
sum	30	(>>100?)	(~0.1?)

Tab. above: The known and the estimated (in brackets) numbers of genera of the theridiid subfamilies in Baltic amber, and extant worldwide, as well their ratios. – From above to below the probably more ancestral to the more derived subfamilies are listed; note the ratio of (about) 1.0 in the first four subfamilies, up to the ratio of probably only 0.03 in the most derived subfamily Theridiinae in which most extant genera exists (see below).

Because of their occurrence mainly in higher strata of the vegetation the Theridiidae are well qualified in considering a comparison of the fossil spider fauna with the extant fauna and to conclude on the spider's biodiversity of the Early Tertiary. (Caused by the traps of sticky resin mainly in higher strata of the vegetation adult members of taxa like Mygalomorpha or Gnaphosidae are under-represented in the fossil resins).

According to my present knowledge I estimate (1) that we now may know more than two third of the genera of the Eocene Baltic amber Theridiiae, and (2) that the Eocene theridiid spider fauna was more – at least as – diverse as the extant European fauna. (3) The most dramatic change in the theridiid fauna concerns the most advanced subfamily Theridiinae, which is by far most diverse today (see the fig. below):
The – probably 2 or less – Eocene genera of the Theridiinae represent only 7% of the 30 genera of the family Theridiidae; on the other hand represent 23 extant European theridiinae genera 57% of the about 40 European theridiidae genera of today. That means (a) that the relative percentage of the theridiinae genera increased within the last about 40 million years by ca. 800% (!), and (b) that the diversification of this most successful theridiid subfamily – the Theridiinae – happened apparently (at least in Europe) much later than in the other theridiid subfamilies besides the Argyrodinae.

Remark: Similar findings – they are even more pronounced – concern several other spider subfamilies, for example the Erigoninae of the Linyphiidae which were absent in the Eocene, and the Salticinae (as well as other advanced subfamilies) of the Salticidae which are unknown from the Eocene (apparently even absent).

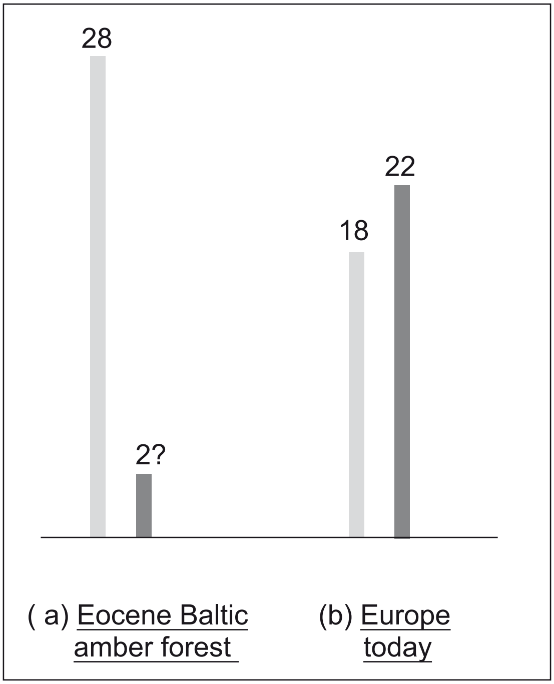


Fig. above: Number of genera of the family Theridiidae, (a) in Eocene (Baltic) amber, and (b) in Europe today. The advanced Theridiinae are shown on the right and the remaining genera on the left. Note the enormeous shifting ratio of both groups after a span of almost 50 million years!

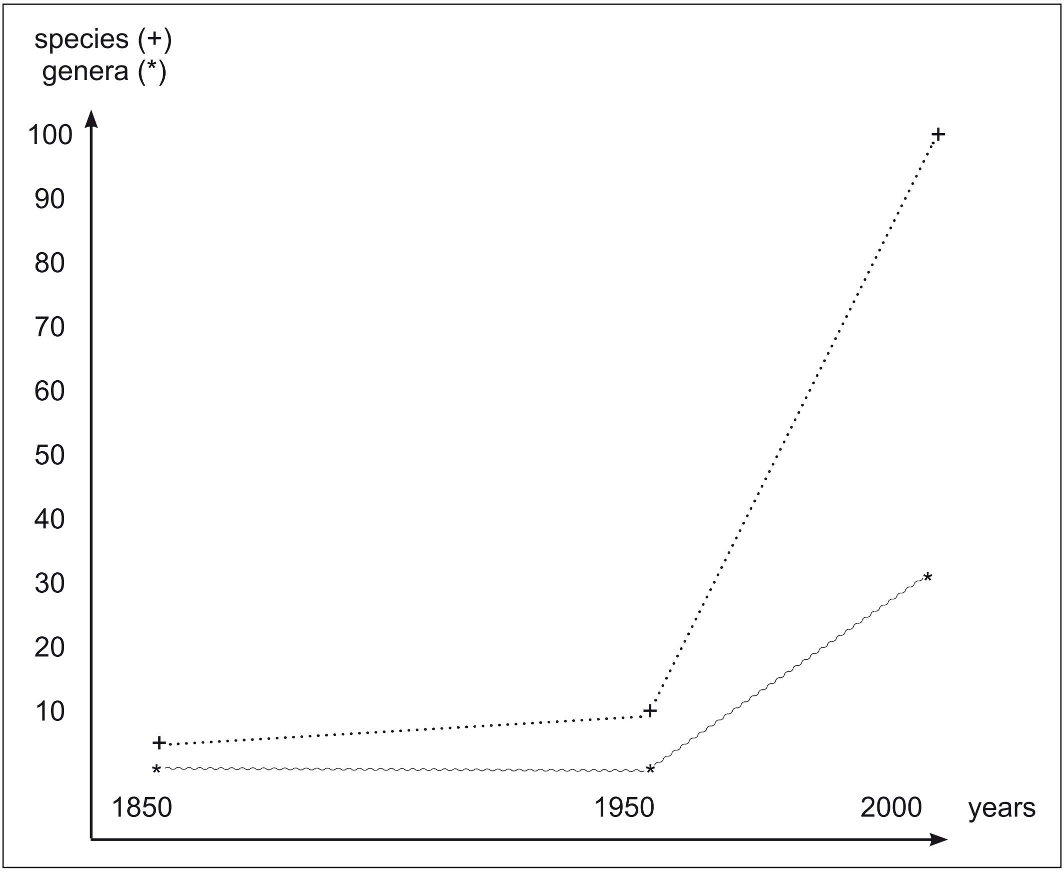
“HISTORICAL TAXONOMY” of theridiid spiders of the Eocene European amber forests and SYNONYMY

Our knowledge of fossil Theridiidae in Baltic and other Eocene European amber(s) increased mainly in four steps besides the description of 5 species by MARUSIK & PENNEY (2005); questionable taxa are not included, new combinations and synonyms: See below:

(1) KOCH & BERENDT (1854) published as pioneers in this matter members of 3 nominal genera: *Clya* n. gen., *Flegia* (a junior synonym of *Episinus*), and “*Theridium*” (misidentifications, the species are now transferred to different genera, but not to *Theridion*, see below), with 7 new species (about two dozen specimens);

(2 + 3) PETRUNKEVITCH (mainly 1942 and1958) added the new genus *Eomysmena* and several new species of different genera; see the synonyms below (*Flegia*: See *Episinus*; *Dipoena*: See *Lasaeola*; *Theridion*: Diverse misidentifications);

(4) in this paper I add 27 genera (24 are described for the first time) with 78 new species which are based on hundreds of type specimens, more than 15 000 specimens from Baltic, Bitterfeld, Romanean, and Ukrainean deposits; several thousand fossil spiders were studied more or less closely. Now we know almost 100 Eocene theridiid species of 30 genera (more species and slightly more genera than are known from Central Europe today); see the fig. below:



SYNOPSIS of the theridiid taxa in Baltic amber (including questionable taxa and selected species which were erroneously described e. g. under *Erigone*, *Mysmena* and *Theridion*):

Remarks: (1) Numerous taxa of fossil spiders which were described by KOCH & BERENDT (1854) and by PETRUNKEVITCH are based on juveniles which most often can not determined with certainty to a certain species or genus or even to the family level. As a result these authors placed several taxa in wrong subfamilies or even families (e. g. the Linyphiidae and the Theridiidae). – (2) Subfamily names and foundation of the synonymies: See below. – (3) See also the remarks on certain synonymies and resurrections below (subfamily Asageninae), and problems caused by the paper of MARUSIK & PENNEY (2005).

(1) Taxa described by PETRUNKEVITCH:

Astodipoena PETRUNKEVITCH 1942 = *Eomysmena* PETRUNKEVITCH 1942 (**n. syn**.).

Dipoena sensu PETRUNKEVITCH = *Lasaeola* SIMON 1881 s. l.

Eodipoena PETRUNKEVITCH 1942 = *Eomysmena* PETRUNKEVITCH 1942 (**n. syn**.); species see below (Asageninae).

Eomysmena PETRUNKEVITCH: Species see below (Asageninae).

Eomysmena consulta PETRUNKEVITCH 1958 ?= *E. moritura* PETRUNKEVITCH 1942 (**quest. n. syn**.).

Flegia succini PETRUNKEVITCH 1942 = *Pseudoteutana stigmatosa* (KOCH & BERENDT 1854) (**n. syn**.).

Impulsor PETRUNKEVITCH 1942 (described in Linyphiidae) = *Episinus* WALCKENAER 1809 (**n. syn**., **n. relat**.).

Malleator PETRUNKEVITCH 1942 (described in Linyphiidae) = *Episinus*, see WUNDERLICH (2004: 1306).

Medela PETRUNKEVITCH 1942 (sub Thomisidae!) with its type species *baltica* (juv. holotype PIHUB no. 18138-A, seen), may be a member of the Theridiidae; the specimen is ventrally covered with a white emulsion, the legs are fairly stout, its bristles are thin and relatively long.

Mictodipoena PETRUNKEVITCH 1958 = *Episinus* WALCKENAER 1809 (**n. syn**.), see below.

Mictodipoenini PETRUNKEVITCH 1958 (sub Mictodipoeneae) = Episinae: Episini (**n. syn**.), see below (Episini).

Municeps PETRUNKEVITCH 1942: The generotype *M. pulcher* is based on a juvenile spider, body length 1.8 mm. According to the long tarsi, the wide labium, the small chelicerae and the widely spaced posterior coxae this is a questionable genus of the family Theridiidae. The eye field is narrow in the generotype but fairly wide in the second species of the genus, *M. minutus* PETRUNKEVITCH 1958 which may not be congeneric.

Mysmena sensu PETRUNKEVITCH 1942 and 1958 = member of the family Theridiidae. The holotype of *Mysmena succini* (PETRUNKEVITCH 1942) (sub *Eomysmena*; see PETRUNKEVITCH (1958: 158), not seen) is a juvenile male. Its body length – 1.7 mm – is distinctly larger than in *Mysmena*, and also the well developed comb of tarsus IV indicate that this species is a member of the family Theridiidae but not of the Anapidae: Mysmeninae; its generic relationships remains unclear.

Nanomysmena PETRUNKEVITCH 1958 = *Clya* KOCH & BERENDT 1854, see WUNDERLICH (1986: 27). *N. aculeata* and *N. munita* PETRUNKEVITCH 1958 are dubious species which are based on juvenilies.

Steatoda succini PETRUNKEVITCH 1942 (holotype ♀ (fig. 31) and paratype (juv. ♂) = Theridiidae indet.

Theridion simplex KOCH & BERENDT 1854 and sensu PETRUNKEVITCH (1942, 1958) (female; not seen) (see the remark below): One or two quite unsure taxa; even the family relationship appears unsure to me.

Theridion sp. indet. sensu PETRUNKEVITCH (1942: 267) (not seen): A "very young spiderling", body length 1.1 mm. According to PETRUNKEVITCH a colulus is absent but it could well be hidden in my opinion. Its relationships are quite unsure, it is not a *Theridion*, see the following remark.

Remark: Fossil members of the genus *Theridion* WALCKENAER 1805 are unknown from Baltic amber, and are even completely absent to my knowledge.

(2) Taxa described by KOCH & BERENDT (1854):

Clythia KOCH & BERENDT 1854: Not a taxon of the family Theridiidae, see WUNDERLICH (2004: 1392). The generotype – according to PETRUNKEVITCH (1958: 381) *C. calma* KOCH & BERENDT 1854 – is according to MENGE in KOCH & BERENDT (1854: 46, 49) probably a member of the family Agelenidae. *Clythia gracilenta* MENGE 1854 as well as *C. leptocarena* MENGE 1854 are nomina nuda.

Erigone stigmatosa KOCH & BERENDT 1854 = *Pseudoteutana stigmatosa* (KOCH & BERENDT 1854) (**n. comb**., **n. relat**.) (Asageninae). (*Erigone* is a genus of the subfamily Erigoninae of the Linyphiidae; this genus and even the whole subfamily Erigoninae are unknown from Baltic amber).

Gea obscura KOCH & BERENDT 1854 = *Clya obscura* (**n. comb.**)

Theridion sensu KOCH & BERENDT (1854): KOCH & BERENDT (1854: 33–37) described seven species sub *Theridion*; most species are based on females or juvenile spiders, see the remarks above. – *T. hirtum* (part.: ♀) is a member of *Acrometa* PETRUNKEVITCH (Synotaxidae), *T. granulatum* is a member of *Clya* KOCH & BERENDT; according to MENGE in KOCH & BERENDT (1854: 37) T. *alutaceum* may be synonym with *granulatum*. I studied the female holotype of *alutaceum* (PIHUB) and regard it as a Theridiidae indet. The spider is completely and well preserved in a darkened piece of amber. Mainly dorsally the body is covered with a white emulsion, the area of the colulus is hidden, the epigyne (fig. 30) is a triangular pit which is partly covered with a white emulsion. Measurements (in mm): Body lengt 2.3, prosomal length ca. 1.0, length of tibia I 0.85. The sternum is not rugose, the eye field is narrow, the anterior median eyes are distinctly the largest. The legs are stout, the tibial bristles are fairly long, the comb of tarsus IV is well developed, the trichobothrium of metatarsus I is situated in the middle of the article.

Mizalia globosa KOCH & BERENDT 1854: The single known type is a subadult male. I did not get the opportunity to study the holotype (it has not been found in the Palaeontological Institute of the Humboldt University). This species was removed from the genus *Mizalia* – a member of the family Oecobiidae – by MENGE (in KOCH & BERENDT (1854: 43), and transfered with hesitation (!) to *Theridion* WALCKENAER 1805. Members of the genus *Theridion* (see the nomina nuda below, which were described by MENGE) – as well as probably of the whole subfamily Theridiinae – are unknown from Baltic amber. Although the relationships of *globosa* were doubted by MENGE as well as by MARUSIK & PENNEY (2005: 213) the latter authors regarded the name *globosa* as praeoccupied sub *Theridion*, and proposed the new name *Theridion berendti*. Because of the dubious relationships of *globosus* – and the absence of the genus *Theridion* in Baltic amber – the new name *berendti* is not justified – not praeoccupied –, and is therefore regarded here as a junior synonym of "*Mizalia" globosa* KOCH & BERENDT 1854 (**n. syn**.). It may be problematical to propose a new name for a species which relationships are quite unsure, and without investigation of type material. Probably the holotype of *globosa* will be discovered in the fossil material of the Humboldt University Berlin in the future.

The dubious members of *Thyelia* KOCH & BERENDT 1854 (probably various families) are listed in the family Agelinidae by PETRUNKEVITCH (1958: 370); one species was listed with *Amaurobius* and *Clubiona* by MENGE (p. 51). See WUNDERLICH (2004: 1392, 1485). The dubious species (family?) which were described sub *Zilla* are listed in the family Araneidae by PETRUNKEVITCH (1958: 372) with a question mark?; see WUNDERLICH (2004)

(3) Taxa described by MENGE in KOCH & BERENDT (1854):

Antopia MENGE 1854 ?= *Eomysmena* PETRUNKEVITCH 1942 (**quest. syn**.);
Antopia Menge is listed under Linyphiidae by PETRUNKEVITCH (1958: 377), but its type species – according to PETRUNKEVITCH *Mizalia obscura* KOCH & BERENDT – seems to me to be a member of the Theridiidae (*Eomysmena*?) or of the Araneidae/Zygiellidae. A second nominal congeneric species – *Mizalia punctulata* KOCH & BERENDT 1854 – may be a member of the Theridiidae (*Eomysmena*?). Material of both species has not been found in the PMHUB.

Corynitis MENGE in KOCH & BERENDT (1854): According to the numerous leg "spines" most probably a genus of the family Mimetidae, see WUNDERLICH (2004: 1261), and not a synonym of *Episinus*, see MARUSIK & PENNEY (2005: 215).

Euryopus MENGE in KOCH & BERENDT 1854 (p. 40: *Euryopus*, p. 124: *Euriopus*): According to the very short diagnosis a questionable genus of the Theridiidae, and a nomen nudum; material is most probably lost.
Theridium bufurcum, T. chorius, T. clavigerum, T. crassipes and *T. setulosum* were

already listed as nomina nuda by MARUSIK & PENNEY (2003: 215). Material is lost to my knowledge. See the remark on the Eocene *Theridion* above.

(4) Taxon described by BERLAND (1939):

Lithyphantes anticus BERLAND 1939 ?= *Episinus anticus* (BERLAND 1939) (**quest. n. comb**.), see below.

LIST OF THE SUBFAMILIES, GENERA AND SPECIES OF THE FAMILY THERIDIIDAE IN BALTIC AMBER:

The relationships of some taxa are questionable, see Enoplognathinae, Pholcommatinae and Theridiinae.
Listed are members of 8 subfamilies, 30 genera – names of the 4 surviving extant genera are heavily printed –, 24 n. gen., almost 100 species, 78 n. sp.
Only three genera of three subfamilies (Asageninae, Episinae and Hadrotarsidae) include half of the fossil species: From these most diverse genera – *Clya* (13 species), *Episinus* (23 species) and *Lasaeola* (12 species) – are 48 species listed (= half of all known theridiid species in Baltic amber). Atleast 10 species are known from the genus *Eomysmena* (Asageninae), in which the relationships of numerous species are unsure.

(1) **ASAGENINAE**:

Clya KOCH & BERENDT 1854: *abdita* n. sp., *calefacta* n. sp., *gracilis* (PETRUNKEVITCH 1958), *granulata* (KOCH & BERENDT 1854), *lugubris* KOCH & BERENDT 1854, *obscura* (KOCH & BERENDT 1854), *palanga* (MARUSIK & PENNEY 2005), *petrunkevitchi* (MARUSIK & PENNEY 2005), *pseudogracilis* (MARUSIK & PENNEY 2005), *rotata* n. sp., *supercalefacta* n. sp., *superspiralis* n. sp., *tricurvata* n. sp.
Eoasagena n. gen.: *scutata* n. sp
Eomysmena PETRUNKEVITCH 1942: *aviceps* n. sp., ?*bassleri* (PETRUNKEVITCH 1942), *calefacta* n. sp., *crassa* (PETRUNKEVITCH 1958), ?*kaestneri* (PETRUNKEVITCH 1958), *militaris* (KOCH & BERENDT 1854), *moritura* PETRUNKEVITCH 1942, *nielseni* (PETRUNKEVITCH 1958), ?*obscura* (KOCH & BERENDT 1854), *oculata* (PETRUNKEVITCH 1942), ?*punctulata* (KOCH & BERENDT 1854), *recta* n. sp.
Eoteutana n. gen: *hirsuta* n. sp.
Nanosteatoda n. gen.: *breviscutum* n. sp., *trisetae* n. sp.
Protosteatoda n. gen. (Enoplognatinae?): *gutta* n. sp.
Pseudoteutana n. gen.: *stigmatosa* (KOCH & BERENDT 1854).
Unispinatoda n. gen.: *aculeata* n. sp.

(2) **ENOPLOGNATHINAE:**

Eolyrifer n. gen.: *longitibialis* n. sp.

Hirsutipalpus n. gen.: *varipes* n. sp.
Succinobertus n. gen.: *adjacens* n. sp.

(3) **PHOLCOMMATINAE**:

Balticpholcomma n. gen.: *scutatum* n. sp.
Cymbiopholcomma n. gen.: *dudum* n. sp.
Globulidion n. gen.: *cochlea* n. sp.
Obscurpholcomma n. gen.: *tegens* n. sp.
Rugapholcomma n. gen.: *patellaris* n. sp.
Succinura n. gen. (relationships questionable): *aciesaeta* n. sp., *bellavista* n. sp., *circuita* n. sp., *dubia* n. sp., *fuscoruber* n. sp., *ovalis* n. sp.
Vicipholcomma n. gen. (relationships questionable): *spiralis* n. sp.

(4) **PHORONCIDIINAE**:

Ulesanis L. KOCH 1872: *antecessor* n. sp., *frontprocera* n. sp., *longicymbium* n. sp., *ovalis* n. sp., *parva* n. sp. (Compare *Praetereuryopis*, questionable Hadrotarsinae).

(5) **HADROTARSINAE**:

Euryopis MENGE 1868 s. l.: *araneoidea* n. sp., *bitterfeldensis* n. sp., *nexus* n. sp., *streyi* n. sp.
Lasaeola SIMON 1881 s. l.: *acumen* n. sp., *baltica* (MARUSIK & PENNEY 2005), *bitterfeldensis* n. sp., *communis* n. sp., *dunbari* (PETRUNKEVITCH 1942), *furca* n. sp., *germanica* (PETRUNKEVITCH 1958), *infulata* (KOCH & BERENDT 1854), *larvaque* n. sp., *latisulci* n. sp., *sexsaetosa* n. sp., *sigillata* n. sp.
Praetereuryopis n. gen.(relationships questionable): *phoroncidoides* n. sp.

(6) **EPISINAE**:

(6a) **Episini**:

Episinus WALCKENAER 1805: *anapidaeque* n. sp., ?*anticus* (BERLAND 1939), *appendix* n. sp., *arrodens* n. sp., *balticus* (MARUSIK & PENNEY 2005), *bulla* n. sp., *clunis* n. sp., *cochlear* n. sp., *cymbialis* n. sp., *dimidius* n. sp., *eskovi* MARUSIK & PENNEY 2005, *isopteraque* n. sp., *latus* n. sp., *longimanus* (KOCH & BERENDT 1854), *longisoma* n. sp., *mordellique* n. sp., *musculus* n. sp., *mutilus* (PETRUNKEVITCH 1958), *nasuticymbium* n. sp., *neglectus* (PETRUNKEVITCH 1942), *regalis* (PETRUNKEVITCH 1958), *stridulans* (PETRUNKEVITCH 1958), *transversus* n. sp.

(6b): **Spinitharini n. trib.**:

Caudasinus n. gen.: *bispinosus* n. sp., *caudatus* n. sp., *regeneratus* n. sp.
Mimetidion n. gen.: *furca* n. sp.
Spinisinus n. gen.: *parvioculi* n. sp., *splendidus* n. sp.
Spinitharinus n. gen.: *bulbosus* n. sp., *cheliceratus* n. sp., *coniectus* n. sp., *curvatus* n. sp., *cymbioseta* n. sp.

(**ARGYRODINAE**: A faked piece of "amber" – most probably heated copal from Madagascar, see below – includes a specimen of *Argyrodes* sp. indet.).

(7) **ANELOSIMINAE**

Kochiuridion n. gen.: *pecten* n. sp.

(8) **THERIDIINAE** (doubtful):

Balticoridion n. gen. (relationships questionable): *dubium* n. sp.
Clavibertus n. gen. (relationships questionable): *parvus* n. sp., *prominens* n. sp.

DESCRIPTIONS OF THE TAXA IN BALTIC AMBER as well as of few related not European extant taxa: Episinae: Episini; ?Pholcommatinae: Magnopholcommatini n. gen. as well as notes on extant taxa

Key to the subfamilies: See above.

Key to the genera: See the descriptions of the subfamilies below.

Remarks on the most frequent theridiid spiders in Baltic amber: Almost two third of the theridiid specimens in Baltic amber are members of only four genera: *Clya, Eomysmena, Episinus* and *Lasaeola* s. l.; most frequent are *Clya* and *Lasaeola*. At least the males of three of these GENERA (except *Episinus*) are easily to recognize:

- Prosoma distinctly rugose/wrinkled, embolus spirally, long to very long (figs. 68, 93, photos 161f) (a spiral embolus exists also in other genera – e. g. in *Acrometa* – and families in which the prosoma is not distinctly rugose) . . . . *Clya* (Asageninae)

- Prosoma similar rugose, male clypeus densily covered with conspicuous hairs (figs. 108–110, photos 190f) . . . . *Eomysmena* (Asageninae)

- Basal cheliceral articles ususually very small (fig. 256; compare fig. 371!), prosoma not rugose, in the male dorsally very high, with a very long clypeus, and frequently with deep furrows (fig. 246, photos. 260f). . . . . *Lasaeola* s. l. (Hadrotarsinae)

- Anterior legs long (fig. 333, photo 301) to very long, opisthosoma long-oval, prosoma not rugose, fovea long and deep (figs. 340, photos 301, 306). (Members of related genera may be similar) . . . . *Episinus* (Episinae)

Remarks on some of the most frequent SPECIES in Baltic amber: *Pseudoteutana stigmatosa* (KOCH & BERENDT 1854) (Asageninae) is one of the most frequent species at all in Baltic amber. Its prosoma is rugose like in *Clya* and *Eomysmena* but its embolus is sickle-shaped (figs. 142–144). – *Hirsutipalpus varipes* n. gen. n. sp. (Enoplognathinae) is relatively frequent, too; its bulbus is fairly small (figs. 166–167). Some species of *Clya* (Asageninae) and *Lasaeola* (Hadrotarsinae, see above) are also quite frequent.

1. ASAGENINAE (= Latrodectinae)

The subfamily Asageninae has a cosmopolitical distribution; most taxa occur probably in the Northern Hemisphere. Its small members are frequent in Baltic amber, especially specimens of the genus *Clya* KOCH & BERENDT 1854; specimens of *Eomysmena* are not rare, and *Pseudoteutana stigmatosa* is one of the most frequent species in Baltic amber. (Among this subfamily are – extant – the largest and most poisenous members of the Combfooted Spiders (Theridiidae): Representatives of the genus *Latrodectus* WALCKENAER 1805, the “Widows”).
With this paper the number of genera of the subfamily Asageninae is enlarged from currently 8 (6 extant and 2 extinct) to ca. 14 (at least 6 genera are extant, 8 fossil genera are extinct). AGNARSSON (2004: 467) listed only three – extant – genera of the Asageninae: *Crustulina, Latrodectus* and *Steatoda* s. l. (fossil genera were ignored). Besides the extant nominate genus *Steatoda* and the widely accepted genera *Crustulina* and *Latrodectus* I resurrect – from *Steatoda* SUNDEVALL 1833 – the genus *Asagena,* and as subgenera *Lithyphantes* and *Stearodea,* and I regard *Craspedisia* and *Helvidia* as members of the Asageninae, too. Most members of the now accepted

extant genera occur in Europe (*Craspedisia* and *Helvidia* are exceptions), all the 8 fossil genera which are known from Baltic amber are extinct: To the previously described genera *Clya* and *Eomysmena* I add in this paper the new genera *Eoasagena, Eoteutana, Nanosteatoda, Protosteatoda, Pseudoteutana* and *Unispinatoda*. So we know now from a single Tertiary area, the Eocene Baltic amber forest, more (extinct) genera of the Asageninae than today worldwide; but in my opinion most probably several extant tropical genera of the Asageninae have to resurrect in the future, see below. – This ancestral theridiid subfamily – like the Enoplognathinae – was apparently more diverse in the Early Tertiary than today.

Ecology:

(a) Prey: Members of several Asageninae species feed on ants (compare photo 32); an ant with *Eomysmena* sp. indet., F1715/CJW, see below.– The largest extant Asageninae – e. g. members of *Latrodectus* – live at the ground and feed on large prey (e. g. beetles). Comparable large fossil Asageninae in Baltic amber are unknown because large "ground spiders" were captured only very rarely in the fossil resin.

(b) Preferred biotopes, habitats and strata of the vegetation: Almost all extant spiders prefer open biotopes and are dwellers on or near the ground at hidden places, e. g. under stones, and few live in higher strata at (and hidden below) the bark of trees in contrast to most other Theridiidae – e.g. members of *Lasaeola* (Hadrotarsinae), *Episinus* (Episinae) and most Theridiinae – which prefer higher strata of the vegetation. The very high frequency of certain Asageninae (*Clya*, *Eomysmena, Pseudosteatoda*) in Baltic amber – most Theridiidae in this fossil resin are members of this subfamily – should result from their occurrence in higher strata, probably at the bark of trees, too. This change in the ecological preferrence of the Asageninae during the Tertiary may be caused by the competition by members of the Theridiinae which diversified later than the Asageninae during the Tertiary – probably during the Oligocene –, which prefer higher strata of the vegetation, and which displaced most Asageninae in higher strata. – According to the presence of only a single specimen in three fossil genera – *Eoasagena, Eoteutana, Protosteatoda*) and only two specimens in a fourth genus (*Nanosteatoda*) – the members of these genera may already have been dwellers at the ground and may only occasionally (by ballooning?) have drifted to the fossil resin.

Distribution: Extant: Cosmopolitical, most genera are holarctic distributed; fossil: Surely known from the Early Tertiary (Eocene) European (Baltic, Bitterfeld, Ukrainean), and the Miocene Dominican amber (only *Craspedisia*, the only fossil genus which survived from a Tertiary forest).

Remarks on the synonymy, priority, ranges and the names of the taxa:

(1) Subfamily:

The name Asageninae SIMON 1894 (sub Asageneae) is older than Latrodectinae SIMON 1914 (sub Latrodecteae) and well in use, see e. g. SIMON (1914), WIEHLE (1937); contra AGNARSSON (2005). – In his work on fossil spiders PETRUNKEVITCH (1942) – following SIMON – did not separate Hadrotarsinae (sub Dipoeninae) and Asageninae (= Latrodectinae). SIMON (1914) included *Enoplognatha* and *Robertus* in his Asageninae, and did not mention the Enoplognathinae separately as he previously did. Some authors unite Enoplognathinae, Phoroncidiinae and Pholcommatinae – that may be correct or not – but I do not unite them, see the diagnoses and the key to the subfamilies above.

(2) Genera:

Remarks: Before certain genera were synonymized with *Steatoda* s. l. by LEVI & LEVI (1962) most of the former authors knew well the differences between the various genera of the Asageninae which are listed in the Katalog of the Aranea, 1 by ROEWER (1942). Apparently the conspicuous similarities and CONVERGENCES in the colour of the body, the position of the lateral eyes – a character which was overwightened in my opinion by some authors –, the structures of the bulbus in different genera, as well as the large and hairy colulus, and the conspicuous intrageneric differences in the shape of the epigyne may have played a role in the lumping of genera by LEVI & LEVI. According to my investigation there are clear diagnostic characters of the resurrected genera; see the diagnoses, the key to the genera and subgenera, and the paragraph on the variability below. – Regarding the subgenera: See the paper no. 13 “Different views on Taxonomy...” in this volume.

LEVI & LEVI (1962) (see also below) regarded the genera *Ancocoelus, Argyroelus, Asagena, Asagenella, Eucharia, Lithyphantes, Stearodea, Steassa*, *Stethopoma*, *Teutana* and – with a question mark – also *Moero* (see below, = Cyatholipidae) as synonyms of *Steatoda* SUNDEVALL 1833, which is the oldest name.

In this paper I remove from their synonymy (gen. resurr.) the following taxa from *Steatoda*: *Asagena* (as genus of its own)*, Lithyphantes* and *Stearodea* (as subgenera of *Steatoda*); see also the special case of *Teutana* (below). *Steatoda* has probably to split up into several further subgenera or even genera, mainly from SE-Asia, e. g. *Stethopoma* THORELL 1890 (type species *Steatoda cingulata* (THORELL) (in which a hood-shaped paracymbium exist), and gen. indescr. with its type species *Steatoda wangi* ZHU MINGSHENG 1998 (in which the opisthosoma bears a dorsal scutum). – The most diverse genus is *Steatoda* (syn.: *Teutana*), and ALL THE SPECIES OF THE ASAGENINAE WORLDWIDE WHOSE RELATIONSHIPS ARE NOT YET KNOWN, SHOULD BE LISTED PROVISORICALLY UNDER *STEATODA* until they – and their subgenera – are revised. I regard *Asagenella* SCHENKEL 1937 (holarctic) as a synonym of *Steatoda*, *Argyroelus* HOGG 1922 (Vietnam) as a questionable synonym of *Steatoda*. *Eucharia* C. L. KOCH 1835 is praeoccupied by *Eucharia* HUEBNER 1802 and was regarded as synonym of *Steatoda* by LEVI & LEVI (1962: 21). *Moero* O. PICKARD-CAMBRIDGE 1904 has turned out to be a member of the family Cyatholipidae. The relationships of *Stethopoma* THORELL 1890 (Sumatra, see below: *Steatoda*) have to revise.

The type species of *Steatoda* SUNDEVALL 1833 is *Aranea castanea* (CLERCK 1757) – see LEVI & LEVI (1962: 28) and LEVY & AMITAI (1982: 14) – which is a typical species of the genus *Teutana* SIMON 1881 (type species: *Aranea triangulosa* WALCKENAER 1802. So *Teutana* has to be regarded as a junior synonym of *Steatoda*. Certain authors believed erroneously *Aranea bipunctata* LINNAEUS 1758 being the type species of *Steatoda*, see LEVI & LEVI (1962: 28), but *bipunctata* is actually the type species of *Stearodea* O. PICKARD-CAMBRIDGE1902, which I regard as a subgenus of *Steatoda* s. l..

Remarks on the extant genera *Ancocoelus*, *Craspedisia*, *Helvidia*, *Icona, Proboscidula* and *Steassa*: The subfamiliar relationships and the synonymy of the genera *Ancocoelus* SIMON 1894 (Tasmania), *Craspedisia* SIMON 1894 (America and China, see below), *Icona* FORSTER 1955 (New Zealand) and *Steassa* SIMON 1910 (South Africa, ♂ unknown) are not sure, see LEVI & LEVI (1962: Tab. 2). LEVI & LEVI (1962: 60–62) compared these genera with *Steatoda*. In *Craspedisia* the position of the paracymbium (fig. 37) is retrodistal (ectal) as in the fossil Asageninae. LEVI & LEVI (1962) compared the genus with *Crustulina* and *Steatoda*. According to AGNARSSON (2004: 468) *Craspedisia* may well be a member of his Pholcommatinae, but Pholcommatinae – see its diagnoses and descriptions below – are usually dwarf spiders which have small anterior median eyes, a redbrown colour of body and legs and reduced teeth of the paired tarsal claws. *Helvidia* (from Sumatra) (figs. 42–43) was transferred by LEVI (1970) from Araneidae to Theridiidae, and regarded as closely related to *Enoplognatha* but – according to the rugose prosoma, the scutate opisthosoma (like in *Steatoda wangi*) and the structures of the bulbus – I transfer the genus here to the Asageninae. *Proboscidula* MILLER 1970 (extant, Africa) may be a member of the Asageninae, too, see KNOFLACH (1995). *Ancocoelus* SIMON (Tasmania) may be a genus of its own; it has to revise. – I had no opportunity to study specimens of the genera *Ancocoelus*, *Craspedisia* (except a fossil), *Helvidia, Icona, Proboscidula* and *Steassa*.

Eocene genera: *Antopia* MENGE in KOCH & BERENDT 1854 in Baltic amber: See above (Synonymy) and below: *Eomysmena* (probably a younger synonym).

(3) Species:
Besides few species of *Eomysmena* and *Clya* (= *Nanomysmena*) – see below – few species were previously described from Baltic amber and were placed in the Asageninae: *Steatoda succini* PETRUNKEVITCH 1942 and *Lithyphantes anticus* BERLAND 1939; both were based on female holotypes, their males are unknown. I consider the holotype of *Lithyphantes anticus* as a questionable member of *Episinus,* and the holotype of *Steatoda succini* (epigyne fig. 31) – as well as the paratype, a juvenile male – as Theridiidae indet., see below. *Erigone stigmatose* KOCH & BERENDT 1854: See *Pseudoteutana* n. gen..

Diagnosis of the Asageninae: Colulus large and usually bearing three or more (in large spiders up to more than ten) hairs (figs. 47, 70, 111) (only two hairs exist in small members as *Clya* and some *Crustulina*), body and legs basicly strongly sclerotized, prosoma including the sternum usually rugose with raised hair bases; at least the anterior legs bear most often ventral hair-bearing cusps (both are absent in *Latrodectus*, in some members of *Steatoda* – in which the colulus bears 3 or more hairs –, and in few fossil genera; prosomal-opisthosomal stridulatory organ (figs. 38, 76) very well developed (except in Latrodectinae), eye field narrow (fig. 108). Four PMS AC spigots, see AGNARSON (2004: 467). Paracymbium: shape very variable, well developed; plesiomorphicly – in *Craspedisia*, *Helvidia* and in all fossil taxa (!) – not distinctly sclerotized, and in a retrodistal-ectal position (figs. 37, 63), but strongly sclerotized and in an internal position (figs. 34, 48–49, 56) in the extant taxa except *Craspedisia* and *Helvidia*. Capture web with gumfooted lines, and with a peripheral (hidden) retreat in extant spiders (unknown in fossil spiders).

Remark regarding the function of the colulus: Its function is unknown and it has been regarded funtionless by several authors – but why is it so large in most Asageninae and bears up to more than ten hairs in members of this subfamily? Because of its position and bearing hairs I suppose (it makes sense) that the colulus has a sensory – proprioreceptory? – function at least in large and ground-living spiders of this subfamily. In members of the subfamily Theridiinae – which are mainly dwellers of higher strata – a colulus is completely absent (lost).

Further characters: Distinct concave cheliceral furrows are usually absent, the opisthosoma has usually an oval shape (it is globular in the giant females of *Latrodectus*) and may be slightly flattened, the cephalic part is fairly elevated in some taxa. Most spiders possess stout legs. The body length is most often 2–10 mm (largest females in egg-bearing *Latrodectus* and some *Steatoda*, but only 1.4 mm in *Nanosteatoda*). Among the Asageninae are the largest members of the Theridiidae, and the only case of sexual dimorph female gigantism (in the extant genus *Latrodectus*). At least members of certain genera – e. g. *Latrodectus* and some *Steatoda* – possess a strong venom which is dangerous to large insects and vertebrates as well. The colour of body and legs is usually dark to black brown (the legs are usually annulated) with white or coloured spots or stripes on the opisthosoma but light brown in few species of *Steatoda* s. l. like *triangulosa*.

Tribes: I distinguish three tribes of the Asageninae:

(a) Pseudoteutanini **n. trib**. (type genus: *Pseudoteutana* n. gen.) in which – in contrast to the remaining tribus – the paracymbium has an ectal position and is only weakly sclerotized. Colulus usually with 2–3 hairs (rarely exists a small aditional hair, fig. 111). Distribution: Disjunct, the Americas – incl. Tertiary (Miocene) Dominican amber forest –, China, and Early Tertiary (Eocene) Baltic amber forest. The Baltic amber forest has a connecting position in this relict taxon. Extant genera: *Craspedisia* (fossil in Dominican amber as well), and *Helvidia*; fossils/extinct genera in Eocene European ambers: *Clya*, *Eoasagena, Eomysmena, Eoteutana, Nanosteatoda, Protosteatoda, Pseudoteutana*, *Unispinatoda*. 8 of 10 genera are extinct and only known from Baltic amber, only *Craspedisia* and *Helvidia* are extant genera.
(b) Asagenini SIMON (type genus: *Asagena* SUNDEVALL 1833) with a strongly sclerotized intern paracymbium (similar to Latrodectini), and with large promarginal cheliceral tooth or teeth (similar to most Pseudoteutanini). Colulus with 2 hairs in most small spiders but up to more than 10 hairs in large spiders. Distribution: Cosmopolitical; unknown from fossils. Genera: *Asagena, Crustulina, Steatoda* (subgenera *Lithyphantes*, *Steatoda* and *Stearodea*) and probably further genera which have to resurrect or still to describe for the first time, see above and the next paragraph.

(c) Latrodectini SIMON (only the nominate genus *Latrodectus* WALCKENAER 1805) with a smooth prosoma, reduced stridulatory files, small chelicerae, no promarginal cheliceral teeth or cusps of the legs, a modified cymbium, a strongly sclerotized intern paracymbium, a long and coiled embolus (fig. 46), sexual cannibalism, female gigantism and strong venom. Male colulus usually with 3–5 hairs, female colulus usually with 10–12 hairs (one pair is large). Distribution: Cosmopolitical, mainly cosmotropical; unknown from fossils.

Relationships: Probably Enoplognathinae is most related – as already supposed by SIMON (1914: 278) – and may be the sister group of the Asageninae; in the Enoplognathinae taxa exists a similar paracymbium and a large colulus, too (the colulus may also bear more than two hairs, see below), and a concave cheliceral furrow is also absent or weakly developed as in the Asageninae, but the (extant) members of the Enoplognathinae are only weakly sclerotized (an opisthosomal scutum is only present in the extinct new genus *Hirsutipalpus*), a rugose prosoma and ventral leg cusps are absent, the leg and prosomal colour is usually redbrown as in the Pholcommatinae which may (also) be strongly related to the Enoplognathinae. – Episinae possesses also an oval – but usually more slender, and frequently flattened – opisthosoma, and usually – apparently basicly – a retrodistal (marginal) paracymbium but the opisthosoma is weakly sclerotized, a rugose prosoma and ventral leg cusps are absent.

Phylogeny, origin, extinction and relationships of the genera:

(1) Probably the large and hairy colulus, the well developed prosomal stridulatory files, the retroectal paracymbium, and the well developed comb of tarsus IV – which exist in the Asageninae – are basic characters of the Theridiidae, and therefore I regard Asageninae being the most basal branch of this family, see above. Furthermore – according to BENJAMIN & ZSCHOKKE (2003: 301) – Asageninae build the most basic type of capture webs within the Theridiidae: "...we might consider the behaviour of *Latrodectus* and *Steatoda* to be the primitive condition in the theridiids.".
(2) Most of the extant genera are known from the Holarctic Region, much fewer in the tropics and in the Southern Hemisphere; thus the origin of the Asageninae may well be the Holarctic Region, but the knowledge of taxa of the Southern Hemisphere is still restricted.
(3) According to our current knowledge no genus survived from the Early Tertiary Baltic amber forest up to now or up to the Miocene Dominican amber forest.
(4) According to my investigation Asageninae diversified at least two times, (a) latest in the Early Tertiary – 8 genera are now known from Baltic amber – and (b) after the existence of the Baltic amber forest, probably in the Oligocene: At least 6 genera exist today which all are different from the fossil genera of the Baltic amber forest.
(5) Due to the position and the sclerotization of the paracymbium the extant and fossil taxa of the Asageninae are quite different; apparently the position of the paracymbium and the intensity of its sclerotization shifted – probably already during the Early Tertiary – in one or two branches, see above, the paragraphs "Bulbus-cymbium lock mechanism, paracymbia...".
Craspedisia and *Helvidia* are two of the most interesting genera of the Asageninae

(their relationships are unsure): In respect to the kind of their paracymbium – weakly sclerotized and in an ectal position as in all the fossil taxa and in contrast to all remaining extant genera – these may be members of an old branch of this subfamily, of the tribus Pseudoteutanini. *Craspedisia* may be the "key genus" for the understanding of the evolution of the branches of the Asageninae. The special disjunct distribution of the genus *Craspedisia* and of the whole tribus Pseudoteutanini as well – tropical Americas (extant and Miocene), China and Early Tertiary Baltic amber forest – indicates (a) the cosmopolitical distribution of *Craspedisia* in the Early Tertiary, (b) *Craspedisia* (and *Helvidia*) being relict genera of the Asageninae, and (c) Pseudoteutanini being an old/ancestral branch of this subfamily.
(6) Strongly related taxa are (see below): (a) probably *Asagena* and *Crustulina*, (b) *Craspedisia* and *Helvidia*, (c) *Lithyphantes*, *Stearodea*, and *Steatoda* and (d) the fossil genera, especially *Eomysmena* and *Eoteutana* as well as probably *Eoasagena* and *Nanosteatoda*. Close relationships of the extinct genus *Clya* and the extant genus *Latrodectus* are unknown; both may be branches of their own besides their extant and fossil relatives; I will not exclude that the weakly sclerotized *Latrodectus* may be the sister group to the remaining Asageninae, see the paragraph "Relationships" below.
(7) A sure proof of fossil Theridiidae from the Cretaceous is wanting; from that period I would firstly expect representants of or related to the ancestral Asageninae.

Intrasubfamiliar and intrageneric variability, similarities and convergences within the Asageninae (selected characters):

(1) Most often body and legs are strongly sclerotized (hardened and mainly blackbrown), usually the epigaster is strongly sclerotized and the prosoma is strongly sclerotized and rugose (figs. 36, 42–43, 88, 108f, 126, 133, photos 163, 191f) but in *Latrodectus* and *Protosteatoda* it is smooth, and in *Stearodea*, *Latrodectus* as well as in some *Steatoda* as *triangulosa* the epigaster is only weakly sclerotized (probably reversals). Prosomal wrinkles and leg cusps are stronger developed in the male sex. The opisthosoma may be hardened (stronger in the male, e. g. leathery in *Crustulina* and *Helvidia*) or it even bears a dorsal scutum, so in ?*Steatoda wangi* ZHU MINGSHENG 1998 (China) as well as the fossil genera *Eoasagena* and *Nanosteatoda* (females unknown). – The evolution of these sexual dimorphic differences may be caused by ants which could be more dangerous to the more vagile male spider – which are searching for females – than to females which are protected for most of the time in their capture web.

(2) Eye lenses: (a) The lenses of the lateral eyes are most often contiguous (fig. 51) but in certain taxa they are separated by about their diameter (*Latrodectus,* some *Steatoda*) (similar to fig. 55) or about by their radius (e. g. in some *Asagena* up to one diameter and *Steatoda septemmaculata*; an intrageneric variability). Distinctly separated lateral eyes evolved several times convergently within the Asageninae. – (b) The anterior median eyes are usually not larger than the remaining eyes but in *Helvidia*, *Steatoda*: *Stearodea* and in *Steatoda latifasciata* (intrageneric variability) lenses of the anterior median eyes are distinctly larger than the others.

(3) The ventral margin of the clypeus has a medial gap (sector) in the extant genus *Stearodea* (fig. 50) and the extinct genus *Eomysmena* (arrow in fig. 110); an indistinct gap is present in some species of *Steatoda*.

(4) In most extant Asageninae the fangs are stout (but slender in *Crustulina*) in contrast to the (usually small) fossil spiders in Baltic amber in which the fangs are long and slender. Apparently the smallest spiders possess fangs which are more slender.

(5) Teeth of the cheliceral "margins": Usually in the male the anterior "margin" of the cheliceral "furrow" bears at least one tooth (the posterior "margin" is smooth), but in both sexes of *Helvidia* and *Latrodectus* teeth are absent on the anterior "margin", too. Remark: In the Asageninae – as in some Enoplognathinae (*Enoplognatha*) – a concave cheliceral furrow with "sharp" margins is absent, so true furrows are not existing in these taxa.

(6) The sternum is usually rugose and (a) not or only slightly prolongated between the posterior coxae in all extant genera except *Craspedisia*, *Crustulina* and *Helvidia*, but it (b) widely separates (up to their diameter) the posterior coxae in all fossil genera as well as in the extant genera *Craspedisia*, *Crustulina* and *Helvidia* (fig. 39).

(7) Ventral hair-bearing cusps of (at least) the anterior legs of males (fig. 146) are most probably apomorphic for Asageninae. They are weakly developed – or even absent – in the female sex and reduced in some taxa, even absent in *Latrodectus*, very well developed in male *Crustulina* and *Steatoda cingulata* (THORELL 1969), and strongly developed (spoon-shaped) in male *Asagena* (legs I/II) (fig. 32). Some of these spoons are sexual-dimorph developed in the male sex – as "clasping spines" – which play a role in the mating behaviour (fixing the females during copulation). – (Sexual size dimorphism: See below, no. 17).

(8) Usually exist two dorsal bristles on tibia IV (unknown to me in *Helvidia*), but in few taxa the distal tibial bristle is absent: In *Asagena* (sexual-dimorphic short bristles in the male members of this genus), *Crustulina*, *Eoasagena* and *Nanosteatoda*. In *Steatoda cingulata* THORELL 1869) bristles of tibia IV are probably completely absent. We have losses three, four or even five times independently within the Asageninae.

(9) A trichobothrium on metatarsus IV is usually absent in the Asageninae and its position on metatarsus I–II is in the basal half (unknown in *Helvidia*), but it is present on metatarsus IV in *Asagena*. Its position is in the distal half e. g. in *Asagena* and *Steatoda cingulata* (THORELL). – Remark on a probable reversal: According – e. g. to the derived intracymbial position of the paracymbium – *Asagena* is surely not an ancestral genus of this subfamily, and so I regard the existence of a metatarsal IV trichobothrium being a **REVERSAL** in this genus; in my opinion a reversal is more likely than numerous losses separately in this subfamily. – In *Crustulina guttata* a trichobothrium on metatarsus III is absent in contrast to other congenerics (and to other taxa of the Asageninae) – an intrageneric variability.

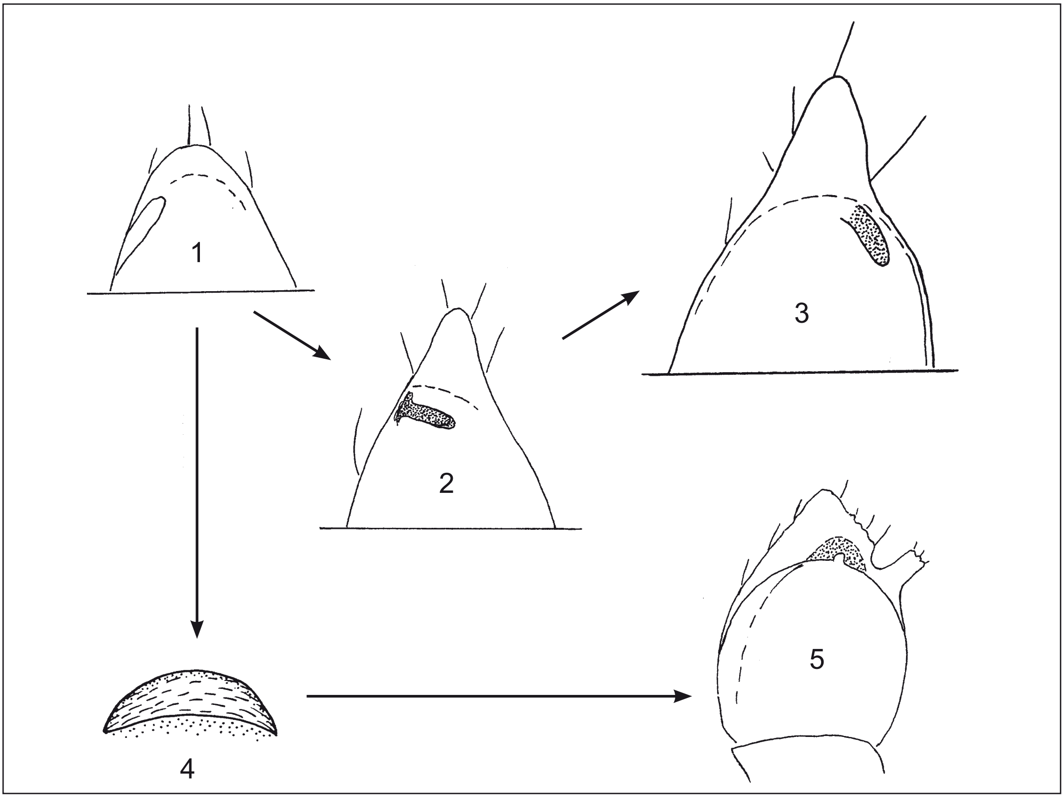
(10) The legs are covered with conspicuous longer hairs in the fossil genus *Eoteutana* (photos 199–200) in contrast to other members of the Asageninae.

(11) The number of the hairs of the colulus is frequently higher than two (a pair), mainly in large members, e. g., 9–12 in *Latrodectus* sp. (usually 3–5 in the small males, usually 9–12 in the large females, one pair of these hairs is large; this is a sexual dimorphism connected with the sexual size dimorphism) as well as in *Steatoda* (*Lithyphantes) albomaculata* and *Steatoda paykulliana* (fig. 47), but there are only 2–3 hairs in small spiders, 2 in some *Crustulina* as well as in the extinct genera *Clya, Pseudoteutata* (figs. 70, 140) and probably in *Protosteatoda*, and 3 in *Eoasagena, Eoteutana,* and *Nanosteatoda* (figs. 128, 135) (their number is unknown in *Helvidia* and *Unispinatoda*); there is a greater number in *Eomysmena*. (See this character in Anelosiminae and Enoplognathinae, too).

(12) The retrolateral margin of the cymbium may function as a conductor of the embolus in such taxa in which a long and coiled embolus exists: In peculiar species of the extinct genus *Clya* (figs. 98, 102) and in the extant genus *Latrodectus* (fig. 46). These are doubtless convergences in these genera which are not strongly related. (See also this character in *Succinura* n. gen. (Pholcommatinae), *Kochiuridion* n. gen. and *Kochiura* ARCHER (Anelosiminae)).

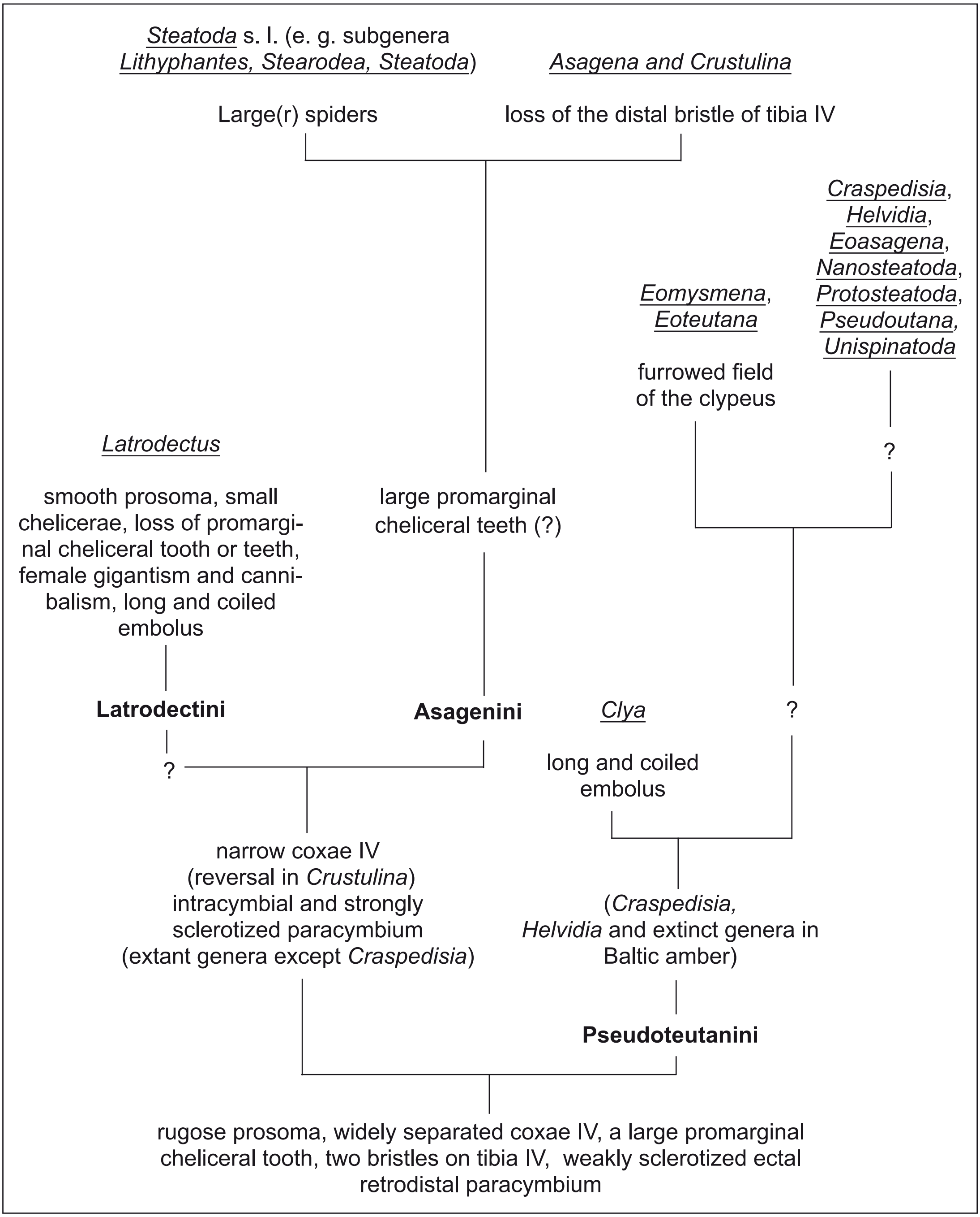
(13) The position and the intensity of sclerotization of the paracymbium (see the figs. below) is very variable within the Asageninae: In all extinct taxa of the Baltic amber forest it is not or very weakly sclerotized and situated ectal retrodistally in a similar position, fig. A (1)). In most of the EXTANT taxa it is – contrarily – strongly sclerotized (dark brown) and situated inside the cymbium (intracymbial) in a quite variable position, figs. A (2–5)), more or less similar within a single genus. Exceptions are the extant genera *Craspedisia* and *Helvidia* which have a retroectal and only weakly sclerotized paracymbium as in the fossil genera. Usually the paracymbium is hook-shaped, figs. A (2, 3) but in *Crustulina* and some species of *Steatoda* – e.g. *Steatoda cingulata* and *S*. sp. indet. from Laos (SMF) – it is hood-shaped (figs. A (4, 5); in *Steatoda* (*Lithyphantes*) *albomaculata* its position is near the prodistal margin, fig. A (3) (unique within the Asageninae it shifted to the opposite side of the cymbium!), in *Steatoda latifasciata* SIMON its position is midway, in *Steatoda* (*Stearodea) borealis* (HENTZ) it is partly hook-shaped and partly hood-shaped and in *Latrodectus* it is strongly modified.

(14) A **LARGE** theridiid tegular apophysis (TTA) evolved several times within the Asageninae, e. g. in *Steatoda* (*Stearodea)*; it stands strongly out from the bulbus in *Steatoda* (*Lithyphantes)* (fig. 57), and evolved in a similar way in *Asagena americana* (fig. 35) – a surprising case of convergence!



Figs. A (1–5): Shifting of the paracymbium in the evolution of the Asageninae in extinct (fig. A (1)) and extant taxa (figs. A (2–5)). Ventral aspect of the right cymbium (bulbus removed), distal parts only in figs. 1–3, paracymbium solely in fig. 4.

(1) *Pseudoteutana* sp., an extinct taxon which existed ca. 40–50 million years ago in the Early Tertiary European amber forests. Note the ancestral position of the finger-shaped and only weakly sclerotized ECTAL paracymbium at the retrodistal margin of the cymbium which exist in extant spiders only in *Craspedisia* and *Helvidia*.
(2) *Steatoda(Steatoda) grossa* (C.L. KOCH 1838), extant, Germany. Note the strongly sclerotized and HOOK-shaped paracymbium, which has been shifted inside the cymbium and is directed prolaterally. (In ?*Steatoda cingulata* (THORELL) exists a hooded paracymbium).
(3) *Steatoda* (*Lithyphantes*) *albomaculata* (DE GEER 1778), extant, Germany. Note the **PRO**marginal position of the intracymbial paracymbium.
(4) *Steatoda (?Steatoda) cingulata* (THORELL 1890), extant, China: A HOOD-shaped, strongly sclerotized internal paracymbium – the most derived kind of paracymbia within the Asageninae besides *Crustulina*.
(5) *Crustulina guttata* (WIDER 1834), extant, Germany. Note the strongly sclerotized flat and HOOD-shaped paracymbium which shifted in the prolateral direction inside of the cymbium to an internal position. In *Crustulina* exists one of the most derived kind of paracymbia within the Asageninae besides ?*Steatoda cingulata*. (In the genus *Crustulina* exists an additional prodistal outgrowth of the cymbium).



Probable relationships of the extinct and extant genera of the Asageninae.
The relationships of *Clya* and *Latrodectus* are most unsure, the relationships of *Craspedisia* and *Helvidia* are also not sure.

(15) An additional tegular apophysis (ATA) is usually weakly sclerotized (distinctly sclerotized in *Steatoda* (*Lithyphantes) albomaculatus*) and originates between the TTA and the embolus; it is fringed in at least some of the fossil taxa. I found it in the extant *S. albomaculatus* (not fringed) (see the fig. 57) and – apparently convergently evolved – in the extinct genera *Eomysmena* and *Pseudoteutana* (fringed) (see the figs. 123, 143), and probably in *Unispinatoda*. I will not exclude its existence in the other fossil taxa – in which its existence is unknown – as well as in some species of *Steatoda;* further studies are needed.

(16) The embolus is strongly coiled/looped in *Latrodectus* (fig. 46) and evolved convergently similar in the extinct genus *Clya* (fig. 100); in these genera exist also a large/ wide cymbium – see no. (12) – and bulbus in contrast to most other Asageninae. – A shorter and sickle-shaped embolus exists in most extant members of *Steatoda* (fig. 53–54, 58), and evolved convergently in the extinct genus *Pseudoteutana* (fig. 143).

(17) A sexual size dimorphism (a result of female gigantism) exists in *Latrodectus* and is – to our actual knowledge – absent in the other asagenine genera, but the females of most of the extinct genera are unknown. I never found an unusually large female of the Asageninae in the Baltic amber.

Remark: Taking into account the numerous “similarities”, convergences and reversals of these characters in the genera of the Asageninae I would be eager to see the result of a computer-based cladistic analysis of their relationships, although few of these characters are probably incorrectly estimated by me.

Key to the extant and fossil genera – and selected subgenera of *Steatoda* s. l. – of the subfamily Asageninae:

Remarks: (1) The extant genera *Icona* FORSTER 1955 (New Zealand) and *Proboscidula* (Africa, relationships unsure) are not included in this key. The tibiae of *Proboscidula* are bristleless, the prosoma is not rugose and the posteriorly wide sternum bears modified hairs which may be glandular, a retrodistal-ectal paracymbium exists, see KNOFLACH (1995). – (2) The extinct genera in Baltic amber are *Clya, Eoasagena, Eomysmena, Eoteutana*, *Nanosteatoda*, *Protosteatoda, Pseudoteutana* and *Unispinatodea*, see nos. 9–15; the female of these fossils is only known in *Clya* and *Eomysmena*. – (3) In several genera the tibia IV bears 2 dorsal bristles; only a single tibial bristle (in the basal half) is known to me from *Asagena*, *Crustulina*, *Eoasagena*, *Nanosteatoda* and probably ?*Steatoda cingulata*. – (4) Coxae IV are widely separated by the sternum in *Crustulina*, *Craspedisia*, *Helvidia* (fig. 43), and in all of the extinct genera.

1 Male clypeus with a slender anterior projection (fig. 36), paracymbium as in the fossil genera of the Baltic amber forest (fig. 37). Extant (the Americas and China) and fossil in Dominican amber. . . . . *Craspedisia*

- Clypeal projection absent, paracymbium similar or different (inside the cymbium). Extant and fossil in Baltic amber.. 2

2(1) Prosoma – at least the male sternum – usually rugose (figs. 42–43, 108f, photos 191f) and/or some articles of leg I and/or the pedipalpal femur ventrally usually with cusps (figs. 32, 146) (prosoma smooth and leg I articles without hair-bearing cusps in some members of *Steatoda* and some fossil taxa). Lateral eyes contiguous or distinctly separated, cymbium modified only in *Crustulina* (fig. 40). ANTERIOR CHELICERAL “MARGIN” – except in *Helvidia* , no. 8 – WITH AT LEAST ONE TOOTH. A long AND COILED embolus exists only in the extinct genus *Clya* (e. g. fig. 90). Extant and fossil. 3

- Prosoma smooth, ventral cusps on leg I and the pedipalpal femur absent, lateral eyes widely spaced (similar to fig. 55), anterior cheliceral “margin” smooth, cymbium strongly modified, embolus long and strongly coiled (fig. 46), female gigantism – small males. Extant (mainly cosmotropical and subtropical) . . . .*Latrodectus*

3(2) ♂: Cymbium with a large PRODISTAL ectal process (figs. 40). Epigyne raised in a sclerotized transverse bridge. Coxae IV widely separated by the sternum (fig. 39, as in *Craspedisia*, no. 1). Prosoma strongly rugose. Extant, cosmopolitical. . . *Crustulina*

- ♂: Cymbium without a prodistal process. Epigyne different. Coxae IV widely separated by the sternum in the fossil taxa and in *Helvidia* from Sumatra (no. 8). Prosoma strongly rugose (e.g. in *Asagena* and *Eomysmena*) or not. 4

4(3) Coxae IV widely separated by the sternum (similar to fig. 39). Position of the weakly sclerotized paracymbium retrodistally on the ectal cymbial margin (figs. 63, 115–116). Extant (*Helvidia*) or extinct in Baltic amber. 8

- Coxae IV close together. Paracymbium strongly sclerotized and hidden within the cymbium (figs. 34, 41, 48). Extant. 5

5(4) Metatarsus IV with a trichobothrium (unique in the Asageninae!), tibia IV with a single dorsal bristle in the basal half. Prosoma strongly rugose, with numerous denticles on its margin. ♂: Femur and/or tibia I or II with spoon-shaped outgrowths (fig. 32), basal part of the embolus with a "seam" (figs. 33, 35), epigyne with a transverse bridge. Almost cosmopolitical. . . . . *Asagena*

- Metatarsus IV without a trichobothrium, tibia IV usually with 2 dorsal bristles. ♂: Femur and tibia I–II without spoon-shaped outhgrowths but frequently with cusps. . . . . .
. . . . *Steatoda* sl. l...6

6(5) Anterior median eyes distinctly larger than the anterior lateral eyes (fig. 51), gap of the ♂-clypeus present (fig. 50; more weakly developed in *bipunctata*), opisthosoma weakly to fairly flattened, theridiid tegular apophysis very large (figs. 53–54). Holarctic. . . . . Subgenus *Stearodea*

- Anterior median eyes usually not larger than the anterior lateral eyes (*Steatoda latifasciata* is one of few exceptions), gap of the ♂-clypeus most often absent, opisthosoma usually not flattened (rarely slightly flattened in some members of the subgenus *Steatoda*), theridiid tegular apophysis small to very large 7

7(6) ♂: Gnathocoxae usually with tubercles (fig. 55) (less distinct in small spiders), paracymbium in a PRODISTAL (!) POSITION (fig. 56), bulbus with an additional tegular apophysis and another large tegular apophysis which stands widely out (fig. 57). E. g. *L. albomaculatus* . . . . Subgenus *Lithyphantes*

- ♂: Gnathocoxae smooth, paracymbium in a retrodistal (fig. 48) or midway position, bulbus variable, an additional tegular apophysis is most often absent, a tegular apophysis which stands widely out exists occasionally. (= "*Teutana*") . . . . Subgenus *Steatoda*

8(4) Anterior median eyes largest, their area strongly protruding (fig. 42), male pedipalpus figs. 44–45. Extant (Sumatra). . . . . *Helvidia*

- Anterior median eyes not largest, their area not strongly protruding, male pedipalpus different. Extinct, in Baltic amber 9

9(8) ♂: Clypeus very long, bearing a field of long hairs and a distinct medial gap (fig. 108–110, arrow in fig. 110). Embolus very wide at its base, abruptly thin in the distal half (figs. 117f). Epigyne of a probably congeneric female with a wide groove (fig. 125b). Body length 3–4.1 mm. . . . . *Eomysmena*

- No such hairs of the ♂-clypeus nor a distinct medial gap of the clypeus, embolus different. Body length 1.4–3 mm 10

10(9) ♂-pedipalpus (figs. 97–99) with a long and coiled embolus. . . . . *Clya*

- Embolus not long and coiled, hidden in some taxa 11

11(10) Body length 1.4–1.6 mm, opisthosoma with a dorsal scutum in the basal half (photos), tibia IV with a single dorsal bristle in the basal half (fig. 131). 12

- Body length at least 2 mm, dorsal opisthosomal scutum absent, tibia IV with 2 dorsal bristles. 13

12(11) Eye field ca. 0.35 mm wide, prosoma high, cephalic profile convex (fig. 103), ♂-pedipalpus figs. 104–107 . . . . *Eoasagena*

- Eye field ca. 0.27 mm wide (fig. 134), prosoma low (fig. 133), ♂-pedipalpus figs. 132, 136. . . . . *Nanosteatoda*

13(11) Legs covered with conspicuous long hairs (photos 199–200), pedipalpus (fig. 129) with the conductor longer than the tip of the cymbium . . . . *Eoteutana*

- Legs with normal hairs, conductor not longer than the tip of the cymbium (figs. 142–144, 147) 14

14(13) Prosoma and/or sternum strongly rugose (similar to fig. 133). Chelicerae not distinctly diverging 15

- Prosoma incl. sternum smooth; pedipalpal femur with retroventral denticles (fig. 138). Chelicerae distinctly diverging, with a large tooth (fig. 137). Pedipalpus (fig. 138): Cymbium retrobasally with a hair-bearing outgrowth . . . . *Protosteatoda*

15(14) Tibia and metatarsus I with a row of distinct ventral cusps (fig. 146). ♂-pedipalpus (fig. 147): One of the distal tibial hairs distinctly longer and stronger than the other hairs, cymbium apically without bristle-shaped hairs, questionable embolus thick. . . . .*Unispinatoda*

- Tibia and metatarsus I without ventral cusps. ♂-pedipalpus (figs. 141–145): Tibia distally with several long hairs of about the same length, cymbium apically with bristle-shaped hairs, embolus sickle-shaped, of medium length. . . . . *Pseudoteutana*

The extant genera of the Asageninae (in alphabetic order):

Remarks: The position of the paracymbium is inside the cymbium (on the back, internal) in all extant genera except *Craspedisia* and *Helvidia*; usually it is +/- hook-shaped in these genera but in *Crustulina* it is distinctly hood-shaped (fig. 41). IF NOT OTHERWISE NOTED: At least few articles of the anterior legs bear – at least in the male – ventral cusps, tibia IV bears two dorsal bristles, the position of the metatarsal trichobothrium is usually in the basal half, and the colulus bears more than 2 (up to ca. 10) hairs. – Not included are few not Palaearctic extant genera like *Icona* FORSTER and *Proboscidula* MILLER (relationships questionable), see above.

Asagena SUNDEVALL 1833 (**gen. resurr**. from *Steatoda*) (figs. 32–35)

Diagnosis: Metatarsus IV with a trichobothrium (fig. 32), tibia IV with a single dorsal bristle only, male with 1–4 ventral “thorns” (clasping spurs) in two rows on femur II (fig. 32), paracymbium as in fig. 34, basal part of the long embolus with a “seam”, distal part of the embolus enclosed by the long conductor, epigyne with a transverse bridge which has shallow depressed areas anteriorly and posteriorly from the bridge, see LEVI & LEVI (1962).

Further characters: Short-legged spiders with a long clypeus, a rugose prosoma which bears numerous denticles on its margin, lateral eyes separated by less than 1/3 up to 1 of their diameters, male femur I as well as tibia I and/or II most often thickened, position of the metatarsal trichobothria in the distal half, tibial bristles thin, in the male tibia III–IV bristles sexually-dimorphic short in contrast to I–II (and the female), ventral hair-bearing cusps existing on all male femora, tibiae and metatarsi except tibia and metatarsus III, opisthosoma hardened (leathery), ♂-pedipalpus e. g. figs. 31–35.

Relationships and reasons for the resurrection: According to KNOFLACH (1996: 402) the genital-morphological characters of *Asagena* are seemingly near the *Steatoda fulva*-group; in my opinion the *fulva*-group is identical with *Asagena*. *Asagena* and *Steatoda* s. l.) differ in several characters of morphology and sexual behaviour (and therefore I resurrect *Asagena*): In the trichobothriotaxy (metatarsus IV bears no trichobothrium in *Steatoda*), in the chaetotaxy (probably in all members tibia IV bears 2 dorsal bristles in *Steatoda*), in the sexual dimorphism of the bristles on tibia IV and femoral "thorns" in the male sex which are absent in *Steatoda*, in the transverse bridge of the epigyne in *Asagena*, and in the embolus which has a membraneous inside in the basal half in *Asagena*. – In *Crustulina* tibia IV bears also a single dorsal bristle only, the spiders are short-legged and strongly sclerotized but the numerous differences indicate no close relationship: The sternum is wide posteriorly, a trichobothrium on metatarsus IV is absent, the position of the metatarsal trichobothrium is in the basal half, the tibial IV bristle is not shortened in the male, the anterior male femora are not or only weakly thickened, clasping spurs are absent, the pedipalpal patella is strongly thickened, a prodistal cymbial outgrowth exists, and the shape of the paracymbium is different. Corresponding sexual behaviour of *Asagena* and *Crustulina*: See KNOFLACH (1996).

Type species: *Asagena phalerata* (PANZER 1801) (= *Phalangium phaleratum* PANZER 1801).

Further species (see KNOFLACH (1996)): *americana* EMERTON 1882, *brignolii* KNOFLACH 1996 (**n. comb**.) (from *Steatoda*), *fulva* (KEYSERLING 1882) (from *Lithyphantes*), *italica* KNOFLACH 1996 (**n. comb**.) (from *Steatoda*), *meridionalis* KULCZYNSKI 1894, *pulcher* (KEYSERLING 1882) (**n. comb**.) (from *Lithyphantes*) and *medialis* (BANKS 1898) (**n. comb**.) (from *Lithyphantes*).

Remarks: *americana* (similar bulbus structures in *S. albomaculata*!) and *meridionalis* were already correctly considered as members of *Asagena* by EMERTON rsp. KULCZYNSKI.

Distribution: Mainly holarctic; Central America.

Craspedisia SIMON 1894 (figs. 36–37)

Diagnosis: Male clypeus with a finger-shaped anterior projection (fig. 36), the sternum separates the coxae IV by almost their diameter.

Further characters: Prosoma rugose, anterior median eyes relatively large, cheliceral promargin with a larger tooth, opisthosoma scutate, with a sclerotized ring around pedicel and with a sclerotized epigaster, the large colulus bears a pair of hairs, the embolus is short in the American species, and long in the Chinese species.

Relationships (see also above): According to the kind of the paracymbium (fig. 37) – weakly sclerotized and in a retroectal position – as well as the posteriorly wide sternum the genus *Craspedisia* is most probably a member of the Protosteatodini and most related to *Helvidia* THORELL in which the anterior median eyes are the largest and a clypeal outgrowth as well as cheliceral teeth are absent. The coxae IV of *Craspedisia* are widely spaced like in *Crustulina* and in the extinct genera in Baltic amber.

Type species: *Umfila cornuta* KEYSERLING 1891.

Distribution: Extant: Central and South America – see LEVI (1963) – and China: *C. longioembolia* YIN et al. 2003; a relict distribution; fossil: Tertiary Dominican amber, see WUNDERLICH (1988). *Craspedisia* is the only genus of the Asageninae which is known from a fossil (Miocene), and from extant specimens as well.

Crustulina MENGE 1868 (figs. 38–41)

Diagnosis: Tibia IV with a single dorsal bristle only, coxae IV widely separated by the sternum (fig. 39) (as in the fossil genera); ♂-pedipalpus (figs. 40–41): Patella strongly thickened, cymbium with a large prodistal outgrowth, paracymbium hood-shaped internal basal outgrowth of the embolus toothed. ♀: Epigyne raised in a sclerotized transverse bridge.

Further charcters: Body length only 1–3 mm, short-legged and strongly sclerotized spiders with rugose prosoma which bears numerous distinct denticles and small hairs between a pair of pits, male sternum elongated between coxae II–IV, metatarsal IV trichobothrium absent, metatarsal III trichobothrium present except in *C. guttata* (*), opisthosoma more or less hardened and with sclerotized ring around pedicel in both sexes (fig. 38), only two hairs of the colulus in some specimens, strong ventral cusps usually on all male femora (at least on femur I).
(*) A rare case of intrageneric variability in the sequence of metatarsal trichobothria in the family Theridiidae.

Relationships: See *Asagena*.

Type species: *Crustulina guttata* (WIDER 1834) (= *Theridium guttatum* WIDER 1834).

Further species: E. g. *altera* GERTSCH & ARCHER 1942, *scabripes* SIMON 1881, and *sticta* (O. PICKARD-CAMBRIDGE 1861).

Distribution: Holarctic.

Helvidia THORELL 1890 (figs. 42–45)

Diagnosis (♂; ♀ unknown): Anterior median eyes largest, and their area strongly protruding (fig. 42), "margins" of the cheliceral "furrow" without teeth, coxae IV widely separated by the sternum (fig. 43), pedipalpus (figs. 44–45): Position of the weakly sclerotized paracymbium retroectal, embolus long.

Relationships: LEVI (1970) transferred the genus from the Araneidae to the Theridiidae; he compared it with *Enoplognatha*, but according to the rugose prosoma, the posteriorly wide sternum and the structures of the pedipalpus I regard *Helvidia* related to *Craspedisia,*and as a member of the Asageninae (Protosteatodini), see above.

Type species: *Helvidia scabricula* THORELL 1890 (the only known species).

Distribution: Sumatra.

Latrodectus WALCKENAER 1805 (fig. 46)

Diagnosis: Lateral eyes spaced by their diameter or more, basal cheliceral articles small, margins of their “furrow” toothless, prosoma smooth stridulatory organ reduced, ventral leg cusps absent, cymbium and paracymbium strongly modified, embolus (fig. 46) very long and coiled, vulva with paired dumbbell-shaped receptacula; female gigantism, very strong venom, and female cannibalism.

The **relationships** are unsure, see the key; the genus is the only member of a tribus of its own (Latrodectini), see above. In the remaining genera of the Asageninae “promarginal” cheliceral teeth are most often present (absent in *Helvidia*), the prosoma is usually rugose and ventral leg cusps are usually present at least in the male. A long and coiled embolus exists – convergently evolved – also in the extinct genus *Clya* which – with respect e. g. to its rugose prosoma, the cheliceral teeth and the position of the paracymbium – is not strongly related.

Type species: *L. tredecimguttatus* (ROSSI 1794) (= *Aranea 13-guttatus* ROSSI 1794).

Further species: See the cataloges of the Araneae.

Distribution: Cosmopolitical, mainly tropical and subtropical; unknown from fossils.

Steatoda SUNDEVALL 1833 **s. l**. (figs. 47–58)

Synonyms and subgenera (up to now they are partly regarded as subgenera or species-groups, see LEVI & LEVI (1962), here as subgnera (see also above): *Lithyphantes* THORELL 1869, *Stearodea* O. PICKARD-CAMBRIDGE 1902, *Steatoda* SUNDEVALL 1833 (= *Teutana* SIMON 1881) (the most diverse subgenus), and most probably *Stethopoma* THORELL 1869. In the type species of *Stethopoma – cingulata* THORELL 1869 from SE-Asia, 1 ♂ coll. DEELEMAN from Sumatra – bristles of tibia IV are probably absent, the prosoma is low, the male femur I is distinctly thickened and bears ventral spoons, the lateral eyes are contiguous, the large and helm-shaped paracymbium (fig. A4 above) has a retrodistal-marginal position and the embolus is hidden). The synonymy of the genera *Ancoelus* SIMON 1894 and *Steassa* SIMON 1910 appear quite unsure to me, see above. – *Asagena* SUNDEVALL 1833 is resurrected in this paper, see above.

Subgenera: Besides the nominate subgenus I regard *Lithyphantes*, *Stearodea* (see below) and probably *Stethopoma* (see above: Synonymy) as subgenera, but there are more species-groups in the Ethiopian and Oriental Regions as well as in the Americas, which may be regarded as subgenera, see e. g. the species-groups sensu LEVI (1962).

Recommendation on (sub)generic names: All species of the diverse genus *Steatoda* and its subgenera – as well as of such strongly related genera which relationships are unclear – should provisorically be listed under *Steatoda* s. l. until they are revised; see the catalogues of Araneae; and all species which can not be regarded as members of the subgenera *Lithyphantes* or *Stearodea* should provisorically be listed under *Steatoda* s. str., but *cingulata* sub *Stethopoma*.

Diagnosis: Usually larger spiders (including the largest Asageninae besides *Latrodectus* females), ♀ up to more than 1 cm long (e. g. in *Lithyphantes*). ♂-pedipalpus (figs. 48–49, 52–54, 56–58): Paracymbium strongly sclerotized, its position inside the cymbium (internal), variable, half way to the promargin in *S. latifasciata* SIMON, and in a prolateral (!) position in the subgenus *Lithyphantes*; usually it is hook-shaped – but hood-shaped in *Steatoda (Stethopoma) cingulata* ZHU 1998 and *S*. sp. indet. from SE-Asia (SMF 3839), or intermediate between both kinds of paracymbia, e. g. in *Steatoda* (*Stearodea*) *borealis*. The embolus is most often fairly long and sickle- or screw-shaped.

Variability of certain further structures: Due to the position of the lateral eyes, sclerotization of the body and prosomal wrinkles as well as the structures of the genital organs *Steatoda* is the most diverse/most variable genus of the Asageninae. The colulus (fig. 47) bears several hairs, up to more than 10 hairs in large females. In *S. cingulata* a distal bristle of tibia IV is apparently absent and the cymbium is elongated. In *S. latifasciata* and *S.* indet. (SMF 3839) from SE-Asia, the anterior median eyes are distinctly the largest in contrast to most other congeneric species. The fangs are slender up to unusually stout. A medial gap of the clypeus exists e. g. in *Stearodea* and in *S.* sp. indet. from SE-Asia. An opisthosomal scutum exists e. g. in *S. wangi* ZHU 1998 from China and *S.* sp. indet. from SE-Asia.

Relationships: *Asagena* and *Crustulina* may be the closest relatives, see above.

Type species: *Steatoda castanea* (CLERCK 1757) (= *Araneus castaneus* CLERCK 1757, *Teutana castanea* auct.).

Distribution: Cosmopolitical.

Subgenus *Steatoda* SUNDEVALL 1833 (= *Teutana* SIMON 1881) (figs. 47–49)

Diagnosis: ♂: Gnathocoxae smooth, paracymbium in an internal retrodistal position and strongly sclerotized (fig. 48) (*), bulbus variable, an additional tegular apophysis is most often absent, a tegular apophysis which stands widely out exists occasionally.

(*) in a midway position (fig. 49) in *cingulata* (SE-Asia) which may be the member of a subgenus of its own: *Stethopoma*.

Type species: See above (the genus *Steatoda*).

Further species: In Europe and North America I consider *castanea* (OLIVIER 1789), *grossa* (C. L. KOCH 1838), *nobilis* (THORELL 1875), *paykulliana* (WALCKENAER 1805), *latifasciata* (SIMON 1873), and *triangulosa* (WALCKENAER 1802) being surely members of the subgenus *Steatoda.*

Relationships: See the key above and the subgenera *Lithyphantes* and *Stearodea*.

Distribution: Cosmopolitical.

Subgenus *Lithyphantes* THORELL 1869 (**n. stat**., **resurr. as subgen.** from *Steatoda*) (figs. 55–58)

Diagnosis: ♂: Gnathocoxae with distinct tubercles (fig. 55), paracymbium in a prodistal position (fig. 56), bulbus (figs. 57–58) with an additional tegular apophysis (ATA) (median apophysis sensu KNOFLACH (1996)), a large tegular apophysis which stands widely out retrolaterally and the distal part of the embolus are partly enclosed by a conductor. Egg sac covered by detritus at least in *albomaculata*, see WIEHLE (1934: 83).

Further characters: The lateral eyes may be separated by almost their diameter (fig. 55), the fangs may bear an anterior hump (fig. 55), the ATA may be distinctly sclerotized (e. g. in *albomaculata*, fig. 57) or scinny (e. g. in *kuytunensis* (ZHU), not drawn by ZHU but existing (person. observ.).

Relationships: The paracymbium has not a prolateral position in the related subgenera *Stearodea, Steatoda* and *Stethopoma*. In *Stearodea* the anterior median eyes are distinctly larger than the anterior lateral eyes and the epigaster is weakly sclerotized, in the subgenus *Steatoda* the male fangs, gnathocoxae and tegular apophyses are different, the embolus is not enclosed by the conductor, the lateral eyes are rarely separated by their radius. To my knowledge an additional tegular apophysis is absent in the subgenus *Steatoda* (as well as in *Stearodea*) and the egg sac (only described by some species) is probably in all species of the subgenera *Stearodea* and *Steatoda* not covered by detritus. – See also below, the extinct genus *Pseudoteutana* n. gen..

Type species: *Aranea albomaculata* DE GEER 1778 (= A*ranea corollata* LINNAEUS 1758), see LEVI & LEVI (1962: 23) (= *Steatoda albomaculata* (DE GEER 1778)).

Further species: *Steatoda incomposita* (DENIS 1957) from S-Europe and probably *Steatoda kuytunensis* ZHU MINGSHENG 1998 from China. The extinct *Lithyphantes anticus* BERLAND 1939 in Baltic amber is regarded here as a questionable member of the genus *Episinus*.

Distribution: The Northern Hemisphere.

Subgenus *Stearodea* O. PICKARD-CAMBRIDGE 1902 (**n. stat**., **resurr. as subgen.** from *Steatoda*) (figs. 50–54)

Diagnosis: Anterior median eyes distinctly larger than the anterior lateral eyes (fig. 51), opisthosoma fairly flattened; ♂: Clypeus with a MEDIAL GAP at the ventral margin (distinctly developed in males of *S. borealis*, fig. 50; weakly developed in the female sex), (prosoma in *S. bipunctata* with short spines, fig. 51), tegular apophysis very large and u-shaped (figs. 53–54), embolus long.

Further characters: Fangs long and slender; ♀: Colulus with ca. 5 hairs, epigaster weakly sclerotized, paracymbium (fig. 52) three-pointed and hook-shaped in *bipunctata*, partly hook-shaped and partly hood-shaped in *borealis*.

Relationships: In the subgenera *Lithyphantes* and *Steatoda* the anterior median eyes are usually not larger than the remaining eyes, the opisthosoma is most often not flattened, posterior spines on the ♂-prosoma and a medial gap of the ♂-clypeus are usually absent, the structures of the male pedipalpus (paracymbium, tegular apophysis) are different. – The gap of the clypeal margin has been convergently developed in a species-group of the subgenus *Steatoda*, and in the extinct genus *Eomysmena* in Baltic amber, see below (fig. 110).

Type species: *Aranea bipunctata* LINNAEUS 1758.

Further species: At least *S. borealis* (HENTZ 1859). (*S. latifasciata* (SIMON 1873) is a member of the subgenus *Steatoda*, *S. americana* EMERTON 1882 is a member of the genus *Asagena*).

Distribution: Holarctic.

The fossil genera of the Asageninae:

Clya **KOCH & BERENDT 1854** (figs. 59–102, photos 8, 10, 25, 29–30, 45, 161–186)

Besides *Orchestina* SIMON (Oonopidae), *Acrometa* PETRUNKEVITCH (Synotaxidae), and *Lasaeola* SIMON the males of the genus *Clya* are the most frequent spiders in Baltic amber; females are very rare. I saw thousands of males in various collections and selected less than 100 for a close study. The males are easily to recognize as members of *Clya* by the combination of their looped/spiral embolus which possess a "peak" on its thick base (photos 175–177), and the rugose prosoma (photo 174). The female is known from *C. obscura*, the internal female genitalia are unknown.

Synonymy: According to WUNDERLICH (1986: 27) *Nanomysmena* PETRUNKEVITCH 1958 is a junior synonym of *Clya*; this synonymy was not accepted by MARUSIK & PENNEY (2005). Because of no differences in the shape of the prosoma, the chaetotaxy and the structures of the male pedipalpus – with a certain variability see below – both genera are doubtless synonym in my opinion. Neither the "embolic peak" nor the paracymbium are shown in the drawings of the pedipalpi of their "*Nanomysmena*" by MARUSIK & PENNEY. For unknown reasons these authors failed to study type material of *Clya* – which is available in contrast to the time of PETRUNKEVITCH, see below – and of *Nanomysmena*, which is also available, and the present author has not been asked for material or for a discussion.

Diagnosis (♂): Pedipalpus (e. g. fig. 63, photos 170f): Embolus long, coiled or spirally (see below), with at least one long loop, partly guided by the cymbial margin, with a large and partly two-partite basal part which bears a "peak" (fig. 67). ♀: See *C. obscura*; the epigyne is unknown. According to the long embolus should the vulva – at least in the derived species – possess very long (spiral or screw-shaped) introductory ducts.

Further characters: Prosoma dorsally, as well as chelicerae and sternum rugose (photo 163, figs. 69, 88), sternum widely separated by the posterior coxae (fig. 69), femora and metatarsi I–II ventrally with bristles on cusps (fig. 77) (at least the leg cusps are most probably absent in the female), cephalic part wide, elevated and separated from the thoracal part by a depression, sequence of the tibial bristles 2/2/1/2, opisthosoma usually with two pairs of sigillae and with sclerotized epigaster. Prosomal stridulatory organ well developed (fig. 76): The strongly sclerotized anterior opisthosomal margin and the rugose posterior part of the prosoma with files. At least in *C. lugubris* exists only a single pair of epiandrous gland spigots (fig. 60). Colulus with a single pair of hairs (fig. 70). ♂-pedipalpus (e. g. figs. 63–64): Tip of the cymbium with a bristle-shaped hair, position of the paracymbium ectal-retrodistally. In contrast to the note of MARUSIK & PENNEY (2005: 204) the embolic spiral is three-dimensional – frequently hard to recognize as three-dimensional: only in such species of *Clya* in which a long embolus exists, e. g. in *rotata* (figs. 98–99) –, but it is two-dimensional in species in which a short embolus exists, e. g. in *lugubris* (fig. 62). Body length 1.9–2.6 mm.

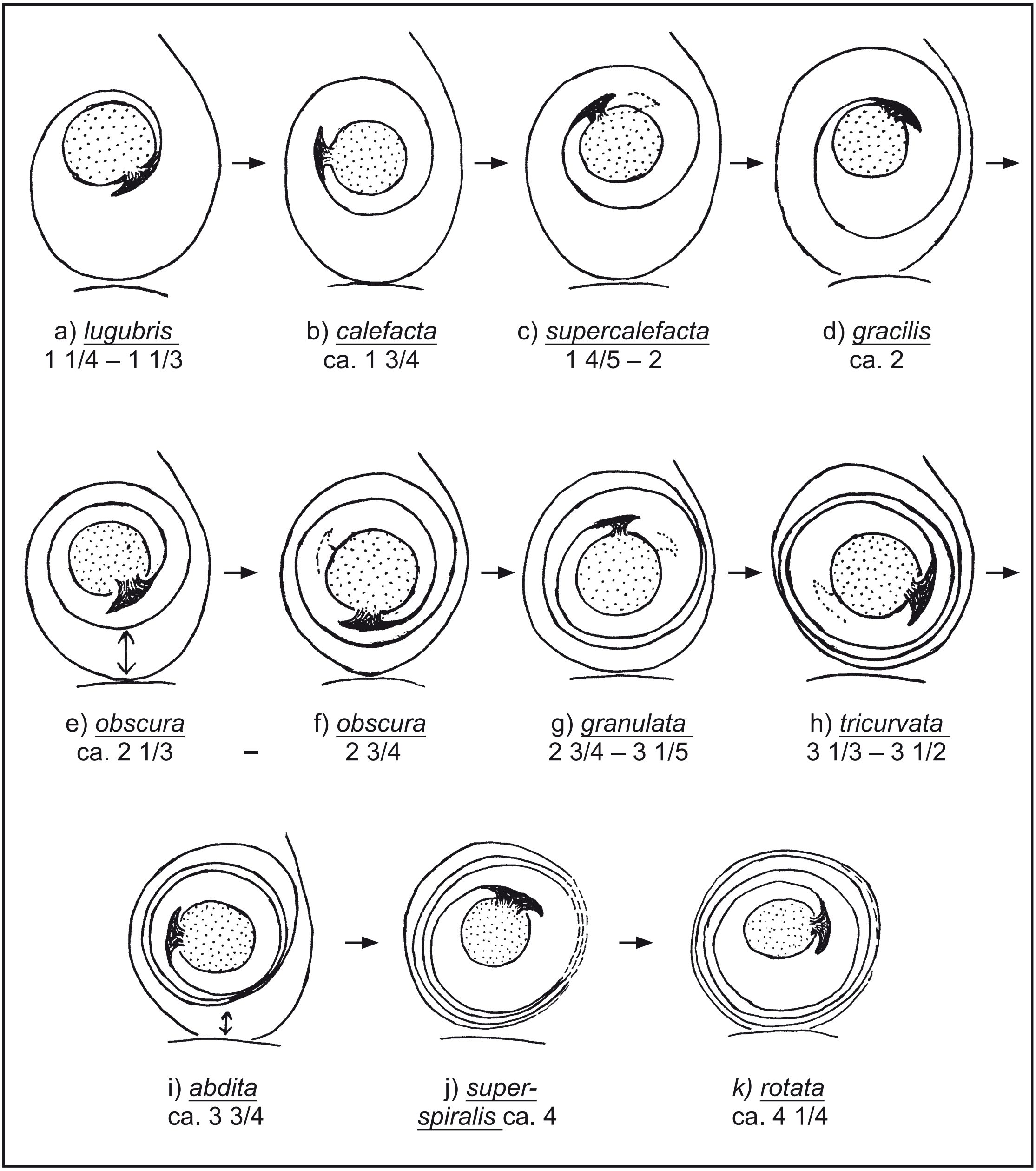
Species and remarks: Four species – *gracilis, granulata, lugubris* (the generotype) and *obscura* – were described in the 19th and 20th century in different genera; MARUSIK & PENNEY (2005) added – sub *Nanomysmena* – *C. palanga, petrunkevitchi* and *pseudogracilis*. Unfortunately it was not possible for me to get type material for a revision of these three species from the Palanga Amber Museum in Lithunia which apparently is not a scientific institution. In contrast to all species which I describe in this paper the males described by MARUSIK & PENNEY (2005) lack seemingly a "peak" of the basal part of the embolus (I suppose that this "peak" was overlooked by these authors), the pedipalpi of *pseudogracilis* seem to be badly preserved, the bulbus of *petrunkevitchi* may be expanded and the posterior median eyes of *palanga* may be covered by bubbles. A revision of these species was impossible and has to be excluded from this investigation. – In this paper I add 6 newly described species. Including not yet described taxa there may be more than a dozen species in Baltic amber, but the rank of the taxa may be unsure, see the paper "Differing subjective views of the taxonomy of spiders" in this volume and below ("Evolution"). I regard some taxa as doubtful, and do not want to exclude – according to the variable shape, length and position of the embolus, see the figs. – that *lugubris* and *obscura* may be "sampling species" and *abdita, rotata* and *superspiralis* may be not different species (but subspecies?). – The most frequent species are *C. obscura*, *granulata*, *lugubris* and *tricurvata*.

Relationships: The prosomal wrinkles, the "cusps" of the anterior legs, and the retrodistal/marginal paracymbium indicate a membership of *Clya* of the Asageninae. Most of the remaining genera of the Asageninae possess more than two hairs of the colulus but smaller representatives may possess only a single pair (fig. 140). – The shape of the embolus of some *Clya*-species is similar to *Kochiura*, in which the sequence of the tibial bristles is 1/1/1/1, the colulus is reduced and a retrodistal (ectal) paracymbium is absent.– See also *Latrodectus* as well as *Kochiuridion* n. gen. (Anelosiminae) (fig. 460).

Distribution: Early Tertiary (Eocene) European (Baltic, Bitterfeld, Ukrainean) amber forests.

Evolution: Why exist emboli of so different length in *Clya*? I do not know a sufficient answer. Are they the result of a fast radiation? Are they caused by sexual selection, i. e. sperm competition between males? – The differing length of the emboli of *Clya* may be the model of an "evolutionary row" of "time taxa"; the embolic loops/spirals reach from more than one (probably the most "primitive" species *calefacta* and *lugubris*) to more than 4 spirals (apparently the most derived species in this respect, *abdita, rotata* and *superspiralis*) (tab.). See the paper no. 13 "Differing subjective views of the taxonomy of spiders" in this volume. – Unfortunately exists no method of absolute dating of the specimens and amber pieces.
Such an "evolutionary trend" – a line of character states – of the embolic lengthening by a large ventral spiral/loop close to the bulbus occurs in numerous spider families of the Oecobioidea: Hersiliidae, the Araneoidea as well as of the RTA-clade – see e. g. JÄGER (2005) –, and originated several times convergently within the family Theridiidae, e. g. in the fossil genus *Clya* (1 to 4 1/4 loops) as well as in the extant genera *Latrodectus* (1 to 6 loops) and *Kochiura* (6 loops in *K. aulica*). Exist in these taxa a limit of 6 loops? Probably we will find a species of *Clya* in the future which has 6 loops of the embolus.

The prolongation of the embolus may be understandable by a clockwise "rotation" of the embolic bulb of the right pedipalpus from the most ancestral *C. lugubris* to the most derived *C. spiralis* and *rotata*.
Two features are conspicuous in the embolus of *Clya*: (1) The shorter the embolus – *calefacta* and *lugubris* (figs. b, 62, 65, 67) – the more long-oval is the shape of the embolus, and two-dimensional; longer (spiral) emboli have an almost circular position and possess a three-dimensional shape, see figs.g, 92, 98, 100); (2) the rarest species in Baltic amber – *abdita, rotata* and *superspiralis* (only the holotypes are known) – possess the longest embolus. Did these species occur in special biotopes or in restricted areas as mountain regions? Are these species the youngest and short-living ones, and are – on the other hand – *calefacta* and the frequent *lugubris* most related to the unknown ancestral species?



a) *lugubris*
1 1/4 – 1 1/3

b) *calefacta*
ca. 1 3/4

c) *supercalefacta*
1 4/5 – 2

d) *gracilis*
ca. 2

e) *obscura*
ca. 2 1/3 –

f) *obscura*
2 3/4

g) *granulata*
2 3/4 – 3 1/5

h) *tricurvata*
3 1/3 – 3 1/2

i) *abdita*
ca. 3 3/4

j) *superspiralis* ca. 4

k) *rotata*
ca. 4 1/4

Tab. Schematic drawings of the right emboli, and the intraspecific variable position of their embolic peaks (which is unknown in some species, but see figs. e–f) in most members of the genus *Clya* (Theridiidae) in a – phyletic? – line. The apical tibial margin (below) and the number of embolic loops/spirals are also noted.

Key to the species of *Clya* (♂):

<u>Remarks</u>: (1) The length of the pedipalpal tibia appears different in various positions. (2) We do not know the intraspecific variability of the length of the embolus – more than 1/4 loop, more than 1/2 loop? –, see e. g. *C. granulata* and *C. obscura*. (3) The position of the embolus appears quite different if the bulbus is not or more or less expanded; see e. g. *C. granulata* n. sp.. This is one of the reasons why the determination of most specimens is difficult. (4) The last loop of the embolus is partly guided between the tegulum and the distal margin of the tibia; the last half of a loop may be hidden by the guiding cymbial margin. (5) In *Clya* the right embolus turns to the left (counterclockwise) as in almost all genera of the Theridiidae. The embolus ends near the tip of the cymbium in all species. (6) The embolic loops are so close together in some bulbi that one can easily overlook one of them. (7) *C. palanga, petrunkevitchi* and *pseudogracilis* – see above – are not included in this key.

	distance between the embolic bulb and the position of the first embolic loop in direction to the tibial margin	
number of embolic loops	long	short
1 1/4 – 1 1/3	*lugubris* (fig. 62)	
~ 1 3/4	*calefacta* (fig. 67)	
1 4/5 – 2 1/5	*gracilis* (fig. 68) *supercalefacta* (fig. 71)	
2 1/4 – 2 3/4		*obscura* (fig. 78f)
2 3/4 – 3 1/5		*granulata* (figs. 89f)
3 1/3 – 3 1/2		*tricurvata* (figs. 92f)
3 3/4 – 4 1/4	*rotata (fig.98.), superspiralis* (fig. 100)	*abdita* (fig. 102)

<u>Above: Key tab. to most species (males) of the genus *Clya* except species which were described by MARUSIK & PENNEY (2005)</u>

<u>In the following the fossil species are described in the sequence of the tab. above:</u>

Clya lugubris KOCH & BERENDT 1854 (figs. 59–66, photos 10, 169–172)

1854 *Clya lugubris* KOCH & BERENDT in BERENDT, Die im Bernstein befindlichen Organischen Reste der Vorwelt, <u>1</u> (2): 31, tab. 3, fig. 19.
1986 *Clya lugubris*, – WUNDERLICH, Spinnenfauna gestern und heute: 27, fig. 337.

Material in Baltic amber: 18♂; holotypus PMHUB, F1569-1581/CJW, F1672-1673/ CJW, F1709/CJW, 1♂ coll. F. EICHMANN no. 03, 1♂ coll. F. KERNEGGER no. 198/ 1994.

Preservation and syninclusions: The holotype is completely preserved in a red-brown piece of amber and is strongly darkened by aging; the structured of the bulbus are difficult to recognize. Most of the remaining specimens are well preserved, some are heated, a dragline exists with the nos. F1571 and 1575, spider's threads are also present with the specimens nos. 1569, 1570 und 1576 (photo), a wasp and a midge with no. 1576, a spiderling with no. 03 of the coll. EICHMANN. A questionable secretion is preserved on the epiandrous spigots of no. 1569, the opisthosoma of no. 1579 is cut off. In the male F1709 the left leg III is amputated through its middle, blood is absent (see the photo 10) and probably the stump has been healed.

Diagnosis (♂; ♀ unknown): Pedipalpus (figs. 61–66) with an oval embolus which describes 1 1/4 – 1 1/3 loops, the position of the peak of the embolic bulb is basally and frequently directed to the tibia.

Description (♂):
Measurements (in mm): Body length 2.1–2.6, prosomal length 1.0–1.25, tibia I 1.2–1.6. Colour: Prosoma and legs dark brown, opisthosoma yellow brown. – Prosoma slightly longer than wide, rugose, clypeus long, cephalic part elevated, fovea distinct. Eyes large, anterior medians largest, posterior row straight, posterior median eyes separated by their diameter; a pair of small hairs is present in the field of the median eyes. Clypeus long and protruding. Gnathocoxae and chelicerae large, fangs long and strongly bent (fig. 59). Posterior opisthosomal stridulatory files well developed. – Legs fairly long, I distinctly longest, order I/II/IV/III, hairs short, patellar and tibial bristles thin, the tibial sequence 2/2/1/2, femora I–II with ventral cusps, metatarsal trichobothrium I in ca. 0.5, metatarsal IV trichobothrium absent. – Opisthosoma oval, with fairly short dorsal hairs and two pairs of sigillae; epigaster distinctly sclerotized. A single pair of epiandrous gland spigots (fig. 60), tracheal fold small and close to the spinnerets, colulus well developed, with a single pair of hairs (F1569). – Pedipalpus (figs. 61–66): Patella slightly longer than wide, the shape of the pedipalpal tibia varies from wider than long to longer than wid, paracymbium well developed, tegular apophysis large, embolus: See above.

Remark: In the drawing of the holotype (in which most parts are darkened) by WUNDERLICH (1986: Fig. 37) the tibia was drawn in an oblique position and actually too short; for the present paper the pedipalpus has been redrawn.

Relationships: See the key tab.; *C. calefacta* is most related.

Distribution: Early Tertiary (Eocene) Baltic amber forest (not – yet? – known from the Bitterfeld deposit).

***Clya calefacta* n. sp.** (fig. 67)

Material: 4 ♂ in Baltic amber; holotypus F1582/BB/AR/CJW, paratypes: F1583-1585/BB/AR/CJW.

Preservation and syninclusions: Holotype: The spider is well and completely preserved in a piece of amber which was heated, a white emulsion and stellate hairs are absent, a spider's thread is preserved right of the spider. – F1583 is well and almost completely preserved in a small yellow piece of amber without stellate hairs, parts of the left legs I–III are cut off, bubbles cover ventral parts of the opisthosoma, a weak white emulsion covers ventral parts e. g. of the pedipalpi, few thin threads including a dragline and a tiny Nematoda: Rhabditida are preserved right below the spider. – F1584 is completely preserved, most parts of the prosoma and legs – the opisthosoma completely – are cut off, stellate hairs are absent, in a separated piece as well. – F1585 is fairly well preserved in a piece of amber which was heated; the left patella II is dorsally cut off and both legs I are cut off through their femora. Some white emulsions are present on the body, stellate hairs are absent, 1/2 male *Episinus* sp. indet. (Theridiidae) is preserved left near to this paratype.

Diagnosis (♂; ♀ unbekannt): Pedipalpus (fig. 67): The embolus describes ca. 1 3/4 loops, embolic peak in a retrolateral (dorsal) position, directed to the base of the paracymbium.

Description (♂):
Measurements (in mm): Body length 2.1 (holotype) – 2.5 (F1583), prosoma: Length 1.0–1.3, width 1.05–1.3, tibia I 1.1 (holotype) – 1.6 (F1583). Transverse diameter of the embolic loops 0.32–0.42.
Colour, body and legs as in *C. lugubris*, position of the metatarsal trichobothria I–II near the middle. Pedipalpus: See above.

Relationships: See the key tab. and *C. lugubris*.

Distribution: Early Tertiary (Eocene) Baltic amber forest.

Clya gracilis (PETRUNKEVITCH 1958) (**n. comb.)** (fig. 68, photos 166–167)

1958 *Nanomysmena gracilis* PETRUNKEVITCH, Trans Connect. Acad. Arts Sci., 41: 193, figs. 188–194 (♂).

Material: Holotypus ♂ in Baltic amber, ZMHUB.

Preservation: The piece of amber is preserved in clarite – see PETRUNKEVITCH (1958: 102) – between glasses. The piece is darkened, orangebrown, body and legs of the spider are dark brown, almost black; the inner parts of the legs appear fragmented (photo), the structures of the bulbus are difficult to observe.

Diagnosis (♂; ♀ unknown): Pedipalpus (fig. 68) with a wide embolic spiral of ca. 2 1/5 loops (*), with a wide distance between the bulbus and the first half loop of the embolus which position is near to the pedipalpal tibia.

(*) Only almost a single loop according to the original description (fig. 190) (!).

Description (♂):
Measurements (in mm): Body length 2.2 mm, prosomal length 1 mm. Body and legs – as far as recognizable – as in *C. lugubris*. Pedipalpus: See above.

Relationships: See the key tab.; *C. supercalefacta* is most related.

Distribution: Early Tertiary (Eocene) Baltic amber forest.

***Clya supercalefacta* n. sp.** (figs.69–73)

Material: 8♂ in Baltic amber; holotypus F1586/BB/AR/CJW; paratypes: 4♂ F1606-1609/CJW, 1♂ from the Bitterfeld deposit coll. M. KUTSCHER in Sassnitz, 1♂ from the Bitterfeld deposit coll. H. GRABENHORST (no. AR-94) in Celle, 1♂ GPIUH.

Preservation and syninclusions: Holotype: The body of the spider is not well preserved in a piece of amber which was heated but both bulbi are well preserved; the distal parts of both legs IV are cut off, strong fissures of the amber hide the view to the spider, stellate hairs are absent in the small piece of amber. – Paratypes (most stellate hairs are not mentioned): The male of the GPIUH is well and completely preserved in a orange-brown piece of amber which was heated. A dragline, a small beetle and some stellate hairs are also preserved. The male of the coll. KUTSCHER is well preserved in a heated piece of amber. – The male of the coll. GRABENHORST is well preserved in a piece of amber which was heated. – F 1606 is fairly well preserved together with a dragline. – F1607 is well preserved, parts of the right legs III and IV are cut off. – Body and legs of F1608 are darkened, remains of a tiny Collembola are preserved in a different layer as the spider; the piece of amber was heated. – The piece of amber F1609 was strongly heated, prosoma and legs of the completely preserved spider are distinctly darkened, the opisthosoma is deformed. Two Diptera (most probably not the prey of the spider) are preserved below the spider and in contact with it in the same layer, remains of a third Diptera are preserved in a different layer.

Diagnosis (♂; ♀ unknown): Pedipalpus (figs. 71–73): Embolus in a slightly oval position, describing 1 4/5 – 2 loops, embolic peak in a distal position (variable), free visible part of the subtegulum usually large, smaller in paratype F1608.

Description (♂):
Measurements (in mm): Body length 2.0–2.2, prosoma: Length ca. 1.1, width ~ 0.9, height 0.7–0.8; tibia I 0.95–1.0.
Colour, body and legs as in *C. lugubris*, position of the metatarsal trichobothrium I near the middle. The coxae IV are widely spaced (fig. 69), the colulus (fig. 70) bears a pair of long hairs. Pedipalpus: See above. In the male F1609 – as in the male of the coll. KUTSCHER – the left bulbus is somewhat expanded and therefore the position of the embolic peak is different to other conspecific males.

Relationships: See the key tab.. In *C. gracilis* the embolus is longer, reaching almost the tip of the embolus, and is in a close position to the pedipalpal tibia after half of a loop.

Distribution: Early Tertiary (Eocene) Baltic amber forest incl. the Bitterfelder deposit.

Clya obscura (KOCH & BERENDT 1854) (**n. comb**.) (figs. 74–86, photos 29–30, 164–165, 173–177)

1854 *Gea obscura* KOCH & BERENDT in BERENDT, Die im Bernstein befindlichen Organischen Reste der Vorwelt, 1 (2): Tab. 3, fig. 13 (♂).
1986 *Clya* sp., – WUNDERLICH, Spinnenfauna gestern und heute: 260–261, fig. 337 (♂, GPIUH).

Material: 23♂1♀ in Baltic amber; holotypus ♂ PMHUB, further ♂: F1587/BB/AR/ CJW, F1589 from the Bitterfeld deposit, F1593, F1594 (1 1/2♂) – 1601 (1600: A male as prey of a spider, 1601: 2♂1♀ – the only known female of this genus!), F1617 (2♂), F1618, F1619-1622, 2♂ GPIUH.

Preservation and syninclusions: Holotype: Its opisthosoma is absent, most articles of the right legs III and IV are cut off, the legs are fairly and the prosoma is strongly darkened by aging, the amber piece has a redbrown colour, some fissures run from its surface to the spider's body and legs. A member of Diptera is preserved in front of the spider. – Remaining material: F1589: The spider is preserved in a larger piece of darker brown amber which was heated. The piece is broken between two layers and stuck together with the help of nail. The spider's body and both bulbi were cracked. The embolus of the left pedipalpus is unrolled and stretched out (fig. 183). – A dragline is preserved e. g. with F1589 and F1619, thin spider's threads are preserved with F1593, F1594, F1596, F1599, F1618, F1619 and F1621. – At the tip of the right embolus of F1593 a stalked droplet is preserved. Another droplet is preserved at the tip of a normal hair of the right chelicera; so the embolic droplet may not be a droplet of sperm, too. – A part of the right embolus is broken off in F1599. – F1600 is spun in in spiders threads, its opisthosoma and parts of the anterior four legs are distinctly deformed, the spider has been sucked out by a spider, probably by a conspecific female, a questionable case of cannibalism (photos 29–30); Diptera and mammals' hairs are preserved in the same piece of amber. – The epigyne of the female F1601 is covered by a white emulsion; the right leg III (through the tibia) and IV (through the patella) of one ♂ of F1601 are amputated. – Acari are preserved with F1594 and 1598, a juvenile Araneae with F 1599, mammal hairs with 1600, Diptera with F1600, 1601 and 1617 (no prey of the spiders), a beetle and a wasp with F 1617.

Diagnosis (♂): Pedipalpus (figs. 78–87): Embolus with 2 1/4–2 3/4 loops, the peak of the embolus has a quite variable position, see below.

Remark: *C. obscura* as described in this paper may be a “sampling species” (some specimens are probably not conspecific with *C. obscura*): Size and loops of the embolus as well as the position of the embolic peak are very variable – see the drawings – and there are intermediates; in some specimens – e. g. F1587, 1589, 1620 and 1621 – the basal part of the embolus is distinctly thinner than in other specimens. We do not know the intrapopular or intraspecific variability; therefore I regard males – e. g. F1617 – in which the position of the embolus differ distinctly from the holotype as only tendatively conspecific.

Description (♂):
Measurements (in mm): Body length 1.9–2.2, prosoma: length ca. 1.1, width 1.0–1.1, height 0.6–0.7; leg I: Femur 1.5, patella 0.55, tibia 1.35, metatarsus 1.28, tarsus 0.55, tibia IV 0.65. Transverse diameter of the embolic loops 0.32–0.37.
Body and legs are very similar to *C. lugubris*. The basal article of the left chelicera is shown in fig. 75, the prosomal-opisthosomal stridulatory organ is shown in fig. 76, the position of the eyes in fig. 74. The position of the anterior metatarsal trichobothrium is near the middle. Pedipalpus (see above): median and tegular apophyses large, embolus long and with wide loops. The embolus of the left pedipalpus of male F1589 is unrolled in an unnatural position beyond the first loop and stretched out in an unnatural position for 1 mm (probably almost 1 1/2 loops) (fig. 83).
Female (most parts of the body are covered by a white emulsion): Measurements (in mm): Body length 2.4, prosomal length ca. 1.2; leg I: Femur 1.0, patella 0.47, tibia 0.65, metatarsus 0.75, tarsus 0.53, cusps of the anterior legs are apparently absent, the pedipalpi are large, their claws are hidden, the epigyne ist covered by a white emulsion. The position of the female is close to the two males in the same piece of amber which most probably are conspecific.

Relationships: See the key tab.; *C. granulata* is most related.

Distribution: Early Tertiary (Eocene) Baltic amber forest incl. the Bitterfeld deposit.

Clya granulata (KOCH & BERENDT 1854) (figs. 88–91, photo 25)

1854 *Theridium graulatum* KOCH & BERENDT in BERENDT, Die im Bernstein befindlichen Organischen Reste der Vorwelt, 1 (2): 36, t. 4, fig. 26.

Material: 15♂ in Baltic amber; holotypus PMHUB, further males: F1404-1405/BB/AR/CJW, F1623-1632 (1627 only the loose right pedipalpus), F1670/BB/AR/CJW, 1♂ Museum Ziemi in Warsaw.

Preservation and syninclusions of the holotype: The spider is completely preserved and strongly darkened in a redbrown piece of amber; some fissures of the surface of the amber piece reach to legs and pedipalpi of the spider. The larva of a mite and some stellate hairs are present in the piece which has been boren through; two bubbles cover parts of the spider's body. – Syninclusions with F1627: Various Acari, 1 Opiliones, numerous Collembola, Diptera, larvae, a Thysanoptera, a leaf, pollen grains, numerous particles of detritus, excrement of insects and stellate hairs.

Diagnosis (♂; ♀ unknown): The embolus (figs. 89–91) describes a wide circle of 2 3/4–3 1/5 loops, large peak of the embolic bulb in a distal position, directed away from the paracymbium.

Description (♂):
Measurements (in mm): Body length 2.0–2.2, prosomal length usually 1.0–1.1; leg I (male F1604/CJW): Femur 1.5, patella ca. 0.55, tibia 1.8, metatarsus 1.75 (tibia and metatarsus of another male (F1605/CJW) are each only 1.3 mm long!), tarsus 0.65;
Body and legs quite similar to *C. lugubris*; the leg length is quite different in the males, the holotype and F1604 are long-legged spiders, F1605 is short-legged although the prosomal length is identic. The anterior tibiae are slightly bent in in F1629. Basal cheliceral article: Fig. 88; the fangs are fairly bent. The position of the metatarsal I trichobothrium is in 0.45 – 0.55 (holotype). Pedipalpus: See above. Variability of the position of the embolic peak: See the figs.

Relationships: See the key tab.. In *C. abdita* the embolus describes ca. 3 3/4 loops.

Distribution: Early Tertiary (Eocene) Baltic amber forest.

***Clya tricurvata* n. sp**. (figs. 92–97, photos 184–185)

Material: 13♂ and a probably conspecific ♂ in Baltic amber; holotypus and a separated piece of amber F1611/BB/ AR/CJW; paratypes: F1590-F1592/BB/AR/CJW, F1603, F1612, F1614-1616 (F1612 from the Bitterfeld deposit, with a separated piece), 1♂ from the Bitterfeld deposit: coll. M. KUTSCHER in Sassnitz, 2♂ in the same piece of amber, Mus. Ziemi in Warsaw, no. 11530. – Probably conspecific ♂: Mus. Naturk. Stuttgart, Do-886-K (the kind of amber has formerly been misidentified as Dominican).

Preservation and syninclusions: Holotype: The spider is well and completely preserved, the opisthosoma is dorsally depressed and ventrally covered with a weak white emulsion; a thin spider's thread is preserved below/behind the spider, a tiny wasp, Diptera (no prey of the spider) and few stellate hairs are preserved with the spider. – Paratypes: The males of the Mus. Ziemi are well preserved in a red-orange piece of amber, their legs and prosoma are darkened, the left leg III of one of the males is lost beyond the coxa by autotomy. – The male of the coll. KUTSCHER is fairly well preserved in a piece which was heated; some leg articles – especially of the left side – are cut off, the opisthosoma is dorsally depressed. – F1590 is well and completely preserved, the opisthosoma is fairly deformed and covered by a white emulsion, 6 Diptera: Nematocera, few Acari, the leg of a beetle and stellate hairs are present in the same piece of amber. – F1591 is well preserved, some leg articles are dorsally cut off. – F1592 is well and completely preserved together with a dragline, a Diptera and stellate hairs. – F1603 is well preserved, dorsal parts of the right metatarsus III and IV are cut off, few stellate hairs are present in the yellow piece of amber which was not heated. – F1612 is fairly well and completely preserved in an orange-brown piece of amber which was heated. The left side of the opisthosoma is depressed by a larger bubble, a thin spider's thread is present. – F1614 is well and completely preserved in a yellow piece of amber, ventral parts of the body are covered with a white emulsion, a Diptera is preserved in a different layer. – F1615 is incompletely and badly preserved in a yellow piece of amber, the dorsal parts of the prosoma and the right pedipalpus are broken off, several leg articles are lost, the amber piece was probably heated. – F1616 is incompletely and badly preserved in a yellow piece of amber, the dorsal parts of the prosoma and the right pedipalpus are broken off, several leg articles are lost, the amber piece was probably heated.

Diagnosis (♂; ♀ unknown): Pedipalpus (figs. 92–95, 97): Embolus in a wide circle of 3 1/3 – 3 1/2 loops, embolic peak in a basal position.
Remark: Due to the – really intraspecific? – variable size of the body as well as size and position of the embolus this species may be one of the "sampling species".

Description (♂):
Measurements (in mm): Body length 1.9 (F1614)–2.5(F1615), prosoma: Length 1.1 (holotype, F1612, F1615) –1.2(F1616), width 1.0–1.1, height above chelicerae 0.55 (F1612, F1614) – 0.7 (e. g. holotype and F1615); leg I (holotype): Femur 1.45, patella 0.45, tibia ca. 1.3, metatarsus 1.05, tarsus 0.55; tibia I (a male from the Mus. Ziemi) 1.1, in F1612 1.4. Diameter of the embolic loops 0.4–0.5 (e. g. in the holotype). The diameter of the embolic loops is 0.4–0.5.
Body and legs quite similar to *C. lugubris*. The prosomal height is very variable. The position of the metatarsal I trichobothrium is in/near the middle of the length of the article. Pedipalpus: See above.

Description of the probably conspecific male: The spider is well preserved, the embolus of the left pedipalpus is preserved – on a layer in the fossil resin – in a quite unnatural position beyond its first loop (fig. 97); the right pedipalpus is covered by a thin layer of white emulsion. A dragline is present and in contact with the left patella IV (fig. 96). The prosoma is 1.1 mm long and 1.05 mm wide. The left patella and tibia are regenerations (fig. 96), the patella is shortened by ca. 60%, the tibia is only 0.25 mm long and has a blunt end; bristles are absent, the hairs are shorter than normal.
The position of the peak of the embolic bulb is as in *C. tricurvata* and I do not want to exclude the conspecifity, but I am in doubt because of the unnatural position of the left embolus.

Relationships: See the tab. of the key; *C. abdita* may be most related.

Distribution: Early Tertiary (Eocene) Baltic amber forest inc. the Bitterfeld deposit.

Clya abdita n. sp. (fig. 102)

Material: Holotypus ♂ in Baltic amber, F1610/BB/AR/CJW.

Preservation and syninclusions: The spider is only fairly well preserved in a yellow piece of amber and is strongly darkened by heating. Most parts of the body are thickly covered with a white emulsion, parts of the prosoma are covered with a silvery emulsion, most parts of the medium articles of the legs I and II are cut off. Few stellate hairs.

Diagnosis (♂; ♀ unknown): Position of the embolus in a wide circle of ca. 3 3/4 loops, embolic peak near to the next loop of the embolus, the peak points to the tip of the cymbium (fig. 102).

Description (♂):
Measurements (in mm): Body length 2.2, prosomal length and width 1.15, height (anterior aspect) ca. 0.55; leg I: Femur 1.75, patella 0.45, tibia 1.15, metatarsus 1.1, tarsus 0.6, tibia IV 0.8, length of the cymbium 0.63.
Colour: Prosoma and legs strongly darkened by heating, opisthosoma covered with a white emulsion.
Body and legs probably similar to *C. lugubris*, position of the metatarsal III trichobothrium in the middle of the article. Pedipalpus (fig. 102): See above. The long prolateral conductor has drifted a bit away from the bulbus as a result of heating.

Relationships: See the key tab., *C. granulata,* C. *rotata* and *tricurvata* are related. In *C. superspiralis* the cymbium is unusually large, the free visible part of the subtegulum is much smaller, the position of the embolic peak is quite different, and the embolus is a bit longer.

Distribution: Early Tertiary (Eocene) Baltic amber forest.

Clya superspiralis n. sp. (figs. 100–101, photos 182–183)

Material: Holotypus ♂ in Baltic amber, F1588/BB/AR/CJW.

Preservation and syninclusions: The spider is almost completely and well preserved in a small yellow piece of amber; the left patella IV as well as the distal tibia and the basal metatarsus are cut off, especially ventral parts of the body are covered with a white emulsion. A lump of questionable pollen grains is preserved 3 mm in front of the spider.

Diagnosis (♂; ♀ unknown): Cymbium unusually large, 1 mm long, allmost as long as the prosoma, second longest embolus of the genus (ca. 4 loops), embolic peak in a distal position (figs. 100–101.

Description (♂):
Measurements (in mm): Body length 2.4, prosomal length 1.1; leg I: Femur 1.6, patella 0.5, tibia 1.5, metatarsus 1.2, tarsus 0.6, cymbium almost 1.0, largest (longitudinal) diameter of the embolic loops 0.75.
Body and legs similar to *C. lugubris*, position of the metatarsal I trichobothrium in 0.45. Pedipalpus: Figs. 100–101.

Relationships: See the key tab.. The cymbium is larger (almost as long as the prosoma) than in all other species of this genus, and the embolus is longer only in *rotata*.

Distribution: Early Tertiary (Eocene) Baltic amber forest.

***Clya rotata* n. sp.** (figs. 98–99, photos 178–180)

Material: Holotypus ♂ in Baltic amber, F1696/BB/AR/CJW.

Preservation and syninclusions: The spider is well preserved in a piece of amber which probably was slightly heatened; three left legs are partly cut off: I through the metatarsus, II through the femur and IV longitudinally through patella and tibia. Few white emulsions exist e. g. at the mouth parts. Fissures at a layer in the amber hide dorsal parts of the spider. A dragline runs backwards from the spinnerets. A member of Diptera is preserved in another layer, stellate hairs are absent.

Diagnosis (♂; ♀ unknown): Embolus with ca. 4 1/4 loops (figs. 98–99), prosoma 1.29 times longer than the cymbium.

Description (♂):
Measurements (in mm): Body length 1.9, prosomal length 0.9, tibia I ca. 0.9, tibia III 0.35, tibia IV ca. 0.55, length of the cymbium 0.7, diameter of the embolic spiral 0.55.
Colour: Prosoma dark brown, legs medium brown, opisthosoma yellow brown. – Body and legs as in the related species, the position of the metatarsal III trichobothrium is in 0.42. – Pedipalpus (figs. 98–99): Patella and tibia short, the embolus describes 4 1/4 loops. The apical aspect of the pedipalpus shows the three-dimensional position of the embolic spiral and the position of the embolic tip at the tip of the cymbium.

Relationships: In *C. rotata* the embolus is longer than in all other known congeneric species. In *abdita* the embolic spiral describes only 3 3/4 loops, in *superspiralis* 4 loops and the cymbium – absolutely and compared with its prosomal length – is larger.

Distribution: Early Tertiary (Eocene) Baltic amber forest.

***Eoasagena* n. gen.** (figs. 103–107, photos 187–188)

Diagnosis (♂; ♀ unknown): Opisthosoma with a dorsal scutum in the basal half (photo), tibia IV with a single bristle in the basal half, pedipalpus (figs. 104–107) with large cymbium and bulbus.

Further characters: Body length only 1.6mm, prosoma high, cephalic part convex (fig. 103), eye field 0.35 mm wide, the fovea is a small deep circular hole, legs slender, position of the metatarsal I trichobothrium in 0.25, colulus with 3 hairs.

Relationships: See the key. A small opisthosomal scutum exists also in *Nanosteatoda*; the prosoma is lower in *Nanosteatoda*, the eye field is only 0.27 mm wide and the structures of the bulbus are different.

Type species: *Eoasagena scutata* n. sp. (the only known species of the genus).

Distribution: Early Tertiary (Eocene) Baltic amber forest.

***Eoasagena scutata* n. gen. n. sp.** (figs. 103–107, photos 187–188)

Material: Holotypus ♂ in Baltic amber and a separated piece of amber, F1732/BB/AR/CJW.

Preservation and syninclusions: The spider is very well and completely preserved in a piece of amber which was fairly heated, ventrally at the left side exist some white emulsions and a larger bubble below the pedipalpi and on the left side of the prosoma; few stellate hairs.

Diagnosis (♂; ♀ unknown): See above.

Description (♂):
Measurements (in mm): Body length 1.8, prosoma: length 0.75, width 0.7; leg I: Femur 1.1, patella 0.25, tibia 0.72, metatarsus 0.8, tarsus 0.53, tibia IV 0.7.

Colour: Prosoma, legs, epigaster and opisthosomal scutum dark brown, remaining parts of the opisthosoma yellow brown.
Prosoma (fig. 103) convex, fine rugose, posteriorly laterally with distinct cusps, fovea deep, few short hairs. Eyes small (lenses partly covered with emulsions), field 0.35 mm wide, posterior row recurved, clypeus only slightly concave, fangs long and slender, sternum distinctly rugose, separating coxae IV by their diameter. – Legs long and slender, order I/IV/II/III, hairs fairly short. Tibial bristles very thin, long, their sequence 2/2/1/1 (or 2/2/1/2?). Femur and tibia I ventrally with only indistinct hair-bearing cusps, comb of tarsal IV fairly well developed, hairs probably not serrated, position of the metatarsal I trichobothrium in 0.25, paired tarsal claws almost smooth, unpaired claw bent in a right angle. – Opisthosoma oval, scarcely covered with short hairs, epigaster strongly sclerotized; two pairs of small dorsal sigillae and a small scutum exist which almost reaches the middle (photo). The colulus bears 3 hairs. – Pedipalpus (figs. 104–107): Femur fairly long, slender, patella longer than wide, bearing 2 thin dorsal bristles, tibia with only indistinct distal hairs, cymbium and bulbus large, paracymbium in a retroectal position, embolus apparently in a hidden position.

Relationships: See above.

Distribution: Early Tertiary (Eocene) Baltic amber forest.

Eomysmena PETRUNKEVITCH 1942 (figs. 108–125b, photos 18, 37, 39, 189–198)

Remarks: (1) *Mysmena* SIMON 1894 is a genus of the Anapidae s. l.: Mysmeninae, and therefore the genus name *Eomysmena* is missleading. – (2) Species of *Eomysmena* have been described under four or even five different generic names, *Androgeus* by KOCH & BERENDT (*militaris*), *Astodipoena*, *Eodipoena* (synonyms of *Eomysmena*), probably *Mizalia punctulata* KOCH & BERENDT 1884and *Antopia* MENGE 1854, as well as *Eomysmena* by PETRUNKEVITCH. Some as congeneric described specimens/ paratypes of *Eomysmena* are members of different genera (!).

?1854 *Antopia* MENGE in KOCH & BERENDT in BERENDT: 43 (**quest. syn.**).
1942 *Eomysmena* PETRUNKEVITCH, Trans. Connect. Acad. Arts Sci., 34: 283.
1942 *Eodipoena* PETRUNKEVITCH, Trans. Connect. Acad. Arts Sci., 34: 271 (**n. syn.**).
1958 *Astodipoena* PETRUNKEVITCH, Trans. Connect. Acad. Arts Sci., 34: 41: 201 (**n. syn.**).

Reasons for the new synonymies and new combinations: (1) *Eodipoen* was based on a single female of its type species *Eodipoena oculata* PETRUNKEVITCH 1942. I studied the holotype (BM In. no. 18740); it is strongly darkened, has a darkbrown discolouration around its body and is embedded in an artificial circular block. The darkening may be the result of heating during the procedure of embedding in the artificial substance. The epigyne is prominent, apparently largely covered by an emulsion and the pit is probably filled by a plug under the emulsion, not looking very similar to the fig. 164 given by PETRUNKEVITCH (1942). – According to the rugose prosomal cuticula, the body length (4 mm), the chaetotaxy and the stout legs I regard this holotype as a member of *Eomysmena* (**n. comb**.), and *Eodipoena* as a junior synonym of *Eomysmena* (**n. syn**.). – (2) *Astodipoena*: According to the long and hairy ♂-clypeus – they were overlooked by PETRUNKEVITCH (1958) –, and the structures of the bulbus *Astodipoena crassa* PETRUNKEVITCH 1958 – the only species of *Astodipoena* – is a clearly member of *Eomysmena*, and therefore *Astodipoena* is a synonym of *Eomysmena* (**n. syn**.). – (3) *Antopia* may be an older synonym of *Eomysmena* but material of the generotype is lost; see the chapter on synonymy above.

Remarks on the synonymy of other nominal species of *Eomysmena* and *Eodipoena*:

Eodipoena baltica PETRUNKEVITCH 1946 – based by PETRUNKEVITCH on a 2.5 mm long adult female – was transferred to *Eomysmena* by PETRUNKEVITCH (1958: 169, 175), but according to the body size of only 2.5 mm it is not a member of *Eomysmena*; its prosoma is not punctuated and its relationships remain unsure.

Eodipoena bassleri PETRUNKEVITCH 1942 – based by PETRUNKEVITCH on a badly preserved female which has a body length of 4 mm – was trasferred to *Eomysmena* by PETRUNKEVITCH (1958: 169, 175). The body length fits in *Eomysmena,* but PETRUNKEVITCH did not mention punctuations of the sternum in the holotype; thus the relationships of this badly preserved specimen remains unsure.

Eodipoena consulta PETRUNKEVITCH 1958 = *Eomysmena consulta* (PETRUNKEVITCH 1958) (**n. comb**.).

Eodipoena germanica PETRUNKEVITCH 1958 = *Lasaeola germanica* (PETRUNKEVITCH 1958) (**n. comb**.).

Eodipoena kaestneri PETRUNKEVITCH 1958: In my opinion most probably a member of *Eomysmena* (**n. comb**.) (see below).

Eodipoena nielseni PETRUNKEVITCH 1958: According to the characters of the holotype, a subad. ♀ (Geol. Palaeontol. Mus. Copenhagen, seen) this species is also a member of *Eomysmena* (**n. comb**.).

Eodipoena oculata PETRUNKEVITCH 1942 = *Eomysmena oculata* PETRUNKEVITCH 1942 (**n. comb**.).

Eodipoena oculata sensu PETRUNKEVITCH (1958): See *Lasaeola* near *L. communis* n. sp. in this paper.

Eodipoena regalis PETRUNKEVITCH 1958 = *Episinus regalis* (PETRUNKEVITCH 1958) (**n. comb**.).

Eomysmena stridens PETRUNKEVITCH 1958 = *Pseudoteutana stigmatosa* (**n. gen., n. syn**.).

Eomysmena succini PETRUNKEVITCH 1942 = Theridiidae indet. (**n. comb**.).

Remark on a species in Mexican amber: According to the short clypeus and the structures of the bulbus of the holotype (not seen) *Eomysmena asta* PETRUNKEVITCH 1971 is not a member of the genus *Eomysmena* (and probably not of the family Theridiidae); its relationships are dubious.

Diagnosis of *Eomysmena*: ♂-prosoma (figs. 108–110, photos 189f): Cephalic part raised, clypeus very long, with a dense field of long and thick hairs and ventrally as well laterally with a wide border of small furrows which possess a medial GAP; ♂-pedipalpus (figs. 112f): Cymbium with very long retrolateral hairs in the distal half, bulbus with a fringed additional apophysis (fig. 114) (which is only recognizable in well preserved specimens), embolus with a wide basal part, and a thin and straight distal part; the epigyne is a wide pit (figs. 124, 125b, photo 197); see also *E. oculata*.

Further characters: Body length usually 3–4 mm (largest Asageninae in Baltic amber), prosoma incl. sternum with hair-bearing cusps (punctuated) in both sexes, legs with some cusps, fovea deep, eye field narrow, sternum separating the coxae IV by ca. 3/4 of their diameter, legs stout (tibia I ca. 1/10 shorter than the prosoma, I and IV about equal in lenght), opisthosoma with two pairs of dorsal sigillae, an epigastral scutum and a scutate ring around spinnerets, posterior stridulating files well developed, colulus large, with 2–5 hairs (fig. 111), males most often with only 3 hairs, unpaired tarsal claw bent in a right angle, paracymbium in a retrodistal-ectal position (figs. 115–116).

Remark on the sexually-dimorphic structures of the male clypeus (figs. 108–110, photos): I did not recognize remains of a secretion or secretory pores in the fields of the anterior hairs and ventral furrows, but in this position such a secretion – a pheromone? – could well have been emitted by males. In the subadult male the hairs are distinctly less developed than in the adult male; such hairs and a modified ventral margin of the clypeus are absent in the female.

Relationships: See *Pseudoteutana* n. gen. and the key.

Type species: *Eomysmena moritura* PETRUNKEVITCH 1942.

Leg amputations (fig. 121) exist at the holotype of *Eomysmena recta* n. sp. and paratype F1707/CJW of this species, in which also a part of a capture web is preserved as well as in *E*. sp. indet., F1702/CJW and in the male of *E. crassa* from the coll. FLEISSNER; a dragline is preserved e. g. with *E.* sp. indet., F1702/CJW, F1714/ CJW, F1724/CJW and *E. recta* n. sp., paratype F1706/CJW; an ant as a questionable prey is preserved with *E*. sp. indet., F1715/CJW (photo 37). Almost all congeneric specimens which I studied have been heated; one of the rare pieces which were not heated is *E*. sp. indet., F1714/CJW.

Distribution: Early Tertiary (Eocene) Baltic amber forest and most probably Ukrainean (Rovno) amber forest. Males of *Eomysmena* are rather frequent in Baltic amber.

Determination: I do not know the true number of species which were described in Baltic amber and not the number of species which are synonyms; see above, the paragraph " Remarks on the synonymy...". – I looked for non-genitalic differences of the species but I failed to find such differences. The shape of the theridiid tegular apophysis seems to be most important in distinguishing the species – it is long and most slender in *moritura*, relatively short and shaped like a birds head in *aviceps* – but there exist several problems: its shape varies strongly in different positions, and it is impossible to figure this apophysis in the same position for all species. In the most often heated spiders the theridiid apophysis as well as the embolus and other structures may be more or less deformed; we do not know the intraspecific variability of the structures of the bulbus. Especially in heated and darkened inclusions the additional (fringed) apophysis (fig. 114) is hard to recognize, and the distal (slender) part of the embolus may be deformed or be broken off, e. g. in the male of the GPIUH.

***Eomysmena aviceps* n. sp.** (fig. 112)

1958 *Eomysmena moritura* sensu PETRUNKEVITCH 1942, Trans. Connect. Acad. Arts Sci., 41: 167–168, figs. 104–107.

Note: *Eomysmena moritura* PETRUNKEVITCH 1942: See below.

Material: Holotypus ♂ in Baltic amber, ZMHUB.

Preservation and syninclusions: The spiders is almost completely preserved, strongly darkened, parts of the left leg III are missing, most parts of the right side are covered with a white emulsion, the structures of the bulbus are fairly well recognizable.

Diagnosis (♂; ♀): Theridiid tegular apophysis bird-shaped, stout, distal part of the embolus long and thin. – Remark: The hook-shaped apophysis sensu PETRUNKEVITCH (1958: Figs. 104, 105, 107) is an artefact.

Description (♂):
Measurements (in mm): Body length 3.5, prosomal length 1.7; leg I: Femur 1.5, patella 0.55, tibia 1.1, metatarsus 1.05, tarsus 0.8.
Prosoma wrinkled, cephalic part raised, fovea large, clypeus as in the genus, partly covered with a white emulsion, posterior stridulatory files present. Legs stout, fairly hairy, I longest, tibial bristles thin. Opisthosoma oval, covered with short hairs, colulus large. Pedipalpus (fig. 112): Tibia slightly longer than the patella, see the diagnosis.

Relationships: In *E. crassa* (PETRUNKEVITCH 1958) the theridiid tegular apophysis is more slender.

Distribution: Early Tertiary (Eocene) Baltic amber forest.

Eomysmena calefacta n. sp. (fig. 113)

Material: Holotypus ♂ in Baltic amber, F1674/BB/AR/CJW.

Preservation and syninclusions: The spider is completely preserved in a clear piece of amber; body and legs are strongly darkened by heating, its dorsal side is partly covered with a white emulsion, bubbles exist above the pedipalpi, in front of the prosoma and between pro- and opisthosoma.

Diagnosis (♂; ♀ unknown): Theridiid tegular apophysis slender and slightly bent (fig. 113), distal part of the embolus long.

Description (♂):
Measurements (in mm): body length 3.9, prosoma: Length 1.8, width 1.6; opisthosoma: Length 2.2, width 2.0, hight 1.65; leg I: Femur 1.4, patella 0.65, tibia 1.3, metatarsus 1.05, tarsus 0.75, tibia IV 1.05.
Prosoma (incl. the sternum) wrinkled, cephalic part raised, clypeus and stridulatory files as in the genus, dorsally with numerous longer and erect hairs. Most parts of the eye field are hidden, anterior median eyes largest. Chelicerae long and strong, fangs long, only slightly bent. Sternum slightly longer than wide, widely elongated between coxae IV. Labium distinctly wider than long, gnathocoxae distinctly longer than wide, converging above the labium. Legs stout, as in the genus, position of the thin basal bristle on tibia I in 0.3. Paired tarsal claws with few long teeth, unpaired claw long and bent in a right angle. Opisthosoma oval, with two (or three?) pairs of dorsal sigillae and a sclerotized ring around the pedicel. Colulus large, distinctly longer than wide, spinnerets stout. Pedipalpus: See above, tibia slightly longer than the patella.

Relationships: Compare *E. moritura* PETRUNKEVITCH 1942.

Distribution: Early Tertiary (Eocene) Baltic amber forest.

Eomysmena crassa (PETRUNKEVITCH 1958) (**n. comb.**) (figs. 114–115, photo 190)

1958 *Astodipoena crassa* PETRUNKEVITCH, Trans. Connect. Acad. Arts Sci., 41: 201, figs. 216–222.

Material: 2♂ in Baltic amber; holotypus ♂, ZMHUB, 1♂ coll. H. FLEISSNER in Bad Nauheim, no. BB561.

Preservation and syninclusions of the male of the coll. FLEISSNER: It is well preserved, some leg articles are cut off, the left leg I is lost beyond the trochanter by an amputation; at the tip of the embolus a lump of questionable sperm is preserved.

Diagnosis (♂; ♀): Theridiid tegular apophysis fairly short, basal part of the embolus widely standing out (figs. 114–115, photo 190).

Description (♂):
Prosomal length 1.7 mm. In the male of the coll. FLEISSNER the additional (fringed) tegular apophysis, the very long retrodistal cymbial hairs, and a lump of questionable sperm at the tip of the embolus are well recognizable.

Relationships: See *E. aviceps* n. sp.

Distribution: Early Tertiary (Eocene) Baltic amber forest.

?***Eomysmena kaestneri*** (PETRUNKEVITCH 1958) **(n. quest. comb.)** (fig. 125b.)

1958 *Eodipoena kästneri* PETRUNKEVITCH, Trans. Connect. Acad. Arts Sci., 41: 184, figs. 163–172.

According to the well developed tarsal comb, the shape of the prosoma, the large basal cheliceral articles, and the position of the eyes *Eodipoena kaestneri* may be a member of the Asageninae (**n. relat**.), and of the genus *Eomysmena* (**quest. n. comb**.). Hairs in the field of the median eyes are absent, the colulus bears a single hair, tibia I is unmodified, the epigyne (fig. 125b) has apparently a pair of large pits (or a single divided pit) which were erroneously called “sperm receptacula” by PETRUNKEVITCH (1958: 188).

Eomysmena militaris (KOCH & BERENDT 1854) (**n. comb**.) (figs. 116–118)

1854 *Androgeus militaris* KOCH & BERENDT in BERENDT: Die im Bernstein befindlichen organischen Reste der Vorwelt, 1 (2): 28, fig. 17.

Material: Holotypus ♂ in Baltic amber, embedded in artificial resin, strongly darkened by aging.

Diagnosis (♂; ♀ unknown): Theridiid tegular apophysis stout and strongly bent (fig. 117).

Body and legs as in the genus. The retrodistal/ectal paracmbium is well recognizable in the holotype but parts of the bulbus structures are hidden.

Relationships: In *E. militaris* the theridiid tegular apophysis is stout and stronger bent than in other congeneric species.

Distribution: Early Tertiary (Eocene) Baltic amber forest.

Eomysmena moritura PETRUNKEVITCH 1942 (figs. 119–120, photo 189)

1942 *Eomysmena moritura* PETRUNKEVITCH, Trans. Connect. Acad. Arts Sci., 34: 284, figs. 259–266, 591.

?1958 *Eodipoena consulta* PETRUNKEVITCH, Trans. Connect. Acad. Arts Sci., 41: 78, figs. 140–148 (**comb. n., quest. n. syn**.).

Material in Baltic amber: Holotypus of *moritura*: BMNH no. 18113; holotypus of *consulta*: ZMHUB.

Preservation: Both males are strongly darkened (probably by heating). In the holotype of *moritura* (photo 189) the opisthosoma is partly thickly covered with a white emulsion, the distal parts of all legs and dorsal parts of both pedipalpis are cut off. Because of the position of the pedipalpi are the bulbus structures of the holotype of *consulta* only insufficiently recognizable.

Diagnosis (♂; ♀ unknown): The theridiid tegular apophysis is very long and slender (figs. 119–120) (in the holotypes of both nominal species).

The prosomal length is 1.7–1.85 mm (holotype of *moritura*). The sickle-shaped apophysis of the holotype of *moritura* is apparently an artefact (fig. 120).

Relationships: *E. calefacta* the theridiid tegular apophysis is stouter.

Distribution: Early Tertiary (Eocene) Baltic amber forest.

Eomysmena oculata (PETRUNKEVITCH 1942) (**n. comb**.)

1942 *Eodipoena oculata* PETRUNKEVITCH, Trans. Connect. Acad. Arts Sci., 34: 272, figs. 160–168, 505 (♀).

Material: Holotypus ♀ in Baltic amber, BMNH no. 18740.

The spider is completely preserved, its prosomal length is 1.8mm, its prosoma bears distinct wrinkles, the legs are stout, the dorsal aspect of the opisthosoma is circle-shaped, the epigyne is prominent and has a large transverse oval pit.

Close **relationships** are unknown without the knowledge of a conspecific male.

Distribution: Early Tertiary (Eocene) Baltic amber forest.

***Eomysmena recta* n. sp**. (figs. 121–123)

Material: Holotypus ♂ in Baltic amber, F1704/BB/AR/CJW.

Preservation and syninclusions: The spider is fairly well preserved in an orange piece of amber which was heated, the dorsal part of the left metatarsus IV is partly cut off, the left leg III has been amputated through the mid of the patella and the left tarsus IV near its end (fig. 121). The stumps have probably been healed. Few threads are preserved below the left pedipalpus. Parts of the opisthosoma are covered with a white emulsion. Remains of insects and the tarsus of an insect (a beetle?) are preserved as syninclusions, stellate hairs are absent.

Diagnosis (♂; ♀ unknown): Pedipalpus (figs. 122–123): Theridiid tegular apophysis almost straight, its position near the additional fringed tegular apophysis.

Description (♂):
Measurements (in mm): Body length 3.3, prosomal length 1.5; leg I: Metatarsus 1.5, tarsus 0.7.
Colour: Prosoma and legs dark brown, opisthosoma light brown, epigaster dark brown.
Body and legs as in the genus; the opisthosoma bears two pairs of sigillae.

Relationships: In the remaining congeneric species the shape of the theridiid tegular apophysis is different.

Distribution: Early Tertiary (Eocene) Baltic amber forest.

“Eomysmena” succini PETRUNKEVITCH 1942

1942 *Eomysmena succini* PETRUNKEVITCH, Trans. Connect. Acad. Arts Sci., 34: 286, figs. 341–346, 606.

The description of this species is based on a juvenile male only. Its body length is 1.7 mm. According to the glabrous prosoma it is most probably not a member of *Eomysmena*. According to the long tarsi PETRUNKEVITCH (1958: 158) regarded *succini* as a member of the genus *Mysmena* but specimens of *Mysmena* are smaller, possess a wide eye field and a comb of tarsus IV is absent. I regard *succini* as a member of the Theridiidae which relationships are unsure.

Distribution: Early Tertiary (Eocene) Baltic amber forest.

Notes on some species of *Eomysmena* indet. (stellate hairs are not mentioned):

(a) ♀ (see also above: The holotype of *E. oculata*, and below: F1876/CJW: 1♂ 1♀ in the same piece of amber):

F1701/CJW (fig. 124, photo 197): The spider is well and almost completely preserved in a piece of amber which was not or only slightly heated; only a small part of the opisthosoma is cut off, the hole has been closed by nail polish. The dorsal side of the spider is covered with a thick layer of a white emulsion. A tiny wasp is preserved in a different layer of the fossil resin. The body length is 3.2mm, the prosomal length ca. 1.6mm, the pedipalpal claws are long, the legs are stout, IV is the longest, the leg order is IV/I/II/III, the tibial bristles are long, the colulus bears 5 hairs, the hair-bearing cusps of the sternum are distinct, the epigaster may be stronger sclerotized, the position of the basal bristle of tibia IV is in 0.28, the long trichobothrium of metatarsus I has a position of 0.62, its bothrium is small. The epigyne (fig. 124) has a 0.14 mm wide pit and a prominent anterior margin; the pit is filled with a PLUG.

(b) ♂:

F536/CJW: Subad. ♂ with a Thysanoptera indet. which was probably sucking in the spiders opisthosoma, see WUNDERLICH (2004: 121, 559, photo 603, the spider under "juv. Theridiidae indet." was identified now by me as *Eomysmena* sp. indet.).

F1565/CJW: The original piece of amber is broken in 5 pieces through the spider's body and through both pedipalpi. Most parts of body and pedipalpi are crumpled in tiny gray particles. The piece is now deposited in the Geol. Palaeont. Inst. Goettingen.

F1698/CJW: The flat piece of amber has a size of 2 x 3.5 mm. The spider is ca. 3.5 mm long, spun in in a larger part of a spider's web in which sticky droplets are preserved. Sternum, opisthosoma and some leg articles are depressed or injured, apparently the spider was the prey of an araneoid spider and sucked out, probably of a conspecific female a case of questionable cannibalism. 1 mm behind the spider's opisthosoma remains of its exuvia are preserved in the same spider's capture web and a tiny mite which is ventrally partly cut off. The clypeus of the exuvia (subad. male) bears only few and thin hairs in contrast to the adult male.

F1699CJW (photo 198): The spider's opisthosoma is probably eaten out from the dorsal side and now filled with amber. A small member of a Thysanura is preserved in the same piece of amber.

F1700CJW (fig. 109, photo 191) originates from the Bitterfeld deposit.

F1702/CJW (fig. 110): A DRAGLINE is preserved with the spider, the right tarsus IV is AMPUTATED near its end, the stump is covered with a white emulsion. Photo 195.

F1703/CJ W: The left leg I of the spider is missing beyond the trochanter, the stump has apparently HEALED, remains of blood are absent. Colulus: Fig. 111.

F1705/CJW: The right half of the spider's opisthosoma is cut off within the amber and filled with amber. Also preserved are a beetle (Elateridae), 1 Thysanoptera and 1 1/2 Diptera. Photo 194.

F1706/CJW: The piece of amber is broken through the dorsal part of the spider, remains of the cuticula are recognizable, the opisthosoma is empty; a spider's DRAGLINE is also present.

F1707/CJW: The spider is preserved together with thin threads of a larger part of a spider's CAPTURE WEB, a mite larva of the family Erythraeidae and 2 Diptera are preserved in a different layer of the amber.

F1710/CJW (photo 18): The spider has been injured, the opisthosoma is strongly depressed from the right side, some threads – including a DRAGLINE – originate at the spinnerets. Decomposing fungi hyphae exist at the mouth parts and some leg articles of the spider.

F1715/CJW (photo 37): The spider is 3.5 mm long; an indet. member of the Formicidae (body length 1.3 mm) is preserved as a probable PREY below the right legs I and II. The ant has drifted away in the resin from the spider's mouth parts to the right side.

Further fossil material: 1♂ GPIUH (coll. HERRLING, photo 196): The distal (slender) part of the right embolus is apparently broken off; 1♂ Mus. Ziemi 10440; a single ♂ each in the CJW: F1708 (photo 192), F1711 (photo 193), F1712 and 1714; 8♂ in the CJW: F1713.

(c) 1♂1♀ in the same piece of amber which was slightly heated, F1876/BB/AR/CJW: The spiders are completely preserved and lying partly in contact whith each other; large parts of the animals are covered with a white emulsion, the epigyne is hidden, the male colulus bears 5 hairs, the length of the bodies is 3 mm (male) and 3.5 mm (female), the prosoma (mainly thoracal part and sternum) are strongly wrinkled (bearing hooks and thin hairs in both sexes), the cephalic region is strongly raised in both sexes. Tiny – ca. 0.005 mm long – "particles" near the genital opening of the male may be remains of a secretion of the epiandrous glands (sperm?). – The male is situated with his left side in front of the female which I regard as conspecific; his bulbi are not expanded and I do not suppose a “post copula”. One mm in front of the male an ant worker is preserved which is not dissected and not spun in. Some spider’s threads run from the males left leg III to the females opisthosoma, another thread is preserved below the body of the female. A large number of tiny (globular?) particles (diameter ca. 0.002 mm) – Bacteria? – is preserved in several layers on different parts of the male, e. g. on the cymbia and on the left gnathocoxa. A small Hymenoptera, a Diptera, a Collembola and stellate hairs are preserved in the same piece of amber.

Eoteutana **n. gen**. (figs. 126–130, photos 199–200)

Diagnosis (♂; ♀ unknown): Legs very hairy (photos 199–200), clypeus with a ventral area of small furrows (fig. 126), without a medial gap, chelicerae diverging (fig. 126). Pedipalpus (figs. 129–130) with a very long conductor which is elongated beyond the tip of the cymbium.

Further characters: Dense field of long clypeal hairs absent, legs stout, colulus most probably with 3 hairs (fig. 128).

Type species: *Eoteutana hirsuta* n. sp. (the only known species of the genus).

Relationships: See the key to the fossil genera. *Eomysmena* is most related and possesses also a clypeal field of small furrows but is has additionally a field of dense hairs and a medial gap. Members of *Eomysmena* are larger spiders, body length usually 3–4 mm.

Distribution: Early Tertiary (Eocene) Baltic amber forest.

Eoteutana hirsuta **n. gen. n. sp**. (figs. 126–130, photos 199–200)

Material: Holotypus ♂ in Baltic amber, F1731/BB/AR/CJW.

Preservation and syninclusions: The spider is fairly well and almost completely preserved in a piece of amber which was heated; the right tarsus III is AMPUTATED, the left pedipalpus has been AMPUTATED basally, coxa and trochanter are small REGENERATIONS (fig. 127). The opisthosoma bears weak ventral emulsions, a large bubble covers most parts of the sternum. Stellate hairs are absent, small particles of detritus are preserved.

Diagnosis (♂; ♀ unknown): See the genus.

Description (♂):
Measurements (in mm): Body length 2.4, prosoma: Length 1.2, width ca. 1.0; leg I: Femur 0.9, patella 0.4, tibia 0.75, metatarsus ca. 0.65, tarsus ca. 0.5, tibia IV 0.77.
Colour: Prosoma and legs dark brown, opisthosoma yellow brown.
Prosoma (fig. 126, photo) with a convex profile, distinct wrinkles and a deep procurved fovea, dorsally with short as well as few long hairs, eye lenses covered with bubbles. Clypeus long, ventrally (anteriorly and laterally) with small furrows similar to *Eomysmena* but without a medial gap, with few thin hairs. Chelicerae diverging, fangs long and slender, gnathocoxae strongly converging, the labium and most parts of the sternum are hidden. – Legs stout and very hairy (photo), order I/II/IV/III, femur I thickened, sequence of the tibial bristles most probably 2/2/1/2, bristle long and quite thin (almost hair-shaped), femur and tibia I with fairly distinct hair-bearing cusps. The tarsal IV comb is hidden, the position of the metatarsal trichobothria is unknown. – Opisthosoma oval, scarcely covered with short hairs, dorsally with 2 pairs of sigillae, epigaster sclerotized, colulus large, with 3 long hairs (fig. 128). – Pedipalpus (figs. 129–130) with stout articles, bristles of the patella unknown, hairs of the distal tibial margin indistinct, paracymbium large, embolus long and slightly bent, guided by a long conductor which is elongated beyond the tip of the cymbium.

Relationships: *Eomysmena* is most related, see above.

Distribution: Early Tertiary (Eocene) Baltic amber forest.

Nanosteatoda **n. gen.** (figs. 131–136, photos 201–205)

Diagnosis (♂; ♀ unknown): Smallest known Asageninae, body length ca. 1.4 mm, prosoma (fig. 133, photos 201f) low, opisthosoma with a small scutum in the basal half, tibia IV with only a single bristle in the basal half, colulus with 3 hairs (fig. 135), pedipalpus (figs. 132, 136) with a large subtegulum; the embolus is hidden.

Further characters: Fovea very low and indistinct, eye field 0.27 mm wide, opisthosoma letarally and posteriorly with furrows.

Type species: *Nanosteatoda breviscutum* n. sp.

Relationships: See *Eoasagena* n. gen.

Distribution: Early Tertiary (Eocene) Baltic amber forest.

Nanosteatoda breviscutum **n. gen.** (figs. 131–132, photos 201–203)

Material: Holotypus ♂ in Baltic amber, F1749/BB/AR/CJW.

Preservation and syninclusions: The spider is well and completely preserved in a small yellow piece of amber and is partly darkned by slightly heating. Parts of the right and ventral side of the opisthosoma are covered with a white emulsion. The opisthosoma is deformed (inclined laterally). Few thin threads are preserved with the spider.

Diagnosis (♂; ♀ unknown): Pedipalpus (fig. 132) with the femur shorter than tibia + cymbium, the subtegulum is ventrally enlarged.

Description (♂):
Measurements (in mm): Body length 1.4, prosomal length 0.7; leg I: Femur 0.65, patella 0.22, tibia 0.5, metatarsus 0.44, tarsus 0.35, tibia IV 0.5.
Colour: Prosoma, legs and opisthosomal scutum dark brown, remaining parts of the opisthosoma yellow brown.
Prosoma slightly longer than wide, low, almost no longer hairs, rugose and with distinct hair-bearing wrinkles. Eyes fairly large, partly hidden or covered with an emulsion, posterior row slightly recurved, posterior median eyes separated by slightly more than their diameter. Fovea low, posterior stridulatory files present, building an entire field. Clypeus fairly short, chelicerae hidden, labium wider than long, gnathocoxae distinctly converging, sternum covered with conspicuous hair-bearing cusps, separating the coxae IV by more than their diameter. – Legs only fairly long and slender, order IV/I/II/III; hairs short, sequence of the thin and fairly long tibial bristles 2/2/1/1 (fig. 131), position of the trichobothrium on metatarsus I–III in the basal half, absent on IV, tarsal organ large, its position in the basal half. The hairs of the tarsal IV comb are bent and appear smooth in a magnification of 150x, the paired tarsal claws bear tiny teeth. – Opisthosoma oval, covered with short hairs and a dorsal scutum in the basal half, epigaster sclerotized, a sclerotized ring exists around the short spinnerets and short stridulatory picks above the pedicel; colulus well developed. – Pedipalpus (fig. 132): Femur shorter than pedipalpal tibia + cymbium, tibia longer than wide, subtegulum large and ventrally enlarged, embolus hidden.

Relationships: In *N. trisetae* the pedipalpal femur is almost long as the pedipalpal tibia + the cymbium and the subtegulum is smaller.

Distribution: Early Tertiary (Eocene) Baltic amber forest.

***Nanosteatoda trisetae* n. gen. n. sp.** (figs. 133–136, photos 204–205)

Material: Holotypus ♂ in Baltic amber, F1748/BB/AR/CJW.

Preservation and syninclusions: The spider is completely and fairly well preserved in a piece of amber which was strongly heated, parts of the ventral side are covered with a white emulsion, parts of legs and opisthosoma are hidden by structures of the amber, the opisthosoma is dorsally deformed (inclined).

Diagnosis (♂; ♀ unknown): Pedipalpus (fig. 136): Femur almost as long as pedipalpal tibia + cymbium, subtegulum only fairly large.

Description (♂):
Measuremants (in mm): Body length 1.4, prosoma: Length 0.7, width 0.65; leg I quite similar to *N. breviscutum*.
Colour, prosoma (figs. 133–134), legs and opisthosoma – as far as recognizable – as in *breviscutum* n. sp.; colulus (fig. 135) well developed, with a pair of short basal hairs and a long apical hair. The dorsal opisthosomal scutum bears a pair of larger sigillae and a second small pair behind the scutum. – Pedipalpus (fig. 136) with a long femur, patella short, tibia longer than wide, subtegum fairly enlarged, embolus hidden.

Relationships: See *N. breviscutum* n. sp.

Distribution: Early Tertiary (Eocene) Baltic amber forest.

***Protosteatoda* n. gen.** (figs. 137–138, photos 206–207)

Diagnosis (♂; ♀ unknown): Chelicerae distinctly diverging and with a large anterior tooth (fig. 137), prosomal cuticula smooth; pedipalpus (fig. 138, photo 207): Femur with retroventral cusps/denticles, cymbium with a retrobasal “outgrowth” (unique in the Asageninae) which bears 4 + 1 hairs, embolus long, thin and bent in a half-circle.

Further characters: Legs long, colulus well developed, its hairs are difficult to recognize, probably exists a pair of short hairs.

Type species: *Protosteatoda gutta* n. sp. (the only known species of the genus).

Relationships: See the key. Close relationships are unknown to me; see below.

Distribution: Early Tertiary (Eocene) Baltic amber forest.

***Protosteatoda gutta* n. gen. n. sp.** (figs. 137–138, photos 206–207)

Material: Holotypus ♂ in Baltic amber, F1733/BB/AR/CJW.

Preservation and syninclusions: The spider is well and almost completely preserved, a white emulsion is present at the right side. The left metatarsus I is AMPUTATED in the basal half, the stump may be "healed", there are no remains of blood. A DRAGLINE and some other thin threads (a part of a capture web without droplets) which are partly in contact with the spider are running outside of a 2.5 cm long "drop" within the piece of amber on which margin the spider is situated. The "drop" is a rolled piece of resin in which 6 1/2 Diptera: Nematocera are enclosed. Remains of plants are also preserved but no stellate hairs.

Diagnosis (♂): See above, the diagnosis of the genus.

Description (♂):
Measurements (in mm): Body length 2.3, prosomal length 1.2; leg I: Tibia 1.1, ca. metatarsus 1.5, tarsus ca. 0.7.
Colour: Prosoma, legs and epigaster dark brown, remaining parts of the opisthosoma yellow brown.
Prosoma not rugose, cephalic part slightly raised, fovea large, the eye lenses are covered with emulsions (the anterior median eyes may be small), clypeus long and concave, chelicerae long and slender, distally distinctly diverging and with a large anterior tooth (fig. 137), fangs long, slender and strongly bent, sternum not rugose, separating the coxae IV by less than their diameter. Prosomal-opisthosomal stridulatory organ well developed. – Legs long and slender, order I/IV/II/III, hairs fairly long, tibial bristles long and thin, their sequence 2/2/1/2, tarsal IV comb well developed, trichobothrium on metatarsus IV absent, its position on metatarsus III in 0.37. The ventral hair-bearing cusps on femur I are small. – Opisthosoma oval, dorsally covered with hairs of medium length, with two pairs of dorsal sigillae, epigaster distinctly sclerotized. – Pedipalpus (see above): Femur with ventral cusps and basal denticles, patella and tibia fairly short, patella with two thin bristles (not drawn), tibia with at least one trichobothrium, position of the paracymbium distal-ectal, the cymbial "outgrowth" is hairless besides 4 + 1 small hair-bearing cusps, distal half of the bulbus with a deep depression.

Realtionships: See the key. Close relationships are unknown to me. The large cheliceral tooth is similar to certain members of the Enolognathinae.

Distribution: Early Tertiary (Eocene) Baltic amber forest.

Pseudoteutana **n. gen.** (figs. 139–145, photos 208–210)

Diagnosis (♂; ♀ unknown): Legs long and slender, I distinctly the longest. Pedipalpus (figs. 141–145): Cymbium apically with few bristle-shaped hairs, bulbus with an additional fringed apophysis.

Further characters: Prosoma with a flat cephalic part, its cuticula fine rugose, the sternum separates the posterior coxae by almost their diameter, legs annulated, two pairs of opisthosomal sigillae exist, epigastral scutum present, colulus with a single pair of hairs only. Pedipalpus (figs. 141–145): Femur very long, cymbium + bulbus small, bulbus with a fringed additional tegular apophysis, conductor funnel-shaped, distal part of the embolus sickle-shaped. Body length 2.4–2.5 mm.

Relationships (see the key): Specimens of *Eomysmena* are larger, their prosomal cuticula is more roughly rugose, the cephalic part is raised, the legs are stout, IV ~ I, the clypeus bears long hairs and possesses a ventral-medial gap, the cymbium bears long retrolateral hairs, the distal (slender) part of the embolus is straight and thinner, its basal part stands widely out. – In the extant genus *Steatoda* (= *Teutana*) s. l. the position and the sclerotization of the paracymbium are different, and an additional tegular apophysis is usually absent, but existing in the subgenus *Lithyphantes*; the lateral eyes are widely separated from each other in *Lithyphantes*, the fangs are thick, and the sternum separates only scarcely the posterior coxae.

Type species: *Erigone stigmatosa* KOCH & BERENDT 1854 (the only known species of the genus).

Distribution: Early Tertiary (Eocene) Baltic and Rovno amber forests.

Pseutoteutana stigmatosa (KOCH & BERENDT 1854) (figs. 139–145, photos 208–210)

1854 *Erigone stigmatosa* KOCH & BERENDT, in BERENDT (ed.): Die im Bernstein befindlichen Organischen Reste der Vorwelt, 1 (2): 38, t. 16, fig. 136. (**n. comb**.).

Synonyms according to the bulbus structures of the holotypes which I studied: *Eomysmena stridens* PETRUNKEVITCH 1958 (**n. syn.**) and *Flegia succini* PETRUNKEVITCH 1942 (**n. syn.**).

Material: (a) Baltic amber: More than 30♂. Holotypes: *Erigone stigmatosa* KOCH & BERENDT: PMHUB; *Eomysmena stridens* PETRUNKEVITCH: Min. Mus. Copenhagen no. 9982; *Flegia succini* PETRUNKEVITCH: Peabody Mus. (Yale University) no.

26723; 2♂ PMMoscow, 1♂ GPIUH; 1♂ coll. F. KERNEGGER; 14♂ F1717/CJW-F1729/CJW, 11♂ F1730/CJW. – I saw further males in collections of different dealers.
(b) Ukrainean (Rovono) amber: 2♂ Mus. Kiev, nos. K-1082, 4300 and UA no. 661.

Remarks on the material: Holotype of *stigmatosa*: The male is fairly well preserved but darkened by aging; most parts of the bulbi are covered with a white emulsion. – Holotype of *stridens*: Most parts of the spider are translucent, probably the result of embedding/heating. – Holotype of *succini*: Body and legs are strongly darkened. – The male F1719 is spun in in a part of a web of an unknown spider together with a fly and 1 1/2 Ephemeroptera. – 4 Acari are preserved with the male F1718. – A male of *Acrometa cristata* PETRUNKEVITCH 1942 is preserved very close to the male of F1723. F1728: The right pedipalpus is amputated beyond its patella, the right patella of leg I is a regeneration.

Diagnosis (♂; ♀ unknown): See the diagnosis of the genus.

Description (♂):
Measurements (in mm): Body length 2.4–2.5, prosomal length 1.1–1.2, femur I 1.5–1.8, tibia I 1.3–1.7, tibia II ca. 1.0, tibia IV ca. 0.8, metatarsus I 1.3–1.7, tarsus I ca. half as long as the metatarsus I.
Colour brown; the legs are annulated; the annulation is best preserved in spiders which are not or only slightly heated, e. g. in F1717/CJW (see the photos).
Prosoma flat, fine rugose, fovea well developed, eyes large, their field wide, posterior row straight, lateral eyes close together, clypeus fairly long, cheliceral promargin with a large tooth or outgrowth (F1719, F1729), sternum rugose, widely prologated between the posterior coxae. Prosomal-opisthosomal stridulatory organ distinct (fig. 139), consisting of tiny sclerotized anterior opisthosomal teeth and posterior prosomal files. – Legs long and slender, I distinctly longest, femur and tibia I with indistinct ventral cups, sequence of the long dorsal tibial bristles 2/2/1/2, position of the trichobothrium on metatarsus I–II in 0.4–0.44, tarsal IV comb well developed. Metatarsus I is bent in some males. – Opisthosoma oval, covered mainly with short hairs, with two pairs of dorsal sigillae, epigaster distinctly sclerotized; colulus (fig. 140) large, with a pair of long hairs.
Pedipalpus (figs. 140–145, photo 210): Femur very long and slender, patella and tibia with a long dorsal bristle in the distal half, tibia 1.5 (e. g. in the holotype) –1.85 times longer than wide, cymbium with 2–3 bristle-shaped hairs, position of the paracymbium retromarginal-distal (ectal), bulbus with a fringed additional tegular apophysis and a long theridiid tegular apophysis, distal part of the embolus sickle-shaped.

Relationships: See the genus. Most bulbus structures of the extant *Steatoda (Steatoda) triangulosa* (WALCKENAER 1802) are surprisingly similar, but (e. g.) the position of the paracymbium is quite different (internal position in *Steatoda*).

Ecology: Due to its frequency – *stigmatosa* is one of the most frequent species in Baltic amber – this species was supposingly a dweller in higher strata of the vegetation – and the bark? – of the extinct resin-producing needle trees of the genus *Pinites*.

Capture web: A larger part of a capture web with sticky droplets is preserved with the male F1720.

Distribution: Early Tertiary (Eocene) European amber forests; Baltic and Ukrainean ambers; an area which has a diameter of 1300 km.

Unispinatoda **n. gen**. (fig. 146–147, photos 211–214)

Diagnosis (♂; ♀ unknown): Legs I–II bear two rows of distinct short ventral cusps (fig. 146); pedipalpus (fig. 147): One of the hairs of the distal tibial margin is bristle-shaped enlarged, very long and strong, distinctly longer than the other hairs, reaching the tip of the cymbium.

Further characters: Prosoma with only few cusps, sternum rugose, sequence of the tibial bristles 2/2/1/1, number of the hairs of the colulus unknown, conductor large, questionable embolus thick.

Type species: *Unispinatoda aculeata* n. sp. (the only known species of the genus).

Relationships: See the key; close relationships are unknown to me. In the extant genus *Asagena* metatarsus IV bears a trichobothrium, the bristle of the male tibia IV is short and thick and the paracymbium has a position inside the cymbium (internal).

Distribution: Early Tertiary (Eocene) Baltic amber forest incl. the Bitterfeld deposit.

Unispinatoda aculeata **n. gen. n. sp**. (figs. 146–147, photos 211–214)

Material: 11♂ in Baltic amber; holotypus F1734/BB/AR/CJW, paratypes: F1735-1741/CJW, 1♂ (F1742) Mus. Brisbane, 1♂ GPIUH, 1♂ from the Bitterfeld deposit coll. M. KUTSCHER.

Preservation and syninclusions (stellate hairs are not listed): The holotype is fairly well preserved, ventrally exist some white emulsions and a bubble on the left side of the opisthosoma, the left leg IV is lost beyond the coxa by autotomy, a DRAGLINE runs backwards from the anterior spinnerets. – Paratypes: The right side of F1735 has been cut off; F1736 is completely preserved, a tiny Diptera: Nematocera is preserved above the right patella I; F1737 is well preserved, some leg articles are cut off; F1738 is completely and well preserved together with a DRAGLINE; F1739 is fairly well and completely preserved, its opisthosoma is deformed; F1740: The piece of amber was strongly heated and has a hole, the spiders opisthosoma is deformed; F1741: Parts of both anterior tibiae are cut off; F1742 is well and completely preserved in a 4 cm long piece of amber, some parts of the spider are covered with a white emulsion. The piece containing the male from the GPIUH was strongly heated, a bubble is preserved between the basal cheliceral articles. The piece from the coll. KUTSCHER was strongly heated, too, its opisthosoma is distinctly deformed at several parts.

Diagnosis (♂; ♀ unknown): See above.

Description (♂):
Measurements (in mm): Body length 1.8–2.0, prosomal length and width 1.0–1.1; leg I: Femur 1.3, patella 0.42, tibia 1.2, metatarsus 0.95, tarsus 0.5, tibia IV 0.7.
Colour: Prosoma, legs and epigastral scutum dark brown, opisthosoma yellow brown, legs annulated.
Prosoma as wide as long, with few cusps, profile convex, with a large fovea, eye field wide, eyes fairly small, posterior row straight to slightly recurved, clypeus long, basal cheliceral articles long, slender and slightly diverging, sternum rugose, the coxae IV widely separating. – Legs long and slender, order I/IV/II/III, I distinctly longest, sequence of the thin dorsal tibial bristles 2/2/1/1, comb of tarsus IV well developed, position of the metatarsal II trichobothrium in 0.75, metatarsal IV trichobothrium absent. Rows of ventral leg cusps/denticles (fig. 146) are present on all femora (weakly developed on III–IV) and on tibia and metatarsus I–II. These cusps/denticles are most probably sexually-dimorphic absent or weakly developed in the female sex like in related extant genera. – Opisthosoma oval, dorsally with two pairs of sigillae and short hairs; epigaster sclerotized, colulus large, with 2 or probably 3 hairs (F1736). – Pedipalpus (fig.147) (see above): Articles only fairly long, patella with 2 long dorsal bristles, paracymbium slender and pointed, position at the ectal margin.

Relationships: See above.

Distribution: Early Tertiary (Eocene) Baltic amber forest incl. the Bitterfeld deposit.

2. ENOPLOGNATHINAE SIMON 1884

Diagnosis: Chelicerae: Basal articles large (figs. 157, 170) (but relatively small in *Eolyrifer*!), with 1–2 (♂) large teeth on the anterior margin, anterior median eyes usually smallest (fig. 152), colulus large, usually with 2 (rarely 1 or 3) hairs (figs. 148–150), cymbium and bulbus most often slender (figs. 154, 167, 175), paracymbium (figs. 153, 166, 175) in a retrodistal-ectal position, with a needle-shaped prolongation.

<u>Further characters</u>: Clypeus usually not or only weakly protruding (but see *Eolyrifer*!) (fig. 151), sequence of the thin tibial bristles 2/2/1/1 in the extant genera *Enoplognatha*

and *Robertus*, 1/1/1/1 (fig. 161) or 2/2/1/2 (fig. 171) in the fossil genera in Baltic amber, dorsal opisthosomal scutum usually absent (present in the extinct genus *Hirsutipalpus* n. gen., fig. 165, which relationships are unsure). Most extant spiders live near the ground similar to most extant Asageninae. In the fossil Enoplognathinae – in contrast to extant Enoplognathinae and members of most other theridiid subfamilies – I found not a single case of leg autotomy but amputations and healing effects of leg articles (fig. 162) are not rare. This character may be an adaptation to the dangerous prey of these spiders – ants – which most probably injured numerous fossil spiders, see *Hirsutipalpus varipes* n. sp. (figs. 162–163).

Genera: Extant: *Enoplognatha* PAVESI 1880, *Robertus* O. PICKARD-CAMBRIDGE 1879 and probably *Selkirkiella* BERLAND 1924, see AGNARSSON (2004: 476); fossil/extinct: *Eolyrifer* n. gen., *Hirsutipalpus* n. gen. and *Succinobertus* n. gen.

Relationships: WIEHLE (1937: 217) – apparently following SIMON (1914) – considered *Enoplognatha* and *Robertus* as closely related and I agree with this authors, but according to ARNEDO et al. (2004) these genera are not closely related. With respect to AGNARSSON (2004) *Enoplognatha* and *Robertus* are members of the Pholcommatinae, but according to the large colulus (which may bear more than two hairs), the large basal male cheliceral articles which bear large teeth on their promargin (especially ♂ of *Enoplognatha* already existing in the Eocene fossils) as well as of the soft opisthosoma (except *Hirsutipalpus*) I distinguish two subfamilies, the Eno-plognathinae and the Pholcommatinae. Almost all members of both subfamilies are dwellers on the ground and possess a redbrown colour of body and legs, most taxa occur in the Northern Hemisphere. – SIMON (1914: 278) regarded *Enoplognatha* and *Robertus* as related to *Steatoda* and its kin within the enlarged subfamily Asageninae. I agree that the Asageninae are closely related to the Enoplognathinae but I consider both being separate subfamilies. In the Asageninae body and legs are usually strongly sclerotized, the prosoma is usually distinctly rugose (*Latrodectus* is one of the rare exceptions), and a needle-shaped prolongation of the paracymbium is absent. – In the Episinae the clypeus is ventrally usually strongly protruding, the basal cheliceral articles are usually smaller, large teeth on the cheliceral promargin are absent, the opisthosoma is long and usually – in the extant taxa – flattened, the colulus is usually smaller, and a pair of strong hairs exists usually in the field of the median eyes.

Distribution: Extant: Widely distributed but mainly holarctic; fossil known from the Early Tertiary (Eocene) Baltic amber forest (first fossil report; all genera are extinct).

Variability of structures: (a) Enoplognathinae possesses usually – apparently basicly – a soft opisthosoma; *Hirsutipalpus* – in which a dorsal opisthosomal scutum exists – is the only known exception. – (b) The number of dorsal tibial bristles varies strongly in this subfamily, see the diagnosis and the key; the ancestral sequence of these bristles – 2/2/1/2 – exists in two extinct genera: *Eolyrifer* and *Succinobertus*; it is reduced in the extinct genus *Hirsutipalpus* to 1/1/1/1 and in the extant genera *Enoplognatha* and *Robertus* to 2/2/1/1. – (c) The number of hairs on the large colulus is also quite variable (figs. 148–150): Among 12 specimens of *Robertus lividus* (BLACKWALL 1836) from Austria and Germany (CJW) I found ten specimens whith a pair of long hairs (fig. 149), one male in which only a single long hair exists in a central position (fig. 148) and a single female with an additional short third hair in a central position between the long paired hairs (fig. 150). Is the unpaired hair an atavistic structure and a hint to the existence of such a third hair in the ancestors of this genus and subfamily? The only other theridiid subfamily in which I found more than a pair of colular hairs is the ancestral Asageninae – a hint to its strong relationships?

Ecology: Most extant members of the Enoplognathinae are dwellers at or near the ground; spiders of the extant *Enoplognatha ovata*-group – as an exception – live in higher strata of the vegetation. Due to their relatively high frequency in Baltic amber at least the members of the extinct *Hirsutipalpus varipes* n. gen. n. sp. were dwellers of higher strata of the vegetation.

Key to the extant and fossil genera of the subfamily Enoplognathinae:

Remark: Not included is the extant genus *Selkirkiella* BERLAND 1924 which has a strongly enlarged conductor, see AGNARSSON (2004: 476).

1 All tibiae bear only a single dorsal bristle in a position near the base of the article (fig.161), opisthosoma with a dorsal scutum (fig. 165), pedipalpus: Figs. 166–170. Fossil in Baltic amber . . . .*Hirsutipalpus*

- Sequence of the dorsal tibial bristles 2/2/1/1 (fig. 171), opisthosoma soft. Extant . . 2

- Sequence of the dorsal tibial bristles 2/2/1/2, opisthosoma soft. Fossil in Baltic amber 3

2(1) Opisthosoma dorsally unicoloured, sternum short posteriorly, reaching only half (middle) of the coxae IV. ♂: Chelicerae not largely diverging, bearing no powerful tooth; ♀: The posterior margin of the cheliceral furrow bears 1–2 tiny teeth. . . . . . .*Robertus*

- Opisthosoma dorsally most often (except e. g. in certain *E. caricis*) with a folium or with spots, sternum long posteriorly, reaching the posterior part of the coxae IV. ♂: Chelicerae largely diverging and usually with at least one powerful tooth (similar to fig. 156; compare fig. 137!); ♀: The posterior margin of the cheliceral furrow bears a single larger tooth . . . . *Enoplognatha*

3(1) Eye field raised, clypeus distinctly concave, ventrally distinctly protruding (fig. 151), male pedipalpus (figs.153–154): Tibia very long, embolus indistinct. . . . . *Eolyrifer*

- Eye field not raised, clypeus almost straight, ventrally not protruding (fig. 169), male pedipalpus (figs. 175–178): Tibia not very long, embolus long and free visible, bulbus with a fringed apophysis. . . . .*Succinobertus*

The extant European genera:

Enoplognatha PAVESI 1880

Diagnosis: Sequence of the dorsal tibial bristles 2/2/1/1, opisthosoma usually with a folium, markings or spots (except in some specimens of *E. caricis*), sternum posteriorly long, reaching the posterior part of the coxae IV. ♂-chelicerae enlarged, diverging and bearing at least one large tooth, the retromargin of the ♀-chelicerae bears a single larger tooth. ♂-pedipalpus e. g. fig. 150a).

Relationships: See *Robertus*.

Distribution: Almost cosmopolitical, mainly holarctic.

Robertus O. PICKARD-CAMBRIDGE 1879

Diagnosis: Sequence of the dorsal tibial bristles 2/2/1/1, opisthosoma dorsally unicoloured, sternum posteriorly short, reaching only the basal half (middle) of the coxae IV. ♂: Chelicerae not strongly enlarged and diverging, without a LARGE tooth; ♀: Cheliceral retromargin with 1–2 TINY teeth.

Relationships: In *Enoplognatha* the sternum is longer posteriorly, the opisthosoma bears usually dorsal markings (see above), the ♂-chelicerae are enlarged, diverging and bearing at least one large tooth, the retromargin of the ♀-chelicerae bears a single – larger – tooth.

Distribution: Holarctic.

The fossil genera in Baltic amber:

***Eolyrifer* n. gen**. (figs. 151–154, photos 215–216)

Diagnosis (♂; ♀ unknown): Prosoma almost circular, sequence of the dorsal tibial bristles 2/2/1/2 (similar to fig. 171), eye field raised, clypeus strongly concave and protruding (fig. 151), anterior median eyes small and in a more dorsal position (fig. 152), ♂-pedipalpus (figs. 153–154): Tibia unusually long and hairy, bulbus very small.

Further character: Basal cheliceral articles only fairly large.

Type species: *Eolyrifer longitibialis* n. sp. (the only known species of the genus).

The **relationships** are unsure. According to the relatively small anterior median eyes, the large colulus which bears two hairs, the kind of the paracymbium and the small bulbus *Eolyrifer* may be related to *Robertus* O. PICKARD-CAMBRIDGE 1879, but in *Robertus* – as in *Enoplognatha* PAVESI 1880 – tibia IV bears only a single bristle. In *Hirsutipalpus* n. gen. (see the key) all tibiae bear a single dorsal bristle. The ventrally protruding clypeus and the relatively small basal cheliceral articles are similar to the Episinae and unusual in the Enoplognathinae.

Distribution: Early Tertiary (Eocene) Baltic amber forest.

***Eolyrifer longitibialis* n. gen. n. sp.** (figs. 151–154)

Material: 2♂ in Baltic amber; holotypus F1751/BB/AR/CJW, paratypus and a separated piece of amber F1752/BB/AR/CJW.

Preservation and syninclusions: The holotype is almost completely and well preserved, the tips of the legs III and IV are cut off, remains of a white emulsion are preserved e. g. below the mouth parts, on the prosoma, and on parts of the bulbi, numerous tiny bubbles exist below and above the spider; complete stellate hairs are absent. – The paratype is completely preserved in a piece of amber which was heated; some brown darkenings exist around the spider's body, the opisthosoma is dorsally depressed (concave), ventrally exist few remains of a white emulsion. Few particles of detritus are present, an almost 0.2 mm long Psocoptera is preserved left of the spider. In the separated piece of amber some stellate hairs are enclosed.

Diagnosis (♂; ♀ unknown): Pedipalpus (figs. 153–154) with an unusually long and hairy tibia and a very small bulbus; embolus hidden.

Description (♂):
Measurements (in mm): Body length 1.8, prosoma: Length 0.9, width 0.85; leg I: Femur 1.7, patella 0.4, tibia 1.25, metatarsus 1.3, tarsus 0.8, tibia IV 1.0; pedipalpus: Femur 0.8, tibia 0.55.
Colour yellow brown to medium brown (the prosoma).
Prosoma (figs. 151–152) almost as wide as long, dorsally with few longer hairs, fovea short and deep, eyes partly covered with white emulsions, field fairly wide, anterior median eyes fairly small, in a more dorsal position, the remaining eyes large, a pair of thin hairs exist in the field of the median eyes. Clypeus long, concave and protruding ventrally, basal cheliceral articles only fairly large, mouth parts hidden, coxae IV separated by almost their diameter, stridulatory files not recognizable. – Legs long and slender, order I/IV/II/III, sequence of the tibial bristles 2/2/1/2, paired tarsal claws probably toothless, unpaired claw long and bent in a right angle, position of the metatarsal trichobothria I–III in the distal quarter of the article. – Opisthosoma oval, without dorsal scutum or sigillae, hairs fairly long, epigastral scutum present, colulus longer than wide, probably bearing a pair of hairs, spinnerets short. – Pedipalpus (figs. 153–154): Femur and tibia long, patella and tibia with long and almost bristle-shaped hairs, position of the paracymbium at the cymbial margin and apically with a short ”spine”, bulbus unusually small, its structures are partly covered with a white emulsion and difficult to recognize, the questionable embolus is small.

Relationships: See the genus.

Distribution: Early Tertiary (Eocene) Baltic amber forest.

Hirsutipalpus **n. gen.** (figs. 155–168, photos 221a–221b)

Diagnosis (♂; ♀ unknown): Opisthosoma with a dorsal scutum (figs. 164–165), sequence of the dorsal tibial bristles 1/1/1/1, their position near the base of their article, cheliceral promargin with 3 teeth (figs. 156–158) (one is very large), pedipalpus (figs. 166–167, photo 221b) with a small bulbus and a short embolus.

Further character: Fangs very long and slender (figs. 156–157).

Type species: *Hirsutipalpus varipes* n. sp. (the only known species of the genus).

Relationships: See the key; I regard *Hirsutipalpus* as a questionable member of the Enoplognathinae and do not want to exclude relationshipips to the Asageninae. A dorsal opisthosomal scutum exists as in the Pholcommatinae and some Asageninae. *Hirsutipalpus* is the only genus of the Enoplognathinae in which a dorsal opisthosomal scutum exist and the number of tibial bristles is reduced to 1/1/1/1.

Distribution: Early Tertiary (Eocene) Baltic amber forest incl. the Bitterfeld deposit.

***Hirsutipalpus varipes* n. gen. n. sp**. (figs. 155–168, photos 221a–221b)

Material 16♂ in Baltic amber: Holotypus F1775/BB/AR/CJW; paratypes: F1776-1788 (1786 with a separated piece of amber, 1785 from the Bitterfeld deposit; F1787 has been given to the AMNH); 1♂ coll. LIEDTKE in Itzehoe no. 445, 1♂ from the Bitterfeld deposit is kept in the coll. M. KUTSCHER in Sassnitz.

Preservation and syninclusions: The holotype is completely and very well preserved in a small yellow piece of amber which most probably was slightly heated; a white emulsion is absent, remains of questionable SPERM are preserved on the conductor of both pedipalpi (figs. 166–167); paratype F1776 is fairly well preserved below a layer which contains numerous small bubbles; dorsal parts of body and legs are covered with a white emulsion, distal articles of the left leg II are cut off; paratype F1777 is completely and well preserved in a piece of amber which was slightly heated, the right side is partly covered with a white emulsion, the part of a tiny and headless Collembola is preserved behind the spider, stellate hairs are absent; F1778 is almost completely preserved in a piece of amber which was slightly heated; the left leg II is AMPUTATED near the base of the tibia (figs. 162) and HEALED, few remains of a white emulsion cover the ventral side of the spider, the dorsal opisthosomal scutum is cut off; 5 1/2 Diptera: Nematocera (no prey), a small insect larva, a member of the Sternorrhyncha, 1/2 Acari and few remains of stellate hairs are preserved in the same piece of amber; F1779 is well and completely preserved in a piece of amber which was slightly heated; few remains of a white emulsion exist on the spiders body; an ant, a mite and a tiny male spider of *Fossilanapis* sp. indet. (Anapidae: Anapinae) are also preserved but no stellate hairs. The anapid spider is preserved in a different layer of the resin, the ant is embedded in the same layer as the spider in a distance of 1.2 cm. Right of the ant – and partly in contact with the spider – are remains of thin threads preserved which well may be spider's threads, and thus I do not want to exclude that the ant was the prey of the spider. I found no injuries of the ant which has a body length of almost 3 mm; F1780 is completely but only fairly well preserved, the opisthosoma is deformed in front of the dorsal scutum, white emulsions exist mainly anteriorly, questionable REMAINS OF POISON are preserved at the tip of the left fang (fig. 168), parts of a large arthropod leg and the tiny larva of a mite are also preserved but no stellate hairs; F1781 is completely preserved in a larger piece of amber which was slightly heated, only few remains of a white emulsion exist below the mouth parts, 1/2 beetle, 1/2 Diptera and few remains of stellate hairs are also enclosed; F1782 is well and almost completely preserved in a piece of amber which was slightly heated; its ventral side is partly covered with a white emulsion, the right patella I is cut off, the right tibia IV is broken near its end (fig. 163), the metatarsus is amputated in its basal half, apparently the stump is closed and HEALED. The fracture of the tibia happened probably on a layer within the fossil resin. 4 1/2 Diptera (apparently no prey of the spider) are the syninclusions; F1783 is fairly well preserved and heated, the ventral side is covered with a white emulsion, the opisthosoma is shriveled, deformed and probably injured (photo), the spider is in contact with at least two thin spider's threads which are difficult to recognize. The male has probably been the prey of a – conspecific? – spider, and thus this may well be a case of CANNIBALISM. Most leg tips of the spider are cut off as well as both anterior legs through their tibia; F1784 is completely preserved and darkened by heating; opisthosoma, sternum and mouth parts are covered with a white emulsion, parts of the opisthosomal scutum are free. Remains of some Diptera as well as – in front of the spider – remains of an Acari and a Collembola are the organic syninclusions; F1785 is darkened by heating, most parts of opisthosoma and legs and some parts of the prosoma are covered with a white emulsion, the opisthosoma is somewhat deformed, a larger air bubble is preserved right of the prosoma; F1786: Mainly most parts of the opisthosoma are covered with a white emulsion, parts of the right tibia IV are cut off from the dorsal side; a DRAGLINE is preserved, other organic inclusions are absent. According to the "sweet" smell during dry grinding this piece of amber was not heated; F1787 is incompletely preserved: The dorsal part of the opisthosoma is cut off, the tips of the left tarsus I and the right tarsus II as well as the right patella I are cut off, ventral parts of body and legs are covered with a white emulsion.

Remark: Among 16 males I found three leg amputations and two broken legs but not a single case of leg autotomy.

Diagnosis (♂; ♀ unknown): Pedipalpus (figs. 166–167) with a hairy tibia, a small bulbus and a short questionable embolus.

Remark: The length of prosoma and femur I are very variable – ca. 100% (!) – like e. g. in certain other Theridiidae and Linyphiidae; with some hesitation I regard this variability as intraspecific because I found – so far as recognizable – no differences in the structures of the bulbus, but the cheliceral teeth (figs.) are also quite variable!

Description (♂):
Measurements (in mm): Body length 1.7–2.2, prosoma length 0.7–1.3; leg I (the short-legged holotype): Femur 1.2 (up to 2.3 in large spiders like paratype F 1784), patella 0.2, tibia 1.05, metatarsus 0.85, tarsus 0.43, tibia IV 0.7; pedipalpus: Patella 0.14, tibia 0.17.
Colour (if not darkened by heating): Prosoma, legs, dorsal opisthosomal scutum and epigastral scutum medium to dark brown, opisthosoma yellow brown.
Prosoma (figs. 15–160, 168) ca. 1.25 times longer than wide, hairs short, fovea low, eyes (fig. 155) fairly small, posterior row slightly procurved, anterior median eyes smallest, posterior median eyes separated by more than their diameter, basal cheliceral articles large, promargin with 1 large and 1 or 2 smaller teeth – very variable! – fangs long and slender, labium free, not rebordered, wider than long, coxae IV separated by almost their diameter, prosomal-opisthosomal stridulatory organ (fig. 160) fairly well developed. – Legs (figs. 161–163) long to very long (in larger specimens; apparently allometric growth), femur I distinctly longer than the prosoma (see above), I distinctly longest, order I/II/IV/III, sequence of the dorsal tibial bristles 1/1/1/1, their position near the base of the article, metatarsus I–III bear a trichobothrium, its position on I in ca. 0.3, comb of tarsus IV existing. – Opisthosoma (figs. 164–165) oval, covered with short hairs and an oval dorsal scutum which bears two pairs of sigillae, epigastral

scutum present, colulus large (its hairs are unknown), spinnerets short. – Pedipalpus (figs. 166–167) (see above): Patella shorter than the tibia, both articles bear a dorsal bristle.

Relationships: See the genus.

Distribution: Early Tertiary (Eocene) Baltic amber forest incl. the Bitterfeld deposit.

Succinobertus **n. gen.** (figs. 169–178, photos 221c–221f)

Diagnosis (♂; ♀ unknown): Sequence of the dorsal tibial bristles 2/2/1/2 (fig. 171), prosoma almost as wide as long, cheliceral promargin with 3 teeth (fig. 170); ♂-pedipalpus (figs. 175–178): Cymbium apically like being cut off, one of the functional conductors is fringed.

Further characters: Clypeus (fig. 169) ventrally not elongated, fovea low, coxae IV separated by the sternum by almost their diameter, position of the paracymbium distal-ectal, embolus long.

Type species: *Succinobertus adjacens* n. sp. (the only known species of the genus).

Relationships: See the key.

Distribution: Early Tertiary (Eocene) Baltic amber forest incl. the Bitterfeld deposit.

Succinobertus adjacens **n. gen. n. sp.** (figs. 169–178, photos 221c–221f))

Material: 9♂ in Baltic amer; holotypus F1764/BB/AR/CJW; 5 paratypes F1765/CJW-F1769/CJW (1766 together with a small separated piece of amber), 1♂ Mus. Ziemi no. 5679; 1♂ coll. KRÜMMER in Greifswald no. 2209 from the Bitterfeld deposit; 1♂ coll. KUTSCHER in Sassnitz from the Bitterfeld deposit.

Preservation and syninclusions: The holotype is completely and well preserved in a piece of amber which was slightly heated, remains of a white emulsion exist on the right side of the spider and anteriorly; a spider's thread is running along the spider's left side; stellate hairs are absent. – F1766 is well preserved, dorsal parts of the right patella and tibia I are cut off. – F1766 is well preserved, the dorsal half of the opisthosoma and parts of the left legs III and IV are cut off. – F1767 is completely preserved and darkened by heating. A tiny Collembola and a small wasp are also preserved but no stellate hairs. – F1768 is completely preserved but dorsally hidden by fissures of the resin and ventrally by a white emulsion. – F1769 is completely preserved, the opisthosoma is covered with a white emulsion, few stellate hairs are also preserved. –The male from the Museum Ziemi is completely and fairly well preserved, partly covered with a white emulsion; e larger bubble exists below the right leg II, a mite is preserved right of the spider. – The males from the Bitterfeld deposit are preserved in pieces of amber which are more or less heated, they are completely preserved; with the male from the Museum Ziemi is a mite enclosed, with the male of the coll. KRÜMMER a tiny Diptera: Nematocera.

Diagnosis (♂; ♀ unknown): Pedipalpus (figs. 175–178) Tibia shorter than the patella, the tip of the embolus is situated within a (second) functional conductor (apparently the theridiid tegular apophysis) near the tip of the cymbium.

Description (♂):
Measurements (in mm): Body length 1.5–1.9, prosoma: length 0.7–0.9, width ca. 0.8; leg I: Femur 1.05, patella 0.35, tibia 0.9, metatarsus 0.73, tarsus 0.43, tibia IV 0.7.
Colour in the not heated/darkened spiders: Prosoma medium brown, legs and opisthosoma light brown.
Prosoma (figs. 169–170) about as wide as long, with short hairs and a low fovea. Eyes fairly large, field fairly wide (F1765), posterior row slightly procurved, posterior median eyes separated by about their diameter; strong hairs in the field of the median eyes are absent. Clypeus long, almost straight, basal cheliceral articles fairly large, promargin with 3 teeth, fangs slender, labium wider than long, not fused to the sternum, coxae IV separated by their diameter, posterior prosomal stridulatory files not recognizable. – Legs fairly short and hairy, order I/II/IV/III, sequence of the dorsal tibial bristles 2/2/1/2, position of the metatarsal trichobothrium I–III just in front of the middle of the length of the article, absent on IV; comb of tarsus IV well developed. – Opisthosoma egg-shaped, with two pairs of dorsal sigillae, not scutate, covered with short hairs, epigaster probably hardened, epiandrous gland spigots as in fig. 172, colulus (figs. 173–174) large, bearing 1–2 long hairs. – Pedipalpus (figs. 175–178): Patella longer than the tibia, cymbium apically as being cut off, paracymbium in a retroectal position, weakly sclerotized, with a pointed tip, bulbus with a long embolus which is situated in or near the furrow of a fringed conductor and distally/apically in a second divided functional conductor which may be the theridiid tegular apophysis.

Relationships: See the genus.

Distribution: Early Tertiary (Eocene) Baltic amber forest incl. the Bitterfeld deposit.

3. PHOLCOMMATINAE

Most Pholcommatinae are small to tiny and short-legged spiders similar to the Phoroncidiinae (but see the Australian genus *Magnopholcomma* n. gen. which relationships are quite unsure!). In most genera – in all genera of the Baltic amber forest – the male opisthosoma is armoured; the prosoma is frequently more or less fine rugose. The male prosoma – usually the clypeus – bears outgrowths in some taxa (figs. 184–188, 212–213, photos 224–226, 241–243). – Pholcommatinae were apparently more diverse in the Eocene of Europe (7 genera are known from the Baltic amber forest; two of these – *Succinura* and *Vicipholcomma* – have questionable subfamiliar relationships, see the subfamily Theridiinae) than they are today (3 genera: *Pholcomma, Theonoe*, and *Carniella*, the latter has recently been introduced to Europe). The relatively rareness of fossils – I know only ca. 30 specimens in Eocene Europe ambers – may result from their main occurrence on or near the ground, and their only rare presence on the bark of needle trees which produced the fossil resin.

Diagnosis: Basicly – e. g. in all Eocene taxa – strongly armoured spiders; the opisthosoma bears a large dorsal scutum at least in the male sex (see e. g. photo 224) but not in the female. Anterior median eyes usually small (figs. 181, 188, 192, 199) (large in the extant genus *Magnopholcomma* which may be a member of a subfamily of its own, fig. 213), and closer to laterals than to each other (fig. 208). Prosoma usually fine rugose (photo 223), labium fused to the sternum in most taxa (fig. 215) (but a free sclerite in the frequent European species *Pholcomma gibbum*), colour of body and legs usually red- or orange-brown (photos 223, 231), body length usually 1–1.5 mm.

Further characters: Usually short-legged spiders (length of patella + tibia not longer than the length of the prosoma), frequently with relatively short metatarsi and long tarsi (not in *Magnopholcomma*), dorsal tibial bristles present (they may be indistinct and short, especially in *Succinura* n. gen.). In several genera – e. g. *Carniella*, *Magnopholcomma*, *Proboscidula* (extant), and *Globulidion* (extinct) – the male prosoma (usually the clypeus) bears outgrowths (photos 224–226, 241–243 figs. above as well as figs. 184–188, 212–213). Prosomal stridulatory files or spines may exist (figs. 212–213), the comb of tarsus IV may be strongly reduced or even absent. Ground-living tiny spiders except *Magnopholcomma*. Dwarfism: Body length usually 1–1.5mm (but in the extant genus *Magnopholcomma* – which relationships are unsure – 3.8mm). Paracymbium very variable, usually in an ectal-retrodistal position (figs. 179, 193, 219) similar to the Enoplognathinae; absent in this position – most probably internal – in *Carniella, Succinura* and *Vicipholcomma*, position unknown in *Globulidion*.

Relationships: Apparently Enoplognathinae is most related, see above. – Most of the Phoroncidiinae – members of some taxa are similar but they are not closely related in my opinion – are also small to tiny and short-legged. Their body is always strongly armoured, too, but dorsal tibial bristles are absent, their colour is most often dark brown (usually not redbrown), the eye region is projecting/overhanging the clypeus in BOTH sexes (a conspicuous prosomal sexual dimorphism and an outgrowth of the male clypeus – like in certain Pholcommatinae – are absent), the scutate and most often HIGH opisthosoma bears usually humps and small/tiny (lateral) SCUTA IN ROWS (quite different to the Pholcommatinae), the colulus is strongly reduced and hidden in a quite LARGE (tube-shaped) sclerotized ring IN BOTH SEXES, the anterior median eyes are large and usually not closer to laterals than to each other. – A rugose prosoma exists also in most members of the Asageninae, and rarely an opisthosomal scutum as well; see the key to the subfamilies above.

Distribution: Extant: Cosmopolitical (mainly on the Northern Hemisphere); fossil: Eocene Baltic amber forest incl. the Bitterfeld deposit.

(a) **Key** to the European extant and fossil (Eocene Baltic amber) genera of the subfamily Pholcommatinae:

Remarks: (1) The extant *Pholcomma* is one of the rare genera of this subfamily in which the labium is a free sclerite. – (2) The opisthosomal scutum is about as wide as long in *Obscurpholcomma, Succinura* and *Vicipholcomma* but distinctly longer than wide in *Balticpholcomma*, *Cymbiopholcomma, Globulidion, Pholcomma* and *Rugapholcomma*. – (3) The length of the dorsal opisthosomal hairs in the basal half is about 0.02 mm in *Globulidion*, most often 0.04–0.05 (up to 0.07) mm in *Cymbiopholcomma, Pholcomma*, and *Vicipholcomma*, usually 0.07–0.08 (up to 0.1) mm in *Balticopholcomma*, *Obscurpholcomma, Rugapholcomma* and *Succinura*. – (4) A retrodistal paracymbium is absent in *Carniella, Succinura* and *Vicipholcomma*.

1 Metatarsus III without a trichobothrium, dorsal opisthosomal scutum absent in both sexes, ♂-pedipalpus: Tibia very long, patella 2 to 3 times longer than wide, body length only 0.9–1.3 mm (♀). Extant. 2

- Metatarsal III trichobothrium present, dorsal opisthosomal scutum present in the male, ♂-pedipalpus (figs. 180, 204): Patella usually up to 1 1/2 times longer than wide (long in *Rugapholcomma*, fig. 194), body length 1.1–2.0 mm. Extant (*Pholcomma*) or extinct (the remaining genera). 3

2(1) ♀ with paired genital openings, ♂ without clypeal outgrowth, retrobasal paracymbium absent. . . . . *Theonoe*

- ♀ with an unpaired genital opening, ♂-clypeus with a large erect outgrowth (fig. above), retrobasal paracymbium present. Introduced to Europe from SE-Asia . . . . . . Carniella

3(1) Sequence of the dorsal tibial bristles 1/1/1/1 or tibial bristles absent (few *Succinura*), tarsi about as long as metatarsi. ♂: Prosomal outgrowth present (*Globulidion*, figs. 184–188) or absent (*Succinura*). Baltic amber. ♀ unknown 4

- Sequence of the dorsal tibial bristles 2/2/1/1, tarsi about as long as metatarsi. ♂: Prosomal outgrowth absent (♀ unknown). Extinct, in Baltic amber. 5

- Sequence of the dorsal tibial bristles 2/2/1/2 (unsure in *Rugapholcomma*), the tarsi may be distinctly shorter than the metatarsi. ♂: Prosomal outgrowth absent. Extant (*Pholcomma*) and extinct. 6

4(3) ♂-prosoma: Cephalic part bulging to a dorsal outgrowth, bearing the eyes (fig. 184–188); pedipalpus (figs. 189–190): Long tibial outgrowth absent, cymbium wide, bulbus short, embolus spirally. . . . . Globulidion

- ♂-cephalic part not bulging; pedipalpus (figs. 195f): Tibia with a long retroventral outgrowth, cymbium slender, guiding distally and retrolaterally the embolus by a row of short marginal hairs, bulbus very long and tegulum very large . . . . Succcinura

5(3) Prosomal profile convex (fig. 207), posterior eye row recurved (fig. 208), long spiral tegular apophysis present (figs. 210-211). Body length 1.25–1.5 mm. . . Vicipholcomma

- Prosomal profile straight, posterior eye row procurved, spiral tegular apophysis absent (fig. 180). Body length only about 1.1 mm. . . . . Balticpholcomma

6(3) Labium a free sclerite (with a small unsclerotized white furrow between labium and sternum). In the European species *P. gibbum*: Tarsi distinctly shorter than metatarsi, two pairs of receptacula seminis, and femur I distinctly thicker than the remaining femora. Extant . . . . .Pholcomma

- Labium fused to the sternum (similar to fig. 215). Tarsi about as long as metatarsi. ♀ unknown. Extinct, in Baltic amber 7

7(6) ♂-pedipalpus (fig. 194) with an unusually long patella. Prosoma strongly rugose
. . . . Rugapholcomma

- Pedipalpal patella not unsusually long 8

8(7) Prosoma strongly rugose (photos 227–228), ♂-pedipalpus (fig. 191): Cymbium long but distally not widened, tegulum ventrally strongly protruding . . . . . Obscurpholcomma

- Prosoma fine rugose (photo 223), ♂-pedipalpus (figs. 183–184): Cymbium distinctly widened distally-ventrally, tegulum not distinctly protruding, a lanceolate apophysis (fig. 183b) may be difficult to observe . . . . .Cymbiopholcomma

(b) Description of the fossil taxa of the Pholcommatinae in Baltic amber:

***Balticpholcomma* n. gen.** (figs. 179–180, photo 222)

Diagnosis (♂; ♀ unknown): Sequence of the dorsal tibial bristles 2/2/1/1, tarsi as long as the metatarsi, long opisthosomal scutum (photo); pedipalpus (figs. 179–180) with a long embolus, a distinct tegular apophysis is absent.

Further characters: Tiny spiders (♂ 1.1mm long), prosoma fine rugose, most dorsal hairs of the opisthosoma in the basal half usually 0.07–0.08mm long (up to 1mm).

Type species: *Balticpholcomma scutatum* n. sp. (the only known species of the genus).

Relationships: See the key and *Cymbiopholcomma* n. gen. In *Vicipholcomma* n. gen. the opisthosomal scutum is as long as wide, the prosomal profile is straight, the posterior eye row is procurved the embolus is longer and an additional spiral tegular apophysis is present. In *Obscurpholcomma* n. gen. are the dorsal hairs of the short opisthosoma of the same length, but the opisthosoma is almost as wide as long, tibia IV bears 2 dorsal bristles and the genital structures are different. In the extant genus *Pholcomma* tibia IV bears 2 dorsal bristles and the prosoma is distinctly convex.

Distribution: Eocene Baltic amber forest.

***Balticpholcomma scutatum* n. gen. n. sp.** (figs. 179–180, photo 222)

Material: Holotypus ♂ in Baltic amber, F1797/BB/AR/CJW.

Preservation and syninclusions: The spider is completely and fairly well preserved in a piece of amber which was not heated; the ventral side is thickly covered with a white emulsion, a particle of insect's excrement is preserved above the spider's opisthosoma, a mite and a larger fly are enclosed in different layers of the fossil resin; few stellate hairs are also present.

Diagnosis (♂; ♀ unknown): See above.

Description (♂):
Measurements (in mm): Body length 1.1, prosomal length and width 0.55; leg I: Femur ca. 0.47, patella 0.18, tibia 0.37, metatarsus 0.28, tarsus 0.28, tibia IV 0.37, opisthosomal scutum 0.67 long and 0.57 wide.

Colour: Prosoma, legs and opisthosomal scutum medium to dark redbrown, soft parts of the opisthosoma light brown.
Prosoma (photo 222) as wide as long, fairly low, fine rugose, profile dorsally straight, covered with short hairs, fovea indistinct; most eye lenses are hidden, posterior row procurved similar to *Cymbiopholcomma*, posterior stridulatory files present, most mouth parts hidden, fangs long and thin, sternum as wide as long, fine rugose, separating the coxae IV by more than their diameter. – Legs stout, tarsi as long as metatarsi, hairs short, order of their length I/IV/II/III, tibial bristles almost as long as the tibial diameter, their sequence 2/2/1/1, metatarsi I–III bear a trichobothrium, its position on I in 0.36, comb of tarsus IV well developed, unpaired tarsal claw short. – Opisthosoma oval, with a large dorsal scutum which is longer than wide and bears fairly long hairs. Epigaster scutate, the short spinnerets are surrounded by a sclerotized ring, the area of the colulus is hidden. – Pedipalpus (figs. 179–180): Femur stout, patella and tibia slightly longer than wide, paracymbium in a retrodistal-ectal position; bulbus (most parts are covered with a white emulsion) with a longer embolus which may cover 2/3 of a loop.

Relationships: See above.

Distribution: Eocene Baltic amber forest.

***Cymbiopholcomma* n. gen**. (figs. 181–183b, photo 223)

Diagnosis (♂; ♀ unknown): Sequence of the dorsal tibial bristles 2/2/1/2, the opisthosoma bears a long scutum (photo 223); pedipalpus (figs. 182–183a): Cymbium distinctly widened distally-ventrally (arrow in fig. 183), embolus long, and with a large basal outgrowth, a lanceolate apophysis (fig. 183b) may be difficult to observe (in *C. dudum*). (The function and the origin on the bulbus of this quite unsusual apophysis are unknown).

Further characters: Prosoma fine rugose, posterior eye row slightly procurved (fig. 181), dorsal opisthosomal scutum distinctly longer than wide, most dorsal hairs of the basal half of the opisthosoma 0.04–0.05mm long, tegular apophysis large, a conductor hide the middle part of the embolus.

Type species: *Cymbiopholcomma dudum* n. sp..

Relationships: See the key, e. g. *Obscurpholcomma* n. gen. and *Succinura* n. gen. *Balticpholcomma scutata* – which may be most related – is only 1.1 mm long, its tibia IV bears only a single bristle, the cymbium is not strongly widened distally; a lanceolate apophysis of the bulbus and a distinct tegular apophysis are absent.

Distribution: Eocene Baltic amber forest.

***Cymbiopholcomma dudum* n. gen. n. sp.** (figs. 181–183)

Material: 2♂ in Baltic amber; holotypus and 2 separated pieces of amber, F1796/BB/AR/CJW, paratypus Mus. Ziemi in Warsaw no. 5685.

Preservation and syninclusions: The holotype is fairly well preserved in a yellow piece of amber which was not or only slightly heated; the ventral side is thickly covered with a white emulsion, parts of the left patella I are split off, the left leg IV is cut off at the end of the tibia, the right legs III and IV are cut off beyond their tibia. Left of the spider is a part of a larger leg of a Diptera preserved, in the large separated piece of amber are two Diptera and few stellate hairs enclosed. – The paratype is completely preserved in a piece which was strongly heated, remains of a white emulsion covers its ventral surface; right in front of the spider are the larva of a mite and a stellate hair preserved.

Diagnosis (♂; ♀ unknown): The bulbus (fig. 183) bears a distinctly bent lanceolate apophysis which is difficult to observe (not drawn), the tegular apophysis is long and slender, the basal part of the embolus is “swollen”.

Description (♂):
Measurements (in mm): Body length 1.4–1.5, prosomal length and width 0.63; leg I: Femur 0.72, patella 0.2, tibia 0.55, metatarsus 0.55, tarsus 0.31, tibia IV 0.5; opisthosomal scutum: Length 0.95–1.05, width 0.73–0.8.
Colour: Prosoma, legs and opisthosomal scutum redbrown, remaining parts light brown.
Prosoma as wide as long, fine rugose, almost hairless, with a low fovea, eyes (fig. 181) fairly large, posterior median eyes largest, posterior row very slightly procurved, clypeus long and not protruding, mouth parts hidden, basal cheliceral articles of medium size, sternum as wide as long, separating the coxae IV by more than their diameter. – Legs only fairly long, tarsi distinctly shorter than the metatarsi, hairs indistinct, order of their length I/IV/II/III, sequence of the fairly long tibial bristles 2/2/1/2, metatarsi I–III bear a trichobothrium, its position on II in 0.3. Ventral hairs of tarsus IV straight, unpaired tarsal claws distinctly shorter than the paired claws. – Opisthosoma with a large dorsal scutum which is distinctly longer than wide, fine rugose and covered with short hairs; sigillae are absent. Epigaster strongly sclerotized, sclerotized ring around the spinnerets present, colulus fairly small, hairs not observable. – ♂-pedipalpus (figs. 182–183): Patella and tibia with a small dorsal bristle, patella almost globular, tibia short and wide, cymbium distinctly widened distally-ventrally, paracymbium in a retro-ectal position, tegular apophysis long, slender and bent, lanceolate bulbus apophysis (not drawn and difficult to observe) bent distally, embolus long, describing almost one loop, basally “swollen”, in the middle of its length guided by a – probably narrow – conductor near to the cymbial margin.

Relationships: In *C. spiculum* the tegular apophysis and the basal outgrowth of the embolus are stouter, the lanceolate bulbus apophysis is longer and almost straight; the conductor and the subtegulum are apparently larger but the position of the subtegulum which is drawn in fig. 183a) is more basally than in fig. 183).

Distribution: Eocene Baltic amber forest.

***Cymbiopholcomma spiculum* n. gen. n. sp**. (figs. 183a–183b, photo 223)

Material: Holotypus ♂ in Baltic amber, F2110/BB/AR/CJW.

Preservation and syninclusions: The spider is almost completely preserved, only the left leg I is absent beyond the patella by an amputation or by autotomy. Most parts of the ventral side are covered with a white emulsion, the opisthosomal surface has dorsally in the basal half an artificial silvery modification which is apparently caused by the preservation. Stellate hairs are absent in the small piece of amber which apparently was slightly heated.

Diagnosis (♂; ♀ unknown): Pedipalpus (fig. 183a–183b): Tegular apophysis stout, lanceolate apophysis very long and almost straight, base of the embolus with a stout outgrowth which has an almost triangular shape.

Description (♂):
Measurements (in mm): Body length 1.35, prosoma 0.6 long and wide; leg I: Femur 0.7, patella 0.2, tibia 0.51, metatarsus 0.45, tarsus 0.31, tibia II 0.4.
Colour dark redbrown (probably the original colour or slightly darker).
Prosoma wide as long, fine rugose, hairs and fovea indistinct, posterior stridulatory files absent, eyes only fairly large, similar to *dudum*, posterior row straight, clypeus long, mouth parts and sternum hidden. – Legs only fairly long, order I/IV/II/III, hairs indistinct, tibial bristles thin, their sequence 2/2/1/2, position of the metatarsal trichobothrium I/II in 0.31/0.35; the comb of tarsus IV is not observable. – Opisthosoma depressed, dorsally completely covered by a large oval scutum which is scarcely covered with short hairs; at least a single pair of sigillae exists in the middle of the opisthosomal length. The epigaster is covered by a large scutum, the spinnerets are hidden. – Pedipalpus (figs. 183a–183b): Femur slender, patella short, tibia wide, distal part of the cymbium with the paracymbium hidden, subtegulum prolaterally protruding, conductor large, embolus long, describing about one circle, with a large basal outgrowth, hidden by the conductor in its middle part, a long and slender lanceolate apophysis is almost straight and directed to the patella, its origin is not observable.

Relationships: See *C. dudum* n. sp.

Distribution: Eocene Baltic amber forest.

***Globulidion* n. gen**. (figs. 184–190, photos 224–226)

Diagnosis (♂; ♀ unknown): Prosoma with a prolongated and „swollen“ cephalic area (a fairly low outgrowth) which bears the eyes (figs. 184–188), opisthosoma with a large dorsal scutum (figs., photos)), sequence of the dorsal tibial bristles 1/1/1/1, pedipalpus (figs. 189–190) with a very long and spiral embolus, and distally with a screw-shaped part of the embolus + conductor.

Further characters: Tiny spiders (body length 1.4mm), tarsi about as long as the metatarsi, sternum posteriorly twice as wide as the diameter of a coxa IV.

Type species: *Globulidion cochlea* n. sp. (the only known species of the genus).

The **relationships**: are unsure (the area of the colulus is hidden). According to the shape and the structure of the low opisthosoma *Globulidion* is more likely a member of the Pholcommatinae than of the Phoroncidinae in which the area of the eyes is overhanging the clypeus, too, but this region is much more narrow in the Phoroncidiinae in which dorsal tibial bristles are absent, tiny hair-bearing opisthosomal plates (scuta) exist as well a large (tube-shaped) sclerotized ring around the spinnerets. – The shape of the "swollen" cephalic part of *Globulidion* is unique within the family Theridiidae. See also the key to the genera of the Pholcommatinae.

Distribution: Eocene Baltic amber forest.

***Globulidion cochlea* n. gen. n. sp.** (figs. 184–190, photos 224–226)

Material: 2♂ in Baltic amber; holotypus and 3 separated pieces of amber, F1789/BB/AR/CJW; paratypus, F1790/BB/AR/CJW.

Preservation and syninclusions: Holotype: The spider is embedded in a clear yellow piece of amber which was heated; it is well and completely preserved, most ventral parts are covered with a white emulsion but the sternum is free: below the left femur I a large bubble is preserved, below the right femur I a small bubble; a stellate hair lies right in front of the spider. In the separated pieces of amber some stellate hairs, a small particle of insect excrement, and particles of detritus are preserved. – The paratype is completely but only fairly well preserved close to a Diptera; parts of the spider are hidden by fissures in the amber and by white emulsions. A tiny Acari, a small Diptera and remains of a third Diptera are preserved in front of the spider.

Description (♂; ♀ unknown):
Measurements (in mm): Body length ca. 1.4, prosoma: Length incl. the cephalic outgrowth 0.8, width 0.5; leg I: Femur 0.41, patella 0.15, tibia 0.26, metatarsus 0.21, tarsus 0.2, tibia II 0.25, tibia III 0.2, tibia IV 0.29, metatarsus IV 0.23, tarsus IV 0.24.
Colour of the heated spiders dark brown.
Prosoma (figs. 184–189) distinctly longer than wide, scarcely covered with short bristles, with a large cephalic outgrowth which is separated from the thoracal part by a furrow, and which bears the eyes which are partly covered with emulsions and difficult

to recognize. Openings of glands are not recognizable. Eyes fairly small and in a wide field, posterior row strongly recurved. Clypeus long, mouth parts hidden. – Legs fairly stout, order IV/I/II/III, tarsi about as long as the metatarsi. Dorsal bristles: Patellae 2, tibiae 1, its position on I in 0.16, length on I slightly more than the tibial diameter. Position of the trichobothrium on metatarsus I in 0.55, hairs of the comb of tarsus IV straight and probably smooth. – Opisthosoma (figs. 184–186, photos) oval, fairly flattened, with a large dorsal scutum which is distinctly longer than wide, punctuated and with tiny hairs (in the basal half only about 0.02 mm long); two pairs of sigillae; the area of colulus and spinnerets is hidden in both males. – Pedipalpus (figs. 189–190): Femur slender, patella thick, tibia wide, directed ventrally and with long apical hairs, cymbium large, not modified, area of the retrodistal paracymbium hidden; I do not want to exclude that its position is inside the cymbium; most parts of the bulbus are hidden; embolus and conductor: See the genus.

Relationships: See the genus.

Distribution: Eocene Baltic amber forest.

***Obscurpholcomma* n. gen**. (fig. 191, photos 227–228)

Diagnosis (♂; ♀ unknown): Sequence of the dorsal tibial bristles 2/2/1/2, prosoma distinctly rugose (photos), opisthosomal scutum present; pedipalpus (fig. 191) with a large subtegulum and a ventrally strongly protruding tegulum.

Further characters: Dorsal opisthosomal scutum distinctly longer than wide, posterior eye row straight, most dorsal opisthosomal hairs in the anterior half 0.07–0.08 mm long, cymbium long.

Type species: *Obscurpholcomma tegens* n. sp.; the only known species of the genus.

Relationships: *Succinura* n. gen. has also a large subtegulum but in *Succinura* the prosoma is not rugose, the tibial bristles are reduced, the opisthosoma is almost as wide as long, a retroectal paracymbium is absent, the embolus is thicker in its basal part, is guided by short and bent hairs of the cymbial margin (fig. 195) and as well as of an outgrowth of the pedipalpal tibia, and the tegulum is ventrally less protruding.

Distribution: Eocene Baltic amber forest.

***Obscurpholcomma tegens*. n. gen. n. sp.** (fig. 191, photos 227–228)

Material: 2♂ in Baltic amber, holotypus F1798/BB/AR/CJW, paratypus and a separated piece of amber F1799/BB/AR/CJW.

Preservation and syninclusions: The holotype is completely and excellently preserved between three layers of a piece which was heated; remains of a white emulsion exist only on ventral parts of the opisthosoma. The opisthosoma is ventrally "depressed"; probably the spider did not feed for a longer time. Also preserved are remains of stellate hairs, two splinters of amber and several small ballets of insect's excrement. – The paratype is completely preserved in a piece of amber which was heated; the left leg IV is amputated beyond the patella; dorsal parts of body and legs are covered with a white emulsion, the ventral side is partly hidden by a layer in the amber and fissures as well. Several stellate hairs are also preserved.

Diagnosis: See the genus.

Description (♂):
Measurements (in mm): Body length 1.2 (holotype) – 1.4; holotype: Prosoma: Length 0.7, width 0.63, height 0.4; leg I: Femur 0.7, patella 0.22, tibia 0.58, metatarsus 0.5, tarsus 0.38, tibia IV 0.5; opisthosomal scutum: Length 0.95, width 0.75.
Colour (heated) dark brown.
Prosoma (photos 227–228) distinctly rugose, indistinctly covered with short hairs, fovea low, eyes of medium size, posterior row straight, anterior median eyes smaller than posterior median eyes which are separated by almost their diameter, clypeus weakly protruding, basal cheliceral articles shorter than the clypeus, most mouth parts are hidden, the rugose sternum separates the coxae IV by more than their diameter. Posterior stridulatory files are most probably absent. – Legs fairly stout and hairy, order I/IV/II/III, tarsi distinctly shorter than metatarsi, sequence of the dorsal tibial bristles 2/2/1/2, bristles thin and fairly long; at least metatarsi I–II bear a trichobothrium, its position on I–II is in 0.3, comb of tarsus IV well developed, unpaired tarsal claws distinctly smaller than the paired claws. – Opisthosoma dorsally completely covered by a scutum which is distinctly longer than wide, sigillae are absent, ventrally it is almost completely scutate including a ring around the spinnerets; anterior-ventral ?stridulatory picks are present and a tiny colulus as well. – Pedipalpus (fig. 191) with stout articles, patella with a long dorsal bristle in the distal half, cymbium long, paracymbium in a retrodistal-ectal position, subtegulum large, tegulum protruding, embolus long.

Relationships: See the genus.

Distribution: Eocene Baltic amber forest.

***Rugapholcomma* n. gen.** (figs. 192–194, photo 229)

Diagnosis (♂; ♀ unknown): Prosoma rugose (photo 229, fig. 192), opisthosoma completely covered with an oval and relatively flat scutum, tibia IV with 2 dorsal bristles; pedipalpus (figs. 193–194): Patella almost three times longer than wide, embolus long, in a retrolateral position.

Type species: *Rugapholcomma patellaris* n. sp., the only known species of the genus.

The **relationships** are unsure; apparently there are no closer relationships to other genera in Baltic amber, see the key. In the extant genus *Pholcomma* THORELL 1869 the prosoma is higher, the anterior median eyes are smaller, and the pedipalpal patella is short. See below, the female of the Pholcommatinae indet.

Distribution: Eocene Baltic amber forest.

***Rugapholcomma patellaris* n. gen. n. sp.** (figs. 192–194, photo 229)

Material: Holotypus ♂ in Baltic amber and a separated piece of amber, Muzeum Ziemi in Warszawa no. 1849/13.

Preservation and syninclusions: The spider is completely but only fairly well preserved in a piece of amber which was heated. In contact with the legs of the spider are fissures at both sides which hide the view on the spider. A white emulsion covers parts of body and legs. Few thin spider's threads are preserved e. g. behind and left of the spider, a ballet of insect's excrement is situated right in front of the spider, a tiny insect larva is also preserved, stellate hairs are absent.

Diagnosis: See above.

Description (♂):
Measurements (in mm): Body length 1.8, prosoma: Length 1.0, width 0.92, femur I 1.0, leg IV: Femur 1.0, patella 0.3, tibia 0.8, metatarsus 0.62, tarsus 0.4, pedipalpal femur 0.5.
Colour dark brown (darkened by heating).
Prosoma (fig. 192, photo 229) not raised, rugose and with wrinkles which partly build lines, fovea low, posterior stridulatory files absent; eye field rather narrow, area of the anterior median eyes not protruding and not reduced, posterior row straight, posterior median eyes largest, separated by their diameter, clypeus long, not widely protruding ventrally; mouth parts and most parts of the sternum are hidden. – Legs fairly long,

slender, order probably I/IV/II/III, hairs short, sequence of the dorsal tibial bristles most probably 2/2/1/2 (only on II are 2 thin dorsal bristles observable which are 1.3 times longer than the tibial diameter. Comb of tarsus IV probably absent, position of the trichobothria on the metatarsi I–III unknown, absent on IV. – Opisthosoma (photo 229) depressed dorsoventrally, ventrally hidden, dorsally completely covered by an oval scutum which is not rugose and which bears short hairs (in the basal half they are up to 0.1mm long); its anterior margin has an edge which is somewhat concave (inclined) in the middle. – Pedipalpus (figs. 193–194) with a long and slender femur, patella almost three times longer than wide, tibia fairly short, dorsal bristles of patella and tibia may be absent, cymbium large, retromarginal paracymbium in the middle of the cymbial length (!); most parts of the bulbus are hidden, the embolus is long, in a retrolateral position.

Relationships: See the female of the Pholcommatinae indet. below.

Distribution: Eocene Baltic amber forest.

Succinura n. gen. (figs. 195–206, photos 230–238)

Diagnosis (♂; ♀ unknown): Dorsal tibial bristles strongly reduced, absent, or tibiae only with a single short bristle near their base (see below), opisthosoma covered with a large dorsal scutum which is almost as wide as long (photos); pedipalpus (photos, figs. 195f): Tibia with a long retroventral outgrowth which guides the distal part of the embolus, cymbium long and slender, with a hairy retrolateral furrow as well as hairs which are strongly bent to the bulbus and guide the retrolateral part of the long embolus, retrodistal/ectal paracymbium absent, bulbus very long and subtegulum very large.

Further characters: Dorsal tibial bristles are apparently absent in *circuita* and *fuscoruber,* and short – in a basal position – at least on I in *bellavista, dubia* and *ovalis*. Prosoma finelly rugose or with rows of punctures, posterior eye row almost straight (fig. 199), posterior prosomal files absent but a rugose area is present, legs stout (photos), tarsal comb IV indistinct, paired tarsal claws probably toothless, colulus with a pair or a single hair (fig. 202), embolus describing more than one loop (figs. 195f).

Type species: *Succinura bellavista* n. sp.

Relationships (see the key): *Cymbiopholcomma* and *Obscurpholcomma* n. gen. may be closest related; in these genera the sequence of the dorsal tibial bristles is 2/2/1/2, the tarsi are distinctly shorter than the metatarsi and the structures of the pedipalpus are quite different, e. g. the cymbium is wide. – In contrast to most other Pholcommatinae a retroectal paracymbium is absent in *Succinura* (an internal paracymbium may be present) (a retrodistal paracymbium is also absent in *Carniella* and *Vicipholcomma*). The reason for the absence of a retroectal paracymbium in this genus may be the existence of a row of short hairs at the cymbial margin which guide the embolus and can not co-exist with such kind of a paracymbium. – In *Kochiura* ARCHER (Anelosiminae) (fig. 453) exist also hairs of the cymbial margin which guide the embolus but in *Kochiura* – and other Anelosiminae – the opisthosoma is soft, the hair of the colulus is longer, the position of the eyes is different, the bulbus is short and the tip of the embolus is near the tip of the cymbium but not guided by an outgrowth of the pedipalpal tibia. Because of so many differences I regard the row of cymbial hairs in these two genera as convergently evolved.

Distribution: Eocene Baltic amber incl. the Bitterfeld deposit.

Key to the species of *Succinura* (♂):

Remarks: (1) The weakly sclerotized theridiid tegular apophysis may be deformed by the process of embedding in the resin or by artificial heating. (2) The original red-brown colour of body and legs is not characteristic for certain fossil species but may have changed in some specimens to dark gray-brown by heating (in *S. fuscoruber* the redorange-brown colour has stood a heating, see the photo 231).

1 Large basal part of the embolus distinctly longer than wide (e. g. fig. 195) 2

- Large basal part of the embolus about circular or wider than long (e. g. fig. 204). . .5

2(1) Large basal part of the embolus in a fairly oblique position, tegulum very large (fig. 204) . . . .*fuscoruber*

- Large basal part of the embolus in a longitudinal position (figs. 195, 203, 205) 3

3(2) apical part of the cymbium large (fig. 203). . . . .*dubia*

- Apical part of the cymbium small (figs. 195, 205) 4

4(3) Retrolateral margin of the large basal part of the embolus convex, theridiid terminal apophysis large, shape of the embolus more oval (fig. 205) . . . . *ovalis*

- retrolateral margin of the large basal part of the embolus concave, theridiid tegular apophysis small (fig. 195) . . . . *aciesaeta*

5(1) Large basal part of the embolus distinctly wider than long (fig. 200) . . . . . *circuita*

- Large basal part of the embolus almost circular (figs. 197–198). . . . .*bellavista*

Succinura aciesaeta n. gen. n. sp. (figs. 195–196)

Material: Holotypus ♂ in Baltic amber, Zool. Mus. Copenhagen, coll. A. K. ANDERSEN (28-3 1968).

Preservation and syninclusions: The spider is fairly well preserved, the ventral part of the opisthosoma is cut and broken off, a white emulsion and bubbles cover dorsal parts of the body.

Diagnosis (♂; ♀ unknown): Pedipalpus as in figs. 195–196; the theridiid tegular apophysis does not reach the tip of the cymbium.

Description (♂): Measurements (in mm): Body length 1.3, tibia I ca. 0.5. Colour, body and legs – so far recognizable – quite similar to *dubia* n. sp. Metatarsus I–III bear a trichobothrium, position of the long trichobothrium on metatarsus I in 0.33. – Pedipalpus (figs. 195–196): See above. The right bulbus is partly expanded; patella slightly longer than wide, tibia wider than long, subtegulum large, the embolus describes about one loop.

Relationships: See the key.

Distribution: Eocene Baltic amber forest.

Succinura bellavista n. gen. n. sp. (figs. 197–198, photos 233–235)

Material: 2♂ in Baltic amber, holotypus F1830/BB/AR/CJW, paratypus and a separated piece of amber F1825/BB/ AR/CJW.

Preservation and syninclusions: The holotype is completely and well preserved, the piece of amber was heated, white emulsions and stellate hairs are absent. Remains of two Collembola – questionable prey – are preserved near the spider in the same layer. – The paratype is well and completely preserved in a piece of amber which was heated and has fissures left and behind the spider. Few spider's threads are located near the spider, an Acari in the separated piece of amber; stellate hairs are absent.

Diagnosis (♂; ♀ unknown): Pedipalpus (figs. 197–198): Large basal part of the embolus circular to slightly wider than long.

Description (♂):
Measurements (in mm): Body length 1.25–1.3, prosoma: length 0.65, width 0.55, length of tibia I 0.38. Colour: Dark brown. Body and legs quite similar to *dubia*. In the paratype

are the large lung covers well visible and the position of the metatarsal I trichobothrium is in 0.33.

Relationships: In *S. circuita* is the large basal part of the embolus distinctly wider than long.

Distribution: Eocene Baltic amber forest.

Succinura circuita **n. gen. n. sp**. (figs. 199–200)

Material: Holotypus ♂ in Baltic amber, F1817/BB/AR/CJW.

Preservation and syninclusions: The spider is completely and fairly well preserved, most parts are hidden by layers of the amber and legs, the opisthosoma is dorsally depressed, few remains of a white emulsion are present on the ventral side, most legs are drawn to the right direction. A thin spider's thread runs along the right leg II to the right side (droplets are absent). 2 Acari and some stellate hairs are preserved in the same piece of amber.

Diagnosis (♂; ♀ unknown): Pedipalpus (fig. 200): Large basal part of the embolus distinctly wider than long.

Description (♂):
Measurements (in mm): Body length 1.25, prosomal length ca. 0.5, length of tibia I 0.37. Colour: Light brown. Body and legs quite similar to *S. dubia*, eyes: Fig. 199, pedipalpus: Fig. 200.

Relationships: See the key and *S. bellavista*.

Distribution: Eocene Baltic amber forest.

Succinura dubia **n. gen. n. sp**. (figs. 201–202, photos 236–237)

Material: Holotypus ♂ in Baltic amber and a separated piece of amber, F1816/BB/ AR/ CJW.

Preservation and syninclusions: The spider is completely preserved and dorsally thickly covered with a white emulsion; two fissures are running longitidunally around the spiders opisthosoma, large bubbles cover dorsally the right side of the prosoma, the ventral side is well observable, few stellate hairs are also preserved, some air bag pollen grains are preserved in the smaller one of the separated pieces of amber.

Diagnosis (♂; ♀ unknown): Pedipalpus (fig. 203, photo 237) with a long and slender theridiid tegular apophysis which is as long as the distally visible part of the cymbium.

Description (♂):
Measurements (in mm): Body length 1.2, prosomal length 0.65; leg I: Femur ca. 0.65, patella 0.17, tibia 0.42, metatarsus 0.32, tarsus 0.32, metatarsus III 0.21, tarsus III 0.25, tibia IV 0.46.
Colour medium grey brown.
Prosoma (fig. 201) dorsally hidden, chelicerae of medium size, not diverging, anterior cheliceral margin with 3 or 4 teeth, fangs long and slender, gnathocoxae converging above the labium which is wider than long and separated from the sternum by a seam; probably it is a free sclerite. The sternum separates the coxae IV by 1 1/2 of their diameter. Stridulatory files unknown. – Legs short, order IV/I/II/III, metatarsi about as long as tarsi, comb of tarsus IV weakly developed, tibiae bristleless or with a thin (hair-shaped) dorsal bristle near the base, position of the metatarsal trichobothria unknown. – Opisthosoma dorsally and ventrally strongly armoured, with a short ring around the spinnerets, colulus (fig. 202) with a single bristle; probably only a single pair of epiandrous gland spigots. – Pedipalpus (fig. 203): See above, the diagnoses of the species and the genus; patella and tibia short, a hidden paracymbium may exist inside the cymbium, the tegulum bears few tiny teeth.

Relationships: See the key.

Distribution: Eocene Baltic amber forest.

***Succinura fuscoruber* n. gen. n. sp.** (fig. 204, photos 232–233)

Material: Holotypus ♂ in Baltic amber, F1827/BB/AR/CJW.

Preservation and syninclusions: The spider is completely and excellently preserved in a piece of amber which was slightly heated; a larger bubble and remains of a white emulsion cover most parts of the sternum. – A part of a dragline runs from the anterior spinnerets downwards. A small Diptera: Nematocera is preserved in the same piece of amber, stellate hairs are absent.

Diagnosis (♂; ♀ unknown): The large basal part of the embolus is in a fairly oblique position, the tegulum is very large (fig. 204).

Description (♂):
Measurements (in mm): Body length 1.35, prosomal length 0.65, length of tibia I 0.4.
Colour red orange-brown (probably the original colour). Body and legs quite similar to *S. dubia*, position of the trichobothrium on metatarsus I in 0.33. Pedipalpus: Fig. 204.

Relationships: See the key.

Distribution: Eocene Baltic amber forest.

Succinura ovalis n. gen. n. sp. (fig. 205)

Material: Holotypus ♂ in Baltic amber, F1829/BB/AR/CJW.

Preservation and syninclusions: The spider is completely and well preserved in a piece of amber which was heated, the ventral side is thickly covered with a white emulsion, numerous stellate hairs are present in the same piece of amber.

Diagnosis (♂; ♀ unknown): Large part of the embolus very long (fig. 205).

Description (♂):
Measurements (in mm): Body length 1.35, prosomal length 0.7, length of tibia I 0.4.
Colour: Medium brown. Body and legs quite similar to *S. dubia*; the prosoma bears dorsally few rows of punctures. Pedipalpus (fig. 205) with a very long basal part of the embolus.

Relationships: See the key.

Distribution: Eocene Baltic amber forest.

Succinura sp. indet. (8♂)

F1818/BB/AR/CJW: The colour of the spider is dark redbrown. Pedipalpus: Fig. 206. The dorsal half of body, legs and right pedipalpus are cut off or broken off. Thin spider's threads are preserved ventrally and right of the spider (droplets are absent). A half juvenile spider (Dionycha) is lying behind the spider.

F1826/BB/AR/CJW and a separated piece of amber: The spider is well and completely preserved, its colour is redbrown.

F1828/BB/AR/CJW and a separated piece of amber: The spider is complete and thickly covered with a white emulsion, its colour is redbrown (photo 238). A Collembola is preserved in the separated piece of amber.

F1831/BB/AR/CJW and a separated piece of amber: The spider is completely preserved and ventrally thickly covered with a white emulsion. Remains of a small Diptera are preserved in the separated piece of amber.

F1832/BB/AR/CJW and 3 separated pieces of amber: Parts of the spider are cut off, its colour is light brown, its colulus bears a single pair of hairs. A complete larva of a Blattaria is preserved in one of the separated pieces of amber.

F1833/BB/AR/CJW: The spider is completely preserved, ventral parts are covered with a white emulsion. Its colour is dark redbrown. Some Acari and stellate hairs are also preserved.

F1834/BB/AR/CJW: The spider is completely preserved, the colour is dark brown, most parts are thickly covered with a white emulsion.

F1835/BB/AR/CJW: The spider is completely preserved and thickly covered with a white emulsion, its colour is dark redbrown. Two tiny Collembola are also preserved.

***Vicipholcomma* n. gen**. (figs. 207–211, photos 239–240)

Diagnosis (♂; ♀ unknown): Sequence of the dorsal tibial bristles 2/2/1/1, a large opisthosomal scutum is present (fig. 207); pedipalpus (figs. 208–211): Retrodistal paracymbium absent, embolus long and spirally, describing 1 3/4 loops.

Further characters: Prosoma fine rugose, posterior eye row recurved, tarsi as long as the metatarsi, length of the dorsal opisthosomal hairs in the anterior half most often 0.04–0.05 mm.

Type species: *Vicipholcomma spiralis* n. sp. (the only species of the genus).

Relationships: See the key; *Balticpholcomma* may be closest related, see above. In *Globulidion* n. gen. exists a long and screw-shaped embolus, a prosomal outgrowth is present, and the sequence of the dorsal tibial bristles is 1/1/1/1. A spiral embolus exists also in *Clya* KOCH & BERENDT 1854 (Asageninae); specimens of *Clya* are larger and the opisthosoma is soft. A retrodistal paracymbium is also absent in *Succinura* in which the pedipalpal structures are different.

Distribution: Eocene Baltic amber forest.

***Vicipholcomma spiralis* n. gen. n. sp.** (figs. 207–211, photos 239–240)

Material: 2♂ in Baltic amber; holotypus and a separated piece of amber, GPIUH no. 4632, paratypus and a separated piece of amber F1927/BB/AR/CJW.

Preservation and syninclusions: Holotype: The spider is completely and well preserved directly between two layers in the fossil resin; the ventral side is thickly covered with a white emulsion. In the separated piece are a Diptera: Nematocera and a tiny wasp preserved; stellate hairs are absent. – The paratype is completely preserved in a piece of amber which was slightly heated; the chelicerae and the ventral side of the body are partly hidden by a fissure and a white emulsion. A gas bubble is preserved between the prosoma and the right femur II.

Diagnosis: See the genus.

Description (♂):
Measurements (in mm): Body length 1.25–1.5 (paratype), prosoma: Length 0.63, width 0.6; leg I: Femur 0.6, patella 0.21, tibia 0.47, metatarsus 0.35, tarsus 0.35, tibia IV 0.43, opisthosomal scutum 0.8 long and wide (0.9 x 0.83 in the paratype).
Colour: Prosoma, legs and opisthosomal scuta red brown, remaining parts of the opisthosoma of the holotype light brown.
Prosoma (figs. 207–208, photos) almost as wide as long, fine rugose, covered with short hairs, cephalic profile convex, fovea low, stridulatory area hidden, eyes large, posterior row recurved, posterior median eyes probably largest, separated by more than one diameter, anterior eyes smaller, most mouth parts and sternum hidden, basal cheliceral articles fairly long. – Legs (photos) fairly stout, hairs indistinct, sequence of the dorsal tibial bristles 2/2/1/1, bristles fairly long, the basal bristle on tibia I is 1.7 times longer than the tibial diameter. Metatarsi I–III bear a long trichobothrium, its position on II in 0.31–0.35, the bothria are small. Position of the long trichobothrium on metatarsus II in 0.35, its existence on metatarsus IV unknown, unpaired tarsal claws distinctly shorter than paired claws, comb of tarsus IV indistinct. – Opisthosoma (fig. 207, photos) oval, anterior margin straight and wide (paratype), with a larg dorsal scutum which is about as wide as long, ventral part soft with the exception of a small sclerotized ring around the spinnerets, area of the colulus hidden, lung covers large (paratype). – Pedipalpus (figs. 209–211) with fairly short articles, patella slightly longer than wide, tibia high and distally distinctly widened, retrodistal paracymbium absent (paratype), cymbium blunt, protruding apically, embolus originating retrolaterally, only less than one loop of the spiral embolus is visible in the holotype but there may be more than 1 3/4 loops (paratype), other bulbus sclerites may exist or are hidden.

Relationships: See the genus.

Distribution: Eocene Baltic amber.

Pholcommatinae indet. (photos 27–28)

Material: 1♀ in Baltic amber, SMF, F16/BB/AR/CJW.

The habitus – especially the large and flat dorsal opisthosomal scutum of this female in Baltic amber – see the photos 27–28, and WUNDERLICH (2002: 357, fig. 3) – is similar to *Rugapholcomma patellaris* n. gen. n. sp., see above (♂; ♀ unknown). This female is smaller (body length 1.3mm, prosomal length 0.65mm), the length of metatarsus/tarsus IV is 0.25/0.27mm, most tarsi are about as long as the tarsi, but metatarsus III is 1.4 times longer than tarsus III, tibial bristles are apparently absent, the lung covers are small, the epigaster bears a large scutum, a large scutum exists around the spinnerets, too, the colulus is large. – I do not want to exclude that both taxa are congeneric.

(c) The extant European genera of the Pholcommatinae:

Carniella THALER & STEINBERGER 1988

Diagnosis: Sequence of the dorsal tibial bristles 2/2/1/2, trichobothrium of metatarsus III absent, opisthosomal scutum absent in both sexes; ♂: Clypeus with an outgrowth (fig. 19 above) which is directed dorsally and is only weakly developed in *C. schwendingeri* KNOFLACH 1996, retrobasal “paracymbium” present, ♀ with an unpaired genital opening. Body length about 1 mm.

Relationships: See *Theonoe* and the key above.

Distribution: Originally SE-Asia – see KNOFLACH (1996) –; Central Europe (introduced at first to Austria and Germany); apparently an expansive species.

Pholcomma THORELL 1869

Diagnosis: Sequence of the dorsal tibial bristles 2/2/1/2, trichobothrium of metatarsus III present, (femur I in the type species *P. gibbum* distinctly thicker than the remaining femora, and prosomal profile distinctly convex); ♂: Dorsal opisthosomal scutum present. LABIUM A FREE SCLERITE, two pairs of receptacula seminis in *P. gibbum*. Body length 1.3–2.7 mm.

Relationships: *Carniella* and *Theonoe* are most related, see the key; the labium is fused to the sternum in these genera.

Distribution: Cosmopolitical, mainly holarctic. (According to YOSHIDA (1985: 10) *Crustulina grayi* CHRYSANTHUS and *C. lugubris* CHRYSANTHUS from New Guinea may belong to *Pholcomma*).

Theonoe SIMON 1881

Synonymy: *Marianana* GEORGESCU 1989 (**n. syn**.). – According to the absence of a trichobothrium on the metatarsi III–IV of the Roumanian caverniculous tiny and six-eyed female holotype which I studied, as well as the teeth of the cheliceral margins (3 teeth on the anterior margin), the widely spaced coxae IV, the long tarsi (they are distinctly longer than the metatarsi), and epigyne/vulva I regard *Marianana* as a junior synonym of *Theonoe*.

Diagnosis: Sequence of the dorsal tibial bristles 2/2/1/2 (?), trichobothrium of metatarsus III absent, opisthosomal scutum absent; ♀: Epigyne with a pair of genital openings. Body length 1–1.2 mm.

Relationships: In *Carniella* the ♂-clypeus bears an outgrowth, a retrobasal "paracymbium" exists and the female genital opening is unpaired.

Distribution: Mainly holarctic.

(d) List of further extant genera of the Pholcommatinae which do not occur in Europe and which relationships are unsure (see AGNARSSON (2004: 468–469):

Cerocida SIMON 1894, ?*Magnopholcomma* n. gen., *Proboscidula* MILLER 1970: See above (Asageninae), *Selkirkiella* BERLAND 1924 (South America; partly sub *Anelosimus*), *Stemmops* O. PICKARD-CAMBRIDGE 1894, and *Styposis* SIMON 1894.

(e) Description of an extant taxon which is probably not a member of the Pholcommatinae:

MAGNOPHOLCOMMATINI n. trib.

Diagnosis (♂; ♀ unknown): Larger spiders, body length 3.8mm, a single pair of opisthosomal stridulatory spines only (figs. 212–213), prosoma (figs. 212–213, photos 241–243) with a bipartite fovea and a large globular clypeal outgrowth, without a field of dense hairs in the gap to the clypeus; pedipalpus (figs. 219–220, photo 244) with a retrodistal marginal and partly intern, hook-shaped paracymbium and a long embolus which is guided and hidden by a long conductor.

Further characters: All tibiae bear a single bristle only, cheliceral promargin with 3 large teeth (fig. 214), labium fused to the sternum (fig. 215), two pairs of epiandrous gland spigots (fig. 217), colulus large, bearing two long hairs (fig. 218). Dwellers of higher strata of the vegetation, capture web unknown.

Type species: *Magnopholcomma n. gen*., the only known genus of the tribus.

The **relationships** are quite unsure; the taxon is probably not a member of the ground-living Pholcommatinae but independent. According to the clypeal outgrowth – which is comparable with the outgrowth in *Proboscidula* (fig. 21a) – and which exists in a similar shape in other subfamilies, too –, the small chelicerae, the labium – which is fused to the sternum –, and the redbrown colour of body and legs the genus *Magnopholcomma* is similar to members of the Pholcommatinae, but the remaining Pholcommatinae are small or even tiny short-legged and frequently armoured spiders, and their anterior median eyes are usually smaller. Therefore I regard *Magnopholcomma* only provisionally as a member of the Pholcommatinae. – In the Enoplognathinae the basal ♂-cheliceral articles/teeth are larger, a prosomal outgrowth is unknown, and the prosomal-opisthosomal stridulatory organ is different. – Probably exist no close relationships to the Episinae in which the chaetotaxy as well as the shape of clypeus and colulus are different, the kind of stridularory organ is different, too, and from which a clypeal outgrowth is unknown.

Distribution: Eastern Australia (Queensland).

***Magnopholcomma* n. gen.** (figs. 212–220, photos 241–244)

Diagnosis, relationships and **distribution**: See above.

Type species (by monotypy):

Magnopholcomma globulus **n. gen. n. sp**. (figs. 212–220, photos 241–244)

Material: E-Australia, Queensland, Lamington National Park near Brisbane, shaken from a tree in the rain forest, holotypus ♂ JW leg. in VIII 1992; Queensland Museum in Brisbane.

Diagnosis (♂; ♀ unknown): Position of the metatarsal I trichobothrium in 0.43, epigaster weakly sclerotized, pedipalpus: Figs 219–220.

Description (♂):
Measurements (in mm): Body length 3.8, prosoma: length 1.8, width 1.55; leg I: Femur 1.7, patella 0.55, tibia 1.6, metatarsus 1.6, tarsus 0.85, tibia IV 1.2.
Colour: Prosoma and legs red orange brown (the colour remains unchanged in alcohol for 15 years), opisthosoma dorsally and laterally medium gray, ventrally and dorsally-medially light grey.
Prosoma (figs. 212–215, photos 241–243) oval, not rugose, with few anterior long hairs, a single hair between the anterior median eyes, fovea bipartite, eyes of medium size, posterior row straight, posterior median eyes separated by more than their diameter, anterior median eyes not larger than the laterals, posterior stridulatory files absent but an undivided field of short stridulatory picks exists. Clypeus long, bearing an almost globular outgrowth which bears longer dorsal hairs; I did not find secretory pores. Basal cheliceral articles small; furrow: Anterior margin with 3 teeth, posterior margin with a single tiny tooth, labium wider than long, fused to the sternum, gnathocoxae distally wide. Sternum long, small elongated between coxae IV. – Legs fairly long and slender, hairs fairly distinct, order I/IV/II/III. Two thin and long dorsal patellar bristles, all tibiae bear a long and thin (hair-shaped) bristle in the basal half. Paired tarsal claws with long teeth, unpaired claw distinctly smaller (fig. 216). Metatarsus I–III bear a trichobothrium, its position on I is in 0.43. Tarsal organ large, its position on I in 0.35. Comb of tarsus IV well developed, "teeth" of the hairs short. – Opisthosoma (figs. 212–213) fairly long, not elongated beyond spinnerets, dorsally with longer hairs, soft, epigaster not stronger sclerotized, anteriorly with a single pair of bent and thickened stridulatory spines; a pair of paired epiandrous gland spigots exists (fig. 217); colulus (fig. 218) of medium size, bearing a pair of long hairs, spinnerets stout. – Pedipalpus (figs. 219–220, photos 243–244): Articles fairly stout, patellar and tibial bristles absent, tibia with a dorsal trichobothrium, cymbium not modified, paracymbium in a transitional – partly ectal retrodistal, and partly (more) internal – position, strongly sclerotized and hook-shaped, bulbus prominent, theridiid tegular apophysis apically bipartite, embolus long and thin, in its natural position hidden by the long functional conductor.

Relationships: See above.

Distribution: E-Australia (Queensland, Lamington National Park near Brisbane).

4. PHORONCIDIINAE

Phoroncidiinae are small to tiny, heavily armoured spiders in which the eye region is overhanging the clypeus in both sexes (photo 251) and usually humps or spines exist on a high opisthosoma which usually is overhanging the clypeus (figs. 221, 223, 226 photos 245f). The subfamily has a mainly tropical distribution. No taxon has been described from Eocene Baltic amber or other previous geological periods to species level up to now. Specimens of *Ulesanis* L. KOCH 1872 (and the subfamily Phoroncidiinae) are rare in Baltic amber; I found only 22 of these conspicuous spiders (5 species) among ca. 100 000 specimens. In respect to the high percentage of females (18%) among the spiders in Baltic amber – in contrast e. g. to fossil Enoplognathinae and Pholcommatinae – I conclude that these fossil spiders may have been dwellers of higher strata of the vegetation, and that their rareness is a result of their preference of tropical regions (resp. warm localities) similar e. g. to the Borboropactidae, Deinopidae and Tetrablemmidae as well as most Dipluridae in the Baltic amber forest. (We have to consider that – due to their unusual body shape or large size – the striking fossil females of these families cannot easily be overlooked).

According to the rareness of the fossil members of *Ulesanis* on the one hand, and the relatively high frequence of pairs – 1x 2♂, 2x 1♂1♀ in the same piece of amber on the other hand – I do not want to exclude that these spiders have been kleptoparasites or – more likely in my opinion – social living spiders. Spider's threads near to some of the fossil spiders originate probably from other spiders (their hosts?). – Several spiders in the same piece in Baltic amber in fairly RARE species are also known from *Eohahnia* (Dictynidae: Hahniinae) and *Balticoroma* (Anapidae: Comarominae) besides the most frequent specimens of *Orchestina* (Oonopidae: Orchestininae).

Diagnosis: Dorsal tibial bristles absent (at least in the fossil and extant European taxa), eye region usually strongly raised, projecting/overhanging the clypeus (figs. 223, 226, photos 245f) (*), opisthosoma voluminuous, high and strongly armoured, usually with dorsal humps and/or strong spines (stronger developed in the female) and scutate plates (they are usually tiny or small and impressed) which bear a hair near its centre or in an anterior position (figs. 223, 226–227) (*), most often overhanging the prosoma (figs. 221, 223, 226); prosomal-opisthosomal stridulatory organ reduced, comb of tarsus IV, and claw of the ♀-pedipalpus strongly reduced or probably even absent, colulus as if sunk in a hollow within a sclerotized ring around the spinnerets, reduced (fig. 232); it may be replaced by two hairs. Paracymbium large, its position distal retro-ectal (figs. 228–229).

(*) See *Praetereuryopis* n. gen. in Baltic amber (figs. 321–325, photos 295–297), a questionable genus of the subfamily Hadrotarsinae.

Further characters: Dwarfism: Most often minute spiders, body length less than 1mm to (rarely) 3mm, with a cryptic and probably mimetic shape (opisthosomal humps or spines – see KNOFLACH & PFALLER (2004: photos 4a–b): Resting position in *Ulesanis paradoxa* (sub *Phoroncidia*) –, eye field wide, legs usually quite stout (more slender in *Phoroncidia* s. str.), IV or I longest, tarsi and metatarsi more or less equal in length. Peculiar leg spines, bristles or bristle-shaped hairs may exist, which are quite unusual in the family Theridiidae: Strong ventral and and probasal bristles/spines on tibia and metatarsus I in the male of *P. aculeata* WESTWOOD, see WUNDERLICH (2004:1841, 1851, fig. 20), and a prolateral bristle-shaped hair of tarsus (!) II in both sexes in *Ulesanis paradoxa* (LUCAS) (fig. 222). Dorsal tibial bristle-shaped hairs may exist but NO BRISTLES OR SPINES IN THIS POSITION; the patellae may bear dorsal bristles. Anterior margin of the cheliceral furrow with at least one tooth, posterior margin smooth. The shape of the paracymbium is variable. Tegular teeth (sub "tegular spines" may exist, see AGNARSSON (2004: Figs. 62 A, D). In the fossil spiders existed probably a capture web, see below.

The **relationships** and the number of genera are unsure. – Due to the diagnostic characters Phoroncidiinae is not strongly related to the Pholcommatinae. According to AGNARSSON (2004: 617) *Stemmops* and *Cerocida* are related to the nominate genus *Phoroncidia* but their relationships are dubious in my opinion, see the remarks of ARNEDO (2004: 241). AGNARSSON (2004) did not want to exclude that *Phoroncidia* (s. l.) may be sister to Hadrotarsinae; the colulus is reduced in most taxa. In Hadrotarsinae exists small basal cheliceral articles, long fangs, and usually/basicly exist tibial bristles; small and impressed hair-bearing sclerotized opisthosomal plates evolved Hadrotarsinae apparently convergently rarely to the Phoroncidiinae: In *Praetereuryopis*, see below. – In the armoured members of the family Tetrablemmidae (superfamily Dysderoidea) (which may possess a similar shape) are leg bristles absent, too, but the lateral furrows of the opisthosoma possess sharp margins, and the genital structures are quite different and simple.

Distribution: Extant: Almost cosmopolitical, MAINLY TROPICAL; fossil: Eocene Baltic amber forest incl. the Bitterfeld deposit.

Remark on the splitting, and on the genera of the Phoroncidiinae: In my opinion the diverse genus *Phoroncidia* WESTWOOD 1835 has to split up again. LEVI & LEVI (1962: 26) lumped several genera; they listed ten synonyms and one questionable synonym (*Wibrada* KEYSERLING 1886) of *Phoroncidia*; all these taxa have to revise; some of them may be regarded as subgenera, others have to resurrect. I regard *Ulesanis* L. KOCH 1872 as a genus of its own besides *Phoroncidia* (**n. resurr**.), which includes all extant holarctic species, most species of the Northern Hemisphere, several species of SE-Asia as well as the fossil species in Baltic amber; see below (synonymy): The genus *Oronota*. In *Ulesanis* the anterior eye row (in anterior aspect) is procurved (straight in *Phoroncidia* s. str.), the legs are stout (photos) (longer and slender in *Phoroncidia* s. str., fig. 221), dorsal opisthosomal humps exist usually (fig. 223) (they are absent or different in *Phoroncidia*), and opisthosomal spines are absent (present and frequently long in *Phoroncidia* s. str., fig. 221). *Phoroncidia* is apparently a true pantropical genus which occurs mainly in the Southern Hemishere. It is remarkable that in the type species of *Phoroncidia* – *aculeata* WESTWOOD 1835, see WUNDERLICH (2004) – the legs are only fairly stout, in contrast to other congeneric species, the opisthosomal spines are short and tibia and metatarsus I bears strong ventral bristles/spines in the male.

Parts of ?capture webs – which may be not conspecific! – are preserved with the female paratype of *Ulesanis longicymbium* n. sp. and with the paratype of *U. antecessor* n. sp. (coll. KERNEGGER no. 296/2002).

***Ulesanis* L. KOCH 1872** (figs. 222–237, photos 251–258)

Synonymy: Certain authors regard *Oronota* SIMON 1871 as an older synonym of *Ulesanis* L. KOCH 1872 or a junior synonym of *Phoroncidia* WESTWOOD 1835, see UBICK et al. (2006: 311, 327), but I regard the type species of *Phoroncida* – see WUNDERLICH (2004: 1841, figs. 19–21 p. 1851) – as not congeneric with *Oronota* (*Epeira paradoxa* LUCAS 1846). Material of the generotype of *Ulesanis* – which may be not congeneric with the generotypes of *Oronota* – was not available to me. Therefore I do not want to exclude that the fossil species in Baltic amber – which I regard as congeneric with *paradoxa* – have to transfer to *Oronota* (together with the extant species of Europe), which may be a genus of its own.

Diagnosis, relationships, biolology and ecology of the fossil spiders: See above (“Remark on splitting...”). Position of the metatarsal trichobothria in the basal half, III bears a trichobothrium at least in *U. paradoxa* in which the pointed labium is seemingly bipartite, with a scinny triangular distal third.

Distribution: Most probably almost cosmopolitical. (I regard *U. personata* L. KOCH 1871 – Samoa – as congeneric with *paradoxa*). Europe species: Three extant species are known from the South of Europe, and five fossil species in Baltic amber; these are described below.

Key to the species of *Ulesanis* in Baltic amber:

Remark: The male is unknown in *U. frontprocera*, the female is unknown in *U. ovalis;* the conspecifity of the females is unsure in *longicymbium* and *parva*.

1 Body legth 1.1mm (♂) – 1.2 mm (♀), opisthosomal hump absent, ♂-pedipalpus: Fig. 237. . . . .<u>*parva*</u>

- Body length 1.4 – 2.2 mm (♀), opisthosomal hump usually existing (figs 226, 230) but absent in *ovalis* and indistinct in *antecessor* 2

2(1) ♀-opisthosoma with a very high dorsal hump in the anterior half (photo 253); ♂ unknown . . . . <u>*frontprocera*</u>

- ♂ ♀-opisthosoma with a lower dorsal opisthosomal hump in the distal half or in the middle or without hump 3

3(1) Opisthosoma wide and dorsally with a distinct posterior hump (fig. 230, 235, photos 254f) which is larger in the female. ♂-pedipalpus (figs. 233–234) with a very long cymbium; the embolus originates in a distal position . . . . <u>*longicymbium*</u>

- Opisthosoma with an indistinct dorsal hump near the middle (fig. 276) or without a hump. ♂-pedipalpus (figs. 228, 236): Cymbium short; the embolus originates near the pedipalpal tibia. 4

4(3) Opisthosoma with a quite indistinct dorsal hump (fig. 226). ♂-pedipalpus (figs. 228–229, photos 245f): Subtegulum small, the embolus originates near the pedipalpal tibia . . . . <u>*antecessor*</u>

- Opisthosoma globular, without humps. ♂-pedipalpus (fig. 236, photo 257): Subtegulum very large, the embolus originates retromarginally near the middle of the cymbial length; ♀ unknown . . . . <u>*ovalis*</u>

<u>Description of the species in Baltic amber</u>:

<u>Remark</u>: In the fossils I observed not a single case of leg autotomy or leg amputation.

Ulesanis antecessor **n. sp.** (figs. 226–229, photos 245–252)

Phoroncidia indet. sensu WUNDERLICH (1986: 42, 260, photo 336).

Material: 10♂1♀ in Baltic amber (some are probably not conspecific); 2♂, holotypus and paratypus in the same piece of amber, F1801/CJW; further paratypes: 4♂ F1801-

1803/CJW and 2109/CJW; 1♂+1♀ F1800/CJW; 1♂ coll. F. KERNEGGER in Hamburg no. 296/2002. – 5♂1♀, probably conspecific and not so well preserved spiders in Baltic amber: ♂: F1809-1811/CJW, 1♂ coll. F. KERNEGGER no. 320/94 (enclosed in artificial resin by F. K.), 1♂1♀ GPIUH coll. SCHEELE no. 43.

Preservation and syninclusions: The holotype is completely and well preserved in a piece which was slightly heated, a fissure runs longitudinally along the spider's body, a white emulsion is absent, a single thread of a dragline is present. The paratype in the same piece of amber is also completely and well preserved in a distance of 2.6 cm to the holotype, a white emulsion is absent, a double dragline below the spider is running forewards, two thin spider's threads are preserved below the spider; stellate hairs are absent. – 1♂1♀paratypes, F1800/CJW are preserved in a distance of 3 mm from each other in a piece of amber which was slightly heated. Both spiders are completely and fairly well preserved, remains of white emulsions are present. Few stellate hairs and 1/2 Diptera are also preserved. – F1802 is completely and well preserved, white emulsions exist on its ventral parts; few stellate hairs. – F1803 is completely preserved with some stellate hairs in a piece of amber which was heated, a white emulsion is absent. – F2109 is complete, most ventral parts are covered with a white emulsion, bubbles are preserved below the right pedipalpus, the structures of the right pedipalpus are well observable. Syninclusions are 2 tiny Acari, detritus, and remains of a spider at the surface of the piece of amber. – The male of the coll. KERNEGGER is well and completely preserved; its left side and parts of the ventral side are covered with a white emulsion, the right side of the opisthosoma has been injured, parts of its surface are lost. A dragline and thin spider's threads – of this spider? – are preserved behind the spider, few tiny ?sticky droplets are preserved, too.

Diagnosis: Opisthosoma dorsally with a low hump (covexity) in/behind the middle (fig. 226, photos 245f); ♂-pedipalpus (figs. 228–229): Embolus long, its origin near the pedipalpal tibia, the thick basal part bears a pointed outgrowth (peak) which is directed to the paracymbium.

Description:
Measurements (in mm): Body length ♂ 1.4–1.7, ♀ 2.2; prosomal length ♂ 0.6, ♀ ca. 0.8; leg I ♂ : Femur 0.5, patella 0.17, tibia 0.38, metatarsus 0.28, tarsus 0.29, tibia IV 0.38.
Colour mainly dark brown, opisthosoma "silvery".
Prosoma (figs. 226, photos 245f) about as wide as long and high, distinctly rugose; the wide eye region highly raised and overhanging the long clypeus. Eyes fairly large, anterior row procurved in frontal aspect, anterior median eyes largest, posterior median eyes separated by more than one diameter. Basal cheliceral articles short, fangs probably long and slender, gnathocoxae long converging about the free labium which is wider than long and not pointed apically, sternum rugose, separating the coxae IV by more than their diameter; the stridulatory area is hidden. – Legs (photos) stout, order I/IV/II/III, covered with hairs of medium length, tibiae distally slightly thickened, tarsi as long as metatarsi, patellae with 1/1 thin dorsal bristles, tibiae most probably without dorsal bristles but with bristle-shaped hairs, position of the trichobothrium on metatarsus I–II in 0.4–0.44, comb of tarsus IV weakly developed or absent. – Opisthosoma (photos, figs. 226–227) dorsally and ventrally completely heavily armoured, usually overhanging the prosoma, with a low dorsal hump in the middle or just behind the mid-

dle, lateral furrows and small hair-bearing impressed sclerotized plates; the position of the hair is in the anterior half; at least two pairs of small sigillae. A long, tube-shaped sclerotized ring exists around the stout spinnerets (photo), a small colulus bears a pair of hairs similar to U. *longicymbium* n. sp. (fig. 232). – Pedipalpus (figs. 228–229): Patella and tibia slightly longer than wide, cymbium fairly short, paracymbium large, in a retro-ectal position, apically with a hair-shaped structure, tegular apophysis large, embolus originating near the pedipalpal tibia, basal part with a peak, distal (slender) part long. – The female genital area is hidden.

Relationships: According to the structures of the bulbus *U. paradoxa* (LUCAS 1846) (extant, N-Africa and S-Europe, fig. 225) is more closely related than the remaining fossil species in Baltic amber (see the key and the figs.); the embolic outgrowth (peak) is shorter and the tegular apophysis is bent apically in *paradoxa*. *U. antecessor* may be very close to the ancestor of *U. paradoxa*.

Distribution: Eocene Baltic amber forest; the most frequent species in Baltic amber.

***Ulesanis frontprocera* n. sp.** (photo 253)

Material: Holotypus ♀ in Baltic amber, F1805/BB/AR/CJW.

Preservation and syninclusions: The spider is well and completely preserved in a piece of amber which was slightly heated; a white emulsion is absent, remains of stellate hairs are present.

Diagnosis (♀; ♂ unknown): Opisthosoma as high as long, with a large dorsal hump just in front of the middle (photo 253).

Description (♀):
Measurements (in mm): Body length 1.7, prosomal length ca. 0.8; leg I: Femur 0.58, tibia ca. 0.4, tibia IV ca. 0.4.
Colour, prosoma (photo 253) and legs as in *U. antecessor* n. sp., the mouth parts are hidden. Opisthosoma (photo 253) as high as long, with a large blunt dorsal hump just in front of the middle, and with 3 pairs of sigillae; the genital area is hidden.

Relationships: In the other fossil species the opisthosoma is distinctly lower.

Distribution: Eocene Baltic amber forest.

***Ulesanis longicymbium* n. sp.** (figs. 230–235, photos 254–256)

Material: 3♂1♀ in Baltic amber; holotypus F1807/BB/AR/CJW, paratypes: 1♂ F1808/BB/AR/CJW, 1♀ F1804/BB/AR/CJW, 1♂ GPIUH (coll. C. GRÖHN no. 2957).

Preservation and syninclusions: The holotype is completely and well preserved in a small piece of amber which was heated; body and legs are somewhat transparent and partly covered with a white emulsion. – Paratype F1808 is almost completely preserved at the margin of a piece of amber which was heated. The left part of the opisthosoma is injured and partly lost, the left patellae I and II were broken off with a piece of amber and are lost, the left part of the spider has been covered with nail polish by the present author; stellate hairs are absent. – Paratype F1804 is completely preserved in a piece of amber which was strongly heated, body and legs are slightly deformed, spider's threads connect numerous parts of detritus, 2 tiny Acari and few Collembola – which most probably were no prey of the spider – are also preserved. – The paratype from the GPIUH is well and completely preserved in a large piece of amber which was slightly heated.

Diagnosis: Opisthosoma (figs. 230, 235, photos 254f) wide, with a distinct dorsal hump in the distal half which is much larger in the female which I tentatively regard as conspecific with the male. ♂-pedipalpus (figs. 233–234): Cymbium very long, the long embolus originates in a distal position and is partly covered by the pedipalpal tibia.

Description:
Measurements (in mm): Body length 1.8 (♂) – 2.2 (♀), prosomal length 0.7 (♂) – 0.8 (♀); leg I (holotype): Femur 0.7, patella 0.3, tibia 0.5, metatarsus 0.4, tarsus ca. 0.37, tibia IC ca. 0.47; ♀: Tibia I 0.5, tibia IV 0.6; opisthosoma ♂ holotype: Length 1.25, width 1.3, hight 0.9, ♀: Length 1.8, hight incl. hump 1.8, width ca. 1.5.
Colour – the spider was heated – brown as in *U. antecessor*.
The shape of the ♂-prosoma (fig. 230) is similar to *U. antecessor* n. sp., the labium is pointed apically, the colulus is well observable and bears a pair of tiny hairs (fig. 232), the anterior margin of the opisthosoma is straight, it bears dorsally ca. 8 pairs of sigillae (♂ from the GPIUH). The position of the metatarsal trichobothrium is unknown. The deformed ♀-prosoma and legs are not well preserved; the strongly armoured opisthosoma bears dorsally a distal hump which is larger in the female. At least in the female tibia IV is longer than I. Pedipalpus (see above) with short patella and tibia; the basal part of the embolus bears a pointed outgrowth.

Relationships: See the key. The opisthosoma is more narrow and the cymbium is shorter in the remaining fossil species.

Distribution: Eocene Baltic amber forest.

Ulesanis ovalis n. sp. (fig. 236, photos 257–258)

Material: 2♂ in Baltic amber: Holotypus from the Bitterfeld deposit, F1805/BB/AR/CJW, paratypes coll. F. KERNEGGER in Hamburg no. 299/2002. The piece of amber has been embedded in artificial resin by F. KERNEGGER.

Preservation and syninclusions: The holotype is completely and only fairly well preserved at the margin of a small piece of amber which was slightly heated. Most parts of the spider are hidden by fissures and white emulsions but the ventral side of the bulbus of the left pedipalpus is well observable. – The paratype of the coll. KERNEGGER is completely preserved, mainly the ventral and left sides are covered with a white emulsion. Also preserved is a spider's thread in contact to remains of a larger insect on which some hyphae were growing.

Diagnosis (♂; ♀ unknown): Opisthosoma almost globular, without a hump. Pedipalpus (fig. 236) with a large tegulum and a thin embolus which originates in a retromarginal position in the middle of the cymbial length.

Description (♂):
Measurements (in mm): Body length 1.4–1.6, prosoma: Length ca. 0.6, width ca. 0.5, height 0.6; leg I: Femur 0.5, patella 0.2, tibia 0.35, metatarsus 0.29, tarsus 0.28, tibia IV 0.33.
Colour, prosoma and legs – as far as visible – as in *U. antecessor* n. sp. The opisthosoma is almost globular, humps are absent. The position of the metatarsal trichobothrium is as in *antecessor*. – Pedipalpus (fig. 236; see above) with stout articles, patella slightly longer than wide, tibia about as long as wide, the tegular apophysis is long and claw-shaped bent at its end.

Relationships: See the key. *U. parva* is smaller, the shape of its embolus is different.

Distribution: Eocene Baltic amber forest, incl. the Bitterfeld deposit.

Ulesanis parva n. sp. (fig. 237)

Material in Baltic amber: Holotypus ♂ from the Bitterfeld deposit, coll. EICHMANN No. AR-41; later most probably stored in the GPIUH; 1♀ paratype F1812/BB/AR/ CJW.

Preservation and syninclusions: The holotype is completely and fairly well preserved in an orange piece of amber which was heated, partly hidden by fissures; a white emulsion is absent. The spider was injured: The opisthosoma is depressed from the left side. Three small pieces of bark, few stellate hairs, 2 Diptera and a beetle (Staphylinidae) are also preserved. – The paratype is is completely preserved in a piece of amber which was heated, the cephalic part, the genital area and the opisthosomal dorsal-anterior parts are hidden by a white emulsion, a short remain of a dragline and few Collembola are also preserved.

Diagnosis: Opisthosomal hump absent, smallest Phoroncidiidae in Baltic amber, body length 1.1 (♂) – 1.2 (♀) mm; ♂-pedipalpus: Fig. 237.

Description:
Measurements (in mm): Body length ♂ 1.1, ♀ 1.2, prosomal length ♂ ca 0.33, ♀ ca 0.45; leg I (♂): Femur 0.44, patella ca. 0.11, tibia ca. 0.22, metatarsus 0.18, tarsus 0.2; ♀-leg I: Tibia 0.3, metatarsus 0.22, tarsus 0.26.
Colour of the spider which was heated: Prosoma and legs dark brown, opisthosoma medium to dark grey brown.
Prosoma and legs quite similar to *U. antecessor* n. sp., the anterior eye row is slightly procurved, position of the metatarsal trichobothrium unknown, opisthosoma without a dorsal hump, with ca. 10 dorsal sigillae in the male, with numerous tiny plates which bear a hair in the middle.
♂-pedipalpus (fig. 237) (see above) with stout articles. ♀-pedipalpus slender.

Relationships: See the key*. U. parva* is the smallest known fossil species of the genus; an opisthosomal hump is also absent in *U. ovalis* n. sp.

Distribution: Eocene Baltic amber incl. the Bitterfeld deposit (holotype).

5. HADROTARSINAE (= Dipoeninae, Euryopinae)

Most taxa of this subfamily occur in the tropics. Specimens of the genus *Lasaeola* in the wide sense are frequent in Baltic amber and other fossil resins; I saw thousands. The male prosoma is most often very high in these spiders and bears frequently strong dorsal furrows (sexual dimorphism, photos, figs. 256, 258, 242, photos 259f). Members of other genera – *Euryopis* and the peculiar *Praetereuryopis* – are quite rare in Baltic amber.

Diagnosis: Basal cheliceral articles usually small to very small (smaller in the male sex (figs. 256, 292, 310, 321), rarely larger like in some species of *Coscinida* (fig. 327), cheliceral margins usually without teeth, fangs usually long and slender (fig. 305) but rarely short (fig. 297), gnathocoxae strongly converging (figs. 247, 259), tarsus I frequently distally (+/- ventrally) bearing +/- grouped and flat-tipped sensory hairs – see AGNARSSON (2004) – which may be similar to a scopula (fig. 316) (absent e. g. in some fossil taxa in Baltic amber, and in *Coscinida*). Peculiar shape of the hairs of the comb of tarsus IV, usually modified female pedipalpal claw, prosomal-opisthosomal stridulatory organ (posterior prosomal files) absent, two pairs of receptacula seminis (figs. 302, 304, 332) (few exceptions), capture web reduced or absent; mainly ant eaters.

Further characters: Prosoma usually as wide as long, not seldom with strong dorsal furrows in the male (fig. 242) and high to very high (photos 264, 273), eye field usually narrow, and anterior median eyes usually largest (fig. 242), but anterior median eyes small e. g. in *Coscinida* (figs. 328, 483), and eye field wide e. g. in the fossil ?*Euryopis araneoides* n. sp. (fig. 307), cheliceral promargin usually smooth, but e. g. in *Coscinida asiatica* with a tooth, labium triangular or wider than long (figs. 247, 259) – both characters in contrast to AGNARSSON (2004: 26), who studied the characters of this (sub)family only superficially in few taxa –, leg IV most often longer than I, the (anterior male) tarsi may be thickened, anterior median spinnerets sclerotized medially and with files in numerous taxa, colulus very variable, reduced or even absent (e. g. in *Coscinida*), frequently with a pair of hairs (figs. 238–239), paracymbium in an internal (hidden) position (e. g. fig. 330). Very rarely bears tibia III 2 dorsal bristles.

Remarks: (1) According to my observations in fossil and extant spiders a triangular labium is not a synapomorphy of the Hadrotarsinae, see above, contra AGNARSSON (2004: Fig. 5A). (2) Variability in the chaetotaxy: Intrageneric variability: See the genera *Euryopis* and *Lasaeola*; intraspecific variability: See *Coscinida*. The intrafamiliar variability is extremely high, see the tab. below. (3) The median apophysis can be reduced or even absent within the same genus, within *Euryopis* and *Lasaeola* s. l. – e. g. in “*Emertonella*” and “*Trigonobothrys*” –, similar to the genus *Micaria* WESTRING 1851 (Gnaphosidae), and other spider genera. (In my opinion it is not forcible to create a new genus solely based on a reduced or absent or lost structure, see below: *Euryopis* and *Lasaeola*). (4) Most often exists a short embolus, but e. g. in *Lasaeola dunbari* (PETRUNKEVITCH) (extinct) and in *Dipoena nipponica* YOSHIDA (extant) exists a long(er) embolus. (5) Subgenera may be justified in *Dipoena, Euryopis* and *Lasaeola* like in *Lepthyphantes* MENGE (Linyphiidae); see below, and the paper no. 13, “Different views of the taxonomy...” in this volume.

The relationships are unsure, see Phoroncidiinae and Episininae (questionable relationships). As discussed above the Hadrotarsidae is surely not the basal branch of the family Theridiidae, contra AGNARSSON (2004). On the other hand AGNARSSON (2004: 468) did not exclude “relationships” (convergences?) of the Hadrotarsinae to the Phoroncidiinae; see *Praetereuryopis phoroncidoides* n. gen. n. sp. below. In certain species of *Pholcomma* (Pholcommatinae) exist two pairs of receptacula seminis as in the Hadrotarsinae.

Distribution: Extant: Cosmopolitical, fossil in Tertiary ambers.

Comparison of characters of extant and fossil palaeartic genera (s. l.) of the Hadrotarsinae (*Coscinida* is excluded, see below):

structure	*Dipoena* s.l.	*Lasaeola* s.l.	*Euryopis* s.l. and *Praetereuryopis* (♂)
shape of the opisthosoma	usually as wide as long (♀)	oval (fig. 256)	usually +/- flattened and triangular, tapering posteriorly (photos, fig. 307)
dorsal opisthosomal cuticula	soft	usually soft, rarely scutate and/or with sigillae	usually hardened or scutate, frequently with sigillae (figs. 307, 321)
sequence of the dorsal tibial bristles	2/2/1/2 (long)	very variable, rarely none	very variable, rarely none
structures of the bulbus	complicated, the median apophysis may sticks out	usually complicated, rarely without median apophysis (e.g. “Trigonobothrys”)	simple; the median apophysis may be reduced or absent
vulva	two pairs of receptacula seminis connected by a sclerotized structure	two pairs of receptacula seminis	two pairs of receptacula seminis in the European taxa

Remarks on the genus ***Coscinida*** SIMON 1895 (fossil and extant):

Figs. 326a–d, 327–332, photo 350.

Diagnosis: Colulus and hairs in its position absent, eyes (figs. 326a–b, 327–328) in a compact group (posterior medians largest, anterior medians smallest), clypeus distinctly concave below the eyes, and protruding ventrally, sequence of the tibial bristles apparently quite variable and most often 2/2/1/2 or 2/2/1/1 (in *tibialis*), less frequently 1/1/1/1 (fig. 326c), paracymbium (fig. 330) in an internal position, hook-shaped, epigyne (fig. 331) with a longitudinal furrow.

Further characters (based on *asiatica* and *tibialis*): Leg IV longer than I, position of the metatarsal trichobothrium in the middle or in the distal half, anterior tarsi not thickened, comb of tarsus IV indistinct, coxae IV widely spaced, prosomal-opisthosomal stridulatory organ absent, prosoma narrow anteriorly (more or less pointed) (figs. 326a, 328), basal cheliceral articles small to large (figs. 326a, 327), fangs long and slender, cheliceral margin: Posterior row smooth, anterior margin smooth or with a single small tooth (*asiatica*), labium wider than long (not triangular); claw of the female pedipalpus large, strongly bent, and bearing long teeth, the anterior spinnerets medially more or less sclerotized, ♂-epigaster not protruding, two pairs of receptacula seminis (fig. 332), ♂-pedipalpus as in figs. 326d, 329–330).

Type species: *Coscinida tibialis* SIMON 1895.

Relationships: *Coscinida* is an untypical member of the Hadrotarsinae: The chelicerae are fairly large in *tibialis* (fig. 327) in contrast to the Hadrotarsinae (but see fig. 326a!), peculiar hairs of tarsus I are absent (in *tibialis* and in *asiatica*) in contrast to most Hadrotarsinae, a colulus and hairs in its position are absent like in the Theridiinae, but they are also absent in several (further) Hadrotarsinae. In *Coscinida* exists two pairs of receptacula seminis, and leg IV is longer than I as in the Hadrotarsinae and in contrast to the Theridiinae, the hooked paracymbium is different from the hooded theridiine one; the chaetotaxy, the position of the eyes, the shape of the clypeus and the claw of the ♀-pedipalpus (e. g.) are all different from the Theridiinae, and (more) like the Hadrotarsinae. – LEVI & LEVI (1962: 48) did not want to exclude that *Coscinida* and *Stemmops* may be synonyms, but in *Stemmops* exists only a single pair of receptacula seminis and a small colulus which bears a pair of hairs; leg bristles are most probably absent.

Distribution: Northern Hemisphere: Africa, SE-Asia, Mediterranean, and green-houses in Europe (*C. tibialis*). – Fossils of *Coscinida* are unknown.

Remarks on the genus ***Dipoena*** THORELL 1869 (extant):

According to the characters of the table above probably only few of the chinese species which were published sub *Dipoena* by ZHU MINGSHENG (1998) are true members of the genus *Dipoena* s. str. – congeneric with its type species *melanogaster* (C. L. KOCH 1837) –; at least some of them may well be members of *Lasaeola*; *pelorosa* ZHU MINGSHENG may be an exception – a species of *Euryopis*? A revised – differentiating – diagnosis of this genus is needed, which should be based on the type species, which has a special shape of the ♀-opisthosoma, the median apophysis, and probably of the claw of the ♀-pedipalpus. According to their characters I regard *D. punctisparsa* YAGINUMA 1967 and probably *D. nipponica* YOSHIDA 2002 as true members of *Dipoena*. – Fossils of *Dipoena* are unknown, erroneous determinations exist.

Key to the hadrotarsine genera in Baltic amber:

Remark: Further – extant – genera in Europe are *Coscinida* and *Dipoena*: See the tab. and the remarks above; they are represented here only by *C. tibialis* and *D. melanogaster*.

1 Opisthosoma strongly armoured, and bearing tiny plates (scuta) in rows which bear marginal hairs (figs. 321– 322) (quite similar to the Phoroncidiinae but the opisthosoma is flattened and tibial bristles are present). A single species . . . . Praetereuryopis

- Opisthosoma not strongly armoured, tiny scuta in rows are absent (e.g. fig. 286). . 2

2(1) Dorsal aspect of the opisthosoma more or less triangular (pointing behind) (fig. 307) (not in *nexus*), and usually flattened (fig. 310) (similar to *Praetereuryopis*); ♂: Prosoma without dorsal furrows, cymbium broadly attached to the pedipalpal tibia (figs. 313–314) . . . . *Euryopis* s. l.

- Opisthosoma not triangular or flattened (figs. 256, 258); ♂: Prosoma in numerous species with dorsal furrows (figs. 246, 264), cymbium not so broadly attached to the pedipalpal tibia (figs. 243, 267) . . . . *Lasaeola* s. l.

Lasaeola SIMON 1881

Lasaeola is one of the most diverse/successful and – in the geological sense – within the Tertiary long-existing spider genera at all. Its origin and early diversification happened at least 50 million years ago; during the Tertiary the genus had a wide range, e.g. in Europe (e. g. in the Eocene Baltic amber) and Central America (e. g. in the Miocene Dominican amber) (from the Southern Hemisphere larger deposits of true amber are unknown but species of *Lasaeola* are preserved in (younger) copal of Madagascar).
According to their high frequence in amber – and the ecology of extant relatives – these spiders lived in higher strata of the vegetation, e. g. on trees, and they fed on ants (photo 31) as most congeneric spiders of today live and feed on. Parasitic mites were – rarely – attached to their body already 50 million years ago. At least some females camouflaged their egg sac. Males of numerous species look and looked quite different from females of the same species: There is a striking sexual dimorphism – see the photos 259f and the drawings –: The prosoma is very high in the males of numerous species, and bears strong dorsal furrows (photos 259f, figs. 242, 292). Most males do – regarding their prosomal shape – not look like a "normal" spider, and the high and dorsally folded prosoma may be a hint to the existence of a mimetic camouflage of these spiders, see below, the paragraph "Mimesis".

Synonyms of *Lasaeola*, subgenera and species-groups (see LEVI & LEVI (1962) and the remark above). I regard *Lasaeola* in a wide sense: *Deliana* KEYSERLING 1886 and probably *Dipoenata* WUNDERLICH 1988 may be members of *Lasaeola* s. str., but a revision of the subgenera is urgently needed. *Dipoenata*, *Nactodipoena* PETRUNKEVITCH 1942 – see WUNDERLICH (1988: 148) –, *Trigonobothrys* SIMON 1889 (**n. stat.**) and *Yaginumena* YOSHIDA 2002 are downgraded here to subgenus rank (**n. stat**.). *Umfila* KEYSERLING 1886 (S-America) may be regarded as a further subgenus of *Lasaeola*. – *Micriphantes* sensu KOCH & BERENDT (1858, part.) is *Lasaeola* s. l., see below. – Most species in Baltic amber are members of the *communis*-group which may be related to *castrata* of the *nigra* species-group (subgenus *Yaginumena* YOSHIDA); *dunbari (Nactodipoena), sigillata* and probably *furca* are members of other subgenera. – *Eodipoena* PETRUNKEVITCH 1942: See *Eomysmena* PETRUNKEVITCH 1942.

Remarks: (1) I suppose that strong dorsal furrows of the male prosoma exist only in *Lasaeola* (compare ?*Euryopis araneoides* n. sp. (fig. 307); this idea has to verify or falsify in the future. On the other hand it seems unsure which of those species are members of *Lasaeola* in which such furrows are absent. In some species as *Lasaeola* ("*Dipoena*") *prona* (MENGE 1868) exist only weak furrows. The taxonomical value of the – very variable – sequence of the tibial bristles is unsure, too. – (2) In my opinion at present it would make sense to regard some taxa – e. g. *Nactodipoena* PETRUNKEVITCH (the extinct *dunbari*-group), *Trigonobothrys* SIMON 1889 and *Yaginumena* YOSHIDA 2002 as subgenera of *Lasaeola* until a worldwide revision will be carried out which is urgently needed. Apparently numerous convergences and probably reversals, too, exist in this diverse genus, so that it seems to be extremely difficult to provide an evident cladogram of the species-groups or subgenera.

Diagnosis of *Lasaeola* in a wide sense: Opisthosoma: Shape ovally, usually soft, in several species with sigilla (e. g. in the subgenus *Nactodipoena*), male prosoma very high, in numerous species almost cylindrical and with dorsal furrows (figs. 246, 258, 292, photos 259f).

Further characters and variability: Sequence of the tibial bristles most often 2/2/1/2, in *Dipoenata* (Dominican amber and certain extant species) 1/1/1/1, absent in the type species of *Lasaeola* (*prona*) and in *Yaginumena* – according to YOSHIDA (person. commun.) – at least in *castrata* and *mutilata*. Usually exists a pair of hairs of the colulus (fig. 238) but in *furca* n. sp. and *germanica* (KOCH & BERENDT 1854) exists (in all specimens?) only a single hair (fig. 271). The comb of bent hairs of tarsus IV may be indistinct. Anterior median eyes largest. A scutum of the male opisthosoma exists in certain species, e.g. in *gui* (ZHU MINGSHENG) and *nigromaculata* (YOSHIDA), a median apophysis is absent in certain species as in *nigromaculata* and *pelorosa* (ZHU MINGSHENG). In certain species the epigyne bears a scape, e. g. in the extinct species *Lasaeola communis* n. sp. (fig. 257) and related species.

Type species: *Pachydactylus pronus* MENGE 1868.

Relationships: See the tab. and key above.

A **questionable egg sac** is preserved within a piece of Baltic amber, F1680/BB/AR/CJW which was heated and contains 1♂1♀ and a subad. ♂ of *Lasaeola* sp. indet. The female is 2.9 mm long, her opisthosoma is broken off and empty, few black sclerotized remains of vulva structures are preserved. Also preserved are spider threads, a larger stamen, pollen grains, 3 ants (most probably prey of the spiders), 1 Acari, Diptera etc. as well as a structure which may be an egg sac of the female. It is darkened, 2.7 mm long and 1.3 mm wide and preserved 0.5mm behind the spider's opisthosoma; details are hard to recognize, there may be about 30 questionable eggs. Apparently remains of some spider threads are present on the eggs; furthermore there are numerous hyphae, some of them bear tiny sporangia.

Prey: (Mainly?) ants as in other Hadrotarsinae; see WUNDERLICH (2004: 95), *Lasaeola* sp. indet. (sub *Dipoena*). – Directly left hehind of a female of *Lasaeola* sp. indet. (F1677/BB/AR/CJW) in Baltic amber from the Bitterfeld deposit remains of 3 ants are preserved which are close together and loosely spun in in spider's threads and which most probably have been prey of the spider (photo 31). – Right in front of the male paratype of *L. latisulci* n. sp. (F1534/BB/AR/CJW) an ant is preserved which is ca 2.8mm long, not spun in and probably not injured; the dorsal part of the ant's head is cut off. – See also *Lasaeola communis* n. sp., paratypes with two ants, F1476/BB/AR/CJW and *Lasaeola* sp. indet. (F1680/BB/AR/CJW) (above, with a questionable egg sac). – In some fossil males the tarsi of leg I or II are missing and probably bitten off by ants, see below, *L. dunbari* (fig. 261, photo 9).

Mimesis. The conspicuous high prosoma (figs. 142f, photos 260f) with its dorsal folds of most male *Lasaeola* is unique in spiders; the prosoma is quite lower in the female sex and dorsal folds are absent (sexual dimorphy). The function of the high ♂-prosoma and its folds is unknown. I do not want to exclude a mimetic effect/function of the male prosoma, "imitating" small plant particles on twigs. But why is this modification absent in the female sex? See the paper no. 14 in this volume.

Distribution: Extant: Cosmopolitical (mainly tropical and subtropical); fossil: Tertiary: Miocene Dominican amber, Eocene European ambers: Baltic amber incl. the Bitterfeld deposit (most frequent are *germanica*, *communis* and *infulata*), and Ukrainean (Rovno) ambers (*L. germanica*); subfossil: Copal from Columbia, the Dominican Republic, and Madagascar.

Provisorical key to the palaearctic extant and fossil subgenera of *Lasaeola* (♂):

Remarks: The relationships of some species – like the fossil *Lasaeola furca* and *sigillata*, as well as some extant species which were published sub *Dipoena* by ZHU MING-SHENG – are unsure, and therefore they are not included in this key, see above and no. 4 in the key (remaining groups).

1 Median apophysis absent, embolus and conductor small; dorsal prosomal furrows present. – Extant, Madagascar (incl. in copal), and E-Asia. (= *excisa*-group). . . . . *Trigonobothrys*

- Median apophysis most often present; dorsal prosomal furrows present or absent. – Extant and fossil 2

2(1) Dorsal opisthosomal sigilla present (fig 258), dorsal prosomal furrows present (fig. 258), sequence of the dorsal tibial bristles 2/2/1/2, embolus long and bent almost semicircular (fig. 262). – Baltic amber (*dunbari* PETRUNKEVITCH) and probably extant in SE-Asia (*gui* ZHU) . . . . *Nactodipoena*

- different combination of characters 3

3(2) Seqence of the dorsal tibial bristles 2/2/1/2 (fig. 269), large tegulum, small subtegulum, conductor connected to the tegulum. Dorsal prosomal furrows present (fig. 246). – Extant and fossil in Baltic amber . . . . *L. communis*-group

- Sequence of the dorsal tibial bristles very variable: 2/2/1/2, 1/1/1/1 or tibial bristles absent. Dorsal prosomal furrows present or absent. 4

4(3) Dorsal tibial bristles absent, tegulum very large, conductor conjugated with the tegulum. No distinct dorsal prosomal furrows. – Extant, widely distributed (= *L. nigra*-group sensu LEVI (1953)) . . . . *Yaginumena*

- Sequence of the dorsal tibial bristles 1/1/1/1. Extant and Dominican amber . . . . *Dipoenata*, part. (see below)

- Dorsal tibial bristles present (sequence e. g. 2/2/1/2 in *testaceomarginata*) or absent (e.g. in *prona*), conductor not connected to the tegulum, distinct dorsal prosomal furrows present or absent. – Extant widely distributed and fossil in Baltic and Dominican amber . . . . *Lasaeola* s. str.and remaining subgenera

Key to the species of *Lasaeola* s. l. in Baltic amber (♂):

Remarks: (1) Members of smaller species possess usually smaller leg bristles. (2) Opisthosomal sigilla exist in *dunbari, larvaque* and *sigillata*. (3) Usually exists a pair of hairs of the colulus (fig. 241) but in *germanica* only a single hair (fig. 271). (4) The relationships of *furca* and *sigillata* are quite unsure. (5) *L. baltica* (MARUSIK & PENNEY 2005) (fig. 244) is not included in this key.

1 Prosoma usually posteriorly almost as high as anteriorly and with deep dorsal furrows (figs. 242, 258), photos), opisthosomal sigilla present in *dunbari* (fig. 258) 2

- Prosoma posteriorly usually distinctly lower than anteriorly, with a fovea but without dorsal furrows, opisthosomal sigilla most often present. 7

- Prosoma posteriorly distinctly lower than anteriorly (photo 259), with indistinct furrows in the posterior half, without opisthosomal sigillae. Pedipalpus: Fig. 245. . *bitterfeldensis*

2(1) Opisthosoma dorsally with very short hairs and with sclerotized sigilla (fig. 258), position of the metatarsal I–II trichobothria in ca. 0.5 (unique in the fossil species of *Lasaeola* of the Baltic amber forest), embolus quite long, originating in the basal half of the bulbus (fig. 262). . . . . *dunbari*

- Opisthosoma dorsally with short and long hairs, sigilla absent, position of the metatarsal I–II trichobothrium in 0.27–0.35, embolus short, originating in the distal half of the bulbus (figs. 250, 274) 3

3(2) Body length 2.3–2.6 mm. Cymbium distally bent (fig. 273), median apophysis in a more longitudinal position, with a very low ventral depression (figs. 274f)....*germanica*

- Body length 1.3–2.6 mm. Cymbium distally straight (fig. 248) 4

4(3) Body length (without the protruding clypeus and anterior median eyes) 1.3–1.8 mm, length of the tibial I bristles only 1–1 1/2 of the tibial diameters (fig. 281), pedipalpus: Figs. 282f. . . . . *infulata*

- Body length 1.7–2.6 mm, length of the tibial I bristles at least 2 tibial diameters . . . 5

5(4) Median apophysis with a deep depression which has a distinct median margin (figs. 252f) . . . . *communis*

- Median apophysis without a depression, median margin absent (figs. 243, 293). . . 6

6(5) Tegular apophysis sickle-shaped, with a basal-medial point (fig. 243) . . .*acumen*

- Tegular apophysis as in figs. 293–295 . . . . *latisulci*

7(1) Pedipalpal tibia longer than wide (fig. 299), bulbus as in figs. 298–299, opisthosomal sigilla absent . . . . *sexsaetosa*

- Pedipalpal tibia wider than long (fig.), opisthosomal sigilla absent or present 8

8(7) Tarsi about as long as metatarsi, opisthosomal sigilla distinct, pedipalpus as in fig. 301. . . . . *sigillata*

- Tarsi distinctly shorter than metatarsi, opisthosomal sigilla absent (*furca*) or indistinct (*larvaque*) 9

9(8) Opisthosomal sigilla absent, prosoma lower, bulbus with a furcate structure (figs. 267–268). . . . . *furca*

- Opisthosomal sigilla indistinct, prosoma higher, bulbus as in figs. 289f . . . . *larvaque*

Descriptions of the species in Baltic amber

Lasaeola acumen **n. sp.** (figs. 242–243)

Material: Holotypus ♂ in Baltic amber and a separated piece of amber F1494/BB/AR/THE/CJW.

Preservation and syninclusions: The spider is well and completely preserved, opisthosoma, sternum and some leg articles are ventrally covered with a white emulsion, a fissure is obliquely running through the body. In the separated piece of amber a Collembola, few stellate hairs and a longer branched plant's hair are preserved.

Diagnosis (♂; ♀ unknown): Prosoma high and almost cylindrical, with deep dorsal furrows in the posterior half (fig. 242). Pedipalpus (fig. 243):Tibia as in *germanica*, median apophysis large and without a ventral depression, tegular apophysis sickle-shaped, pointed medially-basally on the basal part of the embolus.

Description (♂):
Measurements (in mm): Body length 2.5, prosomal length and height above the coxae 1.1; leg I: Femur 1.15, patella 0.35, tibia 0.75, metatarsus 0.85, tarsus 0.43, tibia IV 0.68.
Colour: Prosoma and legs medium brown, opisthosoma yellow brown, legs not annulated.
Body and legs similar to L. *germanica* but the prosomal furrows are restricted to the posterior half (fig. 242). Position of the trichobothrium of metatarsus I in 0.3. Pedipalpus: See above.

Relationships: *L. latisulci* is most related, see the key.

Distribution: Eocene Baltic amber forest.

Lasaeola baltica (MARUSIK & PENNEY 2005) (**n. comb.**) (fig. 244)

2005 "*Euryopis*" *balticus* MARUSIK & PENNEY, Arthropoda Selecta (Special Issue No. 1, 2004): 211, figs. 19–20.

According to the strong dorsal prosomal folds *baltica* is a member of *Lasaeola*, probably of the *communis*-group. The body length is only 1.32 mm. There was no opportunity for me to get the loan of the holotype from the Palanga Amber Museum in Lithunia which may not be a scientific institution. The rough figure of the pedipalpus of the male holotype (fig. 244) shows a strongly sclerotized questionable sclerite which is unknown from other fossil species in Baltic amber – an artefact or an emulsion?

Distribution: Eocene Baltic amber forest.

***Lasaeola bitterfeldensis* n. sp.** (fig. 245, photo 259)

Material: Holotypus ♂ in Baltic amber from the Bitterfeld deposit, coll. H. GRABENHORST no. AR-102. The ♂ will most probably deposited in the GPIUH.

Preservation and syninclusions: The spider is fairly well preserved, prosoma and opisthosoma are somewhat deformed, the prosoma is retrofrontally depressed, the left legs III and IV are missing beyond their coxae by autotomy, the opisthosoma is covered with a thin white emulsion and partly by a bubble. A parasitic mite (Acari: Trombidiidae?) is preserved on the left side of the prosoma. The body of the mite is dorsoventrally distinctly flattened and was probably injured together with the spider. – Tiny chrystals of pyrite are also preserved in the small piece of amber but no stellate hairs.

Diagnosis (♂; ♀ unknown): Body length 1.45mm, prosoma oblique and low posteriorly (photo 259), with indistinct furrows in the posterior half, tibial bristles short as in *infulata*. Bulbus (fig. 245): Conductor slender, distinctly bent, tegular apophysis thick.

Description (♂):
Measurements (in mm): Body length 1.45, prosomal length ca. 0.6; leg I: Femur 0.95, patella 0.32, tibia 0.65, metatarsus 0.72, tarsus 0.27, tibia IV 0.55.
Colour of body and legs medium to dark brown.
The prosoma is deformed, high, and probably as in the strongly related *L. infulata* n. sp. but the furrows may be less distinct. Legs and opisthosoma are as in *infulata*. Position of the trichobothrium of metatarsus I in 0.35. The basal bristle of tibia I is as long as the tibial diameter. Pedipalpus: See above.

Relationships: *L. infulata* (KOCH & BERENDT 1854) is most related, see the key.

The mite (see above): Body length 0.57mm, mouth parts hidden by a white emulsion between the anterior femora.

Distribution: Eocene Baltic amber forest, the Bitterfeld deposit.

***Lasaeola communis* n. sp.** (figs. 246–257, photos 260–262)

Material (in Baltic amber), **preservation and syninclusions**: 24♂ and 3♀; holotypus F1472/ BB/AR/CJW: It is completely preserved, the opisthosoma and ventral parts of the prosoma are covered with a white emulsion, a large fissure in the amber is present above and right behind the spider; few stellate hairs. – Paratypes: F1473 – 1489/BB/ AR/ CJW, F1491-1492/ BB/AR/CJW. F1480 has a deformed prosoma, F1483 and a male from the coll. GRABENHORST AR-83 come from the Bitterfeld deposit, F1476 contains 2♂1♀ and 2 ants as well as the abdomen of an ant (Dolichoderinae) as prey, body length ca. 2.3mm, one of them is spun in in threads and parts of their antennae are broken off, the second ant is strongly dissected. Furthermore a midge, a mite and stellate hairs are preserved in the same piece of amber. – F1481 contains 1♂ and 1♀ which were separated from the same piece of amber, F1488 contains 2♂, F1541 1♂1♀, F1511 1♂; 1♂ is preserved in a piece of amber from the Zool. Mus. Copenhagen, "coll. B. MARTENSEN 2-9 (1965)". – With the male F1478 a dragline is preserved, with F1484 a spider's thread.

Remark: According to the variable shape of the tegular apophysis and the medial outgrowth of the median apophysis I do not want to exclude that some specimens may be members of subspecies or even species of their own.

Diagnosis: ♂ with a high and almost cylindrical prosoma and deep dorsal furrows (fig. 246). Pedipalpus (figs. 248f): Median apophysis usually in a more horizontal position but variable, with a deep depression and a distinct sharp medial margin. ♀: Prosomal profile oblique (fig. 256), epigyne (fig. 257) with a pointed scape and a large opening which is wider than long.

Description (♂):
Measurements (in mm): Body length 1.7–2.3, prosomal length (without the protruding eye field) and width about 0.7, height above coxae about 0.6–0.7; leg I: Femur ca. 0.7–0.8, patella ca. 0.25–0.3, tibia ca. 0.55–0.58, metatarsus ca. 0.52–0.55, tarsus ca.0.3–0.35, tibia IV ca.0.45–0.55, basal bristle of tibia I ca. 0.2.
Colour, body and legs as in *germanica*; leg bristles long, opisthosomal sigillae absent. The labium is wide, the gnathocoxae converging (fig. 247). – Pedipalpus (figs. 248f) (see also above): Patella, tibia and embolus similar to *germanica* but cymbium distally not bent, subtegulum very large, tegular apophysis distally more or less funnel-shaped and apically widened (recognizable in peculiar positions only), the medial outgrowth of the large median apophysis has a variable shape.
♀: F1476: Body length 2.1mm, prosomal length 0.9mm, length of tibia I 0.45mm, the opisthosoma is almost globular. The leg bristles and the dorsal opisthosomal hairs are longer than in the male, the prosoma (fig. 256) has an oblique profile and is high anteriorly, without dorsal furrows, the pedipalpal claw is sickle-shaped strongly bent, the epigyne (fig. 257) has a large opening which is wider than long and a pointed scape; the opening may be closed by a plug, the posterior margin is strongly sclerotized.

Relationships: See *germanica* PETRUNKEVITCH 1958 and the key. According to the embolus and the conductor *communis* and related fossil species are similar to the *nigra*-group (see above) but in the *nigra*-group (= *Yaginumena* YOSHIDA) the tegulum is distinctly larger than the subtegulum, the median apophysis is small and tibial bristles are absent.

Prey: The spiders feed on ants as other members of this subfamily, see above (F1476).

Distribution: Eocene Baltic amber forest incl. the Bitterfeld deposit. *Communis* is the second frequent species of *Lasaeola* in Baltic amber and one of the most frequent spider species in this kind of amber.

Lasaeola (Nactodipoena) dunbari (PETRUNKEVITCH 1942) (figs. 258–265, photos 9, 263–265)

1942 *Nactodipoena dunbari* PETRUNKEVITCH,– Trans. Connect. Acad. Arts Sci., 34: 276, figs. 475–483, 627 (♂) (**n. comb.**)

Material: 12♂ 3♀ in Baltic amber, male holotypus of *Nactodipoena dunbari*, Peabody Museum of the Yale University no. 2 (26724); 7♂ F1515-1520/BB/AR/CJW, F1567/BB/AR/CJW, 3♀ F1521-1523/BB/AR/CJW, 1♂ F1917/BB/AR/CJW; 2♂ Mus. Ziemi Warszawa, nos. 14936 and 15467; 1♂ GPIUH.

Remark: The female was unknown up to now.

Preservation: Holotype: The spider – incl. the bulbus structures – is darkened probably by heating, distal parts of the right leg IV are cut off, the opisthosoma is ventrally covered by a white emulsion, the opisthosomal sigilla – overlooked by PETRUNKEVITCH in his original description – are visible. The amber piece is “mounted in clarite” on a slide (PETRUNKEVITCH (1958: 102)). – With the female F1522 and the male F1519 draglines are preserved, with F1518 the larva of an Aphidina.

Diagnosis: Opisthosoma (figs. 258) with two pairs of dorsal sigilla and short hairs, forrows of the high ♂-prosoma as in *communis*. Position of the metatarsal I trichobothrium in almost 0.5 (!). ♂-pedipalpus (figs. 262–263) with a long and bent embolus. ♀-prosoma as in fig. 264, epigyne (fig. 265) with a deep and wide pit.

Description:
Measurements (in mm): ♂: Body length 2.0–2.1, prosomal length and width 0.7; leg I: Femur ca. 0.6, patella 0.33, tibia 0.44, metatarsus 0.38, tarsus 0.28, tibia IV 0.5, dorsal opisthosomal hairs up to 0.1. – ♀: Body length 2.2–2.5, prosomal length ca. 0.9; leg I: Femur ca. 0.6, tibia 0.44, tibia IV 0.55.
Colour: Prosoma and legs medium brown, opisthosoma light brown, legs not annulated, opisthosomal sigillae dark brown.

Prosoma (figs. 258, 264) very high, with distinct dorsal furrows in the male as in *communis* n. sp. which are absent in the female (sexual dimorphism like in numerous other congeneric species); the prosoma is much lower in the posterior half. Posterior eye row procurved, anterior median eyes largest, posterior median eyes separated by their diameter. Clypeus very long, basal cheliceral articles quite short, labium (fig. 259) almost triangular, gnathocoxae converging; the sternum separated the coxae IV by almost their diameter. – Legs stout, femora IV thickened, with long tibial and patellar bristles (fig. 260) and long metatarsal trichobothria, their position on I in almost 0.5. The comb of tarsus IV is not well developed. In the male F1515 the left tarsus I is amputated and apparently the stump is healed. – Opisthosoma (figs. 258, 264) oval, more or less protruding above the spinnerets in the females, dorsally with short hairs which are placed on tiny sclerotized plates (more distinct in the male) and two pairs of sclerotized sigilla; the tiny colulus bears a pair of hairs (F1521). – Epigyne: See above. ♂-pedipalpus (figs. 262–263): Patella about as wide as long, tibia wider than long, tegular apophysis large and bent, embolus long and bent, originating in the basal half.

Relationships: *Dunbari* is the type species of *Nactodipoena* PETRUNKEVITCH 1942 which I downgrade to subgenus rank. It is characterized by: A long embolus, the position of the metatarsal trichobothrium in the middle of the article, and the existence of opisthosomal sigilla (which also exist in other species, see *larvaque*). A long embolus is also present in the – related? – *Lasaeola gui* (ZHU MINGSHENG) (sub *Dipoena*, extant, China) in which the epigynal opening is small and dorsal furrows of the ♂-prosoma are probably absent. I regard *gui* as a member of *Lasaeola* (**n. comb**.) and a questionable member of the subgenus *Nactodipoena*.

Distribution: Eocene Baltic amber forest (unknown from the Bitterfeld deposit).

?*Lasaeola furca* **n. sp**. (figs. 266–269, photo 266)

Material: Holotypus ♂ in Baltic amber and a separated piece of amber, F1557/BB/ AR/ THE/CJW.

Preservation and syninclusions: The spider is well and completely preserved, parts of the opisthosoma are ventrally and at the left side covered with a white emulsion, a bubble is preserved between the basal parts of the left femora III and IV. Left below the spider – in another layer – are two Nematoda: Rhabditida preserved, their body length is 0.35 mm. In the larger separated piece of amber are a fly, a further Rhabditida and some stellate hairs preserved.

Diagnosis (♂; ♀ unknown): Body length only 1.5mm, prosoma without dorsal furrows, posterior eye row slightly recurved (fig. 266), bulbus with a bifurcate structure which may be the embolus (figs. 267–268).

Description (♂):
Measurements (in mm): Body length 1.5, prosoma: Length 0.7, width ca. 0.65; leg I:

Femur 0.85, patella 0.3, tibia 0.7, metatarsus 0.63, tarsus 0.44, tibia IV 0.6, femur of the pedipalpus 0.25.
Colour: Prosoma and legs medium brown, opisthosoma yellow brown.
Prosoma as wide as long, only fairly high, without dorsal furrows, distinctly lower posteriorly, with a distinct but short thoracal fissure. Posterior eye row slightly recurved (fig. 226), anterior median eyes not distinctly the largest, posterior median eyes separated by one diameter, basal cheliceral articles small. – Legs fairly long, with longer hairs, tibial bristles long and thin, sequence 2/2/1/2, position of the basal tibial I bristle in 0.13, position of the trichobothrium on metatarsus I in 0.32, no trichobothrium on metatarsus IV. – Opisthosoma egg-shaped, more scarcely covered with hairs of medium length, sigilla absent, epigaster hidden, the small colulus bears a single hair. – Pedipalpus (figs. 267–268): Femur fairly stout, patella and tibia about as wide as long, tegulum large; a bifurcate structure may be the embolus.

Relationships: According to the small chelicerae *furca* is a member of the Hadrotarsinae; it may be a member of *Lasaeola*. A strongly related species is unknown to me; a furcate apophysis of the bulbus is unusual in *Lasaeola*. The opisthosoma is egg-shaped in contrast to *Euryopis*, the cymbium is unmodified.

Distribution: Eocene Baltic amber forest.

Lasaeola germanica (PETRUNKEVITCH 1958) (figs. 269–279, photos 267–268)

1958 *Eodipoena germanica* PETRUNKEVITCH, – Trans. Connect. Acad. Arts Sci., 41: 181, figs. 149–162 (♂).

Material: 11♂ in Baltic amber: Holotypus Zool. Mus. Humboldt University Berlin; 3♂ Mus. Ziemi in Warczawa, nos. 10598, 10997 and 19967; 7♂ F1466-F1471/BB/AR/CJW and F1566/BB/AR/CJW.

Preservation of the holotype: The spider is completely preserved but darkened probably by heating; therefore the structures of the bulbus are difficult to recognize. Most parts of the right side of the spider are covered with a white emulsion.

Syninclusions: With the male F1470 a beetle (Elateridae) is preserved, with the male F1467 some thin threads of spider's silk.

Diagnosis (♂; ♀ unknown): Prosoma (photo 267) very high, almost cylindrical, with deep dorsal furrows as in *communis* n. sp. Pedipalpus (figs. 272–279, photo 268): Patella raised, cymbium long and bent distally (fig. 273), conductor even longer than the tip of the cymbium, median apophysis in an almost longitudinal position, with a low depression only, tegular apophysis S-shaped, embolus with an oval base and a stout distal part, wide apart from the small tegulum. – Further character: Tibial bristles (fig. 269) very long.

Description (♂):
Measurements (in mm): Body length 2.3–2.6, prosomal length and width 1.0–1.1, height above coxae 0.75–0.85; leg I: Femur 1.3, patella 0.43, tibia 0.9, metatarsus 1.0, tarsus 0.45, tibia IV 0.85; length of the dorsal opisthosomal hairs usually up to 0.35, rarely up to 0.45; basal cheliceral articles 0.3; pedipalpus: Tibia: Length 0.3, width 0.2, patella: Length 0.2, width 0.18.
Colour: Prosoma and legs medium brown, legs most probably not annulated, opisthosoma light brown.
Prosoma (photo 267) high, as wide as long, with long dorsal hairs and a long clypeus, four pairs of deep dorsal furrows which reach the anterior third, a deep pit is present behind the middle. Eyes fairly small, fild narrow, anterior median largest, posterior row slightly procurved, posterior median eyes separated by almost one diameter, lateral eyes touching. A pair of small hairs is present in the field of the median eyes behind the anterior median eyes. Basal cheliceral articles very short, fangs long and slender. – Legs of medium length, order I/IV/II/III, with longer hairs and long bristles on patellae and tibiae, sequence on the tibiae 2/2/1/2, tibia I twice as long as its basal bristle (fig. 269). Trichobothria short and indistinct, their position on I–II in ca. 0.3, absent on IV. Hairs of the tarsal comb almost straight. – Opisthosoma (photo 267) oval, scarcely covered with short and long hairs. One pair of epiandrous gland spigots (fig. 270). Spinnerets stout. The small colulus bears only a single hair (F1468, F1470, fig. 271). – Pedipalpus (see above): Patella dorsally-distally distinctly elevated, bearing 3 dorsal bristles and hairs, tibia twice as wide as long. The median apophysis bears four furrows, median apophysis and subtegulum have a scaly structure. The distal hair of the conductor (e.g. in F1470, fig. 275) may be absent, but it is distinct in the holotype; the furrows of the median apophysis may be quite indistinct (e.g. in F1466). With some hesitation I regard certain differences in the bulbus structures of different specimens as intraspecific variation. The length of the median apophysis is very variable, longest in F1466, shortest in F1566, see the figs. I do not want to exclude that there are different subspecies or even species of their own within the material in question.

Relationships: *L. communis* n. sp. is smaller, its pedipalpal patella is usually also raised, the furrows of the ♂-prosoma are identical, but bulbus and conductor are shorter, the distal part of the cymbium is not bent, the tegular apophysis is funnel-shaped, the position of the median apophysis is more horizontally, it is deeply depressed at the side which is directed to the tegular apophysis and possesses an additional edge.

Distribution: Eocene Baltic amber forest (not known from the Bitterfeld deposit up to now), and Ukrainean (Rovno) amber: Musem Kiev no. K-4300 (the determination is a bit questionable).

Lasaeola infulata (KOCH & BERENDT 1854) (figs. 280–287, photos 269–272)

1854 *Micriphantes infulatus* KOCH & BERENDT,– Die im Bernstein befindlichen Organischen Reste der Vorwelt, <u>1</u> (2) : 40, t. 4, fig. 29 (♂).

?1950 *Nactodipoena infulata*, – PETRUNKEVITCH, Bull Mus. Comp. Zool., 103: 284–285, figs. 51–54, 189–190 (♂ "hypotype").

Material: Numerous males and few females in Baltic amber; holotypus PMHUB, coll. BERENDT no. 7328 (see below); 2♂ from the Bitterfeld deposit, coll. GRABENHORST nos. AR4 and AR155; 3♂ Museum Ziemi in Warszawa nos. 14935, 14937 and probably 19356 (this specimen may be not conspecific); 1♂ from the Bitterfeld deposit, PMHUB, A583; 1♂ from the Bitterfeld deposit coll. M. KUTSCHER; 3♂ F1528-1530/CJW; 1♂ F1814/BB/AR/ CJW; 25♂ incl. 1♂ from the Bitterfeld deposit F1561/CJW; 5♂ F1528-1530, 1532/CJW, F1671/CJW; 3♀ which are probably conspecific F1537-1539/CJW; 9 probably conspecific ♂ F1562/CJW.

Remarks: (1) The female was unknown up to now. – (2) The type series which I studied contained two males in two pieces of amber. The original description was based on a single male but in a footnote MENGE in KOCH & BERENDT (1854: 40) noted that a second male was added after the description. According to the original description of *infulata* I selected the male which is preserved in a more flat piece of amber as the holotype. The second male – in a thicker piece of amber – is congeneric but not conspecific, its prosomal furrow are less distinct, cymbium and bulbus are longer and more narrow, I gave it the provisional no. 7328a). – (3) The male of Nactodipoena infulata sensu PETRUNKEVITCH 1950 may be *infulata* but – according to PETRUNKEVITCH – the bulbus structures are not well visible. – (4) The variability of the bulbus structures indicates that there may be several subspecies or even species in the material which was studied by me (see above and the figs.).

Syninclusions: Draglines exist with several males, e.g. F1530/CJW; with the male F83/ CJW, few mammals hairs with the female F1537/CJW, two ants with one of the 25 males F1561/CJW.

Diagnosis: Dorsal furrows of the ♂-prosoma limited to the posterior half as in *L. acumen* n. sp. (fig. 242), bristles of leg I only about as long as the tibial diameter, conductor bent distally (fig. 282).

Description (♂ ; ♀ see below):
Measurements (in mm): Body length (without the protruding clypeus) 1.3–1.8 (holotype 1.5), ♂ Mus. Ziemi no. 14937 1.8, prosomal length 0.7–0.8; leg I: Femur 0.92, patella 0.29, tibia 0.65, metatarsus 0.62, tarsus 0.32, tibia IV 0.55.
Prosoma (fig. 280, 286) high, with distinct furrows in the posterior half similar to *L. acumen* n. sp. (fig. 242), eye field relatively wide, the anterior median eyes are largest and protruding, posterior row procurved, posterior median eyes separated by ca. 2/3 diameters. – Legs (fig. 281) fairly short, I longest, order I/IV/II/III, sequence of the tibial bristles 2/2/1/2, tibial bristles I–II only 1–1 1/2 tibial diameters long, position of the basal tibial bristle in ca. 0.23, position of the metatarsal I trichobothrium in ca. 0.3. – Opisthosoma (fig. 280, 286) almost egg-shaped, dorsal hairs up to 0.22 mm long, sigilla are absent. – Pedipalpus (figs. 282–285): Patella short, with 2 dorsal bristles, tibia slightly wider than long, conductor distally distinctly bent (only slightly bent in the questionable conspecific male of the Mus. Ziemi no. 19356) (fig. 285), slender distal part of the embolus shorter than the almost globular basal part, tegular apophysis slen-

der, with a probasal outgrowth in the probably conspecific male. There is an additional branch of the tegular apophysis (or the conductor?).

♀ (probably conspecific): Apparently F1537 and 1538 have an egg-bearing opisthosoma, a well visible epigyne exists only in F1539: Measurements (in mm): Body length 2.15, 2.25 and 1.5, prosomal length 0.8, 0.7 and 0.6; leg I (F1539): Femur ca. 0.85, patella 0.25, tibia 0.5, metatarsus + tarsus 0.9. – Prosoma (fig. 286) high, with long dorsal hairs and a long and concave clypeus. Anterior median eyes largest, posterior eye row straight to slightly procurved, dorsal furrows absent (sexual dimorphism), basal cheliceral articles small. Legs stout, the basal bristle of tibia I is not much longer than the diameter of the tibia, position of the metatarsal I trichobothrium in ca. 0.3 (F1539). Opisthosoma (fig. 286) almost globular, covered with short hairs. Epigyne (fig. 287) a small pit which is slightly wider than long (0.05 mm wide) and surrounded by a sclerotized ring.

Relationships: See the key. The shape of the prosoma is e.g. as in *L. communis* which is larger, and the bristles of tibia I are longer.

Distribution: Eocene Baltic amber forest incl. the Bitterfeld deposit. *Infulata* is the most frequent species of *Lasaeola* in Baltic amber and one of the most frequent spider species in this kind of amber.

***Lasaeola larvaque* n. sp.** (figs. 288–291, photos 273–274)

Material: 2♂ in Baltic amber, holotypus and a separated piece of amber F1551/BB/AR/THE/CJW, paratypus F1552/BB/AR/THE/CJW.

Preservation and syninclusions: Holotype: The spider is well and completely preserved, the ventral side is covered with a white emulsion and bubbles. Few thin spiders threads are preserved near the spider, particles of detritus and stellate hairs are present in the separated piece of amber. – Paratype: The spider is fairly well preserved, parts of the left leg II (mainly the tibia) and parts of the left tarsus I are cut off, the opisthosoma and some other parts of the spider are covered with a white emulsion. The small larva of an insect – body length 0.35 mm – is preserved left of the spider, two stellate hairs are present left above the spider.

Diagnosis (♂; ♀ unknown): Small spiders, body length 1.4–1.6 mm. Shape of the prosoma and leg bristles as in *L. sexsaetosa* n. sp. (fig. 296), indistinct opisthosomal sigilla are present. Pedipalpus (figs. 288–291): Tibia wider than long, conductor bent distally, basal part of the embolus large.

Description (♂):
Measurements (in mm): Body length 1.4–1.6, prosoma: Length 0.7–0.8, height ca. 0.65, tibia I 0.55–0.65, tibia IV 0.5–0.55, metatarsus/tarsus of the holotype 0.5/0.32.
Colour: Prosoma and legs medium to dark brown, opisthosoma yellow grey.

Prosoma and legs – as far as visible – as in *L. sexsaetosa*. Opisthosoma oval, soft, with 2 pairs of indistinct sigilla in the holotype. Pedipalpus (fig.288–291) Patella about as wide as long, tibia wider than long, conductor slender, bent distally, basal part of the embolus large, distal part hidden.

Relationships: The shape of the prosoma is as in *L. sexsaetosa* n. sp. (fig. 296) but the pedipalpal tibia is longer than wide in *sexsaetosa* and the bulbus structures are different.

Distribution: Eocene Baltic amber forest.

***Lasaeola latisulci* n. sp.** (figs. 292–295, photos 275–276)

Material: 9 or 10♂ in Baltic amber: Holotypus (left side without white emulsion) and paratypus in the same piece of amber, F1493/BB/AR/THE/CJW; paratypes: F1495-1498/CJW and F1533-1534/CJW (1497-1498 from the Bitterfeld deposit), F1542/ CJW, 1♂ from the Bitterfeld deposit, coll. GRABENHORST no. AR-87; a probably conspecific ♂: F169/CJW.

Preservation and syninclusions: Holotype: The spider is well and completely preserved in a piece which was heated, and is anteriorly in contact with the ventral side of another male (paratype) which is partly covered with a white emulsion, and is completely preserved, too. In the same piece of amber – most often in a different layer – are 1 Acari, 1 Trichoptera, 4 Diptera and few stellate hairs preserved. – Paratypes: F1495: Most parts are covered with a white emulsion, parts of the left leg I are cut off. – F1496 is almost completely preserved, the right side is covered with a white emulsion, few stellate hairs are present. – F1497: The amber piece was heated; it contains stellate hairs and numerous tiny insect's larvae. The spider is well and almost completely preserved, the left tarsus II is missing, the dorsal side of the body is covered with a white emulsion. – F1498 is well preserved, the right side is covered with a white emulsion, parts of the left legs and the left opisthosomal side are cut off, numerous particles of excrement (of termites?) are preserved around the spider. – F1533: The right leg I is missing beyond the coxa, the right leg III is shortened and deformed, probably a regenerate, the body is strongly covered with a white emulsion. – F1534/CJW: The spider is completely preserved in a heated piece of amber, a white emulsion is absent. Just in front of the right tarsus I an ant (body length 2.5 mm) is preserved as a prey of the spider. Furthermore preserved are small particles of detritus and a Diptera which is darkened and deformed. – Near the male F169/CJW several tiny – phoretic? – Nematoda: Rhabditida and a dragline are preserved.

Diagnosis (♂; ♀ unknown): Prosoma (fig. 292) high as in *L. germanica*, dorsal furrows distinct, most often limited to the posterior half. Pedipalpus (figs. 293–295): Tegular apophysis almost straight, median apophysis blunt, without a depression.

Description (♂):
Measurements (in mm): Body length 2.5–2.7, prosomal length ca. 1.1 (–1.3); leg I: Femur 1.4, patella 0.43, tibia 1.2, metatarsus 1.35, tarsus 0.52, tibia IV 1.1.
Colour, legs and opisthosoma as in *L. germanica*, prosoma similar to *L. acumen* n. sp.; the eyes are small, the prosoma very high. Position of the metatarsal I trichobothrium in ca. 0.3. Pedipalpus (see above), embolus of medium size. The shape of the tegular apophysis is quite variable.

Relationships: *L. acumen* n. sp. is most related, see the key.

Distribution: Eocene Baltic amber forest incl. the Bitterfeld deposit.

***Lasaeola sexsaetosa* n. sp**. (figs. 296–300, photos 276–279)

Material: 16♂ in Baltic amber: Holotypus F1543/BB/AR/THE/CJW; paratypes: 11♂ 1 juv. ♂ F1544-F1550/BB/AR/THE/CJW (2♂ 1 juv. ♂ in F1545), F1697/CJW, F1744/CJW and two separated pieces of amber; 2♂ Mus. Ziemi in Warszawa, nos. 3246 and 8584.

Preservation and syninclusions: The holotype is well and almost completely preserved, only retrolateral parts of the left patella and tibia I are cut off, a weak white emulsion exist anteriorly on the prosoma. Few thin spiders threads are preserved in a layer below the spider; stellate hairs are absent. – F1544 (photo 278) is fairly well preserved without a white emulsion, the right legs I–III and the left leg III are missing beyond their coxae by autotomy, the left leg IV is broken off beyond the coxa and lying near the opisthosoma, blood has come out from these stumps, the blood is covered with a white emulsion. In the same layer left of the spider but not in contanct some thin threads of the almost two-dimensional part of a spider's web without droplets are preserved (fig. 300), and a small Diptera. Remains of a tiny insect and stellate hairs are preserved near the threads. – F1545: A two-lined dragline is preserved with one of the adult males. – F1547: The spider is well and almost completely preserved, only the right leg II is missing beyond the coxa. A Trichoptera – body length ca. 5.5 mm – is preserved in another layer near to and left of the spider. – F1548 is well preserved in a 2.7 cm long piece of amber, the right leg III of the spider is missing beyond the coxa by autotomy. – F1549: On the left side of the prosoma a large "bubble" is preserved which bears furrows. – With the well preserved male F1697 the larger part of a capture web including sticky droplets and a mite (body length 0.38 mm) are preserved. – F1744 is completely and well preserved, the autotomized left leg I is situated behind/beyond the spider.

Diagnosis (♂; ♀ unknown): Prosoma (fig. 296) anteriorly distinctly higher than posteriorly, with an almost circular fovea, basal cheliceral articles with about six pairs of anterior bristle-shaped hairs, bristles of tibia I only about as long as the tibial diameter as in *infulata* (fig. 281). Pedipalpus (figs. 298–299): Tibia distinctly longer than wide, conductor quite slender, distal part of the embolus short.

Description (♂):
Measurements (in mm): Body length 1.4–1.7, prosoma: length 0.7–0.8, width ca. 0.75; leg I: Femur 1.1–1.3, patella 0.33, tibia 0.85, metatarsus 1.0, tarsus 0.45. Variability in F1547: Right/left metatarsus + tarsus I: 1.0/0.8 and 0.45/0.4; width of the eye field 0.38.
Colour: Prosoma and legs medium brown, opisthosoma yellow grey, legs not annulated.
Prosoma (figs. 296–297) anteriorly high, posteriorly low, with an almost circular fovea. A pair of small hairs is present in the field of the median eyes. Eye field narrow, posterior row straight, posterior median eyes separated by less than their diameter, anterior medians largest, clypeus very long, basal cheliceral articles small, anteriorly bearing six pairs of bristle-shaped hairs as well as a few short hairs. Labium triangular, gnathocoxae converging. – Legs fairly long, bristles on tibia I about as long as the tibial diameter, their sequence on the tibiae 2/2/1/2. Metatarsus IV without a trichobothrium, position of the metatarsal I trichobothrium in ca. 0.3. – Opisthosoma oval, covered mainly with short hairs, longer hairs are present dorsally in the anterior half. A prosomal-opisthosomal stridulatory organ is absent. Epigaster not sclerotized, spinnerets stout. The colulus is small (F1550), its hairs are not visible. Tracheal spiracle small and near to the spinnerets. Epiandrous gland spigots in two groups. – Pedipalpus: See above; patella and tibia are longer than wide.

Relationships: See the key.

Distribution: Eocene Baltic amber forest (not known from the Bitterfeld deposit).

?*Lasaeola sigillata* n. sp. (fig. 301)

Material: Holotypus ♂ in Baltic amber from the Bitterfeld deposit and two separated pieces of amber, coll. GRABENHORST no. AR-164.

Preservation and syninclusions: The original piece of amber was separated in three parts by the author: A small piece contains the holotype, the second a female of the genus *Lasaeola* (sp. indet. 3, see below) which – according to the larger size, the short tarsi and the long bristles of tibial I – is not conspecific with the holotype; the third piece is the largest and contains numerous particles of detritus as well as particles of insects excrement and stellate hairs. – The holotype is fairly well preserved, the right leg II is missing beyond the coxa by autotomy, some parts are covered with a white emulsion, the opisthosoma is injured and deformed, it is dorsally distinctly depressed. A larger spiny arthropod is preserved directly left above the spider, and – in a different layer – a small Collembola.

Diagnosis (♂; ♀ unknown): Tarsi about as long as the metatarsi, the prosoma is high but bears no dorsal furrows, bristles of tibia I weak, opisthosoma with two pairs of dorsal sigilla. Pedipalpus (fig. 301) with the tibia slightly wider than long.

Remark: I do not want to exclude that the female of ?*Lasaeola* sp. indet. 2 (see below) may be conspecific.

Description (♂):
Measurements (in mm): Body length 1.6, prosomal length 0.7; leg I: Femur 0.57, patella 0.3, tibia 0.5, metatarsus 0.36, tarsus 0.37, diameter of an opisthosomal sigillum 0.7.
Colour: Prosoma and legs medium brown, opisthosoma yellow brown.
Prosoma anteriorly high, posteriorly low, fovea low, posterior eye row probably slightly recurved. – Legs fairly short, III relatively long, tarsi about as long as metatarsi, sequence of the tibial bristles 2/2/1/2, patellar and tibial bristles weak, the basal tibial I bristle is only slightly longer than the tibial diamer. Position of the metatarsal I trichobothrium in 0.31. – Opisthosoma (it is deformed), oval (not triangular), dorsally with short hairs and a pair of large sigilla in front of the middle; a second smaller pair may be present in a more posterior position. – Pedipalpus (fig. 301; see above): Patella about as long as wide, tibia longer than wide, tegulum and subtegulum small, the median apophysis is apparently not visible.

Relationships: See the key. According the the structures of the bulbus I do not know a strongly related species and I regard the relationships as unsure.

Distribution: Eocene Baltic amber forest, Bitterfeld deposit.

Lasaeola sp. indet . 1

Eodipoena oculata sensu PETRUNKEVITCH 1958: 177–178, figs. 137–139.

Material: 1♀ in Baltic amber, Geol. Miner. Mus. Copenhagen no. 9983.

The epigyne of this female has a sclerotized scapus which is wider than in *L. communis* n. sp. A pair of large receptacula seminis is recognizable but not a second pair. The relationships are unsure. Similar is the scapus of the female F1651/CJW in which the epigyne is partly covered by a white emulsion and in *Lasaeola* sp. indet. 4 (see below).

?Lasaeola sp. indet. 2 (fig. 303, photo 287)

Material: 1♀ in Baltic amber from the Bitterfeld deposit, coll. H. GRABENHORST no. AR-156.

Description:
Measurements (in mm): Body length 1.45, prosoma: Length ca. 0.65, width ca. 0.68; leg I: Femur ca. 0.63, patella 0.28, tibia 0.45, metatarsus 0.4, tarsus 0.4, femur IV 0.63, tibia IV 0.53, diameter of the opisthosomal sigilla: Anteriors 0.03, posteriors 0.095, width of the epigynal opening 0.04.
Eyes large, posterior row procurved, posterior medians separated by their radius, clypeus long, basal cheliceral articles small, legs only fairly long, tibial bristles long and thin, their sequence 2/2/1/2. Position of the trichobothrium on metatarsi II left/right articles 0.31/0.37. The hairs of the tarsal IV comb are almost straight. The pedipalpal claw is hidden. The opisthosoma is dorsally strongly depressed in an unnatural way, as wide as long, dorsally scarcely covered with hairs which are up to 0.16 mm long and with two pairs of distinct sigilla, the posterior pair is much larger (see above) and slightly wider separated than the anterior pair. The epigyne (fig. 303) is a very small pit far in front of the epigastral furrow and has a pair of tiny openings.

Relationships: According to the body size and the long tarsi I will not exclude that this female is conspecific with ?*L. sigillata* n. sp.

Lasaeola **sp. indet. 3**

Material: 1♀ in Baltic amber from the Bitterfeld deposit, coll. GRABENHORST no. AR-164 a). A piece of amber containing this female was separated from the piece which contained the holotype of ?*Lasaeola sigillata* n. sp. (see above); according to the larger size, the short tarsi and the long tibial bristles the male holotype of *sigillata* may be not conspecific with this female.

Preservation: The female is well preserved and observable from the ventral side; the left anterior leg is missing beyond the coxa by autotomy.

Description:
Measurements (in mm): Body length 2.5, prosoma length 1.1; leg I: Tibia 0.7, metatarsus 0.8, tarsus 0.45.
The colulus bears a single hair. The epigynal pit is oval, apparently filled with a plug which is 0.11 mm wide and 0.08 mm long. Between this opening and the epigaster is a fold, a second deep fold exist in front of the pit. A scapus is not recognizable.

The **relationships** are unsure.

Lasaeola sp. indet. 4

Material: 1♂ and 1♀ were separated from the same piece of Baltic amber, F1663/ BB/ AR/CJW.

The male is 1.9 mm long, the shape of his high prosoma is similar to *L. communis*, only parts of the right pedipalpus are visible, other parts are covered with a white emulsion. The female is 2.6 mm long, visible from the ventral side, with regard to her very large opisthosoma she may be egg-bearing. The epigyne has a low pit and a scapus which is shorter and wider than in *communis* but longer tan in *L*. sp. 1.

Lasaeola sp. indet. (photo 281)

Material: 1♂ in Baltic amber, F83/BB/AR/CJW near a male of *Hyptiotes* sp. indet.

The body length is 1.5 mm, the right side and the pedipalpi are partly covered with a white emulsion, the prosoma is only fairly high, the anterior median eyes are large and widely spaced, the legs are slender, the sequence of the thin tibial bristles is 2/2/1/2, the shape of the opisthosoma is oval, pedipalpal patella and tibia are short, a sperm duct is well recognizable.

Lasaeola sp. indet. (fig. 304, photo 287)

Material: 1♀ in Baltic amber, coll. C. GRÖHN no. 5910, later probably GPIUH.

The spider is preserved in a piece of amber which was heated, a white emulsion is almost completely absent, the body length of the spider is 2.4 mm, its prosomal length is ca. 1 mm. The large opisthosoma may indicate that this is an egg-bearing female. The prosoma is high, the fangs are long and slender, the pedipalpal claw is tiny, the combs are hidden, the position of the metatarsal III trichobothrium is in 0.38, the epigyne (fig. 304, photo 287) is partly transparent, has frontally a large pit, a sclerotized posterior margin, a scape is absent. There are two pairs of receptacula seminis, the posterior pair is almost touching, larger and less distinct than the anterior pair. – Probably this is the unknown female of one of the species which are described above.

Lasaeola sp. indet. (fig. 302, photos 282–283)

Material: 1♀ in Baltic amber, F1675/BB/AR/CJW.

Preservation and syninclusions: The spider is preserved in a yellow piece of amber which was not heated, consists of several layers and has a size of 3 x 2.3 x 1 cm. The spider's right leg IV is missing beyond the coxa by autotomy, most legs and eyes are hidden by a layer of the fossil resin. After the spider was captured by the sticky resin it was covered three times by the resin: At first the left half of the body and most legs were coated and later on a flood of resin covered most parts of the opisthosoma and the legs except the patella of the right leg I. The right third of the opisthosoma was standing out from the resin into the air and was cut off a bit irregularly. The opisthosoma was then almost completely emptied in a clear way – probably by an insect – and finally filled with the fossil resin (which covered also the small parts of opisthosomal cuticula which were standing out), so that hair bases and remains of (a) the spinnerets (with two bubbles), (b) the petiolus, and (c) the structures of the vulva (fig. 302, photos 282–283) are preserved in a excellent condition. So we can look inside the opisthosoma of this spider in a unique way and can recognize the structures of the vulva in the dorsal aspect. – Also preserved in this piece of amber are 3 Diptera, 1 Collembola, 1 Acari, few particles of detritus, stellate hairs, and numerous small bubbles in a different layer of the spider.

Description of the spider: Body length ca. 2.5 mm, prosoma high, wrinkles are absent, anterior median eyes largest, legs fairly stout, bristles long, opisthosoma oval, dorsal scutum absent, a single dorsal sigillum is preserved just behind the opisthosomal middle; epigyne difficult to recognize, strongly sclerotized and largely standing out. The "hardened" (partly sclerotized?) structures of the vulva are recognizable in an oblique dorsal aspect from the right side: There are two pairs of receptacula seminis, the posterior pair is larger and covered with thin air bubbles (fig. 302, photos 282–283), the distinct introductory ducts are recognizable between the receptacula, and end separately in a large opening.

Relationships: According to the shape of the opisthosoma, the opisthosomal sigilla, the large anterior median eyes and the two pairs of receptacula seminis I suppose that this female is most probably one of the frequent members of the genus *Lasaeola*. It seems impossible to find out her conspecifity with one of the species which are known from the male sex only.

Distribution: Eocene Baltic amber forest.

Lasaeola sp. indet. (fig. 305)

Material: 1♀ in Baltic amber, F1681/BB/AR/CJW.

Body length 2.8 mm, prosoma high, fangs long and slender (fig. 305), epigyne strongly sclerotized and with a protruding scape.

Further material of *Lasaeola* sp. indet.: See above (prey). The epigyne of the female F1677/CJW has a protruding scape. A strongly sclerotized epigyne exists in the female F1898/ CJW.

Euryopis **MENGE 1868 s. l.**

Synonymy of extant genera: Due to the chaetotaxy and the shape of the opisthosoma I regard *Eurypoena* WUNDERLICH 1992 as a subgenus of *Euryopis* MENGE 1868 s. l.. *Emertonella* BRYANT 1945 may be a junior synonym of *Euryopis*, see LEVI & LEVI (1962) or a further subgenus.

Diagnosis: Opisthosoma usually more or less triangular and pointed posteriorly (fig. 307), frequently hardened or even scutate dorsally, and with sigilla (fig. 307); pedipalpus (figs. 308, 313–314, 317, 324–325): Tibia broadly attached to the cymbium, cymbium distally frequently modified by projection(s), median apophysis broadly attached to the tegulum – see LEVI & LEVI (1962: 39) – or absent (e. g. probably in some of the fossil species in Baltic amber, and in the extant species of "*Emertonella*").

Further characters: At least tarsus I is usually more or less thickened (fig. 316); at least in some species the legs are spread out mediograde in the resting position – observed by the present author on the bark of trees in Australia – similar to *Oecobius* (Oecobiidae), see the right legs of *Euryopis bitterfeldensis* n. sp., specimen of the coll. GRABENHORST (photo 288) which shows a "mediograde" position.

Remarks on the conspicuous intrageneric variability: (1) A colulus which bears two hairs exists in certain extant species like *E. laeta* (fig. 306) and *quinquenotata*; in other species the colulus is strongly reduced or even absent, hairs may be absent, too, e. g. in the extant *flavomaculata* and in certain japanese species. (2) The chaetotaxy is also very variable within this genus: The sequence of the dorsal tibial bristles is frequently 2/2/1/2 (e. g. in the extinct *E. nexus* n. sp. as well as in the extant *E. episinoides* and in the japanese species), absent (in "*Eurypoena*"), 2/2/1/1 in *flavomaculata* and *laeta,* and rarely 2/2/2/2 (in *quinquenotata*, in which metatarsus IV bears a trichobothrium and which may be a (sub)genus of its own). (3) A trichobothrium on metatarsus IV is usually absent but existing in *quinqueguttata* and "*Eurypoena*". (4) In few species exist only a single pair of receptacula seminis, e. g. in "*Eurypoena*".

Related genera in Baltic amber: See the key above and the unique extinct new genus *Praetereuryopis* in which the tarsi are slender. ?*Euryopis araneoidea* may be the member of an unnamed genus.

Distribution: Extant: Cosmopolitical; fossil: Eocene Baltic amber forest, mainly the Bitterfeld deposit; with the exceptions of the holotype of *E. araneoides* – which is probably not a member of *Euryopis* –, the holotype of *E. nexus* n. sp., and one of four specimens of *E. bitterfeldensis* which originates most probably from the Kaliningrad deposit. – First fossil record of the genus.

“*Euryopis*” *balticus* MARUSIK & PENNEY 2005: See above: *Lasaeola baltica*.

Key to the species of *Praetereuryopis* and *Euryopis* in Baltic amber (♂):

Remark: See also the ratio of the length of tarsus to metatarsus in the different taxa.

1 Eye field as wide as the prosoma in this region (fig. 307), prosoma with a low depression crossover, pedipalpus: Figs. 308–309 . . . . ?*E. araneoides*

- Eye field narrow, prosoma without a depression, pedipalpus different. 2

2(1) Prosomal profile concave, eye field distinctly raised and protruding (fig. 321), the opsithosoma bears small plates (figs. 321–323), pedipalpus as in figs. 324–325 . . . . *Praetereuryopis phoroncidoides*

- Prosomal profile convex and eye field not raised (fig. 310), pedipalpus different . . . 3

3(2) Pedipalpus (fig. 320): Cymbium with a thick apical spine and distal bristle-shaped hairs, tegulum with conspicuous sperm ducts . . . . *E. streyi*

- Pedipalpus (figs. 313–314): Cymbium without modifications, conspicuous tegular sperm ducts absent . . . . *E. bitterfeldensis*

- Pedipalpus (figs. 317–319): Cymbium without modifications, tegulum with conspicuous sperm ducts . . . . *E. nexus*

?***Euryopis araneoides* n. sp**. (figs. 307–309, photo 292)

Material: Holotypus ♂ in Baltic amber and a separated piece of amber, F1560/BB/AR/CJW.

Preservation and syninclusions: The spider is well and completely preserved in a yellow piece of amber; a dragline runs backwards from the anterior spinnerets, a large bubble is preserved under the mouth parts and the sternum, a white emulsion and stellate hairs are absent.

Diagnosis (♂): Eye field (fig. 307) as wide as the prosoma, prosoma high posteriorly, too, with a depression crossover and a small deep fovea. Pedipalpus (figs. 308–309): Cymbium unmodified, the thin distal part of the embolus is guided by a conductor.

Description (♂):
Measurements (in mm): Body length 1.7, prosoma: Length 0.83, width almost 0.8, hight above the coxae more than 0.35; leg I: Femur 0.75, patella 0.29, tibia 0.53, metatarsus 0.45, tarsus 0.3, tibia IV 0.4; pedipalpal femur ca. 0.25.
Colour: Prosoma, legs, opisthosomal sigilla and epigastral scutum dark brown, opisthosoma yellow brown. – Prosoma (fig. 307) high anteriorly and posteriorly, fine rugose, with a deep foveal pit and a low cross depression in the posterior half, with few dorsal hairs; posterior files are apparently absent. Eyes large, anterior medians largest, field as wide as the prosoma, posterior row recurved, posterior median eyes separated by 1 1/2 diameters. Clypeus long, basal cheliceral articles short, mouth parts and sternum are hidden. – Legs fairly stout, tibial bristles thin, on I–II shorter than the tibial diameter, their sequence 2/2/1/2 (?). Tarsi short, position of the metatarsal trichobothrium in 0.35 metatarsal IV trichobothrium absent, comb of tarsus IV indistinct. – Opisthosoma (fig. 307) distinctly triangular, flattened, almost straight anteriorly, apparently hardened dorsally, with two pairs of dorsal sigilla and few short dorsal hairs on tiny plates; a colulus may be absent. – Pedipalpus (see above) with a short patella and a wide tibia.

The **relationships** are unsure and the assaignment to *Euryopis* is provisonal. The shape of the opisthosoma is as in *Euryopis* but the eye field is quite unusual – similar to the Araneidae –, and the shape of the high prosoma, and the structures of the bulbus are similar to *Lasaeola*. Therefore I do not exclude that *araneoides* may be to regard as a member of a subgenus of *Euryopis* or of *Lasaeola* or even of a genus of its own.

Distribution: Eocene Baltic amber forest.

Euryopis bitterfeldensis n. sp. (figs. 310–314, photos 288–290)

Material: 4♂ in Baltic amber: Holotypus from the Kaliningrad area and two separated pieces of amber, F1750/BB/AR/CJW; 3♂ from the Bitterfeld deposit: A paratype and a separated piece of amber, coll. GRABENHORST no. AR-165, two further paratypes: F1558 and 1559/BB/AR/CJW.

Preservation and syninclusions: The holotype is completely and excellently preserved, the ventral side is partly covered with a white emulsion, a thin thread is preserved left behind/above the spider's body, stellate hairs are absent. – The male from the coll. GRABENHORST is completely and well preserved in a piece of amber which was slightly heated, a thin silvery emulsion covers most parts of the prosoma, legs and pedipalpi. Stellate hairs are absent, remains of excrement droplets are preserved above the spinnerets (fig. 312). – The paratype F1558 is completely preserved and strongly darkened by heating (most probably in an autoclave). The pierced piece originates from an amber necklace. A tiny Collembola is preserved near the spider, stellate hairs are absent. – The paratype F1559 is completely but not well preserved: A thick emulsion and bubbles cover left parts of body and legs, stellate hairs are absent.

Diagnosis (♂; ♀ unknown): Tiny spiders, body length 1.1–1.3 mm, posterior eye row procurved. Pedipalpus (figs. 313–314, photos 289–290) with a wide tibia and a long questionable embolus.

Description (♂):
Measurements (in mm): Body length 1.1–1.3, prosoma: Length 0.48, width 0.46, hight above the coxae 0.4; leg I: Femur 0.36, patella 0.18, tibia almost 0.2, metatarsus ca. 0.23, tarsus 0.18, tibia IV 0.3, pedipalpal femur 0.25.
Colour; holotype: Prosoma dark brown, legs medium brown, opisthosoma yellow brown but dorsal sigilla and scutate epigaster dark brown. The paratype F1558 is darkened by heating, most parts of the paratype F1559 are covered with a silvery emulsion.
Prosoma (fig. 310) almost as wide as long, with few dorsal hairs of medium length, thoracal fissure indistinct. Eyes large, anterior medians largest, posterior row procurved, posterior median eyes separated by ca. one diameter, clypeus very long, basal cheliceral articles small/short, diverging distally, labium wider than long, gnathocoxae converging. The wide sternum separates the coxae IV by almost 1 1/2 diameters. – Legs stout, sequence of length IV/I/II/III, anterior tarsi and metatarsi fairly thickened; the thin bristles of tibia I are slightly longer than the tibial diameter. The long trichobothria are "feathery" (fig. 311) at least on one side, their position on metatarsus I/II is in 0.35/0.31, they are absent on IV. The ventral hairs on tarsus IV are long and straight (paratype F1558). – Opisthosoma (photo, fig. 310) fairly flattened, triangular, dorsally apparently hardened, widely anteriorly and tapering posteriorly; two pairs of dorsal sigilla are present in the anterior half, the posterior ones are larger. Dorsal opisthosomal parts are scarcely covered with short hairs which are up to 0.05 mm long. The epigaster is sclerotized. A colulus is probably absent but a pair of hairs is present in its area (fig. 311). – Pedipalpus (see above): Patella almost globular, tibia wider than long, close to cymbium and bulbus, questionable embolus long.

Relationships: See the key.

Distribution: Eocene Baltic amber forest, most often from the Bitterfeld deposit.

***Euryopis nexus* n. sp.** (figs. 315–319, photos 293–294)

Material: Holotypus ♂ in Baltic amber, F1815/BB/AR/CJW.

Preservation and syninclusions: The spider is completely preserved in a piece of amber which was heated. The body is dorsally covered with a white emulsion; numerous particles of detritus – partly darkened by heating – are preserved in the same piece of amber, stellate hairs are absent.

Diagnosis (♂; ♀ unknown): Sequence of the dorsal tibial bristles 2/2/1/2, opisthosoma long oval and not flattened or triangular, pedipalpus (figs. 317–319): Cymbium not modified, bulbus simple, the large tegulum bears long and coiled sperm ducts.

Description (♂):
Measurements (in mm): Body length 2.0, prosomal length and width 0.8; leg I: Femur ca. 0.6, patella 0.28, tibia ca. 0.53, metatarsus 0.39, tarsus 0.43, tibia IV ca. 0.5.
Colour of the free observable parts medium brown, emulsion almost white.
Prosoma (most parts are hidden) as long as wide, clypeus very long and protruding, eyes difficult to recognize, of medium size, field narrow, posterior row straight or slightly procurved, posterior median eyes separated by about their diameter, basal cheliceral articles small, gnathocoxae strongly converging above the labium which is wider than long, probably not fused to the sternum and pointed apically, sternum longer than wide, almost smooth, separating the coxae IV by more than their diameter. – Legs fairly long and slender, order I//IV/II/III, tarsi slightly thickened and longer than the metatarsi, sequence of the tibial bristles 2/2/1/2, the basal one on tibia I as long as the tibial diameter, femur I (fig. 315) dorsally-basally stronger thickened than the remaining femora and the femora of *E. streyi* n. sp., and dorsally in the basal half distinctly concave, position of the metatarsal trichobothria unknown, unpaired tarsal claws distinctly smaller than the paired claws, short ventral hadrotarsine hairs of tarsus I well developed (fig. 316). – Opisthosoma (photo 293; most parts are covered with a white emulsion) not flattened and not pointed posteriorly, dorsally with a pair of sigilla, the anterior pair is small. – Pedipalpus (figs. 317–319) (see above) with short patella and tibia, paracymbium in a hidden position, embolus in a distal position, somewhat pear-shaped.

Relationships: In *E. streyi* n. sp. from the Bitterfeld deposit the bulbus bears also long and coiled sperm ducts but the cymbium bears strong apical bristles and a thick apical spine.

Distribution: Eocene Baltic amber forest.

***Euryopis streyi* n. sp.** (fig. 320, photo 291)

Derivatio nomini: This species is dedicated to Prof. GERNOT STREY in Göttingen who collected the holotype and will give it to the Geol. Palaeontol. Museum Göttingen.

Material: Holotypus ♂ in Baltic amber from the Bitterfeld deposit, Grube Goitsche, G. STREY leg., coll. G. STREY at the Geolog. Palaeontol. Mus. Göttingen.

Preservation and syninclusions: The spider is completely and fairly well preserved in a small bloc of amber which was slightly heated. The complete opisthosoma as well as most parts of the left side of prosoma and legs are thickly covered with a white emulsion. The distal parts of the right pedipalpus beyond the patella are distorted by ca. 180°. Stellate hairs are absent.

Diagnosis (♂; ♀ unknown): Small spider, body length 1.4 mm, prosoma short and high. Posterior eye row recurved. Pedipalpus (fig. 320): Cymbium distally with bristle-shaped hairs and a thick apical spine, tegulum large, BEARING LONG AND COILED SPERM DUCTS.

Description (♂):
Measurements (in mm): Body length 1.4, prosoma: Length 0.6, hight above coxae 0.5; leg I: Femur 0.5, patella ca. 0.17, tibia ca. 2.7, metatarsus ca. 0.28, tarsus ca. 0.18, tibia IV 0.3, pedipalpal femur 0.2.
Colour: Prosoma and legs dark brown; the opisthosomal surface is hidden.
Prosoma (photo 291) high, dorsally with some long hairs, without furrows, cuticula fine rugose, a fovea may be absent. At least some eyes are large (most eyes are hidden), posterior row recurved, lateral eyes contiguous; clypeus very long, basal cheliceral articles hidden, apparently short. – Legs (partly hidden) fairly stout, sequence of the tibial bristles 2/2/1/2, bristles thin, the basal one on II is almost 1 1/2 tibial diameters long. Metatarsal trichobothria apparently fine feathery (see fig. 311), position on metatarsus I in 0.25. A stronger (almost bristle-shaped) hair is situated retrolaterally in the middle of metatarsus I. Tarsus I is distinctly shorter than metatarsus I. – Opisthosoma hidden by a white emulsion, probably almost globular. – Pedipalpus (fig. 320): Patella almost globular, tibia wider than long and almost attached to the cymbium, cymbium distally with about one dozen bristle-shaped hairs and a strong apical bristle; tegulum and subtegulum large, tegulum with long and coiled sperm ducts. A median apophysis is not visible, the questionable embolus is thin, most parts of the conductor are hidden by a white emulsion.

Relationships: See the key and *E. nexus* n. sp. in which femur I is stronger bent. The opisthosomal shape of the only known specimen is unknown (it is hidden).

Distribution: Eocene Baltic amber forest, the Bitterfeld deposit.

***Praetereuryopis* n. gen**. (figs. 321–325, photos 295–297)

Diagnosis (♂; ♀ unknown): Eye region distinctly raised and projecting (fig. 321), opisthosoma (figs. 321-323, photos 295-297) flattened, triangular and heavily scutate, bearing small plates (scuta) building lateral rows which bear hairs originating at the anterior margin, pedipalpus (figs. 324-325) with a large median apophysis.
Further characters: Tarsi slender, distinctly shorter than the metatarsi, modified ventral hairs apparently absent, cymbium not modified.

Type species: *Praetereuryopis phoroncidoides* n. sp. (the only known species of the genus).

Relationships: According to the depressed and armoured opisthosoma which is pointed behind, the small basal cheliceral articles as well as the structures of the male pedipalpus I regard this genus as related to *Euryopis*; leg bristles and small plates on the opisthosoma are absent in other species of *Euryopis*, the eye region is not protruding in this way, tarsus I is more or less thickened and the cymbium is most often modified and broadly attached to the pedipalpal tibia. – The shape of the raised and protruding cephalic area, and the tiny opisthosomal scuta are quite similar to characters in *Phoroncidia* WESTWOOD and *Ulesanis* L. KOCH of the subfamily Phoroncidiinae, in which the legs are bristleless and usually stouter, a high opisthosoma, a large (tube-shaped) sclerotized ring around the spinnerets, and a retroectal paracymbium exist, see above. Are the shape of the prosoma and the opisthosomal plates really convergences to the Phoroncidiinae or is *Praetereuryopis* a peculiar member of this subfamily? The discovery of a female may confirm the real relationships of this genus. – Hair-bearing scutate small plates exist also in the theridiid genus *Guaraniella* BAERT 1984 (extant, South America) which has a cup-shaped cymbium and quite different structures of the bulbus.

Distribution: Eocene Baltic amber forest.

***Praetereuryopis phoroncidoides* n. sp.** (figs. 321–325, photos 295–297)

Material: 6♂ in Baltic amber; holotypus ♂ and a separated piece of amber, F1791/ BB/ AR/CJW; paratypes: F1792-1795/CJW, 1♂ coll. J. VELTEN in Idstein.

Preservation and syninclusions: Holotype: The spider is well and completely preserved below a layer which contains numerous small and tiny particls of detritus; the sternum is partly covered with a bubble, the opisthosoma is ventrally partly covered with a bubble and a white emulsion; 3 thin spider's threads inclusively a dragline are preserved left of and behind the spider; numerous particles of detritus and insect's excrement are preserved in the separated piece of amber. – Paratype F 1792 is completely preserved in a piece of amber which was heated, the opisthosoma and ventral parts of prosoma and legs are covered with a white emulsion, a questionable bite mark – caused by a spider? – exist just right in front of the spinnerets (fig. 323). Furthermore preserved are most parts of a female *Orchestina* sp. indet. (Araneae: Oonopidae) with a questionable dragline at the margin of the piece of amber, 1 Diptera, stellate hairs, particles of insect's excremet (a large one closely behind the spider), particles of detritus, stellate hairs and few thin spider's threads. – Paratpe F1793 is well and completely preserved in a piece of amber which was slightly heated; the mouth parts are partly covered with a white emulsion. Syninclusions in different layers: 2 Acari, 1 Myriapoda (Diplopoda: Synexidae: *Phryssonotus* sp. indet.), 1 Formicidae, 2 Diptera: Nematocera, 1 Psocoptera, insect's excrement, stellate hairs and pollen grains as well as few remains of sthin spider's threads in contact to the spider; a sac-shaped structure is present below the spider's right leg IV. – Paratype F1794 is completely preserved in a yellow piece of amber which was not heated; most parts of all sides of body and legs are covered with a white emulsion. – Paratype F1795 is completely preserved, parts are hidden by a white emulsion and fissures in the amber; also preserved are stellate hairs and pollen grains incl. air bag pollen grains. – Paratype coll. J. VELTEN: The spider is completely and well preserved in a larger yellow piece of amber which was slightly heated; a white emulsion is absent, the anterior median eyes are covered with an emulsion as in most fossil spiders, the ventral side of the right bulbus is turned to the dorsal side. A dragline runs from the anterior spinnerets to the left tarsus IV. Remains of a tiny arthropod is preserved left of the spider, and a tiny Diptera behind the spider; few stellate hairs.

Diagnosis (♂; ♀ unknown): Eyes large and in a compact group, pedipalpus (figs. 324–325) with short articles, a large median apophysis and a fairly stout embolus.

Description (♂):
Measurements (in mm): Body length 1.5–1.8, prosoma: Length 0.6–0.75 (F1792), width 0.6–0.7; leg I (paratype of the coll. VELTEN): Femur 1.0, patella 0.25, tibia 0.4, metatarsus 0.43, tarsus 0.28, tibia IV 0.4.
Colour of prosoma and legs most often dark brown (photos; probably darkened by heating) but in F1792 and F1794 red-brown (photo), opisthosoma yellow brown.
Prosoma (fig. 321–322) almost smooth, almost as wide as long, profile concave, cephalic part distinctly raised, fovea small and almost circular, stridulatory files hidden, eyes large and in a compact group, protruding on a narrow area, posterior row recurved, anterior and posterior median eyes largest, anterior median eyes separated by their diameter, posterior median eyes by their radius. Basal cheliceral articles small, teeth of their furrow are hidden, fangs usually hidden and difficult to recognize, most probably long and slender, labium almost triangular, not fused to the wide sternum, which separates the coxae IV by more than their diameter. – Legs fairly short, covered with short hairs, order I/IV/II/III, dorsal tibial bristles ca. as long as the tibial diameter, their sequence 2/2/1/2. The left metatarsus III of the ♂ of the coll. VELTEN bears a bristle in the dorsal half which is slightly shorter than the tibial diameter; the right metatarsus IV of F1793 bears apparently 2 bristles in the basal half. A metatarsal trichobothrium is present on I–III, their position on I–II is in 0.42–0.43. Unpaired claws small, bent in a right angle. – Opisthosoma (figs. 321–323, photos) almost triangular, flattened; dorsally, ventrally and laterally heavily armoured, dorsally and laterally covered with small hair-bearing sclerotized plates (scuta), laterally with long folds, with a sclerotized ring around the spinnerets, epigaster strongly sclerotized, lung covers large, spinnerets short, colulus tiny or even absent (the area is hard to recognize), hairs are not visible. – Pedipalpus (figs. 324–325): Patella and tibia short, distal tibial bristles weakly developed, position of the paracymbium unsure, apparently inside the unmodified cymbium, median apophysis and conductor large, embolus fairly stout, in a clockwise position of the right pedipalpus.

Relationships: See above.

Distribution: Eocene Baltic amber forest.

6. EPISINAE (= Episininae, Monetinae, Spintharinae)

Remark regarding the name Episinae: I prefer the most often used name Episinae (not Monetinae or Spintharinae) – see e.g. WIEHLE (1937), YOSHIDA (2003) contra AGNARSSON (2004) (Spintharinae) (*). The correct name of the subfamily is Episininae but the common use is Episinae, see IRZN art. 29.5.

(*) In my opinion exists no need to use the name of a taxon simply because of its (partly) American distribution.

Diagnosis (as a COMBINATION of characters only, like in some other theridiid subfamilies): Prosoma usually as wide as long or even wider than long, with a deep fovea (photos 301f), leg I usually very long (photos) (not in the Spinitharini), opisthosoma usually distinctly longer than wide (*Twaithesia* is an exception), and frequently modified in extant taxa (see below), colulus and paracymbium very variable (see below), conductor huge and usually consisting of several parts; strongly reduced capture web (few vertical gum-footed lines in a H-shaped web, fig. 333; unknown in the fossils).
Further characters and variability: Usually with a long clypeus, short basal cheliceral articles and a wide eye field (figs. 371, 383, 440). Posterior cheliceral margin usually smooth but in *Moneta* with a single tooth, anterior margin most often smooth, rarely bearing 1–3 teeth. The variability of the paracymbium is quite remarkable: Four kinds exist in different taxa (two kinds in *Moneta*: An internal (hooded), and a retromarginal “paracymbium” (fig. 382); most often exists an internal paracymbium (e. g. fig. 334, 388); a hooded paracymbium exists in *Chrosiothes, Moneta, Spinisinus*, *Spintharus* and probably in *Caudasinus*; the retrodistal/ectal paracymbium in *Mimetidion* and *Spinitharinus* (figs. 421, 424, 431, 442) may be the basal pattern in this subfamily – see above: “Bulbus-cymbium lock mechanisms of the family Theridiidae” – as in the whole family Theridiidae. Prosomal-opisthosomal stridulatoty organ well developed (fig. 405). Colulus usually small (fig. 400), bearing usually one or two hairs (figs. 420, 379, 386, 43), reduced and probably rarely absent (at least in some *Moneta* and *Monetoculus*). Frequently present are red pigments of the anterior median eyes (not known/preserved in the taxa of the Baltic amber), and – in extant spiders in contrast to the Eocene fossils – opisthosomal humps and/or an inclination (figs. 385, 440), as well as humps or a pair of long hairs in the field of the median eyes (fig. 403). (A pair of – usually smaller – hairs in this position exist also in certain members of other subfamilies, e.g. in some Hadrotarsinae). An almost “tetragnathid resting position” (fig. 333) exists at least in some taxa.

The **relationships** are unsure: (a) According to the reduced capture web, the wide prosoma, the dorsal prosomal furrows, the absence of retromarginal cheliceral teeth and the frequently small basal cheliceral articles the subfamily Hadrotarsinae may be most related; in the Hadrotarsinae the legs are shorter than in most Episinae the leg I is not elongated, and the opisthosoma is most often globular, special tarsal I and metatarsal IV comb setae exist usually as well as two pairs of receptacula seminis, the claw of the female pedipalpus is modified, a prosomal-opisthosomal stridulatory organ is absent. An internal paracymbium is present in the Hadrotarsinae, and also in most Episinae (except in *Mimetidion* and *Spinitharinus*). – (b) According to the reduced capture web and the long opisthosoma Argyrodinae may be related, too.

Tribus: The extinct Spinitharini n. trib. (*Caudasinus* n. gen., *Mimetidion* n. gen., *Spinitharinus* n. gen., and *Spinisinus* n. gen.), and Episini (the remaining fossil and extant genera).

Diversity: No region is known from today to have so many species of Episinae, – and especially of *Episinus* – as the Baltic amber forest. During the Early Tertiary (Eocene); the Episinae was apparently quite more diverse than today; the number of species of *Episinus* in Europe was about three times higher than today.

Prey: See below, *Episinus*.

Distribution: Extant: Cosmopolitical (Episini), fossil: The Eocene European amber forests (Episini, and the extinct Spinitharini, too), and the Miocene Dominican amber forest (Episini).

List of the extant and extinct genera of the Episinae:

(a) Extant: *Chrosiothes, Episinus, Moneta, Monetoculus, Pycnoepisinus, Spintharus* and *Thwaitesia*.

(b) Fossil in Miocene Dominican ambers: *Chrosiothes, Episinus* and *Spintharus*;

(c) Fossil in Eocene European ambers: *Caudasinus* n. gen., *Mimetidion* n. gen., *Spinisinus* n. gen., *Spinitharinus* n. gen. (all are extinct), and *Episinus*.

No extinct genus of the subfamily Episinae is known from Dominican amber (see the somewhat unusual species of *Chrosiotes*), four extinct genera are known from Baltic amber. *Episinus* is a diverse genus which species were and are widely spread; today it has a cosmopolitical distribution and fossil it is known from Tertiary European (incl. Baltic) and Dominican ambers.

Key to the extant and fossil genera of the Episinae:
(See the remark below on further possible genera of the Episinae: Episini!)

1 Posterior median eyes separated from each other by more than three diameters, opisthosoma widest in the anterior half. (Epiandrous gland spigots are absent at least in *S. flavidus*, see AGNARSSON (2004: Fig. 69F)). – Extant (the Americas) and fossil in Dominican amber. . . . . *Spintharus*

- Posterior median eyes (if not reduced) usually spaced by 1–2 diameters, opisthosoma widest in the middle or in the posterior half. 2

2(1) Opisthosoma usually higher than wide, with dorsal hump(s) and silvery spots. – Extant, almost cosmotropical. . . . . *Thwaitesia*

- Opisthosoma usually longer than high, without silvery spots; dorsal humps may exist. 3

3(2) Simple bulbus structures. According to LEVI & RANDOLPH (1974): Opisthosoma ventrally and anteriorly overhanging and black in extant spiders, conductor usually absent but present in species in Dominican amber which may be members of a (sub) genus of their own, see WUNDERLICH (1988: 137–138). – Extant (the Americas, SE-Asia) and fossil in Miocene Dominican amber. . . . . *Chrosiothes*

- Bulbus more complicated. Opisthosoma otherwise, conductor present (e. g. figs. 341, 396) 4

4(3) Metatarsus I ca. 7 to more than 10 times longer than tarsus I, a retrolateral/ectal (not retrodistal!) "paracymbium" exists usually near the middle of the cymbial length (it is absent in *longicaudata* SIMON), as well as a stronger apical hair (fig. 382). Extant (tropical Africa, SE-Asia, Australia). Body length usually 2–3 mm . . . . *Moneta*

- Metatarsus I usually 3–4 times longer than tarsus I, retroectal "paracymbium" absent (a flattened bristle is present in *Monetoculus*, no. 7). Extant and fossil. 5

5(4) Metatarsus I bears a row of strong (spine-shaped) prolateral bristles (fig. 441), bulbus (fig. 443) with a furcate apophysis which stands widely out. **Baltic amber**. . . . . *Mimetidion* n. gen.

- No such strong bristles of metatarsus I nor such apophysis of the bulbus 6

6(5) Anterior median eyes distinctly the largest (figs. 383, 391–393). Extant (tropics) . .7

- Anterior median eyes not distinctly the largest (fig. 340, 371), not rarely the smallest. Extant and fossil. 8

7(6) Posterior eye row straight (fig. 391), body length only 1.4 mm (smallest known Episinae); ♂ (♀ unknown): Cymbium retrolaterally with a strong and flattened bristle which stands out in a right angle (fig. 394). Malaysia . . . . *Monetoculus* n. gen.

- Posterior eye row recurved (fig. 383), body length 5 mm; ♂ (♀ unknown): Cymbium without a retrolateral bristle but with an apical bristle (fig. 387). A special stridulatory organ exists between leg I and II. Kenya. . . . . *Pycnoepisinus* n. gen.

8(6) Tibia I with two rows of long prolateral hairs or even bristle-shaped hairs, proapically with a strong bristle or a pair of strong apical bristles (figs. 399, 435, 437) (except in a single species). ♂: Pedipalpal femur distinctly shorter than the prosoma, short apical cymbium hairs absent, subtegulum large and usually protruding. Spinitharini (excl. *Mimetidion,* see no. 5). Eocene **Baltic amber** 9

- Prolateral tibial I bristle-shaped hairs and proapical tibial bristle(s) absent. ♂-pedipalpus (fig. 340, photos): Femur about as long as the prosoma, cymbium with a row of short retrodistal hairs near the tip in one or two groups. – Extant and fossil in Tertiary (**Baltic**, Ukrainean, Dominican and probably Rumanian) ambers . . . . *Episinus*

9(8) Body length 1.8–2.8 mm. With a pair of usually strong hairs in the field of the median eyes (fig. 403); these hairs are small in *Spinitharinus curvatus*. (In *Episinus* exists rarely a pair of small hairs in this position). Posterior median eyes most often separated by slightly more than their diameter but very variable. Cymbium and bulbus not twisted, paracymbium of the retrodistal/ectal type (figs. 421–422) but probably of the internal/hooded type in *Caudasinus*, subtegulum large to very large (figs. 429, 431, 434). . . 10

- Body length 1.7–1.9 mm. No such strong (only thin) hairs in the field of the median eyes. Posterior median eyes separated by ca. two of their diameters. Cymbium and the flat bulbus are twisted by 180°: The ventral side of the bulbus is directed dorsally (fig. 396), paracymbium of the internal (hooded?) type (fig. 397) . . . . *Spinisinus* n. gen.

10(9) Opisthosoma elongated beyond/above the spinnerets (fig. 440), tibia I with a pair of apical bristles (fig. 435) (the retroapical one may be small), cymbium usually with dorsal bristles (fig. 436) (not in *C. regeneratus*), embolus shorter (fig. 434). . . . .*Caudasinus* n. gen.

- Opisthosoma not elongated beyond the spinnerets (raised above the spinnerets in *S. bulbosus*, fig. 406), tibia I with a single proapical strong bristle only (similar in *Spinisinus*, fig. 399), cymbial bristles absent, embolus longer (fig. 411) . . . . . .*Spinitharinus* n. gen.

(a) EPISINI (= Monetini and Mictodipoenini **n. syn.**, see below)

Diagnosis: Presence of a long to very long leg I (especially the femur), and an internal paracymbium. Further characters: See the Episinae. (Proapical bristles of tibia I are absent).

Type genus: *Episinus* WALCKENAER 1809. Further genera: *Chrosiothes, Moneta*, *Monetoculus* n. gen., *Pycnoepisinus* n. gen., *Spintharus* and *Twaitesia*.

Relationships: See below, the Spinitharini n. trib.

Distribution: Extant: Cosmopolitical; fossil: Eocene Baltic (incl. Bitterfeld), Ukrainean, Rumanian (?) and Miocene Dominican amber forests.

Episinus WALCKENAER 1809

Synonymy of the extant genera:

LEVI & LEVI (1962) synonymized several genera with *Episinus* but *Hyocrea* SIMON 1894 is probably a genus of its own, see the shape of the opisthosoma, and the remark by MARUSIK & PENNEY (2003: 209), and *Molione* THORELL 1892 may be a further genus of the Episini; see the remark by WUNDERLICH (1995: 569).
Moneta O. PICKARD-CAMBRIDGE 1871 (figs. 382) was synonymized with *Episinus* by LEVI & LEVI (1962); but due to the chelicerae, the legs, and the structures of the ♂-pedipalpus both genera are distinctly different; see the key to the genera and the tab. below. SAARISTO (2006) and YOSHIDA (2001) regarded *Moneta* as a member of the subfamily Theridiinae but according to the shape of the prosoma, the teeth on both cheliceral margins, the shape of the opisthosoma (fig. 382a), and the existence of a (small) colulus – personal observation, e. g. *M*. sp. from Australia, and in juveniles of *M. longicaudatus*, as well as structures of the ♂-pedipalpus (fig. 382b) – I regard *Moneta* as a member of the Episinae. See also AGNARSSON (2004: 468).

Notes on the taxa in Baltic amber, new combinations, and new synonyms:

About 8 species of this genus in Baltic amber have been described up to now, e. g. *Episinus balticus* MARUSIK & PENNEY 2005, *Episinus eskovi* MARUSIK & PENNEY 2005, *Episinus longimanus* (KOCH & BERENDT 1854) (sub *Flegia*) (= *Malleator niger* PETRUNKEVITCH 1942, see below). I regard *Eodipoena regalis* PETRUNKEVITCH

1958 (holotype juv. ♂, Geol. Palaeont. Mus. Copenhagen no. 9985, studied in 2005) as a member of *Episinus* (**n. comb**.). – In this paper I add 15 new species but – according to indetermined material in my private collection – there may exist some more undescribed species in Baltic amber. Today we know about half as many species in Europe as are known from the Eocene Baltic amber.

Flegia succini PETRUNKEVITCH 1942: According to the structures of the male pedipalpus *succini* is not a member of *Episinus* but a junior synonym of *Pseudoteutana stigmatosa* (KOCH & BERENDT 1854) (Asageninae) (**n. syn**.), and not of *Episinus* as published by MARUSIK & PENNEY (2005: 210) which did not study the holotype. *Eodipoena kaestneri* PETRUNKEVITCH 1958 was transferred to *Episinus* by MARUSIK & PENNEY (2005: 209), but in my opinion it is a member of *Eomysmena*.

According to the long legs, the shape of the prosoma and the body length of 4 mm I regard *Lithyphantes anticus* BERLAND 1939 (male unknown) being most probably a member of *Episinus* (**n. comb**.) (I do not want to exclude relationships to *Spinitharinus*).

Flegia KOCH & BERENDT 1854, see WUNDERLICH (1978 and 1986: 42) and *Malleator* PETRUNKEVITCH 1942, see WUNDERLICH (2004: 1306); both are synonyms of *Episinus*. In my opinion – according to their characters – *Impulsor* PETRUNKEVITCH 1942 and *Mictodipoena* PETRUNKEVITCH 1958 (see below) are further synonyms of *Episinus* (**n. syn**.). – According to its wide labium and widely speced coxae IV I will not exclude that *Municeps* PETRUNKEVITCH 1942 is also a junior synonym of *Episinus* (**quest. n. syn**.). – According to MENGE (1854: 30) *Corynitis* MENGE 1854 is closely related to *Episinus* but – due to the spiny legs, the very long male pedipalpus and the globular bulbus – *Corynitis* is more likely a – dubious – genus of the family Mimetidae, see WUNDERLICH (2004: 1261).

Mictodipoenini PETRUNKEVITCH 1958 = Episini (**n. syn**.) and *Mictodipoena* PETRUNKEVITCH 1958 = *Episinus* (**n. syn**.)

1958 Mictodipoeneae PETRUNKEVITCH, and *Mictodipoena stridula* PETRUNKEVITCH,– Trans. Connect. Ac. Arts & Sci., 41: 161.

Material: Holotype (juv.) of *Mictodipoena stridula* in Baltic amber, Miner. Geol. Mus. Copenhagen no. 9981.

Remark: The pedipalpal articles of the spider are slightly thickened, so the holotype may be a juvenile male.

In 1958 PETRUNKEVITCH described a monotypic new tribe – Mictodipoeneae –, which he erroneously placed in the Hadrotarsinae (sub Dipoeninae) without marking it as described for the first time and without an explicite diagnosis. Diagnostic characters of this tribus are given in a key (p.157–158) and further characters with the diagnosis of the single genus, *Mictodipoena*. Tribus and genus were based on a single small juvenile and defect fossil spider which has been splitted in two pieces (!).

According to the diagnosis of tribus and genus the tarsi II and III are distinctly longer than the metatarsi II and III and the prosoma is distinctly longer than wide, but in fact – according to my investigation – only tarsus II is slightly longer than metatarsus II. The proportions of leg articles are different in juvenile and adult spiders, and – according to PETRUNKEVITCH (1958: 162) – the right legs I and II are "not yet fully regenerated". PETRUNKEVITCH (1958: Fig. 96) figured the prosoma in an oblique position; actually it is not distinctly longer than wide. The position of the trichobothrium of metatarsus I is in 0.36. The most striking diagnostic character of the genus *Mictodipoena* is a "stridulating organ on the dorsal plate of the pedicel and the ventrally turned dorsal wall of the abdomen." (PETRUNKEVITCH (1958: 158). I cannot confirm the existence of such a stridulatory organ in the holotype. According to the comb of tarsus IV *stridula* is a member of the family Theridiidae, due to the long opisthosoma – it is 1.43 times longer than wide – I regard this species as a member of the Episini: *Episinus* (**n. comb**.), and the Mictodipoenini as a junior synonym of the Episini (**n. syn**.).

Impulsor PETRUNKEVITCH 1942 = *Episinus* WALCKENAER 1805 (**n. syn**.)

Impulsor has originally been described as a monotypic genus of the family Linyphiidae; it was transferred to the Theridiidae by WUNDERLICH (2004: 1306). Recently I studied again the male holotype of the generotype, *Impulsor neglectus* PETRUNKEVITCH 1942, which is kept in the BM, no. 18122. It is badly and incompletely preserved, the dorsal parts of prosoma, opisthosoma and of both pedipalpi are cut off, the area of the colulus is not well recognizable (darkened), the structures of the bulbus are badly recognizable. The body length of the spider is 2 mm, the anterior metatarsus is 1.4 mm long, the sequence of the long tibial bristles is 2/2/1/2, the basal articles of the chelicerae are fairly long, the sternum is not rugose, patella and tibia of the pedipalpus are short. According to its combination of characters – the smooth sternum, the long anterior legs, the chaetotaxy and the structures of the bulbus (so far recognizable) – I regard *neglectus* as a member of *Episinus* (**n. comb**.); the second species of *Impulsor* – *mutilus* PETRUNKEVITCH 1958 – is also a member of *Episinus* (**n. comb**.), see below.

Diagnosis of *Episinus*: Fovea very large and long (photos 398f, fig. 340); ♂-pedipalpus: Femur about as long as the prosoma (photos, fig. 340), cymbium with a row of short retrodistal hairs in one or two groups on a low elevation near the tip (figs. 350, 358, 366) (they may be difficult to observe in fossils), paracymbium of the internal hooked type in a distal position within the cymbium (fig. 334).

Further characters: Prosoma usually about as wide as long, usually with a narrow eye field (photos, figs. 340, 371) which bears a pair of tubercles in several species (not in the Baltic amber spiders), anterior median eyes not the largest, posterior median eyes usually separated by ca. one diameter (rarely up to two diameters), cheliceral retromargin toothless, legs usually long (especially the anterior pair), frequently annulated, the opisthosoma may be widest in the distal half, it may be flattened dorsoventrally and/or bear frequently humps in extant spiders (fig. 333) (humps are absent in the Baltic amber spiders in which the opisthosoma has an oval shape, see the photos; a slightly flattened opisthosoma exists in some fossil species as *clunis* and *balticus*); an epigastral scutum may be present (e.g. in the fossil spiders in Baltic amber). The colulus may be large (fig. 379) or reduced. It is unknown if there is only a single pair of epiandrous gland spigots in all species of this genus as in the fossil *Episinus* sp. indet. 1, fig. 378. Opisthosomal sigilla may exist (e.g. in *E. clunis* n. sp.). An epigynal plug may be present (fig. 381); bulbus faced to the retrolateral side, subtegulum usually small, frequently hidden by the pedipalpal tibia, conductor large and complicated (figs. 342, 377).

Relationships: In *Moneta* O. PICKARD-CAMBRIDGE 1870 the extremely long metatarsi are 7 up to more than 10 times longer than their short tarsi, the eye field is usually wider, the tibial bristles are reduced, the cymbium bears a retromarginal outgrowth ("paracymbium") (except in *longicaudata* SIMON), as well as an apical bristle-shaped longer hair which is bent (fig. 382) in all species, and the subtegulum is usually larger; see the key to the genera of this subfamily, and the tab. below. In *Pycnoepisinus* – which is also related, see the tab. below – the position of the INTERNAL paracymbium is in the middle of the length of the cymbium (fig. 388). The tiny spiders of *Monetoculus*: See the key above and the tab. below.

Selected characters of *Episinus* and related genera:

character	*Episinus*	*Pycnoepisinus*	*Moneta*	*Monetoculus*
length of metatarsus I: tarsus I	3 to 4:1	4:1	ca. 7–10:1	3:1
width of the eye field	relatively (1) narrow (fig. 371)	narrow	distinctly wider than long	relatively narrow (fig. 391)
anterior median eyes	not largest	distinctly the largest (fig. 383)	not the largest	distinctly the largest (fig. 391)
cheliceral retromarginal tooth	absent	absent	1	absent
body length	> 2–5 mm	5 mm	> 2–5 mm	1.4 mm
stridulatory organ between legs I & II	absent	present (fig. 384)	absent	absent
length of the pedipalpal femur	~ as long as the prosoma	distinctly shorter	distinctly shorter	~ as long as the prosoma
cymbium with ...	group(s) of small retroapical hairs (fig. 360) or tiny bristles	apical bristles (fig. 387)	retrolateral "paracymbium" (2)	retrolateral flattened bristle (fig. 394)

---

(1) A wider eye field exists in *E. longabdomenus* ZHU 1998.

(2) It is absent in *longicaudata* SIMON and bears most often a bristle (fig. 382). (A similar bristle exist also in certain species of *Spinitharinus* and a – flattened – bristle exist in *Monetoculus*). In *Moneta* the cymbium bears furthermore a stronger and bent apical – sensory? – bristle-shaped hair (fig. 382).

Ecology; remains of prey (as syninclusions) of the fossil spiders of *Episinus* which are described below: Three Diptera (Brachycera and Nematocera) as well as each a single member of: Coleoptera (Mordellidae), Diptera (photo 34), worker Formicidae, Trichoptera and Isoptera. So ants were not the main kind of prey of these fossil spiders. According the frequent winged insects within the prey these spiders of the Baltic amber forest lived in higher strata of the vegetation – probably on the bark of trees, too – were spiders captured their prey easily by the sticky resin – and not mainly in lower vegetation as most extant spiders. A specimen of *Episinus* as a prey: See photo 38.

Distribution: Extant: Cosmopolitical; fossil in Tertiary Baltic (incl. Bitterfeld), Rumanian, Ukrainean (Rovno), and Dominican amber. *E. longimanus* is more frequent in amber from the Bitterfeld deposit than the other species. Has it been a species mainly from the Bitterfeld part of the large Early Teriary European amber forests?

Provisional **key** to the fossil species of the genus *Episinus* in Baltic amber (♂) which are treated in this paper (in *E. anticus* the male are unknown, in *neglectus* and *mutilus* the male is badly preserved, see above and below):

Remark: Use for the determination mainly the shape of the pedipalpal tibia, the outline of cymbium and bulbus, the shape and the position of the embolus including its distal and its basal parts.

1 Cymbium apically elongated (nose-shaped) (figs. 337, 339) 2

- Cymbium apically not elongated (fig. 346–347) 3

2(1) Width of the bulbus in the middle ~0.25 mm . . . . *nasuticymbium*

- Width of the bulbus in the middle ~0.5 mm . . . . *mutilus*

3(1) Pedipalpal tibia 1.5 times wider than long, bulbus also wide, medially with a long and spoon-shaped conductoral apophysis (figs. 345–347), embolus base well observable, originating in a distal position, partly guided and hidden by the margin of the pedipalpal tibia. . . . . *latus*

- Pedipalpus (fig. 358–359): Tibia only slightly longer than wide, bulbus as in the figs., tegular margin near the apical tibial margin strongly protroding (arrow in figs.) . . . . . .
. . . . *isopteraque*

- Pedipalpal tibia only slightly longer than wide, bulbus fig. 362 . . . . *eskovi*

- Pedipalpal tibia 1.4–2 times longer than wide, distinctly longer than the patella . . . 4

4(3) Pedipalpal tibia about 2 times longer than wide (fig. 340), bulbus as in figs. 341f, embolar part near the tibial margin free observable (similar to no. 10ff) . . . *longimanus*

- Pedipalpal tibia 1.4–1.8 times longer than wide, bulbus different 5

5(4) Embolus near the tibial margin partly hidden by a tegular edge (e.g. figs. 354, (arrow), 363). A large protruding prodistal bulbus sclerite is absent, the lateral eyes are almost touching 6

- Embolus free observable near the tibial margin (e.g. figs. 365, 369, 377) as in *longimanus* (no. 4, fig. 341); a large and ventrally protruding prodistal bulbus sclerite is usually present (absent in *transversus*), the lateral eyes may be distinctly separated . . 12

6(5) The embolus describes a wide prodistal loop (arrow in fig. 348) . . . . . . *dimidius*

- No wide loop of the embolus in this position (e.g. figs. 357, 363) 7

7(6) Strongly sclerotized apical conductor apophysis wide (fig. 363). . . .*mordellidaeque*

- Strongly sclerotized apical conductor apophysis narrow (e.g. figs. 354, 357) 8

8(7) Embolus distally strongly bent (semicircular) (fig. 364) . . . . *musculus*

- Embolus distally semicircular but subtegulum larger (fig. 357) . . . .*cymbialis*

- Embolus distally not semicircularly bent (e.g. figs. 351, 354) 9

9(8) The distinctly convex tegular margin (arrow in fig. 354) is wide retrolaterally and covers the embolus about 2/3 of the length of the apical tibial margin . . . . *bulla*

- Tegular margin straight or concave (e.g. figs. 355, 377) 10

10(9) Strongly sclerotized conductoral apophysis not widened at the tip, basally as wide as distally (arrow in fig. 351) . . . .*appendix*

- Strongly sclerotized conductoral apophysis widened at the tip (long arrow in fig. 355), basally distinctly wider than distally 11

11(10) Conductor near the tip of the embolus wider (x in fig. 355) . . . . *cochlear*

- Conductor near the tip of the embolus more narrow (x in fig. 350) . . . . .*anapidaeque*

12(5) A large and ventrally protruding retrodistal bulbus sclerite is absent; the distal part of the embolus is S-shaped (fig. 377). . . . .*transversus*

- A large and ventrally protruding retrodistal bulbus sclerite is present (figs. 366, 370), the distal part of the embolus is not S-shaped (it may be hidden) 13

13(12) Embolus basally thick, its distal part wide apart from the tip of the cymbium (fig. 369) . . . . *longisoma*

- Width and position of the embolus different, the tip of the embolus points more to the pedipalpal tibia (e.g. fig. 374) 14

14(13) Pedipalpus (figs. 373–375): Distal part of the embolus with its seam thick, diameter ca 0.03 mm, tibia ca. 1.6 times longer than wide . . . . *balticus*

- Pedipalpus (figs. 365–368): Diatsl part of the embolus with its seam thin, its, diameter ca. 0.015 mm, tibia 1.4/1.7 times longer than wide (but it may be more variable) . . 15

15(14) Pedipalpus (figs. 365–366): Tibia ca. 1.7 times longer than wide, with an apical inclination (arrow in fig.); retrodistal bulbus sclerite smaller, position of metatarsal III trichobothrium in 0.4 . . . . *arrodens*

- Pedipalpus (figs. 367–368): Tibia ca. 1.4 times longer than wide, without an apical inclination; retrodistal bulbus sclerite larger, position of the metatarsal III trichobothrium in 0.6 . . . . *clunis*

***Episinus nasuticymbium* n. sp.** (figs. 335–338, photo 311)

Material: Holotypus ♂ in Baltic amber and a separated piece of amber, SMNG, (F2035/BB/AR/CJW).

Preservation and syninclusions: The spider is well and completely preserved in a yellow piece of amber; the ventral side of the opisthosoma is covered with a white emulsion. The left metatarsus I has been amputated at its base, blood is not preserved (fig. 336) Parts of (its?) capture web are preserved e. g. at the tip of the left tarsus IV (fig. 335), and a thin spider's thread, 1.4 mm long, which bears remains of a flattened droplet, are existing right in front below the spider; small particles of detritus are also preserved.

Diagnosis (♂; ♀ unknown): Pedipalpus (figs. 337–338): Patella and tibia short, cymbium small, apically elongated (nose-shaped), width of the bulbus in the middle 0.25 mm.

Description (♂):
Measurements (in mm): Body length 2.2, prosoma: Length 1.0, width 0.85; leg I: Femur 1.6, patella 0.47, tibia 1.15, metatarsus 1.4, tarsus 0.45, tibia II 0.7, tibia III 0.45, tibia IV 0.8; width of the bulbus in the middle 0.25, length of the conductor 0.15.

Colour: Prosoma and legs medium brown, opisthosoma yellow brown.
Prosoma longer than wide, hairs indistinct, fovea apparently small; a pair of thin and long hairs in the field of the median eyes is directed foreward. Eyes of medium size, field large, posterior row slightly procurved, posterior median eyes separated by slightly more than their diameter; posterior stridulatory files may be absent. Clypeus long, not protruding ventrally, basal cheliceral articles long, labium distinctly wider than long, coxae IV separated by about half of their diameter by the sternum. – Legs long and slender,order I/IV/II/III, I distinctly the longest, III distinctly the shortest. Bristles long, their sequence on the tibiae 2/2/1/2. Position of the trichobothrium on the right metatarsus II in 0.13. Paired tarsal claws stout, the unpaired claw not shorter, smooth, bent in a right angle. – Opisthosoma oval, covered rather scarcely with hairs of medium length, dorsally with at least two pairs of sigilla; spinnerets stout, colulus apparently strongly reduced (hidden?). – Pedipalpus (figs. 337–338, photo 311): Femur slender, patella slightly longer than wide, dorsally with 1/1 hair-shaped long bristles, tibia fairly stout, bearing at least one dorsal-basal trichobothrium, cymbium distally abruptly narrow, apically nose-shaped, paracymbium hidden, bulbus fairly slender, the ventral aspect of the embolus is short.

Relationships: The shape of the distal part of the cymbium is quite similar to *E. mutilus* (PETRUNKEVITCH 1958) but *mutilus* is distinctly larger, the width of the bulbus is twice, and the position of embolus and conductor are different.

Distribution: Eocene Baltic amber forest.

Episinus mutilus (PETRUNKEVITCH 1958) (fig. 339) (**n. comb**.)

1958 *Impulsor mutilus* PETRUNKEVITCH, – Trans. Connect. Ac. arts sci., 41: 211, figs. 239–247 (♂) (**n. comb**.).

Material: Holotypus ♂ in Baltic amber, MGM Copenhagen no. 9989.

Preservation: The spider is badly preserved and strongly darkened; the piece of amber has been broken through the spider's body longitudinally and cross through the right bulbus "in the course of polishing" according to PETRUNKEVITCH.

Diagnosis (♂; ♀ unknown): Pedipalpus (fig. 339): Patella and tibia short, cymbium apically elongated (nose-shaped), width of the bulbus in the middle 0.5 mm.

Description (♂):
Measurements (in mm): Body length 3.1, prosoma: Length 1.55, width 1.5; femur I ~2.0 (according to PETRUNKEVITCH 4.0!), diameter of the bulbus in the middle 0.5.
The position of the metatarsal trichobothria are unknown. The darkened structures of the bulbus are difficult to observe, the cymbium is distinctly elongeted apically, the pedipalpal tibia is plate-shaped elongated as in other theridiid males.

The **relationships** were not discussed by PETRUNKEVITCH (1958). According to the shape of the body, the chaetotaxy and the structures of the ♂-pedipalpus *mutilus* is a member of the genus *Episinus* (**n. comb**.). The shape of the cymbium is quite similar to *E. nasuticymbium* n. sp., see above.

Distribution: Eocene Baltic amber forest.

Episinus eskovi MARUSIK & PENNEY 2005 (fig. 362)

2005 *Episinus eskovi* MARUSIK & PENNEY, Arthropoda Selecta (Special Issue No. 1): 210, figs. 14–16 (♂ in Baltic amber).

Remarks: (1) It was not possible to get and study the holotype from the Amber Museum in Palanga, Lithunia; probably the director of this institution did not found the holotype. (2) The bulbus and the long embolus of this species are similar to *E. latus* n. sp.

Episinus longimanus (KOCH & BERENDT 1854) (figs. 340–343, photos 306–309)

1854 *Flegia longimana* KOCH & BERENDT, Die im Bernstein befindlichen Organischen Reste der Vorwelt, 1 (2): 29, t. 3, fig. 18 (♂).
1942 Malleator niger PETRUNKEVITCH, Bull. Mus. Comp. Zool., 103: 300, figs. 83–85, 554 (♂) (**n. syn**.).
1946 Flegia longimana, – PETRUNKEVITCH, Amer. Mus. Novit., 1328: 8–9, figs. 26–32, 72 (male “hypotype”).
1950 *Flegia longimana*, – PETRUNKEVITCH, Bull. Mus. Comp. Zool., 103: 286, fig. 55.

Synonymy: According to the long pedipalpal tibia I regard *Malleator niger* PETRUNKEVITCH 1942 as a junior synonym of *Episinus longimanus* (**n. syn**.).

Material: 7♂ in Baltic amber; holotype PMHUB, MB.A. 164/7280; ♂ “hypotype” AMNH no. 26259; F1439/CJW; the remaining 4 males are from the Bitterfeld deposit: F1428/CJW, F1430/CJW, coll. KUTSCHER K/AR/6 and coll. GRABENHORST AR 85.

Remarks: (1) MENGE in KOCH & BERENDT (1854: 30) mentioned in a footnote 7♂ and 1♀ from his private collection (which is lost now) which he regarded as conspecific. At that time only a single species of *Episinus* (under *Flegia*) in Baltic amber was known, the structures of the bulbus were not studied and therefore the conspecifity of these specimens is quite doubtful. (2) In the same footnote MENGE mentioned a couple of the same species from his private collection in a position close together. According to MENGE the reverse position of these spiders indicate a position ofcopulation but this may well have been a "post copular position". (3) *Flegia longimana* was regarded erroneously as "comb. n." in *Episinus* by MARUSIK & PENNEY (2005: 209) whereas these authors – the same page – noted that *Flegia* – with its type species *longimana* – was already synonymized with *Episinus* by WUNDERLICH (1978).

Preservation of the holotype: It has been enclosed in a larger block of artificial resin; the piece of amber is darkened. The adult male is almost completely preserved, the bulbi are covered with a white emulsion, only an apical bulbus sclerite is observable. – In the remaining males the bulbus structures are well recognizable; with F1430 a dragline is preserved, the male F1429 has lost its opisthosoma before it was entrapped, the left part of its prosoma is cut off. The "hypotype" is in best condition (see the photos), and enclosed in two blocks of one or two substance(s) which is(are) unknown to me.

Diagnosis (♂): Tibia of the pedipalpus 2 times longer than wide (fig.340), distinctly longer than the pedipalpal patella, bulbus (figs. 341–343) with a free observable part near the apical tibial edge and fairly bent distally.

Description (♂):
Measurements (in mm): Body length ca. 2.5, prosoma: Length and width ca. 1.2, leg I: Femur 2.15, patella 0.55, tibia 1.9, metatarsus 2.6, tarsus 0.9, tibia II 1.2, tibia III 0.7, tibia IV 1.6; pedipalpus: Femur 1.2, patella 0.42, tibia 0.55.

Colour (if not darkened by aging or heating) light brown, legs more or less annulated, darkened e. g. at the end of the femora.
Prosoma (photos, fig. 340, photos) wide as long, with a deep thoracal furrow, clypeus long and protruding, eye region raised, posterior row slightly recurved, posterior median eyes separated by about one diameter, larger than the anterior median eyes, lateral eyes almost touching. Chelicerae small. Posterior prosomal stridulatory files distinct. – Legs long, slender and fairly hairy, I distinctly the longest, order I/IV/II/III, metatarsus I slightly bent, sequence of the tibial bristles 2/2/1/2, position of the trichobothrium on metatarsus III in 0.45. – Opisthosoma ca. 1.7 times longer than wide, widest in the middle, covered with hairs of medium length, spinnerets short, epigastral scutum present. – ♂-pedipalpus (figs. 340–343, photos 308–309) with long articles, femur 6.5, tibia 2 times longer than wide, embolus not hidden near the apical tibial edge, fairly bent distally (with a hidden tip).

Relationships: According to the bulbus structures *E. transversus* n. sp. is most related; in *transversus* the pedipalpal tibia is only 1.7 times longer than wide and the shape of the embolus is different.

Distribution: Eocene Baltic amber forest incl. the Bitterfeld deposit: 4 of the 7 males which were studied by me were collected at the Bitterfeld deposit. – Almost half of the specimans which are surely determined as conspecific are preserved in amber from the Bitterfeld deposit. Is this a species mainly from the Bitterfeld fauna?

***Episinus latus* n. sp.** (figs. 344–347)

Material: 2♂ in Baltic amber: Holotypus, F1431/BB/AR/THE/CJW; paratypus and a separated piece of amber, F2080/BB/AR/CJW.

Preservation and syninclusions: Holotype: The spider is well preserved, the right side of the prosoma, the right chelicera as well as the basal parts of the right leg articles I–III and of the pedipalpus are cut off, also the distal parts of the left tarsi III and IV are cut off. Parts of the left side of the opisthosoma and of the left prosomal side above the coxae are covered with a white emulsion, some threads are preserved below the left coxae, some stellate hairs are also present.– Paratype: The spider is well and completely preserved in a yellow piece of amber which was slightly heated; it is dorsally covered with a white emulsion. Both emboli are in their original position, a tiny Collembola is situated above the right metatarsus II. In the separated piece of amber are stellate hairs, Acari, Collembola and two small Diptera preserved.

Diagnosis (♂; ♀ unknown): Opisthosoma only 1.25 times longer than high, steeply raising above the spinnerets. Pedipalpus (figs. 344–347): Patella and tibia short, both as long as wide, bulbus with a large prolateral spoon-shaped conductor (S) (probably part of the funtional conductor), embolus very long, originating in a distal position, partly guided and hidden by the apical tibial margin.

Description (holotype):
Measurements (in mm): Body length 2.0, prosomal length 0.95; leg I: Femur 1.7, patella 0.38, tibia 1.45, metatarsus 1.5, tarsus 0.6, tibia IV 0.9; pedipalpus: Patella 0.2, tibia 0.2 long and wide.
Colour yellow brown, legs not annulated.
Prosoma similar to *E. longimanus*; the area of the stridulatory files is hidden. – Legs long, similar to *E. longimanus*, position of the metatarsal III trichobothrium in 0.36. – Opisthosoma only 1.25 times longer than high, scarcely covered with long hairs, steeply raised above the spinnerets, epigaster scutate. – Pedipalpus: See above. The embolus is well recognizable and not in its natural position in contrast to the paratype.
Remark on the paratype: There are small differences in the structures of the pedipalpus: In the paratype the cymbial part which guides the embolus at the apical part of the tibia is larger than in the holotype, and a small outgrowth exists on the basal part of the spoon-shaped conductor near the base of the embolus.

Relationships: See the key. In *E. nubilus* YAGINUMA 1960 (extant, SE-Asia) the wide bulbus and the position of the embolus are similar.

Distribution: Eocene Baltic amber forest.

***Episinus dimidius* n. sp.** (fig. 348)

Material: Holotypus ♂ in Baltic amber, F1436/BB/AR/THE/CJW.

Preservation and syninclusions: Only a part of the spider is preserved: The ventral part of the body, most parts of the left pedipalpus and of the legs are cut off, most parts of leg pair I are present, the right pedipalpus is well preserved. – A small Diptera: Nematocera is situated close to the spider; a tiny Collembola, few remains of stellate hairs and particles of detritus are also preserved, threads of silk are absent.

Diagnosis (♂; ♀ unknown): The "oblique" shape of the thin embolus (arrow in fig. 348) (which is basally hidden by the tegular margin) is unique in the fossils of this genus, the pedipalpal patella and tibia are rather short.

Description (♂):
Measurements (in mm): Body length ca. 2.5, prosomal length ca. 1.1, femur I 2.0.
Colour: Prosoma and legs light brown, opisthosoma yellow brown.
Most parts of body and legs are missing, the lateral eyes are touching, the shape of the opisthosoma is oval. Pedipalpus: See above.

Relationships: See the key.

Distribution: Eocene Baltic amber forest.

***Episinus anapidaeque* n. sp.** (figs. 349–350)

Material: Holotypus ♂ in Baltic amber, F1438/BB/AR/THE/CJW.

Preservation and syninclusions: The spider is fairly well preserved; the distal part of the opisthosoma, the tip of the right tibia I and parts of both legs IV are cut off, the body is partly covered by a white emulsion. Stellate hairs are absent but some thin spider's threads and a male of *Fossilanapis* sp. indet. (Araneae: Anapidae: Anapinae) are preserved in the same piece of amber.

Diagnosis (♂; ♀ unknown): Pedipalpus (figs. 349–350): Only a small part of the retrolateral cymbial margin (X in fig. 350) is observable in the ventral aspect. The distal part of the embolus is fairly bent.

Description (♂):
Measurements (in mm): Body length 2.6, prosomal length 1.1; leg I: Femur 1.85, patella 0.5, tibia 1.6, metatarsus 1.9, tarsus 0.7; tibia of the pedipalpus 0.4.
Colour light brown.

Prosoma: Most parts are hidden by a white emulsion, the lateral eyes are almost touching. Legs similar to *E. longimanus*, position of the metatarsal II trichobothrium in 0.48. Opisthosoma incompletely preserved, the remains are covered by a white emulsion. Pedipalpus: See above.

Relationships: In *E. musculus* n. sp. a larger part of the cymbial margin is observable, the tegular edge near the apical tibial margin is more oblique and the distal part of the embolus is stronger bent. See also *E. anapidaeque* n. sp.

Distribution: Eocene Baltic amber forest.

***Episinus appendix* n. sp.** (figs. 351–353)

Material (in Baltic amber): Holotypus ♂ and 2 separated pieces of amber, F1439/BB/ AR/ THE/CJW; a questionable ♂ and a separated piece of amber, F1440/BB/AR/ THE/JW.

Preservation and syninclusions: Holotypus: The spider is completely and fairly well – the right pedipalpus very well – preserved in a piece which has been heated; mainly the right legs are in contact with some semicircular and partly darkened fissures, a white emulsion is absent. A thin dragline is running from the anterior spinnerets backwards near to the anterior part of a small Hymenoptera which anterior part is preserved at the margin of the piece of amber. A lump of stellate hairs is preserved right in front of the spider. A mite and several stellate hairs are preserved in the separated piece. – The questionable conspecific ♂ is completely and fairly well preserved, the ventral side of its opisthosoma is covered with a white emulsion, bubbles are present below the sternum and – a small one – under the opisthosoma. Detritus, stellate hairs, and the anterior part of a small fly (in the separated piece of amber) are also preserved.

Diagnosis (♂; ♀ unknown): Pedipalpus (figs. 351–353): Embolus near the tibial margin widely but not protruding hidden by the tegular margin, distal part of the embolus only fairly bent.

Description (♂):
Measurements (in mm): Body length 2.7 – 3.0 (questionable ♂), prosoma: Length 1.1, width 1.0; leg I (holotype): Femur 2.0, patella 0.55, tibia 1.7, metatarsus 2.3, tarsus 0.75, tibia IV 1.4; pedipalpus: Femur 1.15, patella 0.36, tibia: Length 0.4, width 0.25.
Colour: Prosoma and legs medium brown opisthosoma of the holotype light to medium brown (it is hidden in the questionable ♂), legs probably not annulated.
Prosoma almost as wide as long, similar to *E. longimanus*, posterior eye row slightly recurved, posterior eyes separated by their diameter, lateral eyes close together. Legs long and slender, bristles as in *E. longimanus*, position of the metatarsal I trichobothrium in 0.31. Opisthosoma oval, 1.6 times longer than wide, widest in the middle, with at least one pair of distal sigilla; dorsal hairs of medium length, epigaster scutate, colulus with a pair of setae. Pedipalpus: See above.

Relationships: See *E. bulla* n. sp. and the key.

Distribution: Eocene Baltic amber forest.

Episinus bulla n. sp. (fig. 354)

Material: Holotypus ♂ in Baltic amber, F1445/BB/AR/THE/CJW.

Preservation and syninclusions: The spider is only fairly well preserved in an amber piece which is full of bubbles; its left leg II is missing beyond the coxa by autotomy; ventrally the spider is heavily covered by a white emulsion. Remains of a tiny and flattened arthropod are preserved dorsally-posteriorly on the prosoma, few stellate hairs and thin threads of spiders silk are present in the same piece of amber.

Diagnosis (♂; ♀ unknown): Pedipalpus (fig. 354): The distinctly convex (not protruding!) tegular margin (arrow) is wide retrolaterally and covers the embolus about 2/3 of the length of the apical tibial margin in ventral aspect of the bulbus. (The distal part of the embolus is hidden).

Description (♂):
Measurements (in mm): Body length 3.0, prosoma: Length 1.2, width 1.1; leg I: Femur 1.7, patella 0.6, tibia 1.4, metatarsus + tarsus 2.6, tibia IV 1.3; pedipalpus: Femur 1.0, patella 0.25, tibia: Length 0.4, width 0.25.
Colour: Prosoma and legs medium brown, opisthosoma light brown.
Prosoma similar to *E. longimanus*, lateral eyes almost touching. Legs similar to *E. longimanus* but less hairy; position of the metatarsal trichobothria unknown. Opisthosoma oval, widest in the middle, 1.8 times longer than wide, fairly covered with hairs of medium length. Pedipalpus: See above.

Relationships: In *E. appendix* n. sp. the tegular margin which covers the embolus is smaller and not distinctly convex.

Distribution: Eocene Baltic amber forest.

Episinus cochlear n. sp. (figs. 355–356)

Material: Holotypus ♂ in Baltic amber, F1437/BB/AR/THE/CJW.

Preservation and syninclusions: The spider is fairly well preserved at the margin of an amber piece which contains numerous stellate hairs. The left femora III and IV, the left part of the prosoma and the dorsal part of the opisthosoma are deeply deformed/depressed (the spider was injured by a beat); several leg articles are cut off or partly cut off, e. g. most patellae; only the left legs III and IV are complete. Some parts of the spider are covered with a white emulsion. A tiny mite and the larger part of the spider's capture web – without droplets – is present with a small Diptera: Nematocera – body lenght ca. 1 mm – as a prey in it. Apparently the midge has been sucked out.

Diagnosis (♂; ♀ unknown): Pedipalpus (figs. 355–356) similar to *E. anapidaeque* but the conductor near to the tip of the embolus (X in fig. 355) is wider.

Description (♂):
Measurements (in mm): Body length 2.5, prosomal length ca. 1.2, femur I ca. 1.7; pedipalpus: Patella ca. 0.45, tibia: Length ca. 0.4, width ca. 0.25.
Colour light brown.
Prosoma similar to *E. longimanus*, lateral eyes almost touching. Legs incompletely preserved, position of the metatarsal trichobothria unknown. Opisthosoma deformed.
Pedipalpus: See above.

Relationships: The distal part of the conductor (X in fig. 355) is wider than in *E. anapidaeque* n. sp.

Distribution: Eocene Baltic amber forest.

***Episinus cymbialis* n. sp.** (fig. 357)

Material: Holotypus in Baltic amber, F1444/BB/AR/THE/CJW.

Preservation and syninclusions: The spider is fairly well preserved in a small piece of amber; the opisthosoma and left parts of prosoma and of some legs are covered with a white emulsion, a smaller right part of the prosoma as well as the right tarsus and distal parts of the right metatarsus IV are cut off, the right leg I is missing beyond the coxa by autotomy, the prosoma is hollow. Stellate hairs are absent.

Diagnosis (♂; ♀ unknown): Pedipalpus (fig. 357) with a relatively large subtegulum in an oblique position and a distinctly bent distal part of the embolus. The tegular edge hide a part of the embolus.

Description (♂):
Measurements (in mm): Body length 2.65, prosomal length 1.15; leg I: Femur 1.75, patella 0.5, tibia 1.45, metatarsus 1.8, tarsus 0.6; pedipalpus: Patella 0.29, tibia: Length 0.4, width 0.25.
Colour: Prosoma and legs medium brown, opisthosoma yellow brown.
Most parts of the prosoma are hidden. Legs relatively short, position of the metatarsal

I and II trichobothria in 0.45. Opisthosoma oval, widest in the middle, 1.9 times longer than wide, with longer hairs. The epigaster is sclerotized. Pedipalpus: See above.

Relationships: In *E. musculus* n. sp. the subtegulum is smaller and the embolus is stronger bent.

Distribution: Eocene Baltic amber forest.

***Episinus isopteraque* n. sp**. (fig. 358–359)

Material: Holotypus in Baltic amber, F1434/BB/AR/THE/CJW.

Preservation and syninclusions: The spider is well preserved, the right leg I is missing beyond the coxa by autotomy, most parts of the opisthosoma are covered by a white emulsion. A termite (Isoptera) as a prey of the spider is preserved directly left of the spider; the body of the termite is ca. 5 mm long, its abdomen is partly dissected, it is partly spun in in spiders' threads, a clue of threads is preserved on the thorax of the termite, a second one on the abdomen, its right anterior wing covers the left half of the spider's prosoma and some articles of the legs. Particles of detritus and numerous tiny bubbles are present in the same piece of amber but no stellate hairs.

Diagnosis (♂; ♀ unknown): Pedipalpus (figs. 358–359): Only slightly longer than wide, tegular edge near the apical tibial margin strongly protruding (arrow in the figs.), the distal part of the embolus is hidden by a sclerite of the bulbus (ventral aspect).

Description (♂):
Measurements (in mm): Body length 3.2, prosoma: Length 1.2, width 1.1; leg I: Femur 2.0, patella 0.6, tibia 1.75, metatarsus + tarsus 2.65, tibia IV 1.5.
Colour: Prosoma and legs medium brown, legs probably not annulated, opisthosoma light.
Prosoma and legs quite similar to *E. longimanus*; position of the metatarsal trichobothria unknown. Opisthosoma oval, 1.33 times longer than wide, widest in the middle, scarcely covered with long hairs; the epigaster is sclerotized. Pedipalpus: See above. The apical bulbus (conductor) apophysis is long and slender, the distal part of the embolus may be similar to *E*. sp. near *isopteraque* (figs.).

Relationships: In *E.* sp. near *isopteraque* (F1433/BB/AR/THE/CJW) (figs. 360–361) the pedipalpal tibia is longer, 1.35 times longer than wide. In *E. appendix* (and related species) the pedipalpal tibia is also longer and the tegular margin is less protruding.

Distribution: Eocene Baltic amber forest.

Episinus mordellidaeque n. sp. (fig. 363)

Material: Holotypus ♂ in Baltic amber, F1449/BB/AR/THE/CJW.

Preservation and syninclusions: The spider is well and almost completely preserved, only the margins between the right tibia and metatarsus I are cut off. The opisthosoma and few further parts of the spider are covered with a white emulsion. Stellate hairs, parts of detritus, a small piece of leaver moss, a plant's seed and a beetle of the family Mordellidae (body length ca. 3.5 mm) are preserved in the same piece of amber.

Diagnosis (♂; ♀ unknown): Pedipalpus (fig. 363): Strongly sclerotized apical conductor apophysis very wide (arrow), embolus thin, most of its parts near the tibia are hidden by the tegular edge.

Description (♂):
Measurements (in mm): Body length 1.95, prosoma: Length 0.85, width 0.8; leg I: Femur 1.6, patella 0.4, tibia 1.3, metatarsus 1.65, tarsus 0.6, tibia IV 1.1; pedipalpus: Femur 0.8, patella 0.25, tibia: Length 0.35, width 0.2.
Colour: Prosoma and legs medium brown, opisthosoma light.
Prosoma similar to *E. longimanus*, legs slender, position of the metatarsal I trichobothrium in 0.44, opisthosoma oval, similar to *E. cymbialis*. Pedipalpus: See above.

Relationships: See the key.

Distribution: Eocene Baltic amber forest.

Episinus musculus n. sp. (fig. 364)

Material: Holotypus ♂ and a separated piece of amber, F1435/BB/AR/THE/CJW.

Preservation and syninclusions: The spider is well preserved, the mouth parts and the ventral side of the opisthosoma are covered with a white emulsion, the right legs III and IV are missing beyond the coxa by autotomy, the dorsal part of the right tibia III is cut off. Probable remains of muscles are preserved within the anterior femora. Few thin threads of spiders silk are preserved above the left side of the spider. A small Diptera: Nematocera is preserved in the separated piece of amber, stellate hairs are absent.

Diagnosis (♂; ♀ unknown): Pedipalpus (fig. 364): Patella and tibia fairly short, subtegulum small, distal part of the embolus strongly bent, semicircular.

Description (♂):
Measurements (in mm): Body length 2.65, prosoma: Length 1.15, width 1.05; leg I: Femur 1.8, patella 0.52, tibia 1.85, metatarsus 2.35, tarsus 0.65, tibia IV 1.5; pedipalpus: Patella 0.35, tibia: Length 0.4, width 0.3.
Colour: Prosoma medium brown, legs light brown, probably annulated, opisthosoma yellow brown.
Prosoma similar to *E. longimanus*, legs relatively long, position of the metatarsal I trichobothrium near the middle. Opisthosoma oval, widest near the middle, 1.2 times longer than wide, dorsally covered with long hairs. Pedipalpus: See above.

Relationships: See *E. cymbialis* n. sp. and the key.

Distribution: Eocene Baltic amber forest.

***Episinus arrodens* n. sp.** (figs. 365–366)

Material: Holotypus ♂ in Baltic amber, F1456/BB/AR/THE/CJW.

Preservation and syninclusions: The spider is only fairly well preserved, the opisthosoma is dorsally strongly depressed, the prosoma is dorsally injured, too, parts with the eyes are missing within the amber, a white emulsion is absent, several leg articles are cut off, the right legs II and III are complete, the right leg IV is complete except parts of tibia and metatarsus; stellate hairs are absent in the small piece of amber.

Diagnosis (♂; ♀ unknown): Pedipalpus (figs. 365–366): Tibia ca. 1.7 times longer than wide, with an apical inclination (arrow), folded part of the conductor wide, ca. 0.2 mm long, the thin distal part of the embolus is strongly bent, its tip is hidden in the ventral aspect.

Description (♂):
Measurements (in mm): Body length 3.0, prosoma: Length and width 1.15 mm, femur II 1.65.
Colour light brown, legs probably not annulated.
Prosoma as wide as long (the eyes are missing). Legs (most articles are lost) relatively long, position of the metatarsal III trichobothrium in 0.4. Opisthosoma 1.55 times longer than wide, widest in the middle, dorsally covered with long hairs. Pedipalpus: See above.

Relationships: *E. clunis* n. sp. is most related, see the key.

Distribution:Eocene Baltic amber forest.

Episinus clunis n. sp. (figs. 367–368, photos 303–304)

Material: Holotypus ♂ in Baltic amber, F1454/BB/AR/THE/CJW.

Preservation and syninclusions: The spider is well preserved, a weak white emulsion is present on its ventral side, the tibia of the right leg IV and the tip of the left tarsus I are cut off, a bubble of the spiders' excrement is present at the anal opening, a dragline is running backwards from the anterior spinnerets, thin threads are preserved on the spiders' body and below the spider. A small deformed midge is preserved just in front of the spider; it may well have been the prey of the spider. Parts of a larger arthropod's leg and several stellate hairs are also preserved.

Diagnosis (♂; ♀ unknown): Pedipalpus (figs. 367–368): Bulbus with a large and protruding retrodistal apophysis, tip of the embolus hidden in the ventral aspect.

Description (♂):
Measurements (in mm): Body length 3.0, prosoma: Length and width 1.3; leg I: Femur 2.5, patella 0.65, tibia 2.0, metarasus 2.7, tarsus 0.9; pedipalpus: Patella 0.38, tibia: Length 0.35, width 0.22.
Colour light brown, legs probably annulated.
Prosoma (photos 303–304) similar to *E. longimanus*. Legs long and slender, position of the long metatarsal III trichobothrium in 0.6. Opisthosoma long and slender, 2.1 times longer than wide, widest just in front of the middle, dorsally slightly depressed in the middle, with two pairs of fairly distinct sigilla and covered with long hairs, epigaster sclerotized. Pedipalpus: See above. The embolus is not hidden by the tegular margin.

Relationships: *E. arrodens* n. sp. is most related, see the key.

Distribution: Eocene Baltic amber forest.

Episinus longisoma n. sp. (figs. 369–370)

Material in Baltic amber: Holotypus ♂, GPIUH, typ. cat. no. 4295, old coll. SCHEELE no. 358; questionable ♂ F1455/BB/AR/THE/CJW.

Preservation and syninclusions: The holotype is preserved in a 4.5 mm long piece of amber which is fairly darkened by aging and which has been rolled; the spider's left side is partly covered with a white emulsion and lying on a layer, the right pedipalpus is very well preserved, its opisthosoma is distinctly deformed, only five legs are complete, both legs I are missing beyond the coxa by autotomy, the right tibia IV is missing. Left of the prosoma and in front of the bulbi each a bubble is preserved. Numerous stellate hairs are present. Few thin threads are preserved on the right metatarsus IV. – The questionable male is completely and well preserved, the ventral side and parts of the bulbi are covered with a white emulsion.

Diagnosis (♂; ♀ unknown): Prosomal length 1.75–1.8 mm (one of the largest species of this genus in Baltic amber). Pedipalpus (figs. 367–368): Embolus very thick in the basal half, in a transverse/oblique position, free observable near the tibial margin; distal part in a wide loop, widely apart from the tip of the cymbium.

Description (holotype ♂):
Measurements (in mm): Body length incl. the protruding prosoma 3.8, prosoma: Length 1.75, width 1.65; leg II (legs I are lost): Femur 2.3, patella 0.7, tibia 1.7, metatarsus 2.25, tarsus 0.9, femur IV 3.4; pedipalpus: Femur 1.9, patella 0.55, tibia: Length 0.6, width 0.4. The prosomal length of the questionable conspecific male is 1.8.
Colour medium to dark brown, legs probably not annulated, opisthosoma light brown.
Prosoma similar to *E. longimanus* but lateral eyes separated by about their radius; stridulatory organ hidden. Legs fairly long and hairy, position of the metatarsal II trichobothrium in 0.37. The deformed opisthosoma had most probably an oval shape.
Pedipalpus (figs. 367–368): Femur distally distinctly bent, tibia 1.5 times longer than wide, with at least two trichobothria, see the diagnosis.

Relationships: See *E. transversus* n. sp.

Distribution: Eocene Baltic amber forest.

Episinus balticus MARUSIK & PENNEY 2005 (figs. 371–376, photo 302)

2005 *Episinus balticus* MARUSIK & PENNEY, Arthropoda Selecta (Special Issue No. 1): 210, figs. 17.18.

Material: At least 6♂ in Baltic amber: 4♂, F1457-F1458 (now MNHUB), F1460, and F1877/BB/AR/THE/CJW; 1♂ PIHUB; 1♂ from the Bitterfeld deposit, F1459/BB/AR/THE/CJW; 1 probably conspecific ♂, GPIUH, the old coll. SCHEELE no. 1186, 1 probably conspecific ♀, F1452/BB/AR/THE/CJW.

Remarks: (1) I was impossible to get the holotype from the Amber Museum in Palanga, Lithuania. (2) The male from the Bitterfeld deposit may be a subspecies or even a species of its own.

Preservation and syninclusions: F1457: The spider is well but incompletely preserved, the ventral side is covered with a white emulsion, most leg articles are cut off, only the right leg III is complete, the right legs I and IV are lost beyond the coxa by autotomy in the amber, remains of blood are present at both stumps, the right leg II is cut off within the amber through the tibia. A dragline is running from the anterior spinnerets to the tip of the left tarsus IV and than to the spider's opisthosoma; few stellate hairs are also present. – F1458 is fairly well preserved and ventrally covered by a white emulsion, the right leg I is stretched out forewards, both legs IV are cut off through their tibia. Some stellate hairs and mouth parts of an ant are preserved in the same piece of amber. – F1459 is well and almost completely preserved, only the left leg I is lost beyond the coxa by autotomy, few parts of the spider's left side are weakly covered with a white emulsion, stellate hairs are absent. – F1460 is only fairly well preserved, the tip of the right tarsus IV is cut off, the left leg IV is cut off through the femur within the amber, the right side of the body is weakly covered with a white emulsion, the opisthosoma as well as right and ventral parts of the prosoma are covered by tiny "discs" (fissures) which may be the result of heating of the amber. Also preserved are a small piece of moss, some stellate hairs and pyrite. – The probably conspecific male is almost completely preserved, only the left leg IV is lost beyond the coxa by autotomy, the left leg I is stretched foreward, the dorsal and right sides of the body are thickly covered with a white emulsion, stellate hairs, a tiny midge and a drilling are also present in the piece of amber. – The probably conspecific female is fairly well preserved, parts are weakly covered with a white emulsion, the left leg I and the right legs III and IV are are lost beyond the coxa by autotomy, one of these legs is preserved behind the spider. A dragline and some other thread are running through the amber piece. In another layer than the spider a fly is preserved. – F1877 is well and almost completely preserved, its body length is 3.5 mm, the left side of the thorax is slightly deformed.

Diagnosis (♂): Pedipalpus (figs. 373–375): Bulbus slender, distal part of the embolus with its seam thick, its diameter in this part is 0.03 mm.

Description (♂ ; based on the material which is listed above):
Measurements (in mm): Body length 3.3–3.7, prosomal length 1.3–1.5; leg I (F1458): Femur 2.6, patella 0.6, tibia 2.1, metatarsus 3.1, tarsus 0.9, tibia IV (F1459) 2.1, pedipalpal tibia (F1457) 0.57.
Colour: Prosoma and legs medium brown, legs annulated (distinctly in F1458), opisthosoma yellow brown.
Prosoma (figs. 371–372) similar to *E. longimanus* but lateral eyes separated by about their radius. Posterior stridulatory files quite indistinct. Legs long, metatarsus I more distinctly bent than in the shorter legged species and similar to *E. longimanus*. Position of the metatarsal trichobothria: I (F1458) in 0.57, II (F1457) in 0.4. Opisthosoma long and slender, 1.85 times longer than wide (F1457), depressed dorsally, covered with long hairs. Pedipalpus (figs. 373–375): See above. Tibia ca. 1.7 times longer than wide, lateral aspect of the bulbus as in *arrodens* n. sp.

Probably conspecific ♀: Body length 3.0, prosomal length 1.1, opisthosoma 1.5 times longer than wide (probably eggs-bearing), the lateral eyes are separated by about their radius as in males of *E. balticus*, the epigynal pit (fig. 376) is well recognizable; most probably a secretion (plug) covers the inner parts of the pit.

Relationships: *E. arrodens* and *E. clunis* are most related, see the key. E. g. in *E. longisoma* the lateral eyes are separated as in *E. balticus*.

Distribution: Eocene Baltic amber forest incl. the Bitterfeld deposit.

***Episinus transversus* n. sp.** (fig. 377, photo 310)

Material: Holotypus ♂ in Baltic amber, F1432/BB/AR(THE/CJW.

Preservation and syninclusions: The spider is well and almost completely preserved, only the right leg III is missing beyond the coxa by autotomy. The opisthosoma is thickly covered by a white emulsion. Few stellate hairs and thin threads of spider's silk are present near the spider, and several oxidated structures within the amber near the margin of the piece.

Diagnosis (♂; ♀ unknown): Pedipalpus (fig. 377): Embolus in an oblique position, wide apart from the tibial margin, with a slender base and strongly bent distally.

Description (♂):
Measurements (in mm): Body length 3.0, prosomal length 1.2, leg I: Femur 2.0, patella 0.6, tibia 1.7, metatarsus 2.15, tarsus 0.75; pedipalpus: Patella 0.37, tibia: Length 0.4, width 0.23.
Colour yellow brown, legs probably slightly annulated.
Prosoma (most parts are hidden by the legs) similar to *E. longimanus*. Legs long and hairy, position of the metatarsal I trichobothrium in 0.41. Opisthosoma 1.5 times longer than high. Pedipalpus (fig. 377): See above; tibia 1.7 times longer than wide, with at least two trichobothria, cymbium and bulbus long, cymbium 1.4 times longer than wide (ventral aspect).

Relationships: The position of most parts of the embolus is similar to *E. longisoma* n. sp.; *longisoma* is larger, and the position of the distal part of the embolus is quite different. *E. longimanus* n. sp. is related, too.

Distribution: Eocene Baltic amber forest.

***Episinus* sp. indet. 1** (fig. 378–379)

Material: 1♂ in Baltic amber and a separated amber piece, F1442/BB/AR/THE/CJW.

In this male the epiandrous gland pits and spigots as well as the colulus and its pair of hairs are well recognizable. The paired low epiandrous pits bear apparently only a single long spigot (fig. 378), the colulus bears a pair of long hairs (fig. 379).
(The epiandrous glands and spigots are present in male spiders of most taxa; they produce silk which is used for the construction of the sperm web).
A dragline is preserved in this piece of amber which originates on the anterior spinnerets in this spider; draglines are present with numerous fossil spiders of this genus in Baltic amber.

?***Episinus* sp. indet. 2** (fig. 380, photo 312)

Material: 1 subad. ♂ in Baltic amber, F1447/BB/AR/THE/CJW; the piece is broken – through the spider, too – in two pieces.

The spider is well preserved, the left side is covered by a white emulsion., its body length is almost 3 mm, the lateral eyes are separated by at least their radius, the posterior median eyes are small and separated by more than 1 1/2 diameters. Pedipalpus (fig. 380): The long femur is strongly bent, a tibial suture is absent but a row of tiny hairs exist at the prospective tibial margin. The apical pedipalpal articles are as voluminous as the prosoma.

***Episinus* sp. indet. 3**

Material: 1♀ with its prey, a Diptera: Brachycera in Baltic amber, F1451/BB/ AR/THE/ CJW.

The body length of the spider is 3 mm, the epigyne is covered by a white emulsion. Directly right in front of the spider and covered by the right leg I a fly as the prey of the spider is preserved which is 2.6 mm long and partly deformes; few thin threads of silk are also present. Near the fly – but in a different layer – a small beetle and 1 1/2 midges are preserved.

***Episinus* sp. indet. 4**

Material: 1♂ with its prey, a Trichoptera in Baltic amber, F1441/BB/AR/THE/CJW.

The body length of the spider is 2.4 mm. The double thread of a dragline is running backwards from the spinnerets. Closely in front of the spider a Trichoptera is situated which is 2 mm long and which has been the prey of the spider. The Trichoptera is dissected and dorsally covered by thin threads of spider's silk. Also present in the piece of amber are some stellate hairs and (not as prey) are 1 Opiliones, 1 Psocoptera, 1 Diptera, 1 Coccoidea and some Acari.

***Episinus* sp. indet. 5** (fig. 381)

Material: 1♀ in Baltic amber, F1453/BB/AR/THE/CJW.

The boy of the spider is ca. 3.3 mm long, the tip of the opisthosoma is cut off, the amber piece was heated. The position of the metatarsal I trichobothrium is in ca. 0.55. The pit of the epigyne (fig. 381) is 0.58 mm long, much longer than wide, its anterior margin is stronger sclerotized; the pit may be filled with a secration (a plug). In *Episinus* sp. indet. 6 – which may be strongly related – the length of the epigynal groove is only 0.4 mm.

***Episinus* sp. indet. 6**

Material: 1♀ in Baltic amber, F1464/BB/AR/THE/CJW.

The spider is ca. 3.3 mm long, well and completely preserved in an amber piece which has been heated. The right tarsus III is a regeneration, it is shortened to 0.18 mm (the left tarsus III is 0.5 mm long), the number of its hairs is low and the claws are weakly developed. The position of the metatarsal III trichobothrium is in ca. 0.55. The epigynal pit is distinctly longer than wide, 0.4 mm long; a plug may be present. *Episinus* sp. indet. 5 may be strongly related.

Further *Episinus* sp. indet. of the coll. JW

In my private collection 13♂, 3♀ and a questionable ♀ of *Episinus* sp. are kept which are preserved in Baltic amber. Two of the females got numbers: a juvenile female, F1524/BB/AR/CJW and an adult female, F1525/BB/AR/CJW. The prosomal length is 1.5 and 1.4 mm, the length of femur I is 3.6 and 2.2 mm. F1524 shows the legs distinctly annulated (photo 313), F1525 has a deformed/shrunk opisthosoma and has probably been the prey of a spider.

Description of two extant new species and genera of the Episini:

(a) ***Monetoculus* n. gen.** (figs. 392–394)

Diagnosis (♂; ♀ unknown): Anterior median eyes distinctly the largest (figs. 392–393), pedipalpus (fig. 394): Femur as long as the prosoma, cymbium with a flattened bristle on the retrolateral margin which is situated on a weak paracymbial outgrowth. Body length only 1.4 mm (smallest known member of the subfamily Episinae).

Further characters: Femur I 2.7 times as long as the prosoma, tarsus I 1/3 as long as metatarsus I, eye field fairly narrow, bearing a pair of humps, cheliceral retromargin without teeth.

Type species: *M. parvus* n. sp. (the only known species of the genus).

Relationships: *Episinus* WALCKENAER 1809 and *Moneta* O. PICKARD-CAMBRIDGE 1870 are most related, see the tab. above (genera related to *Episinus*).

Distribution: Malaysia.

***Monetoculus parvus* n. gen. n. sp.** (figs. 391–394)

Material: Malaysia, Taman Negara National Park, natural forest, shaken from a tree, JW leg in VIII 1980, holotype ♂ R5/CJW. – Remark: I separated the opisthosoma and the right pedipalpus from the spider's prosoma.

Diagnosis (♂; ♀ unknown; see the genus diagnosis): A pair of humps above the very large anterior median eyes, opisthosoma (figs. 391–392) widened behind, with three larger outgrowths, a medial hump and two pairs of lateral pointed humps. Tarsus I 1/3 as long as metatarsus I. Pedipalpus (fig. 394): The long embolus originates in the basal half of the bulbus and is hidden in almost his second half by a conductor.

Description (♂):
Measurements (in mm): Body length 1.4, prosoma: Length 0.6, width 0.55; leg I: Femur 1.6, patella 0.3, tibia 1.55, metatarsus 1.8, tarsus 0.6, tibia IV is lost; pedipalpus: Femur 0.6, patella 0.23, tibia 0.23.

Colour yellowish, legs annulated: Femora distally in the middle, patella and tibiae distally, metatarsi basally and distally. Below the lenses of the anterior median eyes exist black and redbrown pigments. – Prosoma (figs. 391–393) flat, wide posteriorly, fovea low, eye field only fairly wide, with a pair of humps in the field of the median eyes, posterior row straight, anterior median eyes unusually large. Basal cheliceral articles small, fangs thin, promargin with a single tooth, retromargin smooth, labium wider than long, the sternum separates the coxae IV by almost their diameter. Posterior stridulatory files are apparently absent. – Legs very long (see above) and slender, order I/IV/II/III, femur I 2.7 times as long as the prosoma, tarsus I as long as the prosoma, bristles and most hairs and trichobothria are rubbed off, both legs IV are broken off and lost beyond the patella (by autotomy?), so the tarsal comb is unknown. – Opisthosoma (figs. 391–392) flattened, somewhat triangular, with a small dorsal medial hump and three posterior outgrowths, the laterals bear two pairs of pointed spoon-shaped outgrowths. I did not recognize a colulus but a pair of tiny hairs may be present. Stridulatory picks are absent. – Pedipalpus (fig. 394) with long articles, retrobasally with a long and flattened hair which stands out in a right angle. The long embolus originates in the basal half of the bulbus, almost its distal half is hidden by a large conductor; three sickle-shaped apophyses exist as median apophysis, functional conductor and theridiid tegular apophysis.

Relationships: See above.

Distribution: Malaysia.

(b) ***Pycnoepisinus* n. gen**. (figs. 383–390)

Diagnosis (♂; ♀ unknown): Stridulatory organ between legs I and II (fig. 384), anterior median eyes largest, legs relatively stout (femur I shorter than the prosoma); ♂-pedipalpus (figs. 387–390): Tibia very wide and in close contact to the short cymbium, apically modified: with two outgrowths which bear a spine and 3 bristles.

Further characters: A prosomal-opisthosomal stridulatory organ is absent, metatarsus I 4 times longer than tarsus I, opisthosoma somewhat triangular (fig. 385); Pedipalpus (figs. 397–390): Femur less than half as long as the prosoma, embolus in an almost circular position.

Type species: *Pycnoepisinus kilimandjaroensis* n. sp.

Relationships: According to the shape of the opistosoma, the narrow eye field and the structures of the male pedipalpus *Episinus* WALCKENAER 1809 may be most related, see the tab. above.

Distribution: Tropical Africa (Kenya).

Pycnoepisinus kilimandjaroensis **n. gen. n. sp.** (figs. 383–390)

Material: Kenya, Kilimandjaro, coll. ROEWER 11283, holotypus ♂; SMF.

Diagnosis (♂; ♀ unknown): Posterior eye row recurved (fig. 383), shape of the opisthosoma widened posteriorly (fig. 385), pedipalpus (figs. 387–390) with an apically modified cymbium and a retrolateral paracymbium which is situated in the middle of the length of the cymbium(!).

Description (♂):
Measurements (in mm): Body length 5.0, prosoma: Length 1.9, width 1.7; leg I: Femur 2.7, patella 1.05, tibia 2.75, metatarsus 3.5, tarsus 0.85, tibia IV 2.15; pedipalpus: Femur 0.7, patella 0.4, tibia 0.45.
Colour: Prosoma medium to dark brown, anterior median eyes with redbrown pigment, legs medium brown, not annulated, opisthosoma mainly dark brown, dorsally medially partly yellow brown, ventrally-medially light medium brown.
Prosoma slightly longer than wide, cephalic part distinctly raised, with a deep and long fovea, eye field (fig. 383) narrow, anterior median eyes distinctly largest, posterior row recurved, posterior median eyes separated by almost their diameter, clypeus strongly concave, basal cheliceral articles fairly large, margins smooth, fangs long and slender, labium wider than long, not fused to the sternum, sternum separating coxae IV by 1/3 of their diameter. – Legs fairly stout, covered with dense hairs, order I/IV/II/III, sequence of the thin tibial bristles most probably 2/2/1/2, metatarsus I bent, metatarsi I–III bear a trochobothrium, its position on I is in 0.53, paired tarsal claws with long teeth, distinctly longer than the unpaired claw, comb of tarsus IV well developed. A particular structure consists of a probasal serrated ledge on femur II (fig. 384) and a sclerotized retrolateral area of coxa I which I regard as a stridulatory organ. – Opisthosoma (fig. 385) covered with short hairs, widened behind, with a pair of large sigilla. Colulus (fig. 386) large, with a pair of long hairs. Epiandrous gland spigots indistinct (two tiny pairs on indistinct plates?). – Pedipalpus (figs. 387–390) (see above): Position of the retrolateral intern and hook-shaped paracymbium in the middle of the length of the cymbium, sperm ducts long; the distal part of the embolus is hidden by a long conductor, theridiid tegular apohysis devided.

Relationships: *Episinus hickmani* DI CAPORIACCO 1949 has been described from Kenya, too, based only on a juvenile spider.

Distribution: Kenya.

(b) SPINITHARINI n. trib. (figs. 396–444, photos 26, 42, 314–336)

Diagnosis: Tibia I with two rows of long prolateral bristle-shaped hairs as well as most often a strong proapical bristle (figs. 399, 437), rarely a pair of apical bristles (*Caudasinus*, fig. 435) (absent in the known females of *Spinitharinus* sp. indet. and the male sex of few species of this genus), rarely metatarsus I with a row of long prolateral bristles (*Mimetidion*, fig. 441); paracymbium of the retrodistal type (most *Spinitharinus*, figs. 424, 431) or probably of the internal type: In *Spinisinus, Spinitharinus bispinosus* and *Caudasinus* as well.

Further characters: Posterior prosomal stridulatory files (fig. 405) are present at least in *Spinitharinus* (unknown in *Caudasinus, Mimetidion* and *Spinisinus*), the anterior cheliceral margin may bear at least three teeth (*Spinitharinus bulbosus*), colulus small (fig. 400) (probably absent in some species), bearing usually 1–2 hairs (figs. 420, 433), opisthosomal sigillae are present (fig. 419), strong paired hairs in the field of the median eyes may be present (in most members of *Spinitharinus*, figs. 403, 417); epigyne (fig. 432) probably wider than long, the embolus describes a wide loop (fig. 396, 422).

Behaviour and the special structure of the anterior leg: In the fossil genera *Caudasinus*, *Spinisinus* and *Spinitharinus* exist – at least in the male sex of most species – two rows of long and bristle-shaped prolateral hairs and a strong proapical bristle on tibia I. These bristles and hairs may have been connected with the loss of the capture web, see above (e. g. Phylogeny: "Evolutionary trends"); the single strong apical bristle(s) may have been used as "clasping spine(s)" for fixing the female during the copulation; it has not been found yet in a fossil female or in members of the family Theridiidae besides the tribus Spinitharini. (Strong metatarsal bristle-shaped hairs exist in the extant genus *Selimus* SAARISTO 2006. See also Anelosiminae n. subfam.. Apical bristles of tibia I are absent in both taxa.).

Type genus: *Spinitharinus* n. gen. (Further genera are *Mimetidion*, *Caudasinus* n. gen. and *Spinisinus* n. gen.).

Relationships: According to the wide and high prosoma with a (usually) large fovea and short basal cheliceral articles as well as the long opisthosoma (figs. 406, 440), and the large and divided conductor I regard – with some hesitation – Spinitharini as a tribus of the Episinae but it may be even a subfamily of its own. In the remaining Episinae – the tribus Episini – long prolateral hairs and large apical bristles of the male tibia I – they are unique in the Spinitharini within the whole family Theridiidae – are absent, and the number of teeth of the cheliceral promargin may be smaller.

Distribution: Eocene Baltic amber forest (incl. the Bitterfeld deposit).

Key to the genera: See above (Episinae).

***Spinisinus* n. gen**. (figs. 396–402, photos 323–327)

Diagnosis (♂; ♀ unknown): Pedipalpus (figs. 396–397, 401–401): The cymbium and the FLAT bulbus are distorted: The ventral side of the bulbus is directed dorsaly, paracymbium probably internal and strongly sclerotized (fig. 397), conductor large and bent in a right angle.

Further characters: Eyes small, posterior median eyes separated by ca. two diameters (fig. 398), a pair of indistinct hairs in the field of the median eyes, fovea long and deep (*parvioculi*), tibia I with a long proapical bristle (fig. 399), existence of opisthosomal sigillae unknown, hairs of the tiny colulus are probably absent in *S. parvioculi*, the distal bristle of the pedipalpal patella is situated on a hump; body length 1.7–1.9 mm.

Relationships: In the most related fossil genus *Spinitharinus* the male tibia I is usually modified as in *Spinisinus* but the body length of males is 1.8–2.8 mm, strong hairs in the field of the median eyes are usually present, a retrodistal (ectal) and weakly sclerotized paracymbium is usually present and the bulbus is not flat and not twisted dorsally. See the key to the genera. In *Caudasinus* the opisthosoma is elongated beyond the spinnerets, the male tibia I bears A PAIR of apical-lateral bristles (figs. 435), the cymbium bears dorsal bristles, and the bulbus is not flat and twisted. In *Mimetidion* metatarsus I bears a row of long and strong prolateral bristles.

Type species: *Spinisinus splendidus* n. sp.

Distribution: Eocene Baltic amber forest.

***Spinisinus splendidus* n. gen. n. sp**. (figs. 396–397, photos 325–327)

Material: Holotypus in Baltic amber and a separated piece, F1416/BB/AR/CJW.

Preservation and syninclusions: The spider is excellently and almost completely preserved in a clear yellow piece of amber, only the right tarsus I and the right tarsus and metatarsus IV are cut off. Most parts of the right side and few parts of the left side of the spider are covered by a white emulsion. Few thin threads of silk are running through the piece of amber, a greater number of stellate hairs is preserved in both pieces of amber.

Diagnosis (♂; ♀ unknown): Pedipalpus (figs. 396–397, photos 326–327): Position of the distal part of the embolus near to the bulbus, basal part of the conductor in an almost cross position, distal part of the conductor away from the tip of the cymbium.

Description (♂):
Measurements (in mm): Body length 1.9, prosomal length 0.8; leg I: Femur 1.5, patella 0.4, tibia 1.2, metatarsus 1.4, tarsus 0.6, tibia IV 0.7, pedipalpal femur ca. 0.4.
Colour yellow brown.
Prosoma (photo 325) wide, partly covered by a white emulsion, fovea hidden, eyes small, situated on a prominent area, posterior row slightly procurved, posterior median eyes separated by almost two diemeters, larger than anterior medians, lateral eyes touching. Clypeus long and concave. Chelicerae small, fangs of medium length. Prosomal files indistinct, sternum elongated between coxae IV. – Legs fairly long, as in *S. parvioculi*, position of the long metatarsal I trichobothrium in 0.3, comb of tarsus IV well developed. – Opisthosoma (photo 325) long oval, widest in the middle, 1.24 times longer than high, scarcely covered with short hairs up to 0.1 mm long. Epigaster sclerotized, a ring around the petiolus exists. The colular area is hidden. – Pedipalpus (see above) with short articles, patella almost wide as long, tibia higher than long. Tiny bubbles are preserved at the origin of the slender part of the embolus.

Relationships: See *S. parvioculi* n. sp.

Distribution: Eocene Baltic amber forest.

Spinisinus parvioculi **n. gen. n. sp**. (figs. 398–402, photos 323–324)

Material: 2♂ in Baltic amber; holotypus and a separated piece, F1415/BB/AR/CJW; paratyus F1813/BB/AR/CJW.

Preservation and syninclusions: The holotype is excellently and almost completely preserved in a clear piece of amber, only the tips of the left tarsi I and II and dorsal parts of the left patella and tibia IV are cut off. Ventral parts are covered by a white emulsion, a bubble is present under the sternum and on both pedipalpal tibiae; bubbles are present on both pedipalpal tibiae. A dragline is running ventrally from the anterior spinnerets via the right leg III to the right metatarsus I. Some stellate hairs are present in both pieces of amber. – The paratype is completely and well preserved – together with stellate hairs in a piece of amber which was heated; the ventral side is thickly covered with a white emulsion. In the separated piece are a Diptera, an Acari and remains of a tiny spiderling preserved.

Diagnosis (♂; ♀ unknown: Position of the embolus in a wide loop (figs. 401–402), basal part of the conductor in an oblique position, position of the distal part of the conductor near the tip of the cymbium.

Description (♂):
Measurements (in mm): Body length 1.7–1.8, prosoma: Length 0.9, width 0.8–0.9; leg I (holotype): Femur 1.4, patella 0.33, tibia 1.05, metatarsus 1.3, tarsus 0.55, tibia IV 0.8; pedipalpal femur ca. 0.4; tibia I of the paratype 1.15.

Colour yellow brown, legs probably indistinctly annulated.
Prosoma as long as wide, with a large thoracal depression. Eyes (fig. 398) small in the holotype, slightly larger in the paratype, posterior row very slightly procurved, all eyes of about the same size, posterior medians separated by ca. two of their diameters. Chelicerae small, most parts are hidden; labium, gnathocoxae and most parts of the sternum are hidden, too. In the paratype a wide posterior field of fine stridulatory files is recognizable. – Legs fairly long, covered with long hairs; I bears two rows of long prolateral bristles and a long, bent proapical spine (fig. 399). Patellae with two dorsal bistles, sequence of the long tibial bristles 2/2/1/2. Metarsal trichobothria short, most probably absent on IV, position on II in 0.34. – Opisthosoma, 1.7 times longer than wide, widest in the middle, scarcely covered with longer hairs. Anterior spinnerets stout, colulus (fig. 400) very small and apparently hairless. In the paratype a wide sclerotized field is recognizable in front of the spinnerets which bears tiny picks. – Pedipalpus (fig. 401–402): See above; femur slender, patella short, tibia about as long as wide, dorsally with three bristles, one in the basal half and a pair distally, the prolateral one longer.

Relationships: In *S. splendidus* n. sp. the eyes are slightly larger, position and shape of the conductor are different, the loop of the embolus is more narrow.

Distribution: Eocene Baltic amber forest.

***Spinitharinus* n. gen**. (figs. 403–432, photos 26, 314–322)

Diagnosis: With a pair of usually strong hairs in the field of the median eyes (fig. 403, 417) (small in *curvatus* and sp. indet. female); strong proapical bristle of tibia I strongly reduced or even absent in the *cheliceratus* species-group. Pedipalpus (figs. 408f, 421–422) with a retrodistal/ectal paracymbium and a large to very large subtegulum.

Further characters: Tibia I bears usually two rows of long bristles (absent in sp. indet., females) and a long proapical bristle (or an apical pair) as in *Spinisinus* (fig. 399) (absent in *bitterfeldensis*, *coniectens*, *cymbialis*, sp. indet., females; unknown in *cheliceratus*); its length is very variable and it may be broken off. Fovea at least as wide as long (fig. 418). Opisthosomal sigilla present (fig. 419); the opisthosoma is not elongated beyond the spinnerets, pedipalpal tibia longer than wide to wider than long, conductor large. Body length ♂ 1.8–2.8 mm, ♀ up to 3.5 mm.

Relationships: According to the structures of the male tibia I – apical bristles and rows of strong prolateral hairs are unique within the family Theridiidae – and the single hair of the colulus *Spinisinus* is most related. In *Spinisinus* STRONG hairs in the field of the median eyes are absent, the existence of opisthosomal sigillae is unknown, an internal paracymbium is probably present, cymbium and bulbus are distorted, the body length is only 1.7–1.9 mm. In *Caudasinus* the opisthosoma is elongated beyond the spinnerets, the male tibia bears a pair of apical bristles, the cymbium bears dorsal bristles, and the structures of the bulbus are different.

Type species: *Spinitharinus bulbosus* n. sp.

Distribution: Eocene Baltic amber forest including the Bitterfeld deposit.

Key to the species of *Spinitharinus* (♂):

1 Tibia I stout, 1.1–1.2 mm long, with strong (bristle-shaped) prolateral hairs and a strong proapical (spine-shaped) bristle (similar to fig. 399); *bulbosus* species-group. 2

- Tibia I more slender, 1.4–1.85 mm long, prolaterally with only fairly strong hairs, without a proapical bristle (a thin bristle exist in *coniectens*); *cheliceratus* species-group 3

2(1) Position of the spinnerets at the end of the opisthosoma. Field of the median eyes with a pair of small and indistinct hairs (fig. 417), pedipalpus figs. 421–426 . . . curvatus

- Opisthosoma raising above spinnerets (fig. 406). Field of the median eyes with a pair of long hairs (fig. 403), pedipalpus figs. 407–412 . . . . bulbosus

3(1) Chelicerae with basal humps (fig. 413), tibia I ca. 1.6 mm long, pedipalpus (figs. 414–416): Cymbium with a strong and bent retrodistal bristle-shaped hair as in *S. cymbioseta* . . . . cheliceratus

- Chelicerae without humps (fig. 430), tibia I ca. 1.4 or 1.85 mm long, bristle-shaped hair present or absent 4

4(3) Tibia I ca. 1.4 mm long, tibia IV < tibia II, cymbium with a strong and bent retrodistal bristle-shaped hair as in *S. cheliceratus* (fig. 431), tibia I with a thin proapical hair, pedipalpus fig. . . . . cymbioseta

- Tibia I ca. 1.85 mm long, tibia IV > tibia II cymbium without such hair, tibia I with a proapical hair which is weakly enlarged, pedipalpus fig. 427–429 . . . . coniectens

***Spinitharinus bulbosus* n. gen. n. sp**. (figs. 403–412)

Material: 3♂ in Baltic amber: Holotypus F1419/BB/AR/THE/CJW, paratypus a) from the Bitterfeld deposit F1420/BB/AR/THE/CJW, paratypus b) and two separated pieces of amber, F1421/BB/AR/THE/CJW.

Preservation and syninclusions: Holotype: The spider is very well and completely preserved, few ventral parts are covered by a white emulsion, gas bubbles are situated below both pedipalpi and the left tibiae III and IV. The spider has been injured, there is a fissure at the right anterior side of the prosoma, opisthosoma and spinnerets are compressed from behind. Threads are present behind the spider as well as on and behind the right femur II. Few stellate hairs are also present. – Patatype a) is only fairly well preserved, a white emulsion covers mainly the dorsal parts of the spider, the spider may have been a prey of an unknown animal: the left leg I is amputated through the tibia near to its end and probably healed (no blood is present), the right leg I is broken between coxa and trochanter by autotomy, the right pedipalpal femur is lose, the right legs III and IV are broken broken through the base of their tibia, the right legs I and II are broken off near their base and lose, the right side of the sternal margin is open, opisthosoma and spinnerets are compressed e. g. from behind; few stellate hairs are also present. – Paratype b) is completely and fairly well preserved, mainly the opisthosoma is almost completely covered with a white emulsion, ventrally of the spider a dragline is running through the piece of amber. A branch of a stellate hair is preserved below the left metatarsis IV.

Diagnosis (♂; ♀ unknown): Opisthosoma raising above the spinnerets (fig. 406), legs fairly stout, tibia I with strong prolateral hairs and a strong proapical bristle; bulbus strongly protruding, embolus longer than the conductor (figs. 408–412).

Description (♂):
Measurements (in mm): Body length 2.6–2.8, prosoma: Length 1.2, width 1.1; leg I: Femur 1.45, patella 0.5, tibia 1.2, metatarsus 1.33, tarsus 0.6, tibia IV 0.77, pedipalpal femur 0.3.
Colour: Prosoma and legs medium brown, legs not annulated, opisthosoma yellow brown.
Prosoma almost as wide as long, fairly flat, with a deeop thoracal furrow, eye field not raised, with a pair of long hairs in the field of the median eyes (fig. 403). Posterior eye row procurved, anterior median eyes slightly the largest, posterior median eyes separated by more than one diameter. Clypeus long and concave, chelicerae fairly small and slender, fangs long and slender, the anterior cheliceral margin bears at least three teeth (visible in the holotype; the posterior margin is hidden). Fine posterior stridulatory files are present (fig. 405). Labium ca 1.7 times wider than long (fig. 404). – Legs fairly stout, slender, hairy, sequence of their length I/IV/II/III, I distinctly the longest. Patellae with 2 dorsal bristles, sequence of the long dorsal tibial bristles 2/2/1/2. Tibia I bears two rows of prolateral bristles and a strong proapical bristle which is 0.1–0.18 mm long and may (partly) be broken off. A comb of tarsus IV is present. Metatarsal trichobothria short, its position on I in 0.25. – Opisthosoma (fig. 406) 1.3–1.5 times longer than high or wide, widest in the middle, covered with short hairs, raised above the spinnerets (distinct in paratype b), antertiorly with short picks (fig. 405). The epigaster is probably hardened. Spinnerets short, the anteriors stout. A small colulus is probably recognizable in the holotype. – Pedipalpus (figs. 407–412): Femur slender, patella and tibia almost as wide as long, patella with a dorsal-distal bristle, tibia with long distal hairs, cymbium in a more medial position, narrow in the middle, subtegulum large, tegulum smaller, medium apophysis large, conductor very large, with a long basal branch and a rounded distal part, embolus long, ending near the tips of conductor and cymbium.

Relationships: *S. curvatus* may be most related, see the key.

Distribution: Eocene Baltic amber forest incl. the Bitterfeld deposit.

***Spinitharinus curvatus* n. gen. n. sp**. (figs. 417–426, photos 318–319)

Material: 3♂ in Baltic amber; holotypus F15127/BB/AR/THE/CJW; paratypus and a separated piece of amber, F1461/BB/AR/THE/CJW; paratypus F1556/BB/AR/THE/CJW.

Preservation and syninclusions: Holotypus: The spider is well preserved in a clear piece of amber which was slightly heated; a white emulsion covers dorsal parts of the prosoma, parts of the right legs I and II are cut off. Three stellate hairs are preserved left in front of the spider. – Paratypus F1461: The spider is well, completely and apparently in its catching position preserved (photo); parts of the ventral side are covered by a white emulsion, a bubble covers parts of the eye region; stellate hairs are absent. – Paratypus F1556: The spider is well and completely preserved together with a dragline.

Diagnosis (♂; ♀ unknown): Legs fairly stout, tibia I with strong anterior hairs and a strong proapical bristle similar to fig. 399; paired hairs in the field of the median eyes weak (fig. 417), pedipalpus figs. 421–426, with a short and bent apical conductor.

Description (♂):
Meaurements (in mm): Body length 2.2–2.5, prosomal length and width 1.0–1.15; leg I (paratypus): Femur 1.5, patella 0.4, tibia 1.1, metatarsus 1.3, tarsus 0.55, tibia IV 0.8; width of the eye field 0.5, diameter of a posterior median eye 0.05 (holotypus).
Colour: Prosoma and legs medium brown to dark brown (in the heated holotypus), opisthosoma light brown.
Prosoma (photos 318–319) as long as wide, with a long clypeus and short basal cheliceral articles, fovea deep, is a cross position. Eye field wide. posterior median eyes separated by almost 1 1/2 diameters (holotype); most eyes of the paratype are are hidden, a pair of weak hairs is present in the field of the median eyes (fig. 417). – Legs fairly stout, sequence of the length I//IV/II/III, I distinctly the longest, sequence of the long tibial bristles 2/2/1/2. The left tibia I of the paratype F1461 is – teratologically – bent, the right tibia I is straight. Tibia I bears two rows of prolateral bristles and a proapical bristle. Position of the metatarsal I trichobothrium in 0.35. – Opisthosoma 1.13 times longer than wide, covered with short – up to 0.15 mm long – hairs. Three pairs of dorsal sigilla are visible in the holotypus (fig. 419). The epigaster is sclerotized, the colulus bears only a single hair (fig. 420). – Pedipalpus (figs. 421–426): In the holotypus the retrodistal paracymbium is visible in both pedipalpi (in contrast to the other congeneric specimens) (see above). Embolus long and bent (the tip of the right one may be broken off), its tip close to a short and pointed part of the conductor.

Relationships: *S. bulbosus* may be most related, see the key.

Distribution: Eocene Baltic amber forest.

***Spinitharinus cheliceratus* n. gen. n. sp**. (figs. 413–416, photos 313–317)

Material: 2♂ in Baltic amber: Holotypus F1418/BB/AR/THE/CJW; paratype F1746/ BB/ AR/CJW from the Bitterfeld deposit.

Preservation and syninclusions: Holotype: The spider is fairly well preserved, both anterior legs and the left leg II are cut off through their femur, the right patella IV is cut off, both posterior legs and the right leg III are darkened by oxidation, a white emulsion covers thickly the ventral side of the spider and some dorsal part, bubbles cover parts of the pedipalpi, the left tarsus and metatarsus and the sternum. – Paratype F1746 is completely and well preserved in a heated piece of amber. Remains of a white emulsion are present on the right side of the opisthosoma, a larger bubble on its left side.

Diagnosis (♂; ♀ unknown): Legs slender, a strong proapical bristle of tibia I is absent, chelicerae with a basal hump (fig. 413), cymbium with a retrolateral bristle-shaped hair (R in fig. 415).

Description (♂):
Measurements (in mm): Body length 2.6, prosoma: Length 1.0–1.15, width 1.05; leg I of the paratype: Femur ca. 2.0, patella ca. 0.45, tibia 1.6, metatarsus 1.9, tarsus 0.6; leg II of the holotype (most parts of leg I are lost): Femur ca. 1.2, patella 0.37, tibia 0.95, metatarsus 1.1, tarsus 0.55, tibia 0.78, pedipalpal femur 0.5.
Colour yellow brown in the holotype, fairly darkened in the paratype.
Prosoma of the holotype: In the holotype most parts are hidden by a white emulsion; the hairs in the field of the median eyes are thinner than in *bulbosus*. Eyes small, field wide, posterior median eyes separated by almost 1 1/2 of their diameters. Chelicerae anteriorly with humps (fig. 413) which are better recognizable in the holotype, fovea low, eye field wide. The legs of the holotype are covered by a white emulsion, most parts of leg I are cut off. Legs of the paratype slender, order I/II/IV/III, prolateral hairs of tibia I long but not as strong as in bulbosus, more numerous, position of the metatarsal trichobothria I–III in ca. 0.2. Opisthosoma oval, dorsally probably hardened (paratype); colulus with a single hair (paratype). Pedipalpus (figs. 415–416): Patella and cymbium short, cymbium retrolaterally with a bristle-shaped hair (R). Conformation of the bulbus fairly similar to *bulbosus*.

Relationships: In *S. cymbioseta* n. sp. exist also a strong retrodistal cymbial hair but cheliceral humps are absent, the legs are longer and the structures of the bulbus are different.

Distribution: Eocene Baltic amber forest incl. the Bitterfeld deposit.

Spinitharinus coniectens **n. gen. n. sp**. (figs. 427–429)

Material: Holotypus in Baltic amber and two separated pieces of amber, F1426/BB/AR/THE/CJW.

Preservation and syninclusions: The spider is fairly well and completely preserved in a yellow piece of amber, mainly the ventral parts of the opisthosoma as well as some prosomal parts are covered with a white emulsion; bubbles are present at the left side of the prosoma, between the left legs as well as on both bulbi and cymbia. Few remains of stellate hairs and thin threads of spider's silk are also preserved.

Diagnosis (♂; ♀ unknown): Legs slender, ti I bears stronger prolateral hairs but proapically only a slightly stronger hair, pedipalpus as in figs. 427–429.

Description (♂):
Measurements (in mm): Body length 2.75, prosoma 1.2 long and wide; leg I: Femur 2.55, patella 0.6, tibia 1.85, metatarsus 2.6, tarsus 0.7, tibia II 0.9, tibia III 0.65, tibia IV 1.1; pedipalpal femur almost 0.6.
Colour yellow brown, legs indistinctly annulated.
Prosoma as long as wide, with a deep fovea, the posterior area is hidden. Eye field more than two times wider than long, eye small, posterior row procurved, posterior median eyes separated by more than their diameter, anterior median eyes smaller than posterior median eyes. Only the right long hair in the field of the median eyes is recognizable, the second one may be broken off. Chelicerae relatively long and slender, teeth of their furrows hidden, labium 1.8 times wider than long. – Legs long, hairy, sequence I/IV/II/III, I distinctly the longest. Sequence of the tibial bristles 2/2/1/2. Tibia I: See the diagnosis. Metatarsal trichobothria short, their position on III in 0.28. The ventral hairs of tarsus IV are bent but a serrated margin is not recognizable by a magnification of 150x. – Opisthosoma oval, 1.45 times longer than wide, widest in the middle, scarcely covered with short hairs. – Pedipalpus (see above): Femur only fairly long, patella 1.5 times longer than wide, with long hairs and a long, thin and erect bristle in the basal half, tibia 1.7 times longer than wide, with long hairs and a single trichobothrium.

Relationships: See the key.

Distribution: Eocene Baltic amber forest.

Spinitharinus cymbioseta **n. gen. n. sp**. (figs. 430–431, photos 320–321)

Material: Holotypus ♂ in Baltic amber and a separated piece of amber, F1745/BB/ AR/CJW.

Preservation and syninclusions: The spider is completely and well preserved; mainly the opisthosoma is covered with a white emulsion, a fissure in the amber is running longitudinally through the opisthosoma; few stellate hairs.

Diagnosis (♂; ♀ unknown): Legs fairly slender, tibia I with only fairly strong prolateral hairs, a strong proapical bristle is absent, the cymbium bears a strong and bent retrodistal hair (fig. 431).

Description (♂):
Measurements (in mm): Body length 2.0, prosoma: Length ca. 1.0, width ca. 0.9; leg I: Femur 1.65, patella 0.45, tibia 1.4, metatarsus 1.75, tarsus 0.6, tibia IV 0.75, pedipalpal femur 0.43.
Colour: Prosoma and legs medium brown, opisthosoma yellow brown.
Prosoma almost as wide as long, low, fovea indistinct, eye field wide, posterior eye row recurved, posterrior median eyes separated by almost 1 1/2 of their diameters, two long hairs in the field of the median eyes, basal cheliceral articles fairly large, without an anterior hump (fig. 430), teeth of the cheliceral margins hidden. – Legs fairly slender, order I/II/IV////, sequence of the long dorsal tibial bristles 2/2/1/2, position of the trichobothrium on metatarsus I in 0.2. – Opisthosoma 1.6 times longer than high, dorsally scarcely covered with long hairs, dorsally probably hardened or scutate, slightly elongated beyond the spinnerets. – Pedipalpus (fig. 430): Femur long and slender, patella short, tibia wide and plate-shaped, cymbium with an elongeted tipt and retrodistally with a stronger hair, paracymbium hook-shaped, in a retrodistal ectal position, conductor long, embolus screw-shaped.

Relationships: See *S.* **coniectens**, and especially *cheliceratus* in which the cymbium also bears a strong and bent retrodistal hair; see the key.

Distribution: Eocene Baltic amber forest.

Spinitharinus sp. indet. with a parasitic mite (photo 26)

Material: A subad. ♂ with a parasitic mite, F1659/BB/AR/CJW.

Preservation and syninclusions: The spider is completely and fairly well preserved, its ventral side is partly covered with a white emulsion; a dragline is running backward from the spinnerets. A parasitic mite (Acari: Trombidiidae, photo 26) is attached at the right side of the spider's prosoma. The body of the mite is covered with a thin white emulsion.

Descriptions:

(a) <u>The spider</u>: Measurements (in mm): Body length 2.1, prosoma length 0.95; leg I: Femur 1.05, patella 0.32, tibia 0.76, metatarsus 0.68, tarsus 0.48, tibia IV 0.5.

A tiny pair of hairs is present in the field of the median eyes, the fovea is indistinct, the chelicerae are fairly large, strong prolateral hairs/bristles and a proapical spine of tibia I are absent, the position of the long trichobothrium on metatarsus I is in 0.47, the pedipalpal tarsus is pear-shaped thickened.

(b) The mite is 0.6 mm long, its anterior right leg, the fine furrows of its cuticula and some bristles are recognizable. The parasite was apparently sucking behind the right coxa IV; its thick body indicates a rich meal. – A similar mite is preserved on the body of the male holotype of *Lasaeola bitterfeldensis* n. sp.

Spinitharinus **sp. indet., males**

In my private collection 4♂ of the genus *Spinitharinus* are kept which are preserved in Baltic amber: *S*. sp. indet. a-d: F1422, F1424-F1425/BB/CJW, F1514/BB/CJW. F1424 has been embedded in artificial resin after treatment with chemical substances in the Palaeontological Museum of the Humboldt University Berlin (Ms. STENZEL).

Spinitharinus **sp. indet., females** (fig. 432)

In my private collection three females are kept in Baltic amber, F1526/BB/AR/CJW, F1535 and F1536, which I regard as probable members of *Spinitharinus*. In the four females – including *kaestneri* – prolateral bristles and a proapical spine of tibia I are absent and leg I is short as it is characteristic in *Spinitharinus*. So far as visible only a single hair of the colulus exists.

F1526: Below the spider a thin spider's thread is running through the piece of amber, the piece was slightly heated. The distinct fovea of the spider is partly covered with a silvery emulsion. According to the small paired hairs in the field of the median eyes, the normal prolateral hairs of tibia I as well as the absence of a proapical spine of the anterior tibia I do not want to exclude that the female is conspecific with *S. parvus* n. sp. Measurements (in mm): Body length 3.5, prosoma: length 1.25, width 1.1; leg I: Femur 1.5, patella 0.55, tibia 1.15, metatarsus 1.4, tarsus 0.6. The dorsal opisthosomal hairs are up to 0.2 mm long, two or three opisthosomal sigilla are present, the small colulus bears a single hair, the labium is wider than long, the tarsal IV comb is well developed. Position of the metatarsal trichobothria: I in ca. 0.5, III in ca. 0.39 (ca. 0.3 in *S. parvus*). The epigyne is a wide pit (fig. 432).
F1535: The spider and a spider's thread are preserved in a heated piece of amber; the body length is 2.3 mm, the prosomal length is ca. 0.9 mm, tibia I is 0.7 mm long, the colulus is hidden. The eye region is covered with a white emulsion, the chelicerae are large, almost as long as the hight of the prosoma above them.

F1536: Measurements (in mm): Body length 2.3, prosomal length ca. 0.8, tibia I 0.75. The chelicerae are relatively large, a pair of small hairs exists in the field of the median eyes, the colulus bears a single hair, the epigyne is an indistinct pit which is slightly wider than long.

***Caudasinus* n. gen.** (figs. 433–440, photos 328–334)

The genus name is masculine.

Diagnosis (♂; ♀ unknown): Opisthosoma dorsally concave and distinctly elongated beyond the spinnerets (fig. 440). Tibia I bears a pair of apical bristles (fig. 435) (the retroapical bristle is weak in *C. regeneratus*). Pedipalpus (figs. 434, 436, 439): Cymbium with bristle-shaped hairs/bristles, paracymbium hidden and most probably in an intern position, embolus relatively short.

Further characters: Anterior median eyes separated by about their diameter, legs rather short, colulus with a pair of hairs (fig. 433).

Type species: *Caudasinus caudatus* n. sp.

Relationships: In the related genera – *Spinisinus* and *Spinitharinus* – the opisthosoma is not distinctly elongated beyond the spinnerets and dorsally not concave, a retroapical bristle of tibia I is absent, dorsal cymbial bristles are absent and the embolus is longer.

Distribution: Eocene Baltic amber forest.

Key to the species of *Caudasinus* (♂):

1 Cymbial bristles present, embolus in a more basal position (fig. 436) 2

- Cymbial bristles most probably absent, embolus in a more distal position (fig. 439) Retroapical bristle of tibia I thin . . . . *regeneratus*

2(1) Pedipalpus as in fig. 434 . . . .*caudatus*

- Pedipalpus as in fig. 436. Tibia I bears a pair of STRONG apical bristles (fig. 435) . . . .*bispinosus*

***Caudasinus caudatus* n. gen. n. sp.** (figs. 433–434, photo 333)

Material: Holotypus ♂ in Baltic amber, F1878/BB/AR/CJW.

Preservation and syninclusions: The spider is well preserved in a piece of amber which was slightly heated; both patellae I and the dorsal half of the right patella IV are cut off, the opisthosoma is dorsally covered with a thin layer of a white emulsion, bubbles are preserved between the left tibia and femur IV. Remains of some stellate hairs are preserved in the same piece of amber.

Diagnosis (♂; ♀ unknown): Conductor with a basal "rounding" (fig. 434).

Description (♂):
Measurements (in mm): Body length 2.6, prosomal length 1.0, opisthosomal length 1.6, metatarsus I 1.65, tarsus I 0.6, leg IV: Tibia ca. 0.5, metatarsus 0.95, tarsus 0.47, pedipalpal femur 0.6.
Colour: Prosoma and legs medium to dark brown, opisthosoma yellow brown.
Prosoma bearing short hairs, with a pair of hairs in the field of the median eyes. Fovea deep and wide, eyes fairly small, anterior medians protruding, separated by about their diameter, posterior row slightly procurved; most mouth parts are hidden, labium free. The sternum separates the coxae IV by more than their diameter. Posterior stridulatory files unknown (the area is hidden). – Legs fairly short, bearing long hairs, I longest, sequence of the long tibial bristles 2/2/1/2. Two patellar bristles, the distal one very long. Tibia I as in *C. bispinosus* (fig. 435), prolateral bristle-shaped hairs fairly strong developed, comb of tarsus IV well developed, position of the trichobothrium on metatarsus I in 0.28. – Opisthosoma 1.75 times longer than high, scarcely covered with hairs of medium length, distinctly elongated beyond the spinnerets (similar to fig. 440), sigilla unknown (the area is hidden), epigaster sclerotized, spinnerets short, colulus (fig. 433) small, bearing a pair of hairs in a distal position. – Pedipalpus (see the diagnosis; fig. 434) with a short patella and a fairly long tibia, cymbium dorsally-distally with bristle-shaped hairs.

Relationships: In *C. bispinosus* the conductor is almost triangular and the embolus is wider.

Distribution: Eocene Baltic amber forest.

***Caudasinus bispinosus* n. gen. n. sp.** (fig. 435–436)

Material (in Baltic amber): Holotypus ♂, F1563/BB/AR/CJW.

Preservation and syninclusions: The spider is well and completely preserved, the opisthosoma is deformed, the left side is covered with a white emulsion, below the left side of the prosoma lies a large bubble. A thin spider's thread is running cross near the spinnerets above the opisthosoma. More than 20 stellate hairs exist in the same piece of amber.

Diagnosis (♂; ♀ unknown): Pedipalpus: Fig. 436; the conductur has an almost triangular shape.

Description (♂):
Measurements (in mm): Holotype: Body length 2.2, prosomal length ca. 0.9; leg I: Femur 1.65, patella 0.4, tibia 1.1.5, metatarsus 1.4, tarsus 0.6, tibia IV 0.8.
Colour: Prosoma and legs medium to dark brown, legs not annulated, opisthosoma light brown.
Prosoma wider than long, eyes fairly large, a pair of long and bent hairs exists in the field of the median eyes; fovea large, slightly wider than long, clypeus long, basal cheliceral articles short, fangs hidden. – Legs rather short, order I/IV/II/III, I long, femur I is more or less variable bent, sequence of the long dorsal tibial bristles 2/2/1/2 , tibia I bears two rows of strong prolateral hairs (7–8 each row) and a pair of strong (spine-shaped) apical bristles (fig. 435), the retrolateral one is smaller. Position of the trichobothrium of metatarsus I in 0.25. Opisthosoma dorsally covered with longer hairs, with an inclination in the middle and elongated beyond the spinnerets like in fig. 440. A colulus is not surely recognizable, the epigaster is sclerotized. Pedipalpus (fig. 436): Cymbium with half a dozen stronger hairs/bristles in the distal half; a retrodistal paracymbium is most probably absent. Bulbus not much protruding, conductor widened apically at both sides, almost triangular, embolus sickle-shaped, of medium size.

Relationships: See *C. caudatus* n. sp.

Distribution: Eocene Baltic amber forest.

***Caudasinus regeneratus* n. gen. n. sp**. (figs. 437–439, photos 328–332)

Material: Holotypus ♂ in Baltic amber, F1907/BB/AR/CJW.

Preservation and syninclusions: The spider is well and completely preserved in a large yellow piece of amber which was not heated. A larger Trichoptera and a tiny Diptera which bears a parasitic Acari were separated. The anterior part of the prosoma, the right side and some ventral parts of the spider are covered with a white emulsion. The left leg III is a regeneration (photos 331–332, fig. 438), its tarsus is absent, the metatarsus is blunt, tibia and metatarsus are strongly shortened and almost smooth. A phoretic Nematoda: Rhabditida (photo, fig. 437) – body length 1 mm – is preserved below the left anterior tibia and apparently attached near the base of the tibia.

Diagnosis (♂; ♀ unknown): Retroapical bristle of tibia I small, cymbium most probably without dorsal bristles, embolus fairly bent, in a more distal position (fig. 439).

Description (♂):
Measurements (in mm): Body length 2.5, prosomal length 1.1; leg I: Femur 1.75, patella 0.5, tibia 1.3, metatarsus 1.65, tarsus 0.55, tibia IV 0.9.
Colour: Prosoma and legs medium brown, opisthosoma light brown.
Prosoma: Most parts are covered with a white emulsion. – Legs (figs. 437) slender, order I/IV/II/III, bristles thin, sequence as in the genus. Tibia I bears strong prodorsal hairs and a strong proapical bristle, the retroapical bristle is weak. Position of the trichobothrium on metatarsus I is in 0.22, a comb of tarsus IV is apparently absent. – Opisthosoma twice as long as high, covered with fairly short hairs, distally elongated above/beyond the spinnerets which are quite short. – Pedipalpus (fig. 439): Femur slender, patella very short, tibia about as long as wide, cymbium apparently without dorsal bristles, subtegulum large, conductor long, embolus fairly bent, in a more distal position.

Relationships: In *C. caudatus* and *bispinosus* exist distinct cymbial bristles and the embolus has a more basal position; in *bispinosus* exists a pair of strong apical tibial I bristles.

Distribution: Eocene Baltic amber forest.

***Caudasinus* sp. indet.** (fig. 440, photo 334)

Material: 1♂ in Baltic amber, F1423/BB/AR/CJW.
The spider is well preserved, some distal leg articles are cut off, most ventral parts of body, legs and pedipalpi are thickly, the dorsal side of the opisthosoma (fig. 440, photo 334) is weakly covered with a white emulsion, the body length is 2.3 mm, a dragline is present.

***Mimetidion* n. gen.** (figs. 441–444, photos 335–336)

The gender of the name is neuter.

Diagnosis (♂; ♀ unknown): Metatarsus I bears a prolateral row of strong bristles (fig. 441), spinnerets apparently strongly reduced (its wide field is deformed); pedipalpus (figs. 442–444) with a retrodistal/ectal paracymbium and a large furcate apophysis (the TTA?) which stands widely out, the embolus is guided by a large conductor and a sickle-shaped secondary conductor.

Type species (by monotypy): *Mimetidion furca* n. sp.

Relationships: The existence of spine-shaped bristles on the anterior pair of legs is a characteristic pattern of the tribus Spinitharini. The apparently reduced spinnerets are in concordance with the reduced capture web in members of the Episinae. The retroectal-distal paracymbium of *Mimetidion* is similar to members of *Spinitharinus* in which the comb of tarsus IV is well developed, the spination of the legs and the structures of the bulbus are different. – The unusual row of prolateral bristles of metatarsus I – which reminds on certain members of the Mimetidae –, and a furcate tegular apophysis – which is similar to certain members of the Araneidae – are unknown in other members of the Theridiidae. Such strong bristles or spines are rather rare within the superfamily Araneoidea but they exist in several families, in the Araneidae, Linyphiidae, Mimetidae, Theridiidae and Theridiosomatidae; in some members of the family Tetragnathidae exist prolateral thorns of metatarsus I, see e. g. WUNDERLICH (2004: 943, fig. 10). The spine-shaped bristles may occur in both sexes; they are extremely developed in *Chthonos* CODDINGTON 1986 (Theridiosomatidae), in which they exist on tibiae, metatarsi and partly the tarsi of legs I–II, and in numerous members of the Mimetidae in which they are used for capturing spiders. See figs. 23–29 above.

Distribution: Eocene Baltic amber forest.

***Mimetidion furca* n. gen. n. sp**. (figs. 441–444, photos 335–336)

Material: Holotypus ♂ in Baltic amber and a separated piece of amber, F1660/BB/AR/CJW.

Preservation and syninclusions: The piece of amber was slightly heated. The spiders legs are incompletely preserved in an amber piece which was slightly heated, only the right legs III and IV are complete, the left legs I–IV are cut off through their femora, the tarsi and most parts of the metatarsi I and II are cut off, the opisthosoma is somewhat deformed, most parts of body and legs are covered with a white emulsion. – Few thin spider's threads are preserved distally, laterally and ventrally of the opisthosoma; stellate hairs and the distal part of a ca. 1 cm long leg of an Opiliones are preserved right of the spider; a 1.5 mm long beetle is preserved in the separated piece of amber.

Diagnosis: See above.

Description (♂):
Measurements (in mm): Body length 3.3, prosoma: Length 1.7, width 1.7; leg I: Femur 2.9, patella ca. 1.0, tibia ca. 2.3, tibia IV 1.65, pedipalpal femur 0.75.
Colour unsure because of a white emulsion, apparently mainly light.
Prosoma wider than long, with short hairs and a distinct fovea. 8 large eyes in a narrow field close together, anterior median eyes apparently the largest, posterior row straight, posterior median eyes separated by ca. 3/4 diameter, hairs in the field of the median eyes unknown. Clypeus distinctly longer than the eye field, chelicerae longer than the eye field, fangs long, too, mouth parts hidden. – Legs fairly long; various articles are

cut off, conspicuously covered with numerous long hairs, tarsus III–IV distinctly shorter than metatarsus III–IV, femora bristle-less, all patellae with 2 dorsal bristles, sequence of the dorsal tibial bristles 2/2/1/2, metatarsal III preening comb and tarsal IV comb absent. Remains of the right metatarsus I (fig. 441) show strong and widely spaced prolateral bristles, short bristles between them are absent. The paired tarsal claws bear probably only a single tooth, the unpaired claw is strongly bent and relatively small. – Opisthosoma soft, somewhat deformed, oval, slightly longer than wide, high, without humps, dorsally scarcely covered with long bristles; the area of the spinnerets is wide, deformed and partly hidden; the spinnerets look like sunk in and are strongly reduced, the area of the colulus is hidden. – Pedipalpus (figs. 442–444, photos 335–336): See the genus; the tibia bears 2 dorsal bristles, the stout cymbium bears distally long and strong hairs in an irregular row, the bulbus is wide, a questionable median apophysis exist near the the centre of the bulbus near the embolus.

Relationships: See above.

Distribution: Eocene Baltic amber forest.

7. ARGYRODINAE

This subfamily has mainly a tropical distribution; sure members in Baltic amber are unknown, see above and below (fake). – Most species are easily recognizable by the opisthosoma which bears silvery markings and is posteriorly elongated beyond the spinnerets, the anterior outgrowths of the male prosoma (fig. 445b), the complete absence of tibial bristles, and the long unpaired tarsal claws which are strongly bent; see the key to the theridiid subfamilies above.

Diagnosis: Dorsal tibial bristles completely absent, unpaired tarsal claws (at least in the female) longer than the paired claws (fig. 445c), ♂-prosoma usually with 1–2 projections (figs. 445b, 446) which may bear hairy areas, opisthosoma usually more or less extending beyond the spinnerets (fig. 445b) and with silvery markings. Capture web reduced or absent; most spiders are kleptoparasites or araneophages, see AGNARSSON (2004).

Further characters: ♂-clypeus long, a clypeal projection is absent e.g. in ?*Argyrodes incertus* WUNDERLICH 1995 from the Canary Islands; colulus present and bearing (usually?) a pair of hairs, paracymbium in an ectal retrodistal position. According to AGNARSSON (2004: 469) “venterolateral suprapedicellate setal proprioreceptors” are absent in the Argyrodinae.

Genera: *Argyrodes* SIMON 1864 s. l. is the very diverse nominate genus; some of its species-groups may be regarded as genera of their own, e. g. the *cancellatus* group = *Bellinda* KEYSERLING 1884), see AGNARSSON (2004: 468–469), as well as *Ariamnes* THORELL 1869, *Deelemanella* YOSHIDA 2003 (probably = *Argyrodes orbitus* group), *Faiditus* KEYSERLING 1884, *Neospintharus* EXLINE 1950, *Rhomphaea* L. KOCH 1872 and *Spheropistha* YAGINUMA 1957. A revision is needed.

Relationships: Episinae or Hadrotarsinae may be most related, see above and ARNEDO et al. (2004).

Distribution: Extant: Cosmopolitical, mainly tropical; fossil: Tertiary Dominican amber forest, see WUNDERLICH (1988). (A fake in Baltic amber: See below).

***Argyrodes (Ariamnes) copalis* n. sp.** (figs. 446–449) (photos 337–338)

Material: Holotypus ♂ in copal from Columbia, probably from Pena Blanca, F1691/CC/AR/CJW.

Preservation and syninclusions: The spider is well preserved just below the surface and corner (the pedipalpi) of the piece of young fossil resin. The piece of copal has numerous fissures at its surface. Bulbi and eyes are partly hidden, the right legs I and II are cut off through the base of their femur, the left femur I is cut off near its end. – Syninclusions (apparently no prey of the spider): 1 Formicidae, 1 small Lepidoptera, 1 tiny Coleoptera, 5 Diptera and remains of insects. – The holotype is now stored in paraffin.

Diagnosis (♂; ♀ unknown): Opisthosoma vermiform, almost 13 times longer than the prosoma; cephalic part (fig. 446) with two hairy areas, the dorsal hairs are directed forewards, the anterior hairs upwards; tibia II bears distally-retroventrally 2 short bristles (fig. 447), pedipalpus slender, bulbus with a thick sperm duct (fig. 448).

Description (♂):
Measurements (in mm): Body length 18, prosoma: Length 1.4, width 0.7, opisthosomal length in front of the spinnerets 2.0, diameter near its base 0.45; leg I (most parts are cut off): Femur > 4.5, leg II: Femur 3.2, patella 0.4, tibia 2.55, metatarsus 1.5, tarsus 1.1, tibia III 0.9, tibia IV 3.9.
Colour light yellow brown.
Prosoma (see fig. 446 and the photos 337–338) low, twice as long as wide, most eyes and mouth parts are not sure recognizable. – Legs I, II and IV very long and slender (see the photos), III distinctly the shortest, tibia II retroventrally-distally with two small bristles; no other leg bristles are recognizable, unpaired tarsal claws longer than paired claws. – Opisthosoma (see the photos) vermiform, dorsally-distally with thicker hairs, beyond the spinnerets 8.3 times longer than in front of the short spinnerets, pointed apically. – Pedipalpus (figs. 448–449): Tibia longer than wide, bulbus slender sperm duct wide, embolus apparently hidden.

Relationships: According to the vermiform opisthosoma and the straight clypeus *copalis* is a member of the subgenus *Ariamnes* THORELL 1869. Probably *A. mexicanus* (EXLINE & LEVI 1962) from Mexico is most related; in *mexicanus* the hairy areas of the male prosoma are different (an anterial field is absent) and the sperm duct within the tegulum is not so wide.

Distribution: Columbia, young resin (copal); the species is probably not extinct.

A faked spider of the Argyrodinae in "Baltic amber"

I regard this single member of the genus *Argyrodes* SIMON 1864 (fig. 445, photos 12–13) as a fake, see the chapter on this matter above. Fossil members of the Argyrodinae are known from copal of Columbia and Madagascar, from Miocene Dominican amber but unknown from Eocene Baltic amber.

8. ANELOSIMINAE n. subfam.

Anelosiminae: WUNDERLICH (2004: 1246); LEVI in UBICK et al. (2006: 236) (nomen nudum).

Only very few members of a single genus are known from Baltic amber, six specimens of *Kochiuridion* n. gen. – Extant genera (see also below): *Anelosimus* SIMON 1891 s. l., *Kochiura* ARCHER 1950, and *Selima* SAARISTO 2006 (with the new subgenus *Clavilosimus*); in my opinion the genus *Anelosimus* has further to split up; see AGNARSSON (2004: 469–470, 476) and SAARISTO (2006) (*Kochiura* and *Selimus*).

Diagnosis: Colulus tiny (most often) or small, bearing 1 or 2 hairs which are much longer than the colulus and are usually – at least in the extant taxa – inserted in a distal position (figs. 465–469; compare fig. 459 of a fossil species), opisthosoma dorsally most often with a dark longitudinal band (fig. 450) (it may be reduced), in the male sex sclerotized around the pedicel incl. the medial part of the epigaster (except in *Kochiura*). Sequence of the dorsal tibial bristles frequently 2/2/1/2: In *Kochiuridion* (fig. 458) and probably in all species of *Anelosimus* s.l., but 1/1/1/1 in *Kochiura* and *Selimus* (at least in the subgenus *Clavilosimus*), anterior AND posterior margin of the cheliceral furrow bear teeth (they are usually large on the promargin of males (fig. 456), the posterior margin bears two or more small teeth), paracymbium hidden in an internal position of the cymbium; probably loss of viscid elements of the capture web.

Further characters: Legs slender, I longest (IV may be shorter than II), metatarsi I–II frequently bent, gnathocoxae not strongly converging above the labium in the extant taxa but strongly converging in the fossil genus *Kochiuridion* (fig. 457), no gumfooted lines of the capture web; "tendencies" to (a) spine-shaped ventral hairs of metatarsus I or thickened hair bases (fig. 451) in extant species, (b) reduction of the paired colular hairs to a single hair (figs. 459, 465–467), (c) ridges on epigynal plate which may bear an appendage (clavus) (e. g. in the European *Selimus pulchellus* and *vittatus*, fig. 452a)), and (d) sociality/maternal care (unknown in the fossils).

Remarks: To my knowledge and findings a – reduced – colulus exists in all fossil and extant taxa of the Anelosiminae (contra e. g. LEVI & LEVI (1962) and AGNARSSON (2004)); in most members of *Anelosimus* it is sunk in like in a hole (similar to the Phoroncidiinae), the colular area may be hidden by weakly sclerotized cuticula and has to dissect for a closer investigation, compare fig. 468, but doubtless a colulus exists. The tradition of the incorrect observation of the "absence" of a colulus survived surprisingly almost half of a century and generations of taxonomists. – (2) Note that the relationships of the fossil genus *Kochiuridion* are not quite sure; the diagnosis of the Anelosiminae would be different if *Kochiuridion* is excluded from this subfamily.

Type genus: *Anelosimus* SIMON 1891 s. l. (extant); see AGNARSSON (2004: 469–470).

Further genera: *Kochiura* ARCHER (1950) (extant; removed from the synonymy of *Anelosimus* by AGNARSSON (2004: 469)), *Selimus* SAARISTO 2006 (extant), and *Kochiuridion* WUNDERLICH n. gen. (fossil in Baltic amber).

Remark: The extant European species *pulchellus* (WALCKENAER 1802) (from *Aranea*) and *vittatus* (C. L. KOCH 1836) (from *Theridium*) are transferred here from *Anelosimus* to *Selimus* (**n. comb**.), and its new subgenus *Clavilosimus*, see below. *Anelosimus* is not present in Europe.

Relationships: In the Theridiinae exists also an internal and hooded paracymbium and gumfooted lines are lost, too. In contrast to the Anelosiminae a colulus and its hairs, and teeth of the posterior margin of the cheliceral furrow have completely been lost in the Theridiinae *Chrysso* sp. may be an exception, see below); a longitudinally dark band of the opithosoma is very rarely present (convergently evolved).

Distribution: Extant: Cosmopolitical; fossil: In Eocene Baltic amber: *Kochiuridion* n. gen.; *Anelosimus clypeus* WUNDERLICH 1988 in Dominican amber may be a member of the Theridiinae; a colulus is apparently absent.

(a) Key to the extant and fossil European (sub)genera of the Aneloseminae:

1 Gnathocoxae strongly converging above the labium (fig. 457); sequence of the dorsal tibial bristles 2/2/1/2. ♂: Epigaster sclerotized, pedipalpus (figs. 460f) with strong apical tibial bristles and a long embolus in a circular/looped position which is not guided by short hairs of the cymbial margin. ♀ unknown. Extinct, Baltic amber. *K. pecten* . . . . Kochiuridion

- Gnathocoxae (almost) parallel; sequence of the tibial bristles 1/1/1/1. ♂-pedipalpus fairly similar in *Kochiura*. Extant 2

2(1) ♂: Epigaster distinctly sclerotized, pedipalpus (fig. 452) with long cymbium and bulbus and with a long embolic outgrowth. ♀: Epigyne (fig. 452a) with a posterior outgrowth (clavus) which is directed anteriorly. *S. pulchellus* and *vittatus* . . .*Selimus: Clavilosimus*

- Epigaster not sclerotized. ♂-pedipalpus (fig. 453): Tibia with numerous long hairs; the embolus has a circular/loped position and is guided by short hairs of the cymbial margin. ♀: The epigyne is a wide plate, a clavus is absent. *K. aulica* . . . . Kochiura

(b) The extant genus *Selimus* and the new subgenus *Clavilosimus*:

Selimus **SAARISTO 2006** (figs. 450–452)

Type species: *Theridion placens* BLACKWALL 1877 from the Seychelles.

Diagnosis: ♂-pedipalpus (fig. 452): Cymbium long, bulbus long and modified in a special way, embolus with a large basal outgrowth.

Further characters: Prosomal stridulatory files absent, anterior margin of the cheliceral furrow with at least one large tooth, posterior margin with three or more teeth, sequence of the tibial bristles 1/1/1/1 in the European species of the subgenus *Clavilosimus* (unknown in the nominate subgenus), comb of tarsus IV well developed, metatarsal III trichobothrium present, paracymbium hood-shaped.

Relationships: In *Kochiura* – see the key above – exists a coiled embolus, in *Anelosimus* a long basal embolic outgrowth is absent.

Distribution: Seychelles (the nominate subgenus *Selimus*), Palaearctic and N-Africa (the new subgenus *Clavilosimus*).

***Clavilosimus* n. subgen. of *Selimus* (figs. 450–452a)**

Type species: *Theridium vittatum* C. L. KOCH 1836. Further species: *Aranea pulchella* WALCKENAER 1802 (= *Anelosimus pulchellus*).

Diagnosis: Embolus long (fig. 452), epigyne with a large aboral outgrowth (clavus) which is directed foreward (fig. 452a).

Further characters: Ventral cusps of metatarsus I well developed, epigaster sclerotized, the small colulus bears a single hair.

Relationships: In the subgenus *Selimus* SAARISTO 2006 the embolus has a spike-like shape and a clavus of the epigyne is absent.

Remark: SAARISTO (in litt. in IV 2007) regarded *vittatus* and *pulchellus* – part of the *Theridion vittatus*-group sensu WIEHLE (1937: 137) – as members of an unnamed subgenus of *Selimus*.

Distribution: Palaearctic, N- Africa.

(c) The only kown genus in Baltic amber:

***Kochiuridion* n. gen.** (figs. 454–464, photos 339–340)

Diagnosis (♂; ♀ unknown): Sequence of the dorsal tibial bristles 2/2/1/2 (fig. 458), caput convex (fig. 455), basal cheliceral articles rather large, anterior cheliceral margin with at least one large tooth (fig. 456); pedipalpus (figs. 460–463): Tibia with long and strong (bristle-shaped) hairs, cymbium retrolaterally – fairly away from the margin – with a row of long hairs, embolus coiled.

Further characters: Posterior eye row procurved (fig. 454), posterior margin of the cheliceral furrow with at least 2 teeth, gnathocoxae strongly converging above the labium (fig. 456), ventral thickened hair-bases of legs I–II absent, legs I and II longer than IV, body length only 1.3 mm. See also the characters of the subfamily.

Type species: *Kochiuridion pecten* n. sp. (the only known species of the genus).

Relationships: Mainly according to the existence of a tiny colulus which bears a long hair, the toothed margins of the chelicerae, and the absence of a retroectal paracymbium I regard *Kochiuridion* – with some hesitation – as a member of the subfamily Anelosiminae. In the extant genera *Selima* and *Kochiura* the tibiae bear only a single dorsal bristle (their sequence may be 2/2/1/2 in *Anelosimus*), the gnathocoxae are not strongly converging above the labium, and thickened hair bases of legs I–II may exist. In the extant genus *Kochiura* (fig. 453) the embolus is guided by cymbial hairs as in *Kochiuridion* but the conductor is elongated in contrast to *Kochiuridion*; in *Kochiura aulica* (C. L. KOCH 1838) exists a row of long bristle-shaped and "serrated" hairs on the apical tibial margin of the male pedipalpus similar to *Kochiuridion* (but in *Kochiuridion* exist stronger bristles). Because of the absence of such hairs in other congeneric species besides *aulica* and because of the differences in the chaetotaxy and the shape of the gnathocoxae I regard these long tibial hairs as most probably convergently evolved in *Kochiuridion pecten* and *Kochiura aulica*. – In the Eocene genus *Kochiuridion* the basic (ancestral) theridiid sequence of the dorsal tibial bristles – 2/2/1/2 – is still present, while the number of tibial bristles is reduced to a single one in certain extant taxa of the subfamily Anelosiminae, see the key. – In *Succinura* n. gen. (Pholcommatinae) exist stout legs with short metatarsi, only a single dorsal tibial bristle and a dorsal opisthosomal scutum, the posterior median eyes are nearer to the laterals than to each other (most characters are diagnositic for the Pholcommatinae); the embolus is guided by a row of short hairs at the cymbial margin (fig. 203) (similar to the convergently pattern in *Kochiura aulica*), and the subtegulum is much larger.

Distribution: Eocene Baltic amber forest incl. the Bitterfeld deposit.

***Kochiuridion pecten* n. gen. n. sp.** (figs. 454–464, photos 339–340)

Material: 6♂ in Eocene Baltic amber, holotypus from the Bitterfeld deposis, F1820/ BB/ AR/CJW, paratypes: F1821-1824/BB/AR/CJW (F1823 from the Bitterfeld deposit), 1♂ and 3 separated pieces of amber coll. ERNST in Skagen, Denmark.

Preservation and syninclusions: The holotype is well and completely preserved in a heated piece of amber which is broken off and lost with the left legs I and II beyond their patellae; ventrally exist remains of a white emulsion. The spider has been injured: The opisthosoma is dorsally impressed. Stellate hairs as well as the exuvia of a tiny insect larva and some pollen grains (from Fagaceae?) are also preserved. – Paratype F1821 is almost completely preserved in a yellow piece of amber which was not heated, dorsal parts of the right patella I are cut off, mainly the opisthosoma is dorsally covered with a white emulsion. The spider is injured and was probably the prey of a spider (cannibalism?): The right femur I is strongly depressed laterally (sucked out?), the opisthosoma is dorsally distinctly impressed, and the prosoma is distinctly deformed (shrunk) laterally on both sides. A thin spider's thread without droplets is running from the left side sidewards. Few stellate hairs and numerous coffee-pear-shaped pollen grains (fig. 464, photo 440) (originating from a Fagaceae?) are also preserved. – F1822 is completely and quite well preserved, situated in a lateral position on a layer in the amber. Hyphae and the branch of a stellate hair are preserved in the same piece of amber. – F1823 is completely and well preserved without dorsal white emulsions in a piece which was heated; ventrally are few remains of a white emulsion preserved, a bubble exists ventrally between the left femur IV and the opisthosoma; stellate hairs are absent. – F1824 is completely but not well preserved between fissures in the fossil resin; white emulsions are present. The spider has been injured, the opisthosoma is dorsally strongly impressed. Just right of the spider is the drop of amber within the amber enclosed. – The paratype of the coll. ERNST is completely and fairly well preserved together with a lump of stellate hairs; the spider is deposited on its left side on a layer of amber; most parts of its right side are covered with a white emulsion, a double dragline is running backwards from the spinnerets, some pollen grains (probably from a Fagaceae) are preserved just behind the opisthosoma of the spider.

Remarks: Four of the six males are injured/deformed; in the same layer near three of these spiders – an unusual high percentage – are pollen grains (probably of Fagaceae) preserved (fig. 464), see ARNOLD (1998). Fagaceae do not produce resin. From these findings we may conclude that these spiders were probably blown during a stormy weather from an oak or another Fagaceae to a resin-producing tree of the family Pinaceae. These events may explain the rareness of these spiders in Baltic amber and their frequent injuries.

Diagnosis (♂; ♀ unknown): See the diagnosis of the genus. The pedipalpal tibia bears 7 bristles (or bristle-shaped hairs) (fig. 460).

Description (♂):
Measurements (in mm): Body length 1.3, prosoma length 0.65–0.7, width 0.56–0.62; leg I: Femur 1.05, patella 0.4, tibia 0.85, metatarsus 0.8, tarsus 0.38, tibia IV 0.55; pedipalpus: Femur 0.3, patella 0.13, tibia 0.17.
Colour: Prosoma and legs yellow to redbrown, opisthosoma yellow brown.
Prosoma (photos 339–340, figs. 454–457) with few longer dorsal hairs on the convex cephalic part, not rugose, fovea indistinct, eyes small, posterior row procurved, posterior median eyes separated by slightly more than their diameter, clypeus long, basal cheliceral articles longer than the clypeus, fairly diverging in the paratype F1823. Teeth on the cheliceral furrow: Anterior margin with a single large one, posterior margin with at least two small teeth. Fangs very long and slender, labium not wider than long, gnathocoxae strongly converging above the labium, sternum wide, not rugose, weakly elongated between coxae IV. – Legs (fig. 458) long and slender, order I/II/IV/III, II distinctly longer than IV, tarsi distinctly shorter than metatarsi, sequence of the long tibial bristles 2/2/1/2, metatarsal trichobothria I–III present, their position on I in ca. 0.33. Unpaired tarsal claws of medium length, bent in a right angle. – Opisthosoma (figs. 445, 459) egg-shaped, fairly covered with hairs of medium length, epigaster strongly sclerotized. There is a large sclerotized margin around the pedicel and a rugose – stridulatory? – dorsal and lateral field. The tiny colulus is recognizable in the paratypes F1821 and F1822, and bears a long hair. – Pedipalpus (figs. 460–463) (see above): The short patella bears a long dorsal-distal bristle, the tibia is wide and bears 7 long apical

bristle-shaped hairs, cymbium retrolaterally with a row of long and fairly thin hairs away from the cymbial margin, retrodistal paracymbium absent, conductor large.

Relationships: See the genus.

Distribution: Eocene Baltic amber forest, incl. the Bitterfeld deposit.

9. THERIDIINAE

with the questionable report of two genera of the Theridiinae in Baltic amber

Today this is the most diverse subfamily of the Theridiidae; it has a cosmopolitic distribution. Eocene fossils in Baltic amber: I found among thousands of Theridiidae only very few males which probably are members of the subfamily Theridiinae (see below) but no member which is closely related to *Theridion* WALCKENAER 1805 or even to the tribus Theridiini. A colulus may be absent, and an ecternal (retrodistal) paracymbium is absent in these taxa; an internal paracymbium (fig. 472) is recognizable in a single fossil specimen.

According to the egg-shaped or globular shape of the opisthosoma and the absence of a colulus the members of the two genera in question may be members of the Theridiinae, but a convergent loss of the colulus and the presence of the ectal paracymbium as well – like in the genus *Coscinida* of the Hadrotarsinae – cannot be excluded. These spiders – if really Theridiinae – would be the first report of this subfamily in the Early Tertiary, and furthermore its geologically oldest report at all.

From these findings – the rarity or even absence of Eocene Theridiinae – one may conclude that this subfamily diversified not before the Oligocene (see the similar conclusions by MARUSIK & PENNEY (2005)); the exact point of time of its origin remains unknown although its sister taxon – Anelosiminae – is most probably known from the Eocene Baltic amber forest (too), see above.

Diagnosis: Theridiinae is the only subfamily of the Theridiidae which has the following combination of characters (*) (most are “negative characters”): (1) A complete absence of colulus and its hairs (fig. 471) (**); (2) the absence of teeth of the posterior cheliceral margin (***); (3) the absence of a retrodistal/ectal paracymbium, and (4) the presence of an internal paracymbium (fig. 472) (convergently evolved in other subfamilies of the Theridiidae, too, see fig. 330). According to SAARISTO (2006) furthermore (5) the ejaculatory ducts of the “theridiid tegular apophysis 2” lacks always loopings.

(*) A quite similar combination of characters exists in *Coscinida* SIMON 1895 (Hadrotarsinae) in which two pairs of receptacula seminis exist, see above.

(**) This loss happened convergently in different subfamilies, for example within the Hadrotarsinae (e. g. in *Coscinida*), in some Episinae, and probably in certain fossil Anelosiminae (a strong reduction like in the Phoroncidiinae).
(***) Except in male *Arctachaea*; LEVI & LEVI (1962: Fig. 22) reported a species of *Chrysso* as another exception.

Further characters and variability: Usually not tiny spiders but males of *Echinotheridion* and *Tidarren* – as a sexual size dimorphism –, and *Paidiscura* may be only about 1.5 mm long. All tibiae bear at least a single dorsal bristle, sequence of the tibial bristles basicly 2/2/1/2 (reduced numbers: See the tab. below); an intrageneric variability of their number exists in *Paidiscura*. Trichobothrium on metatarsus IV absent, on III basicly present, trichobothrial position most often in the second quarter of the article (see below the tab. and the key to the genera). The teeth of the paired tarsal claws are reduced/absent in *Rugathodes*. Sexual dimorphic outgrowth of the male prosoma very rare, see *Thymoites* (fig. 604). Opisthosoma most often globular and bearing a pattern, in some taxa it is oval or higher than long at least in the female (*Achaearanea, Achaeridion, Echinotheridion, Tidarren*, figs. 482, 485) or wider than long (*Paidiscura*, *Theridula*, figs. 547, 599), dorsal opisthosomal scutum absent, scutate ring around pedicel which covers the epigaster only very rarely existing (e. g. in *Coleosoma*). The male epigaster is distinctly convex (figs. 580–581, 595) in genera of the tribus Theridiini. The chelicerae are large, occasionally enlarged and diverging in the male sex (e. g. in *Phylloneta* and *Rugathodes* (figs. 556, 564); the anterior margin of the cheliceral furrow bears usually 0–1 tooth, rarely more: In *Canalidion*, *Coleosoma* (part.), *Neottiura, Nesticodes* and *Rugathodes*, see the tab. below. The prosomal-opisthosomal stridulatory organ may be well developed, the comb of the tarsus IV is well developed. The male pedipalpus is largest in *Neottiura* (fig. 532), smallest in *Theridula* (fig. 603), Keijia (fig. 523), and *Macaridion* (fig. 530), the cymbium is distally distinctly modified e. g. in *Achaearanea, Echinotheridion, Neottiura*, and *Tidarren*, the internal paracymbium is usually hood-shaped (fig. 573) but hook-shaped e. g. in *Tidarren*, see KNOFLACH & VAN HARTEN (2001), a radix is basicly present but absent in *Achaearanea* and *Theridula* (fig. 603), a median apophysis is absent in *Theridula* (fig. 603), the longest emboli exist in *Paidiscura* (fig. 552), *Sardinidion blackwalli* (fig. 574), and certain *Theridion*. The epigyne has usually a single large introducing opening/groove, e. g. in *Theridion* and *Keijia* (fig. 526) or a pair of openings (e. g. figs. 600, 608), a clavus which is strongly sclerotized and stands widely out, exists e. g. in *Echinotheridion, Neottiura bimaculata* and *Tidarren* (e. g. figs. 507–508), the introductory ducts are short to very long, a single pair of receptacula seminis exists. The capture web is well developed, its kinds are derived, gum-footed lines are absent.

Relationships: Apparently Anelosiminae is most related, see above.

Remarks: (1) The very diverse Theridiinae may be monophyletic – see ARNEDO et al. (2004); in my opinion a larger number of taxa has to study in the future before sure conclusions can be drawn – but I do not want to exclude that they are polyphyletic or paraphyletic; see e. g. the tribus Theridulini.
(2) Doubtless there are numerous undescribed extant tribus of this subfamily, see below.
(3) Questionable relationships: The armoured extinct genera *Succinura* n. gen. and *Vicipholcomma* n. gen. – in which a retrobasal paracymbium and probably a colulus

are absent – are regarded by me as questionable taxa of the subfamily Pholcommatinae, see above, but I do not want to exclude their relationships to the Theridiinae.
(4) Synonymy: See the paragraphs on the synonymy of fossil and extant taxa above and below, e. g. on *Theridion* WALCKENAER 1805. – Fossils: See "*Theridion*" *berendti* MARUSIK & PENNEY 2005 (= *Mizalia globosa* KOCH & BERENDT 1854, ♀), which subfamiliar relationship is very doubtful (fossil females are most often hard to assign to a certain genus), and the remarks on "*Theridion*" *globosum* (PRESL 1822) and "*Theridion*" *oblongum* (PRESL 1822) by MARUSIK & PENNEY (2005: 213). Several names of MENGE in KOCH & BERENDT (1854) are nomina nuda or nomina dubia, and the type material is lost, see MARUSIK & PENNEY (2005: 213–214).

Distribution: Extant: Cosmopolitical; fossil: Tertiary Dominican amber (probably incl. *Anelosimus clypeatus* WUNDERLICH 1988) and probably (relationships are questionable) rarely in Early Tertiary Baltic amber: *Balticoridion* n. gen. and *Clavibertus* n. gen.. See the remarks above on fossil species of "*Theridion*" in Baltic amber.

Tribus in Europe: Here I list only four tribus in which e. g. *Neottiura* and *Rugathodes* *) (both still regarded as Theridiini) are apparently not included; closer investigations are needed:

(1) Achaearanini **n. nom**. (for Achaeini ARCHER 1947; type genus *Achaea* O. PICKARD-CAMBRIDGE 1882 which is – according to LEVI & LEVI (1962: 15) – a homonym of *Achaea* HUEBNER 1823 and an objective synonym of *Achaearanea* STRAND 1929; see IRZN, art. 39. – In the members of this tribus the opisthosoma is usually higher than long (it may bear hump(s)), the cymbium is distally usually distinctly modified, a radix is absent, and the median apophysis is broadly attached to the tegulum or to the embolus.
(2) Echinotheridiini **n. trib**. Type genus *Echinotheridion* LEVI 1963, further genus *Tidarren* CHAMBERLIN & IVIE 1943. Opisthosoma higher than long (similar to the Achaearanini which may be related), dwarf males (in contrast to the Achaearanini), cymbium strongly modified, internal paracymbium HOOK-shaped, conductor very large, epigyne a strongly sclerotized and projecting "knob". Further characters: See below.
(3) The nominate tribus Theridiini: The bulging male epigaster (figs. 580–581, 595) may be an important diagnostic character. It exists e. g. in *Ohlertidion, Sardinidion, Simitidion* and *Theridion* but is absent in the remaining European tribus, e. g. in the genera *Achaearanea, Achaeridion, Canalidion, Heterotheridion, Macaridion, Neottiura, Nesticodes*, *Phylloneta, Rugathodes*, and *Tidarren*. The internal paracymbium is probably hood-shaped in all taxa (numerous taxa have still to study). The limits of this most diverse tribus within the Theridiinae and within the Theridiidae are unknown.
(4) Theridulini ARCHER 1950 (as a tribus within ARCHER's Episinae (!)) (= Theridulinae sensu SAARISTO (2006: 84). *Theridula* EMERTON 1882 (extant, see below) is the only known genus of this taxon, which is characterized mainly by reductions of the structures of the male pedipalpus (conductor, median apophysis and radix are absent) besides the shape of the wide opisthosoma. Because of the mainly only reduced characters I – provisionally – include this taxon in the Theridiinae.

---

*) *Rugarthodes, Phylloneta* and probably *Macaridion* may be members of a further tribus in which the eyes are small, and in the male the epigaster is not bulging, the pedipalpus is small, the chelicerae are large, diverging and bearing an anterior tooth (except in *Macaridion*).

Description of TWO FOSSIL GENERA (questionable Theridinae) in Baltic amber

Balticoridion n. gen. (figs. 470–475, photo 345)

Diagnosis (♂; ♀ unknown): Prolateral hairs of tibia I long and in two rows, their length is 2–3 tibial diameters. Pedipalpus (figs. 472–475): Median apophysis fairly large, questionable tegular apophysis pointed, questionable embolus furcate, in a retrolateral position, the slender part fairly long.

Further characters: Body length 1.25–1.5 mm, sequence of the dorsal tibial bristles 2/2/1/2. Position of the metatarsal I trichobothrium 0.24–0.27. Internal paracymbium (fig. 472): See below.

Type species by monotypy: *Balticoridion dubium* n. sp..

The **relationships** are not sure. According to the (most likely) absence of a colulus and the presence of an internal paracymbium I regard *Balticoridion* likely being a member of the subfamily Theridiinae. – The long prolateral hairs of tibia I are thinner than in the Spinitharini; in contrast to the Spinitharini a colulus and a proapical strong bristle of tibia I are absent. – In *Clavibertus* n. gen. – which apparently is most related – long prolateral hairs of tibia I are absent and the cymbium is elongated.

Distribution: Early Tertiary Baltic amber forest.

Balticoridion dubium n. gen. n. sp. (figs. 470–475, photo 345)

Material: 5♂ in Baltic amber, holotypus F1634/BB/AR/CJW, paratypes: F1633/CJW (with two separated pieces of amber), F1635/CJW (with a separated piece of amber), F1716/CJW (with a separated piece of amber) and F1743/CJW.

Preservation and syninclusions: The holotype is well and completely preserved in a small piece of amber which was slightly heated; ventral parts are partly covered with a white emulsion; stellate hairs are absent. – F1633 is completely and fairly well preserved in a piece of amber which was heated; especially the dorsal side is covered by a white emulsion, thin ?air bubbles are present dorsally on several leg articles. Remains of a Diptera and of stellate hairs are preserved in the separated pieces of amber. – F1635 is well and completely preserved in a heated piece of amber; white emulsions are present on the right side of the body; few stellate hairs are preserved with the spider. – F1716 is completely and well preserved in a yellow piece of amber which was only slightly heated; its dorsal side is thickly covered with a white emulsion. Syninclusions are: 4 Acari, 2 2/2 Diptera, a larva of Aphidina, a scale of a bud, particles of excrement and numerous stellate hairs. – F1743: The right half of the opisthosoma is cut off, the pedipalpi are well preserved.

Diagnosis (♂; ♀ unknown): See the diagnosis of the genus.

Description (♂):
Measurements (in mm): Body length 1.25–1.5, prosomal length and width 0.6–0.65; leg I: Femur 0.95, patella 0.32, tibia ca. 0.7, metatarsus ca. 0.7, tarsus ca. 0.4, tibia IV 0.6; pedipalpal femur ca. 0.25.
Colour: Prosoma and legs medium brown, opisthosoma light brown.
Prosoma (photo 345; most parts are hidden): Thoracal fissure short, eye field not wide, posterior row slightly recurved, anterior median eyes largest, clypeus and chelicerae long, fangs long and slender, cheliceral promargin with a large tooth, labium distinctly wider than long, gnathocoxae strongly converging, sternum smooth, separating the coxae IV by less than their diameter. Posterior stridulating files are indistinct or probably even absent. – Legs hairy (fig. 470) and rather stout, I not much longer than II or IV, sequence of the long tibial bristles 2/2/1/2, position of the metatarsal I trichobothrium in 0.24–0.27. The well developed two-rowed prolateral hairs of tibia I are up to three tibial diameters long in the holotype, only up to two diameters in the paratypes. Comb of tarsus IV well developed. – Opisthosoma oval, almost egg-shaped, with few longer dorsal hairs. Epigaster not protruding, most probably not sclerotized, spinnerets stout; a colulus is most probably absent (fig. 471, F1633), in F1635 a small "bubble" – an artefact or a tiny colulus? – exists, in F1743 the area of the colulus is recognizable, a colulus as well hairs are apparently absent. – Pedipalpus (figs. 472–475) with short articles, patella and tibia about as wide as long, cymbium fairly large. Paracymbium: The paratype F1633 has a translucent cymbial margin in which the internal hooded paracymbium is recognizable (fig. 472). Subtegulum large, median apophysis strongly sclerotized, questionable terminal apophysis pointed, conductor in a distal position, hiding the slender part of the embolus which is fairly long, bent and in a retrolateral position; I am not quite sure that this structure is really the embolus.

Relationships: See the genus.

Distribution: Eocene Baltic amber forest.

***Clavibertus* n. gen.** (figs. 476–481, photos 346–349)

Diagnosis (♂; ♀ unknown): Pedipalpus (figs. 378–379, 381, photo 349): Cymbium distinctly club-shaped elongated.

Further characters: Sequence of the tibial bristles 2/2/1/2, position of the metatarsal I–II trichobothrium in ca. 0.25, pedipalpal patella short.

Type species: *Clavibertus prominens* n. sp., the only known species of the genus.

Relationships: See *Balticoridion* n. gen.

Distribution: Eocene Baltic amber forest.

***Clavibertus prominens* n. gen. n. sp**. (figs. 476–479, photos 347–349)

Material: 8♂ in Baltic amber; holotypus F1770/BB/AR/CJW, paratypes: F1771 (with two separated pieces of amber) – 1774/CJW, F1910/CJW, 1♂ GPIUH, coll. SCHEELE; 1♂ coll. F. EICHMANN in Hannover no. Ar 30.

Preservation and syninclusions: The holotype is well and almost completely preserved in a small piece of amber which was slightly heated; the right leg IV has been amputated beyond the tibia (apparently it is healed), the opisthosoma is deformed (dorsally inclined), two bubbles are preserved below the mouth parts, tiny threads are also present; the paratype F 1771 is well and completely preserved, both anterior legs are stretched forewards, remains of white emulsions are preserved ventrally and on the right side of the spider, numerous stellate hairs are preserved in the same piece of amber; the paratype 1772 is preserved together with a dragline in a piece of amber which was heated; F1773 is almost completely preserved, the left patella I is cut off, the left leg II is amputated at the base of the metatarsus (fig. 477, photo 348), the ventral side of the spider is covered with a white emulsion, a lump of detritus is located on the distal half of the opisthosoma, few stellate hairs are also present; F1774 is completely and well preserved in a large piece of amber which was heated; two large bubbles are preserved in front of the mouth parts; particles of detritus, stellate hairs, a Diptera: Brachycera and numerous tiny Nematoda: Rhabditida are preserved in the same piece of amber; F1910 is well and completely preserved in a piece of amber which was slightly heated; there are remains of only few white emulsions; the male of the GPIUH is fairly well preserved and partly covered with a white emulsion; some stellate hairs as well as the part of a stamen and a Diptera: Nematocera are also preserved; the male from the coll. EICHMANN is completely but only fairly well preserved; most parts are covered with a white emulsion; stellate hairs, air bag pollen grains, 2 Diptera, an arthropos larva and particles of detritus are also preserved. – Amputations of legs – which probably are healed – exist in the holotype and in the paratype F1773 (fig. 477, photo 348).

Diagnosis (♂; ♀ unknown) with a longer embolus which originates near the middle of the length of the bulbus.

Description (♂):
Measurements (in mm): Body length 1.7–1.9, prosoma: Length about 0.9, width about 0.8; leg I: Femur 1.15, patella 0.4, tibia 0.9, metatarsus 0.92, tarsus 0.52, tibia IV 0.57; padipalpus: Femur ca. 0.25, patella ca. 0.16, tibia 0.11.

Colour (if not or only slightly heated): Prosoma and legs medium brown, opisthosoma light brown.
Prosoma (fig. 476, photos 347–348) slightly longer than wide, clypeus ventrally protruding, fovea low, eye field fairly wide, anterior median eyes largest, posterior row straight, posterior median eyes separated by more than their diameter, posterior stridulatory files not visible, basal cheliceral articles fairly long, teeth of their furrow unknown, labium free, wider than long, the sternum separates the coxae IV by almost their diameter. – Legs of medium length, some metatarsi are fairly bent, hairs short, order I/IV/II/III, sequence of the short tibial bristles 2/2/1/2, metatarsi I–III bear a trichobothrium, its position on I–II in ca. 0.22, tarsal IV comb well developed. – Opisthosoma oval, not scutate but epigaster probably hardened, dorsally with fairly short hairs and two pairs of small sigilla, colulus absent (F1910). – Pedipalpus (figs. 478–479, photo 349) with short articles and a fairly large bulbus, cymbium distally clubshaped elongated, paracymbium not observable, embolus long, well visible, basally abruptly broadened.

Relationships: In *C. parvus* n. sp. the origin of the embolus is distinctly more basally.

Distribution: Eocene Baltic amber forest.

***Clavibertus parvus* n. gen. n. sp**. (figs. 480–481, photo 346)

Material: Holotypus ♂ in Baltic amber and a separated piece of amber, F1513/BB/ AR/THE/CJW.

Preservation and syninclusions: The spider is excellently preserved in a clear piece of amber which most probably was slightly heated; the tip of the left tarsus IV as well as parts of the right legs I and II are cut off. A bubble is preserved under the sternum. The opisthosoma is preserved in an unnatural and more vertical position. A white emulsion is absent. Some stellate hairs and few particles of detritus are present in the same piece of amber.

Diagnosis (♂; ♀ unknown): Pedipalpus (fig. 481) with an embolus which originates in a basal position.

Description (♂):
Measurements (in mm): Body length 1.8, prosomal length and width 0.75; leg I: Femur 0.85, patella 0.33, tibia 0.7, metatarsus 0.7, tarsus 0.47, tibia IV 0.46, pedipalpal femur 0.3.
Colour: Prosoma and legs medium to dark brown, opisthosoma light brown.
Prosoma as wide as long, covered with few longer hairs, clypeus ventrally distinctly convex, dorsally concave, fovea fairly small (fig. 480), eye field wide, anterior median eyes largest, posterior row fairly recurved, posterior median eyes separated by ca. 1 1/2 diameters, basal cheliceral articles fairly small; posterior stridulatory files seem to exist. Paired hairs in the field of the median eyes weak. – Legs only fairly long, se-

quence of length I/IV/II/III, covered with short indistinct hairs, bristles also short and indistinct, sequence 2/2/1/2, their length ca. one diameter of tibia I–II; tibia I: See the diagnosis. Position of the metatarsal III trichobothrium in ca. 0.3. The unpaired claw is probably reduced. – Opisthosoma (fig. 346) globular, covered with shorter hairs (up to 0.17 mm long), sclerotized around the pedicel; epigaster not bulging. A colulus is probably absent (the colular area is partly hidden). – Pedipalpus (figs. 481); most parts are hidden by a bubble and an emulsion, the bulbi are bent under the mouth parts; see above) with a short patella and tibia; distal part of the conductor slender and slightly bent dorsally.

Relationships: See *C. prominens* n. sp.

Distribution: Eocene Baltic amber forest.

THE EXTANT GENERA OF THE WEST-PALAEARCTIC THERIDIIDAE,

with special emphasis to the subfamily Theridiinae, see the diagnosis of this subfamily and its tribes in Europe above.

List of the West-Palaearctic genera of the Theridiidae, and selected characters:

There are at least 38 to 41 genera, 22 are members of the Theridiinae

Certain corrections may be necessary because not all west-palaearctic taxa were studied based on well preserved material.
Exclusively dwellers of green-houses are usually not listed; *Coleosoma* is an exception.
Four genera which names are heavily printed, are known as fossils in Baltic amber, too.
The names of the five genera which are described for the first time are market with an asterix.
SUBFAMILIES:
AN = Anelosiminae, AR = Argyrodinae, AS = Asageninae, EN = Enoplognathinae, EP = Episinae, HA = Hadrotarsinae, PL = Pholcommatinae, PR = Phoroncidiinae, TH = Theridiinae;
“red.” = reduced colulus. The colulus is also tiny in other taxa, mainly of the Hadrotarsinae,
tibial bristles: Sequence of the dorsal bristles on tibia I–IV *;
tm III, tm IV: Existence of a trichobothrium on metatarsus III and IV. Their position is usually in the basal half, but more distally in numerous Hadrotarsinae. In three genera their unusual position on I–II within the Theridiinae is noted.
chelical teeth: Number of teeth on the anterior/posterior margins of the cheliceral furrow. “+” means that usually more than a single tooth exist and a variability as well.

Genus	hairy colulus	tibial bristles	tm III/IV	anterior/posterior cheliceral teeth
TH *Achaearanea*	-	2/2/1/2	+/-	0-1/0
TH *Achaeridion**	-	2/2/1/2	+/-	1/0
TH *Anatolidion**	-	2/2/1//2(1?)	+/-	1/0
TH *Arctachaea*	-	2/2/1/2	+/-	♀ 0/0, ♂ 0/1
AR *Argyrodes* s. l.	+	0/0/0/0	+/-	+/+
AS *Asagena*	+	2/2/1/1	+/+	+/-
TH *Canalidion**	-	2/2/1/2	+/-	2/0
PL *Carniella*	+	2/2/1/2	-/-	3/2
TH *Coleosoma*	-	2/2/1/2	+/-	1/0
HA *Coscinida*	-	2/2/1/1(2) **	+/-	0/0
AS *Crustulina*	+	1/1/1/1	+(-)/-	1/0
HA *Dipoena*	+	2/2/1/2	+/-	0/0
TH *Echinotheridion*	-	2/2/1/2	+/-	0-1/0
EN *Enoplognatha*	+	2/2/1/2	+/-	+/1
EP ***Episinus***	+	2/2/1/2	+/-	0/0
HA ***Euryopis*** s. l.	+/-	variable	+/-(+)	0/0
TH *Heterotheridion**	-	2/2/1/2	+/-	1/0
TH *Keijia*	-	1/1/1/1	+(0.9!)/-	0/0
AN *Kochiura*	+ (red.)	1/1/1/1	+/-	+/+
HA ***Lasaeola*** s. l.	+ (red.)	variable	+/-	0/0
AS *Latrodectus*	+	2/2/1/2	+/-	0/0
TH *Macaridion*	-	1/1/1/1	-/-	0-1/0
TH *Neottiura*	-	2/2/1/2	+/-	1-2/0
TH *Nesticodes*	-	2/2/1/2	+(0.6-0.7)/-	1-2/0
TH *Ohlertidion**	-	2/2/1/2	+/-	0/0
TH *Paidiscura*	-	2/2/1/1 or 2/1/1/1	-/-	0/0
PL *Pholcomma*	-	2/2/1/2	+/-	+/+
TH *Phylloneta*	-	2/2/1/2	+(0.25!)/-	0-1/0
EN *Robertus*	+	2/2/1/2	+/-	+/1-2
TH *Rugathodes*	-	2/2/1/2	+/-	2-3/0
TH *Sardinidion*	-	2/2/1/1	+/-	1/0
AN *Selimus*	+	1/1/1/1***	+/-	+/+
TH *Simitidion*	-	2/2/1/2	-/-	0/0
AS *Steatoda* s. l.	+	2/2/1/2	+/-	1-2/0-1
TH *Takayus*	-	2/2/1/2	+/-	1/0
PL *Theonoe*	+	2/2/1/2	-/-	3/2
TH *Theridion*	-	2/2/1/2	+/-	0-1/0
TH *Theridula*	-	2/2/1/2	+/-	1-2/0
TH *Thymoites*	-	2/2/1/2	+/-	1/0
TH *Tidarren*	-	2/2/1/2	+/-	0-2/0
PR ***Ulesanis***	+ (tiny)	0/0/0/0	+/-	+/-

* The tibial bristles may be rubbed off. The sequence of the dorsal tibial bristles is 2/2/1/2 if tibia IV bears 2 dorsal bristles (very rarely 2/2/2/2).

** The sequence of the tibial bristles in *Coscinida tibialis* is apparently variable, usually 2/2/1/1 or 2/2/1/2.

*** The sequence of the dorsal tibial bristles is 1/1/1/1 in the European species of the new subgenus *Clavilosimus* (*S. pulchellus* and *vittatus*) (formerly under *Anelosimus* and *Theridion*) but unknown to me in the nominate subgenus.

New and newer combinations of extant west-palaearctic species of the family Theridiidae:

(See also above – the subfamily Anelosiminae: *Selimus* –, and the next paragraph: The *Theridion vittatum*-group = *Selimus: Clavilosimus*).

Achaearanea tepidariorum (C. L. KOCH 1841) and *A. simulans* (THORELL 1875)
(= *Theridion t., s.*) = subgenus *Parasteatoda t.* and *s.* of *Achaearanea*,
Anelosimus pulchellus (WALCKENAER 1802) and *A. vittatus* (C. L. KOCH 1836)
(= *Theridion p*., *v*.) = *Selimus p*. and *v*. (the subgenus *Clavilosimus* n. subgen.),
Chrysso nordica (CHAMBERLIN & IVIE 1947) = *Arctachaea n*.,
Phoroncidia paradoxa (LUCAS 1846) = *Ulesanis p*. (= *Oronata p*.),
Steatoda *phalerata* (PANZER 1801) = *Asagena p.*,
Theridion aulicum C. L. KOCH 1838 = *Kochiura aulica*,
Theridion blackwalli O. PICKARD- CAMBRIDGE 1871 = *Sardinidion b*.,
Theridion conigerum (SIMON 1914) = *Achaeridion* (n. gen.) *c*.,
Theridion impressum L. KOCH 1881 = *Phylloneta impressa*,
Theridion montanum EMERTON 1882 = *Canalidion m.,*
Theridion nigropunctatum LUCAS 1846 = *Keijia nigropunctata*,
Theridion nigrovariegatum SIMON 1873 = *Heterotheridion* (n. gen.) *n*.,
Theridion ohlerti THORELL 1870 = *Ohlertidion* (n. gen.) *o*.,
Theridion palmgreni MARUSIK & TSELLARIUS 1986 ?= *Takayus p.*,
Theridion simile C.L. KOCH 1836 = *Simitidion s.,*
Theridion sisyphium (CLERCK 1757) = *Phylloneta sisyphia*,
Theridion tinctum (WALCKENAER 1802) = *Keijia tincta*.

Remark: Now all groups of the genus *Theridion* – "*Theridium*" sensu WIEHLE (1937: 136–137) (which were mainly based on the work of SIMON) – are transferred to other genera or even subfamilies, except the "*denticulatum-*" (= *melanurum-*) group (except *blackwalli* and *simile*) which forms the main part of *Theridion* s. str.; see also above: "new combinations", e. g. *Achaearanea* with the subgenus *Parasteatoda*; *Kochiura*, *Anelosimus*, and *Selimus* with the subgenus *Clavilosimus*:

aulicum-group = *Kochiura* (subfamily Anelosiminae!),
bimaculatum-group = *Neottiura*,
instabile-group = *Rugathodes*,
lunatum-group = *Achaearanea*,
nigrovariegatum-group = *Heterotheridion* n. gen.,
notatum-group = *Phylloneta*,
pallens-group = *Paidiscura*,
redimitum-group = part of *Enoplognatha* (subfamily Enoplognathinae!),
tinctum-group = *Keijia*,
vittatum-group = *Selimus* (with the subgenus *Clavilosimus* (*pulchellus* and *vittatus*) and *Kochiura* (*aulica*) (previously *Anelosimus*) (subfamily Anelosiminae!).

The subfamily Theridiinae in the West-Palaearctic

Diagnosis, relationships and tribus: See above.

List of the West-Palaearctic genera of the subfamily Theridiinae

Selected subgenera, species and synonyms

More than half (22) of the about 40 extant West-Palaearctic genera of the Theridiidae are members of the most diverse subfamily Theridiinae; about 50% of these genera are known from a single species only:

Achaearanea STRAND 1929; part.: See the subgenus *Parasteatoda* below, too,
Achaeridion **n. gen**.: *conigerum* (SIMON 1914),
Anatolidion **n. gen**.: *osmani* n. sp.,
Arctachaea LEVI 1957: *nordica* (CHAMBERLIN & IVIE 1947) (= *Chrysso n*.),
Canalidion **n. gen**.: *montanum* EMERTON 1882 (at least),
Coleosoma O. PICKARD-CAMBRIDGE 1882: *floridanum* BANKS 1900,
Echinotheridion LEVI 1963: *gibberosum* (KULCZYNSKI 1899,
Heterotheridion **n. gen**.: *nigrovariegatum* SIMON 1873 (= *Theridion n*.),
Keijia YOSHIDA 2001: *tinctum* WALCKENAER 1802) (= *Theridion t*.),
Macaridion WUNDERLICH 1992: *barretti* KULCZYNSKI 1899 (= *Theridion b*.),
Neottiura MENGE 1868,
Nesticodes ARCHER 1950: *rufipes* (LUCAS 1846) (= *Theridion r*.),
Ohlertidion **n. gen**.: *ohlerti* (THORELL 1870) (= *Theridion o*.),
Paidiscura ARCHER 1950 (from *Theridion*),
Parasteatoda ARCHER 1947: Subgenus of *Achaearanea*; *A*. (*P*.) *simulans* (THORELL 1870) and *tepidariorum* (C. L. KOCH 1841) (= *Achaearanea s*. and *t*.),
Phylloneta: *impressa* (L. KOCH 1881) and *sisyphia* (CLERCK 1757) (= *Theridion impressum* and *sisyphium*),
Rugathodes ARCHER 1950 (from *Theridion*),
Sardinidion WUNDERLICH 1995: *blackwalli* (O. PICKARD-CAMBRIDGE 1871) (= *Theridion b*.) (= *S. perplexum* WUNDERLICH 1995),
Simitidion WUNDERLICH 1992: *lacuna* WUNDERLICH 1992 and *simile* (C. L. KOCH 1837) (= *Theridion s*.),
?Takayus YOSHIDA 2001: *palmgreni* MARUSIK & TSELLARIUS 1986 (=*Theridion p*.),
Theridion WALCKENAER 1805: *denticulatum*-group,
Theridula EMERTON 1882: *gonygaster* (SIMON 1873),
Thymoites KEYSERLING 1884: *bellissimus* (L. KOCH 1879) (= *Theridion b*.),
Tidarren CHAMBERLIN & IVIE 1934: *chevalieri* (BERLAND 1936).

Key to the extant West Palaearctic genera of the subfamily **Theridiinae**

Remarks:

(1) Exclusive dwellers of green-houses are not treated, with the exception of *Coleosoma* (key no. 1) which is relatively frequent.
(2) The genus *Achaearanea* is regarded in a wide sense (including subgenera, the genus *Theridion* is regarded in a strict sense.
(3) About half of 22 genera are known from a single west-palaearctic species only.
(4) The genus *Coscinida* (Hadrotarsinae) possesses certain characters similar to the Theridiinae: A colulus is absent and the basal cheliceral articles are relatively large, see above, and the figs. 327–332.
(5) The sequence of the dorsal tibial bristles in the Theridiinae is basicly and most often 2/2/1/2 (not quite sure in *Anatolidion*); in *Keijia* and *Macaridion* all tibiae bear only a single bristle. Tibia III bears never 2 bristles, the bristles are most often thin, frequently almost hair-shaped (strong in *Coleosoma*), but their position is more erect than in the hairs. In *Paidiscura* (no. 6 below) and *Sardinidion* (no. 5 below) the tibia IV bears exceptionally only a single bristle, the sequence is 2/2/1/1, rarely 2/1/1/1. Notes: (a) If tibia IV bears 2 bristles bear the tibiae I and II also 2 bristles. (b) Tibial bristles on I–II: If there exists only a single one its position is most often in the basal half. If there exists a single bristle in the distal half, a second bristle of the basal half has existed, and has been broken off.
(6) A trichobothrium on metatarsus III exists in all genera except in *Macaridion*, *Paidiscura* and *Simitidion*. – Its position is retrodorsally, most often in the second quarter of the article, frequently near the middle but 0.9–0.95 in *Keijia* (fig. 519).
(7) A dorsal – usually distal – opisthosomal outgrowth (e. g. figs. 484–486, 498, 532) exists – at least in the female sex – in the genera *Achaearanea* (part.: *acoreensis*), *Achaeridion, Arctachaea, Echinotheridion, Neottiura* (part., small) and *Tidarren* (part.).
(8) A distinctly bulging male epigaster (fig. 595) exists in *Theridion* and strongly related genera (probably the most important diagnostic character of the tribus Theridiini, see above), but not in genera like *Achaearanea, Canalidion, Echinotheridion* and *Neottiura* which are or may be not strongly related.
(9) The key starts with a pantropical dweller of green-houses (*Coleosoma*), followed by a genus which has a unique shape of the opisthosoma (*Theridula*), by taxa in which the opisthosoma possesses a dorsal posterior hook (e. g. fig. 484) and by two genera (*Takayus* and *Thymoites*, each a single rare species, nos. 7 and 8), which possess peculiar characters. The sequence of the dorsal tibial bristles is 2/2/1/2 in these taxa, and a trichobothrium on metatarsus III exists (like in *Theridion*, the most diverse genus, no. 19). In certain taxa of no. 9ff the number of tibial bristles is lower than 2/2/1/2, and a trichobothrium on metatarsus III may be absent. The male epigaster is not bulging in the taxa of the nos. 1–8, but it is bulging (fig. 595) in several genera of no. 9ff, e. g. in *Theridion*.

1 Shape of the opisthosoma sexually dimorphic: oval to globular in the ♀ (fig. 504), cylindrical in the male, with a constriction, with a large and more or less sclerotized anterior ring which covers the epigaster and has a divided dorsal lobe (figs. 501–502). ♂-pedipalpus: Fig. 503, epigyne: Fig. 505. Pantropical; in Europe in green-houses. *C. floridanum*. . . . . *Coleosoma*

- Characters different, male opisthosoma without a sclerotized ring 2

2(1) Shape and colour of the opisthosoma quite variable, wider than long, black or bearing white spots in *T. gonygaster* (figs. 598–599, 601–602), with a pair of lateral lobes in about the middle and a dorsal-posterior hump (lobes and hump may be indistinct in the male). *T. gonygaster*: ♂-pedipalpus (fig. 603) small and simple, with a cork-screwed embolus, epigyne (fig. 600) with paired openings. Cosmopolitical, South Europe . . . . *Theridula*

- Characters different; a wide opisthosoma exists also in females of *Paidicura* (no. 11) in which the humps have a more anterior position (figs. 547, 551) and in *Macaridion* (no. 9, fig. 582), in both genera the colour of the smaller body is lighter 3

3(2) The sexually dimorphic dwarf adult males possess only a single pedipalpus. ♀: Opisthosoma higher than long, a dorsal hump may exist IN THE MIDDLE; the epigyne is strongly sclerotized, and bears a scapus which stands widely out (e. g. figs. 507–508). Two genera, Southern Mediterranean, Canary Islands, Madaira 4

- Males with two pedipalpi and no sexual size dimorphism (except an egg-bearing ♀-ophistosoma). ♀: Epigyne usually different, rarely similar (e. g. in *Neottiura*, nos. 6, 15). The ♀-opisthosoma is in some taxa very high (in *Achaearanea* (part.), nos. 6, 19, fig. 484; bearing a dorsal hump POSTERIORLY in: *Achaearanea* (part.), *Arctachea*, *Achaeridion*, and in *Neottiura* (e. g. *uncinata*, no. 6), figs. 484, 485, 496, 533) 5

4(3) ♂: Pedipalpus compact. ♀: Coxa IV without a spur, epigyne with a smaller scapus. *T. chevalieri* . . . . *Tidarren*

- ♂: Cymbium distinctly bilobed, bulbus with large projecting structures (fig. 509). ♀: Coxa in the West-palaearctic species with a basal-medial spur (fig. 506) and epigyne with a larger scapus fig. 507–508. *E. gibberosum*. . . . . *Echinotheridion*

5(3) Opisthosoma (figs. 484, 485, 496, 532) with a dorsal-posterior hump at least in the male, high in the female 6

- Opisthosoma without a dorsal hump, highest in *Achaearanea* (fig. 482, no. 19) . . . 7

6 (5) ♂: Fang (fig. 499) sexually dimorphic thickened in a unique way, pedipalpus: Fig. 500, epigyne: Fig. 497. Holarctic, Hungary. *A. nordica* . . . . *Arctachaea*

- ♂-pedipalpus (figs. 487–489) with a short and straight embolus, vulva: Fig. 490. *A. conigerum* . . . . *Achaeridion*

- ♂-pedipalpus (fig. 532) with a very long and slender femur, ♀: Epigyne/vulva different. E. g. *N. uncinata*. See no. 15. . . . . .Neottiura (min. part.)

- Male unknown, ♀: Epigyne: Fig. 484a. *A. dubitabilis* WUNDERLICH, Canary Islands. See no. 19 . . . . Achaearanea (min. part.)

7(5) Male: Area directly behind the eye field slightly raised, short hairs in the field of the median eyes (fig. 604), pedipalpus: Fig. 606. ♀: Epigyne (figs. 607–608) strongly sclerotized and protruding posteriorly. North Europe. *T. belissimus* . . . . . . .Thymoites

- Area behind the eye field not raised, no hairy field in this position, copulatory organs different 8

8(7) ♂-pedipalpus: Figs. 589–590, ♀: Epigyne (figs. 591–592) with a flat pit which has a strongly sclerotized posterior margin. Sequence of the tibial bristles 2/2/1/2. Poland, NE- Europe; *palmgreni* . . . . ?Takayus

- Copulatory organs different. All tibiae bear only a single bristle in *Keijia* and *Macaridion* (no. 9) but 2 bristles at least on leg I in the remaining genera. 9

9(8) (See the remark no. 8 above). Sequence of the dorsal tibial bristles 1/1/1/1, trichobothrium present on metatarsus III, its exceptional position on I–II is in 0.9–0.95 (fig. 519). ♂-pedipalpus (figs. 520–521) small, the embolus bears a wide and scinny seam. *K. tincta* and *nigropunctata* . . . . .Keijia

- Sequence of the dorsal tibial bristles 1/1/1/1, too, but trichobothrium absent on metatarsus III, and the position of the tiny trichobothria on I–II in ca. 0.3. Eyes unusually small and widely spaced (fig. 527). ♂-pedipalpus (figs. 530–531) small, the embolus bears a wide and scinny seam. The epigyne (fig. 529) bears a pair of small and widely spaced openings. Colour alive green, blanching in alcohol. Madeira, Canary Islands. *M. barretti*. . . . . Macaridion

- Sequence of the dorsal tibial bristles 2/1/1/1, 2/2/1/1 or 2/2/1/2, metatarsal III trichobothrium absent or present, its position < 0.75, most often in the basal half. A small ♂-pedipalpus exists in *Rugathodes* (no. 13) and *Theridula* (no. 2) 10

10(9) Trichobothrium absent on metatarsus III, sequence of the dorsal tibial bristles 2/2/1/1 or 2/1/1/1 (*Paidiscura*) or 2/2/1/2 (*Simitidion*) 11

- Trichobothrium present on metatarsus III, sequence of the tibial bristles 2/2/1/2* . . . 12

- Trichobothrium present on metatarsus III (position on I–II in ca. 0.6), sequence of the tibial bristles 2/2/1/1. ♂-pedipalpus (figs. 573–576) with a long embolus. ♀: Epigynal pit longer than wide. *S. blackwalli* . . . . Sardinidion

11(10) Body length 1.5–2(♀) mm, coxae IV spaced by more (!) than their diameter by the sternum (fig. 548) (even when observed slightly from behind), sequence of the dorsal tibial bristles most often 2/2/1/1 (rarely 2/1/1/1), ♀-opisthosoma (figs. 547,

551) wider than long, in most species with a pair of lateral humps in the anterior half, ♂-opisthosoma oval. Embolus long, free visible, and in an almost circular position (figs. 550, 552) . . . . *Paidiscura*

- Body length 2.3–3.6(♀) mm, coxae IV spaced – frequently distinctly – less than their diameter like in most other Theridiinae, sequence of the dorsal tibial bristle 2/2/1/2, ♀-opisthosoma oval. Male: Chelicerae diverging and bulging basally (fig. 579), conductor extending beyond the tip of the cymbium (fig. 582), embolus only fairly long and bent, partly enclosed by the conductor. *S. lacuna* and *simile* . . . . *Simitidion*

12(10) Metatarsi with a long dorsal-basal bristle-shaped hair (fig. 491) which is larger on the posterior legs (it is longer than the metatarsal hairs and more erect). ♂-pedipalpus (figs. 492–495) with long tegular apophysis, conductor and embolus. (♀ unknown). Anatolia. *A. osmani* n. sp. . . . . *Anatolidion*

- Metatarsal bristle-shaped hair absent, copulatory organs different. 13

13(12) Anterior cheliceral margin with 2–3 teeth (one large tooth exists on the male's diverging articles, figs. 564–566). Paired tarsal claws smooth. ♀: Claw of the pedipalpus smooth, introductory ducts of the vulva partly glandular. (Position of the metatarsal trichobothria usually in 0.4–0.5). ♂-pedipalpus (figs. 567–568) with the small embolus and the conductor in a distal position. . . . . *Rugathodes*

- Anterior cheliceral margin with 0–2 teeth (a smaller tooth and diverging articles exist in the male of *Phylloneta* (figs. 553, 556) (no. 14). Paired tarsal claws and claw of the ♀-pedipalpus with distinct teeth (at least a single large tooth). 14

14(13) The anterior margin of the cheliceral furrow bears 0–1 tooth. Position of the trichobothrium on metatarsus I–II in ca. 0.25. ♂: Chelicerae distinctly diverging (fig. 553, 59), pedipalpus (figs. 561, 557–558) with the femur distinctly bent, and with a long conductor. Epigynal pit distinctly wider than long. Opisthosomal patern typical as in fig. 554. *P. impressa and sisyphia* . . . . *Phylloneta*

- The anterior margin of the cheliceral furrow bears 2 teeth (fig. 605). Position of the trichobothrium on matetarsi I–II in ca. 0.3. ♂: Chelicerae not diverging, pedipalpus (figs. 606–608): Femur straight, cymbium with a basal inclination/depression, embolus in a DORSAL position (fig. 607), hidden in the ventral aspect. Epigyne (fig. 609) a sclerotized plate which bears a pair of sickle-shaped structures which are widely spaced (and a small circular opening). Scandinavia. *C. montanum* . . . . *Canalidion*

- The anterior margin of the cheliceral furrow bears usually 0–1 tooth, see the tab. above. Position of the metatarsal I–II trichobothrium usually >0.3 or even >0.4. ♂-pedipalpus different, the epigyne may be similar. 15

15(14) Clypeus ventrally strongly protruding in both sexes (fig. 532). The Opisthosoma bears a dorsal-distal hump in some species (fig. 532) (distinct in *uncinata*, see no. 6), ♂-pedipalpus (fig. 532): Femur long and slender, 0.6–1.3 mm long, cymbium large and frequently elongated, bulbus large . . . . *Neottiura* (max. part.)

- Clypeus usually not protruding, but protruding in *Theridion* (no. 19) *nasutum* WUNDERLICH from Sardinia. Femur of the ♂-pedipalpus usually 0.3–0.6 mm long (it may be slightly longer in *Heterotheridiion* (no. 17). Cymbium – except in certain members of *Achaearanea* (no. 19) of normal size and not elongated 16

16(15) Position of the trichobothrium on metatarsus I–II in 0.6–0.7. Epigyne (figs. 536–537): Position far in front of the epigastral furrow, strongly sclerotized and protruding; ♂-pedipalpus (figs. 534–535) with an almost straight embolus which bears a large basal outgrowth. *N. rufipes* . . . . *Nesticodes*

- Position of the metatarsal trichobothrium usually in the basal half, copulatory organs different 17

17(16) ♂-pedipalpus (figs. 510–514): Tibia elongated in a slender part, cymbium distally with an outgrowth which bears numerous cusps. ♀: Epigyne (fig. 515) tiny, with a median path and paired pits. *H. nigrovariegatum* . . . . *Heterotheridion*

- ♂-pedipalpus (e. g. fig. 541, 597): Tibia and cymbium different; ♀: Epigyne larger, with a single pit which is usually large (e. g. fig. 545) 18

18(17) ♂: Epigaster distinctly bulging (as in fig. 595), pedipalpus (figs. 541–544): The distal part of the embolus bears tiny cusps. ♀: Epigyne: Fig. 545. E. g. *O. ohlerti* (= *Achaearanea umbratica*) in Central Europe . . . . *Ohlertidion*

- Embolus without cusps, male epigaster bulging (*Theridion*, fig. 595) or not 19

19(18) Opisthosoma higher than long (figs. 482, 484), more or less vertical above the spinnerets (a dorsal-posterior hump may exist, see no. 6), usually with bent dorsal-lateral streaks at least in the female (fig. 483). ♂: Epigaster not bulging (like in the ♀, fig. 482), cymbium distally usually modified, e. g. inclined . . . . *Achaearanea* (max. part.)

- Shape of the opisthosoma more globular (female) or oval (most males), usually with a longitudinal dorsal band at least in the female (e. g. fig. 594). ♂: Epigaster strongly bulging (fig. 595); pedipalpus (fig. 597): Cymbium not modified, convex at the tip, median apophysis large and standing widely out in a prolateral position. The most diverse genus . . . . *Theridion*

---

* Probably 2/2/1/1 in *Anatolidion*, no. 12.

Diagnoses and short descriptions of the extant West Palaearctic genera of the subfamily Theridiinae, a single new species of *Anatolidion,* and remarks on *Keijia.*

The genera are treated in alphabetic order as in the list above.
The generic position of certain species – e. g. *Arctachaea nordica* and *Takayus palmgreni* – is doubtful, and the existence of these genera in the West Palaearctic is therefore unsure.
The club-shaped basal outgrowth of the embolus – lying in a pocket of the tegulum/radix – is apparently a kind of locking mechanism. I found it in several taxa of the subfamily Theridiinae like *Canalidion*, *Phylloneta* (figs. 557–558), *Rugathodes* (fig. 567) and *Theridion*; a systematic taxonomical study of this structure is needed.
The sequence of the dorsal tibial is listed in the order of the legs I to IV. The position of the metatarsal trichobothria is usually in the basal half of the article (fig. 555) if not otherwise reported.
"Cheliceral teeth" refer to the number of anterior/posterior marginal teeth of the cheliceral furrow.

Achaearanea STRAND 1929 (figs. 482–484a)

Diagnosis: Sequence of the tibial bristles 2/2/1/2, trichobothrium on metatarsus III present, cheliceral teeth: 0–1/0. Opisthosoma (figs. 482–484) higher than long, more or less vertical above the spinnerets (a dorsal-posterior hump may exist), usually with bent dorsal-lateral streaks. ♂: Epigaster not bulging (in contrast e.g. to *Theridion*), cymbium distally usually modified, e. g. inclined, radix absent, median apophysis absent or broadly attached to tegulum or embolus.

Further character: In some species the ♀-opisthosoma bears a hump similar to the figs. 484, 485 and 498.

Type species: *Argyrodes trapezoidalis* TACZANOWSKI 1873 (= *Achaea insignis* O. PICKARD-CAMBRIDGE 1882).

Relationships: See *Canalidion*, *Ohlertidion, Phylloneta, Takayus, Theridion* and the key. In some species the shape of the opisthosoma is similar to *Achaeridion* (figs. 485–486) and *Arctachaea* (fig. 498), and bears a dorsal hump.
Parasteatoda ARCHER 1947 (**n. stat**.) is regarded here as a subgenus of *Achaeranea*. The type species is *Theridium tepidariorum* C. L. KOCH 1841; further species in Central Europe are *lunata, mundula, riparia* and *simulans*. See SAARISTO (2006: 69) who regarded *Parasteatoda* as a genus of its own in contrast to LEVI & LEVI (1962) who included it in the synonymy of *Achaearanea*.

Distribution: Cosmopolitical.

***Achaeridion* n. gen**. (figs. 485–490)

Diagnosis: Sequence of the tibial bristles 2/2/1/2, trichobothrium on metatarsus III present, cheliceral teeth: 1/0, opisthosoma (figs. 485–486) at least as high as long, bearing a dorsal-posterior hump. ♂: Epigaster distinctly bulging, pedipalpus (figs. 487–489): Paracymbium a long rim (edge) (neither hood-shaped nor hook-shaped), bulbus with all sclerites, median apophysis sickle-shaped, embolus fairly short, straight and bearing tiny cusps, see *Ohlertidion*. ♀: Epigyne not sclerotized, with a distinct opening. vulva: Fig. 490.

Further characters: Body length only 1.2–1.6(♀) mm. Labium fused to the sternum, opisthosomal hump directed more dorsally in the female (compared with fig. 485). Legs fairly short, position of the trichobothrium on metatarsus I–II in ca. 0.3. Tip of the cymbium with a furrow, the embolus bears a basal outgrowth; ♀: the copulatory ducts long and coiled, shape of the receptacula seminis oval.

Type species: *Theridion conigerum* SIMON 1914. See KNOFLACH (1993), the only known species of the genus.

Relationships: *A. conigerum* has been included in *Achaearanea, Chrysso, Dipoenura*, *Euryopis, Lasaeola* and *Theridion* by different authors, see KNOFLACH (1993), WUNDERLICH (1979) but paracymbium and embolus are different in these genera, and close relationships remain obscure. In *Achaearanea* the male epigaster is not bulging, and a radix is absent (a high opisthosoma and a dorsal hump evolved in several theridiid genera convergently, see e. g. the nos. 4 and 5 in the key above). Regarding *Chrysso* LEVI & LEVI (1962: 47) wrote: "It is not known whether the species placed in this genus are monophyletic." In *Chrysso* the legs are usually long, and the ♀-opisthosoma bears lateral grooves, the embolus is long and bent and tiny cusps are absent. In *Dipoenura* the opisthosomal humps bear four tubercles, the embolus is twisted and cusps are absent. In *Euryopis* and *Lasaeola* (subfamily Hadrotarsinae) are the basal cheliceral articles small, two pairs of receptacula seminis and usually a colulus exist. In *Theridion* s. str. shape and colour of the opisthosoma are different, an opisthosomal hump is absent, shape of paracymbium and median apophysis are different, the embolus is long(er) and bent. In *Arctachaea* the male fang and the shape of the embolus are quite different.

Distribution: Europe.

***Anatolidion* n. gen**. (figs. 491–495)

Diagnosis: Sequence of the tibial bristles 2/2/1/2 (or 2/2/1/1?), trichobothrium on metatarsus III present, cheliceral teeth: 1/0. All metatarsi bear a thin dorsal-basal bristle-shaped hair (fig. 491). ♂-pedipalpus (figs. 492–495): The paracymbium is a wide rim in an apical position, bulbus with all sclerites, median apophysis small, theridiid tegular apophysis and conductor large, embolus long and coiled in several directions.

Further characters: Prosomal-opisthosomal stridulatory organ indistinct or even absent, epigaster not bulging. Hairs of the comb of tarsus IV only slightly bent and weakly serrated. Alveolus in a basal position, basal of a sclerotized rim (edge) (fig. 492), conductor sickle-shaped distally, embolus running in two levels from the ventral to the dorsal position, its distal part is enclosed by the conductor.

Type species: *Anatolidion osmani* n. sp., the only known species of the genus.

Relationships: According to the absence of a colulus and hairs in its position and other characters (see the key to – and the diagnoses of – the theridiid subfamilies above) *Anatolidion* is a member of the subfamily Theridiinae. The existence of metatarsal bristle-shaped hairs is to my knowledge unique within the Theridiidae. In *Theridion* the male epigaster is strongly bulging, paracymbium and conformation of the structures of the bulbus are different. In *Sardinidion* – which may be most related – the sequence of the tibial bristles is 2/2/1/1, the epigaster is slightly bulging, the position of the trichobothrium on metatarsus I–II is in ca. 0.6, position and shape of the – hood-shaped – paracymbium and the conformation of the structures of the bulbus are different (the embolus is also coiled).

Distribution: Turkey (Anatolia).

***Anatolidion osmani* n. gen. n. sp.** (figs. 491–495, photo 351)

Derivatio nominis: The spider is named after the collector of the holotype, OSMAN SEYYAR.

Material: Turkey, Anatolia, Marmaris district, Muola province, Aegean Region, pit fall, holotypus (♂) OSMAN SEYYAR leg. 25. IV. 2006; Erciyes University Science & Art Faculty, dept. of Biology, 38039 Kayseri, Turkey.

Diagnosis: See the genus; ♂-pedipalpus: Figs. 492–495.

Description:
Measurements (in mm): Body length 2.0, prosoma: Length 0.75, width 0.7; leg I: Femur 0.83, patella 0.28, tibia 0.67, metatarsus 0.68, tarsus 0.46, tibia II 0.5,tibia III 0.38, tibia IV 0.5.
Colour (photo 351): Prosoma dark grey brown, cephalic part darker, legs yellow brown, tibiae apically darkened, opisthosoma black, dorsally 2 pairs of white spots, laterally 2 pairs of yellow spots, ventrally uniformly black.
Prosoma (photo 351): almost as wide as long, hairs indistinct, fovea low, ventral margin of the clypeus convex, cephalic part fairly raised and protruding, eyes only fairly large,

posterior row slightly recurved, posterior median eyes smallest, anterior median eyes not much larger than laterals, stridulatory files reduced/absent, clypeus almost twice as long as the field of the median eyes. Chelicerae and fangs of medium size, anterior margin of the cheliceral furrow with a single distinct tooth, posterior margin smooth. Labium twice as wide as long, with a distinct seam to the sternum which is almost as wide as long and which separates the coxae IV by almost their diameter. – Legs slender and fairly long, I > IV, hairs not distinct, tibial bristles long and thin (almost hair-shaped, sequence 2/2/1/2 (probably only a single bristle on IV), all metatarsi bear a long and bristle-shaped basal-dorsal hair (fig. 491), which is distinctly longer and more erect than the remaining hairs but not longer than the longest tibial hairs. Trichobothria exist on metatarsus I–III, their position on I–II is in about 0.3. The position of the tarsal organ I is in 0.37. Comb of tarsus IV: See above. The paired tarsal claws bear short teeth, the unpaired claw is bent in a right angle. – Opisthosoma (photo 351) egg-shaped, scarcely covered with longer hairs; the epigaster is not bulging. Colulus and hairs in its position absent, the median spinnerets are flattened laterally. – ♂-pedipalpus (see above) with a slender femur, a short patella and a wide tibia; the cymbium is not modified, most parts of the median apophysis are hidden in the not expanded bulbus.

Relationships and distribution: See above.

***Arctachaea* LEVI 1957** (figs. 496–500)

Diagnosis (based on the species in Europe, *A. nordica* CHAMBERLIN & IVIE 1947): Sequence of the tibial bristles 2/2/1/2, trichobothrium on metatarsus III present, cheliceral teeth: ♀ 0/0, ♂ 0/1 (large, fig. 499), opisthosoma with a dorsal-posterior hump (figs. 496, 498), male fang distinctly thickened, and partly flattened dorso-ventrally (fig. 499) (a character of *nordica* only?), position of the left embolus counterclockwise (fig. 500), epigyne: Fig. 497.

Further characters: Colour of body and legs pale, eyes small, ventral margin of the male clypeus not convex (but slightly inclined), position of the trichobothrium on metatarsus I–II in the basal half, cymbium basally modified.

Type species: *Arctachaea pelyx* LEVI 1957.

The relationships of *nordica* are quite unsure, see SZINETAR et al. (2002: 307); it has been placed in *Achaearanea, Arctachaea, Chrysso* (see the remark on *Chrysso* above, relationships of *Achaeridion*)*, Theridion* and *Theridula*. Here I follow provisionally UBICK et al. (2004) but *nordica* may be the member of a genus of its own, see the shape of the male fang (unique within the Theridiidae), and the unusual counterclockwise position of the left embolus. See *Achaeridion* which has a similar shape of the opisthosom.

Distribution of *nordica*: Holarctic incl. Hungaria, see SZINETAR et al. (2002).

***Canalidion* n. gen**. (figs. 609–613)

Diagnosis: Sequence of the tibial bristles 2/2/1/2, trichobothrium on metatarsus III present, its position on metatarsus III in ca. 0.3, cheliceral teeth (fig. 609): 2/0. ♂-pedipalpus (figs. 610–612): CYMBIUM WITH A BASAL DEPRESSION which encloses a scinny area and has a strongly sclerotized anterior margin, median and terminal apophyses divided, conductor tube-shaped, embolus short, sickle-shaped and IN A DORSAL POSITION (hidden in the ventral aspect of the bulbus); the epigyne (fig. 613) is a distinctly sclerotized plate which bears a pair of widely spaced sickle-shaped structures and a small genital opening, vulva: See LEVI (1957: Fig: 255).

Further characters: Legs quite indistinctly annulated: ♂: Chelicerae not diverging, epigaster not bulging, clypeus slightly convex, pedipalpal femur straight, paracymbium long and hood-shaped, tegulum with an additional apophysis (not observable in the drawings), the conductor encloses partly the embolus, basal embolic outgrowth existing, lying in a pocket of the tegulum.

Type species: *Theridion montanum* EMERTON 1882. – Further species: *C. montanum* may be a "sampling species": There exist distinct differences in the bulbus structures of males from Minnesota and Alabama, see LEVI (1957: Figs: 252 and 253).

Relationships: LEVI (1957: 71) regarded *montanum* as a member of *Theridion* s. l., ARCHER (1950: 19) as a member of the subgenus *Phylloneta* (see below) of *Allotheridion* ARCHER 1947 which is a synonym of *Theridion* (see below). In *Phylloneta* and *Theridion* the anterior margin of the cheliceral furrow bears only 0–1 tooth, a basal depression of the cymbium is absent, and the position of the embolus is ventrally; in *Phylloneta* furthermore the male chelicerae are diverging and the pedipalpal femur is bent; in *Theridion* furthermore the ♂-epigaster is bulging and a tube-shaped conductor is absent.

Distribution: Holarctic incl. Scandinavia.

***Coleosoma* O. PICKARD-CAMBRIDGE 1882** (figs. 501–505)

Diagnosis (based on the species in Europe, *C. floridanum* BANKS 1900): Sequence of the long and distinct tibial bristles 2/2/1/2, trichobothrium on metatarsus III present, cheliceral teeth: 0–1/0, opisthosoma (figs. 501–502, 504) sexually-dimorphic similar to other congeneric species: oval to globular in the female but cylindrical, frequently with a constriction, and a divided (+/- sclerotized) dorsal lobe anteriorly which covers the epigaster in the male. ♂-pedipalpus: Fig. 503, epigyne: Fig. 505.

Further characters: Position of the trichobothria on metatarsus I–II in ca. 0.3–0.35, body length 1.7–2.2 mm. The male is a sexual-dimorph ant-mimic.

Type species: *Coleosoma blandum* O. PICKARD-CAMBIDGE 1882.

Close relationships: of the genus are unknown.

Distribution: Mainly pantropical; in green-houses in Europe (*C. floridanum*).

***Echinotheridion* LEVI 1963** (figs. 506–509)

Diagnosis (based mainly on the European species): Sequence of the tibial bristles 2/2/1/2, trichobothrium on metatarsus III present, cheliceral teeth: 0–1/0. The sexually dimorphic dwarf adult males possess only a single pedipalpus (the second pedipalpus is lost by self-amputation as in *Tidarren*, see KNOFLACH & VAN HARTEN (2000, 2001), the pedipalpus has a long and divided cymbium (fig. 509). ♀: Opisthosoma higher than long, coxa with a spur (fig. 506), the epigyne (figs. 507–508) is strongly sclerotized and stands widely out.

Type species: *Echinotheridion cartum* LEVI 1963 (female); male: See LEVI (1981). – Species in the West-Palaearctic: *E. gibberosum*, see WUNDERLICH (1992: 410, fig. 606).

Relationships: See *Tidarren* below.

Distribution: Madeira and Canary Islands (*E. gibberosum* (KULCZYNSKI 1899)); the Americas.

***Heterotheridion* n. gen.** (figs. 510–516)

Diagnosis: Sequence of the tibial bristles 2/2/1/2, trichobothrium on metatarsus III present, cheliceral teeth: 1/0. Male epigaster distinctly bulging. ♂-pedipalpus (figs. 510–514) with the tibia elongated in a slender outgrowth, the cymbium bearing a blunt apical outgrowth which bears numerous tiny cusps, and ventrally-basally near the basal alveolus with a large sickle-shaped scinny structure (fig. 511), tegulum with long and coiled ducts. ♀: Epigyne (fig. 515) small, with a median path and paired pits, vulva: Fig. 516.

Further character: Legs very long (especially in the male), anterior median eyes distinctly smaller than posterior median eyes, posterior eye row procurved, ventral margin of the male clypeus convex, internal paracymbium wide and hood-shaped, in a medial-distal position, median apophysis hidden in the not expanded bulbus, conductor large, embolus short and strongly bent.

Type species: *Theridium nigrovariegatum* SIMON 1873; the only known species of the genus.

Relationships: *Nigrovariegatum* has been regarded as a member of *Theridion*; WIEHLE (1937: 144) placed it with hesitation in his *instabile*-group (now *Rugathodes* ARCHER 1950). The shape of the epigyne, the long pedipalpal tibial apophysis, the apical outgowth of the cymbium, shape and position of the median apophysis, and the clockwise position of the right embolus are in contrast to its position in *Theridion*. A close genus is unknown to me.

Distribution: Palaearctic without the north.

***Keijia* YOSHIDA 2001** (figs. 517–526)

Lineatidion sensu SAUER & WUNDERLICH (1995: 170) (nomen nudum).

Diagnosis (based on European species): Sequence of the tibial bristles 1/1/1/1, trichobothrium on metatarsus III present (position on I–II in 0.9–0.95 (!), fig. 519), cheliceral teeth: 0/0, male epigaster fairly bulging, ♂-pedipalpus (figs. 519–521, 523–525) small, with a long conductor and a fairly long embolus which bears a wide and scinny seam in its basal part; epigyne (fig. 526) (at least anteriorly) with a strongly sclerotized margin, and large openings which are widely spaced.

Further characters: Ventral aspect of femur I with black spots typical as in figs. 518 and 522. Anterior median eyes larger than posterior median eyes, ventral margin of the male clypeus almost straight. Colour of the body of the West Palaearctic species as or similar to fig. 517.

Type species: *Keijia maculata* YOSHIDA 2001.

Relationships: In *Macaridion* (Canary Islands and Madeira) the tibiae bear also only a single bristle, the openings of the epigyne are widely spaced, the male pedipalpus is small, and the embolus bears a sciny seam, too, but the eyes are much smaller in *Macaridion*, a trichobothrium on metatarsus III is absent, the position of the metatarsal trichobothrium is in ca. 0.3, the ♀-opisthosoma is wider than long, and the distal structures of the bulbus are different.

Distribution: Holarctic (it has to revise for some species/countries).
Remarks: From the West Palaearctic *K. tincta* (WALCKENAER 1802) (= *Theridion tinctum*) is reported (which apparently has been introduced to North America); *nigropunctata* (LUCAS 1846) (**n. comb**., from *Theridion*) is known from the Mediterranean (on Sardinia I found both species). – Species in Asia: 3 in Japan (YOSHIDA (2003); *Theridion dokuensis* ZHU MINGSHENG 1998 (male unknown) from China may be a member of *Keijia*, too.

Differences of the West Palaearctic taxa *nigropunctata* and *tincta*:

REMARK: Because of the low differences in the two taxa I am not sure about their status as species or subspecies of their own or only an intraspecific variability (*nigropunctata* being a junior synonym of *tincta* in this case). In this paper I regard both provisionally as species of their own because I found differences of the terminal apophysis in different populations.
In the ventral aspect – see figs. 520 and 523–524 – in *nigropunctata* the terminal apophysis (arrows in figs. 520, 523 and 525) is shorter than in *tincta*, not longer than the tip of the embolus (figs. 520–521). I did not found differences of epigyne and vulva in both species. The colour of body and legs varies distinctly within both species; in *nigropunctata* exists ventrally on femur I USUALLY a larger number of SMALLER black spots than in *tincta*, see figs. 518 and 522 (rarely I found the anterior femur largely darkened).

***Macaridion* WUNDERLICH 1992** (figs. 527–531)

Diagnosis: Sequence of the tibial bristles 1/1/1/1, trichobothrium on metatarsus III absent (its position on I–II is in ca. 0.3), cheliceral teeth: 0–1/0, eyes (fig. 527) very small and widely spaced. ♀: Opistosoma (fig. 528) wider than long, epigyne (fig. 529) with a pair of small and widely spaced openings; ♂-pedipalpus (figs. 530–531) small, the embolus bears a scinny seam.

Further characters: Male: Opisthosoma oval, epigaster not bulging.

Type species: *Macaridion barretti* (KULCZYNKI 1899), the only known species of the genus.

Relationships: See *Keijia*.

Distribution: Canary Islands and Madeira.

***Neottiura* MENGE 1868** (figs. 532–533)

Diagnosis: Sequence of the tibial bristles 2/2/1/2, trichobothrium on metatarsus III present, cheliceral teeth: 1–2/0, clypeus (fig. 532) very long and ventrally strongly protruding. Male: Femur IV in some species with a ventral-basal spur, pedipalpus (fig. 532) large to very large, femur long and slender, 0.6–1.3 mm long, cymbium large, asymmetrical, and apically modified/extending, see KNOFLACH (1999).

Further characters: The opisthosoma may bear a dorsal-distal hook (figs. 532–533), male: Ventral margin of the clypeus convex, basal cheliceral articles bulging, opisthosoma long and usually high posteriorly, epigaster not bulging, paracymbium hood-shaped. The males of some species are similar to ants.

Type species: *Aranea bimaculata* LINNAEUS 1767.

Relationships: They are unsure. *Theridion* s. str. is not closely related (contra LEVI & LEVI (1962)): in *Theridion* the clypeus is not protruding (*T. nasutum* is an exception), the male epigaster is distinctly bulging, the pedipalpal femur is shorter than 0.6 mm, the cymbium is smaller and not modified, the structures of the bulbus are different.

Distribution: Holarctic; mainly – and most probably originally – West Palaearctic. *N. bimaculata* is widely distributed, apparently introduced to North America and SE-Asia; the remaining species possess a rather restricted range, see KNOFLACH (1999: 346).

***Nesticodes* ARCHER 1950** (figs. 534–538)

Diagnosis: Sequence of the tibial bristles 2/2/1/2, trichobothrium on metatarsus III present (position on I–II in 0.6–0.7), cheliceral teeth: 1–2/0. ♂-pedipalpus (figs. 534–535) with a sickle-shaped terminal apophysis, and a straight embolus which bears a large basal outgrowth as well as a tooth-shaped structure more distally. Epigyne (figs. 536–538) strongly sclerotized protruding in a position far in front of the epigastral furrow.

Further characters: Male: Ventral margin of the clypeus convex, opisthosoma oval (globular in the female), epigaster not bulging.

Type species: *Theridion rufipes* LUCAS 1849; the only known species of the genus.

The relationships: are unsure, according to the not bulging male epigaster and the structures of the copulatory organs *Theridion* is not strongly related.

Distribution: Mainly pantropical; S-Palaearctic.

***Ohlertidion* n. gen.** (figs. 539–546)

Diagnosis (based on the type species; I am not sure about the correct names of the sclerites of the bulbus): Sequence of the tibial bristles 2/2/1/2, trichobothrium on metatarsus III present (its position on I–II in 0.4–0.6), cheliceral teeth: 0/0, male epigaster distinctly bulging; ♂-pedipalpus (figs. 540–544): Cymbium with a large prodistal outgrowth which is bent ventrally, paracymbium long, hood-shaped, and in a longitudinal position, median apophysis broadly attached to the embolus, radix and conductor existing, embolus long, basally with an outgrowth which lies in a pocket (of the radix?), distally relatively thick and bearing tiny cusps/denticles. ♀: Epigyne: Fig. 545, vulva (fig. 546) according to WIEHLE (1937: 163) with glandular parts.

Further characters: Male: Basal cheliceral articles not diverging/modified, ventral margin of the clypeus strongly convex (fig. 539), right embolus in a clockwise position.

Type species: *Theridium ohlerti* THORELL 1870 (= *Theridium umbraticum* L. KOCH 1872, *Achaearanea umbratica*).

Further species of *Ohlertidion* in the West Palaearctic according to Y. MARUSIK (in litt.): *Theridion thaleri* MARUSIK 1988 (Russia) (**n. comb**.) and *Theridion lundbecki* SÖRENSEN 1898 (sub *T. ohlerti lundbecki*) (Greenland) (**n. stat**., **n. comb**.).

Relationships: The type species has been placed in *Achaearanea* and in *Theridion*; ARCHER (1950: 14) placed it erroneously in his genus *Parasteatoda* (see above, *Achaearanea*, which is quite different). In *Achaearanea* the male epigaster is flat, and a radix is absent; in *Theridion* the cymbium is not modified, the embolus has a different position and possesses no denticles. In *Achaeridion* exist tiny denticles of the embolus, too, but the anterior margin of the cheliceral furrow bears a tooth and the opisthosoma bears a hump. In *Phylloneta* the male chelicerae are different (usually distinctly diverging, bulging basally, and bearing a distal tooth), the median apophysis is not attached to the embolus, and the embolus is not denticulate.

Distribution: Holarctic.

***Paidiscura* ARCHER 1950** (figs. 547–552)

Diagnosis: Sequence of the tibial bristles 2/2/1/1 or 2/1/1/1, trichobothrium on metatarsus III absent, cheliceral teeth: 0/0, coxae IV spaced by more than their diameter by the sternum (fig. 548), the ♀-opisthosoma (figs. 547, 551) is at least as wide as long and bears a pair of anterior-lateral humps in most species, the ♂-pedipalpus (figs. 550, 552) has a flat (disc-shaped) bulbus and a long to very long/coiled embolus. The suspended egg sac has a special shape.

Further characters: Eyes of medium size or small (fig. 549); male: opisthosoma without humps (sexualdimorphy), epigaster not distinctly bulging.

Type species: *Theridion pallens* BLACKWALL 1834.

Further species: *P. dromedaria*, *genistae* (SIMON 1873) (**n. comb**.) (from *Theridion*), *musiva*, *orotavensis*, and *pinicola* SIMON 1873 (**n. comb**.) (from *Theridion*), see WUNDERLICH (1987: 215).

Close relationships are unknown; see *Theridion* and the tab. above. In *Theridion* the sternum is not widely spaced by the coxae IV, the number of tibial bristles and metatarsal trichobothria, and the copulatory organs are quite different. – A trichobothrium on metatarsus III is also absent within the Theridiinae in *Macaridion* and *Simitidion*.

Distribution: Palaearctic; almost all species occur in the West Palaearctic, probably only *pallens* occurs in Russia, too. – *Paidiscura subpallens* (BÖSENBERG & STRAND 1906) sensu YOSHIDA 2003 from Japan is – according to the copulatory organs – a member of another genus.

***Phylloneta* ARCHER 1950** (figs. 553–562) (**n. stat**.)

ARCHER (1950) erected *Phylloneta* as a subgenus of *Allotheridion* (type species: *Theridion pictipes* KEYSERLING 1884). But according to the structures of the ♂-pedipalpus – e. g. the position of embolus and conductor – I regard *Phylloneta* as a genus of its own (**n. stat**.), see below: *Theridion*.

Diagnosis: Sequence of the tibial bristles 2/2/1/2, trichobothrium on metatarsus III present (position on I–II usually in ca. 0.25, fig. 555), cheliceral teeth: 0–1/0; ♂: Basal cheliceral articles distinctly diverging (fig. 553, 556, 559), without a furrow, with a prodistal hump (also existing in the female but smaller), epigaster not protruding, pedipalpus (figs. 57–558, 561–562): Femur bent, thickened in the basal half, and here with hair-bearing cusps, embolus fairly long, bearing a basal outgrowth, partly enclosed by a long conductor. Epigynal pit distinctly wider than long.

Further characters: Dorsal pattern of the opisthosoma usually as in fig. 54: A pair of longitudinal dark bands which are broken by transversal light stripes; eyes small, in a wide field. Male:Ventral margin of the clypeus straight, basal cheliceral articles in the type species with a retrobasal hump (fig. 553), bulging in some species (fig. 560), gnathocoxae lengthened basally like the coxae I (fig. 560). Existence of regurgitationfeeding by females evolved convergently, e.g., in *Anelosimus studiosus* (HENTZ 1850).

Type species: *Theridion pictipes* KEYSERLING 1884 (= *Allotheridion p*., USA, fig. 553). In Europe: P. *impressa* (L. KOCH 1881) (see the **n. comb**. in SAUER & WUNDERLICH (1995: 168)) (from *Theridion*, and *Allotheridion* sensu ARCHER (1950: 21), and *sisyphia* (CLERCK 1757) (see the **n. comb**. in SAUER & WUNDERLICH (1995: 166)) (from *Theridion*).

Relationships: See *Canalidion*, *Ohlertidion* and *Simitidion*. In *Theridion* the ♂-pedipalpus and ♂-chelicerae are not modified in this way, the ♂-epigster is strongly bulging, the pattern of the opisthosoma and the copulatory organs are different. – *Allotheridion* is a synonym of *Theridion*, see below. – In *Rugathodes* – which may be closely related – the paired tarsal claws and the claw of the ♀-pedipalpus are smooth, the anterior margin of the cheliceral furrow bears 2–3 teeth, the position of the metatarsal trichobothria is more distally (usually 0.4–0.5), the male chelicerae bear a large outgrowth, the embolus is smaller and in all species in a more distal position.

Distribution: Holarctic.

***Rugathodes* ARCHER 1950** (figs. 563–569)

Diagnosis: Sequence of the tibial bristles 2/2/1/2, trichobothrium on metatarsus III present (its position on I–II usually in 0.4–0.5), cheliceral teeth: 2–3(!)/0, paired tarsal claws and claw of the ♀-pedipalpus smooth (teeth reduced), ♂-chelicerae (figs. 564–566) diverging, bearing distally at least a single large medial-distal tooth, ♂-pedipalpus (figs. 567–568): The small embolus build half a circle in a distal position. ♀: Epigyne e. g. as in fig. 569, ducts of the vulva partly glandular.

Further characters (see WUNDERLICH (1987: 213) and (1992: 414–417)): Anterior median eyes distinctly smaller than the posterior median eyes (fig. 563), the egg sac is attached to the spinnerets and carried by the female (as in several other theridiid genera). Male: Epigaster not bulging, ventral margin of the clypeus convex,

Type species: *Theridium sexpunctatum* EMERTON 1882.

Relationships: See *Phylloneta*.

Distribution: Holarctic: In the West Palaearctic: *R. acoreensis* and *pico* on the Acores, *bellicosus* and *instabilis* on the European continent; in the Nearctic: *R. sexpunctatus*.

***Sardinidion* WUNDERLICH 1995** (figs. 570–578)

Diagnosis: Sequence of the tibial bristles 2/2/1/1, trichobothrium on metatarsus III present (position in ca 0.6), cheliceral teeth: 1/0, ♂-pedipalpus (figs. 574–578) with a long embolus in three levels. ♀: Epigyne and vulva: See WIEHLE (1937: Figs. 158–159).

Further characters: Male: Ventral margin of the clypeus (fig. 570) convex, basal cheliceral articles basally bulging (fig. 571), epigaster only slightly bulging, paracymbium (fig. 573) in a distal position, ♀: epigynal pit longer than wide. The opisthosoma is completely black in few specimens (person. observ.).

Type species: *Sardinidion perplexum* WUNDERLICH 1995 (= *Theridium blackwalli* O. PICKARD-CAMBRIDGE 1870) (**n. syn**.), the only known species of the genus.

Relationships: See *Anatolidion* n. gen. In *Theridion* the ♂-epigaster is strongly bulging, the shape of the clypeus is different, the sequence of the tibial bristles is 2/2/1/2, the theridiid tegular apophysis and the conductor are different, the position of the embolus is in a single level. – ARCHER (1950: 20) regarded *blackwalli* erroneously as a member of his subgnus *Phylloneta* ARCHER 1950 (see above), but the structures of the bulbus and the sequence of the tibial bristles both are different in these genera.

Distribution: Palaearctic.

***Simitidion* WUNDERLICH 1992** (figs. 579–588)

Diagnosis: Sequence of the tibial bristles 2/2/1/2, trichobothrium on metatarsus III absent, cheliceral teeth: 0/0; ♂-pedipalpus (figs. 582–586, 588): Median apophysis not standing out, embolus partly enclosed by the large conductor, basally without a projection in a tegular pocket (in contrast e. g. to *Theridion*); ♀: Epigyne (fig. 587) with a wide pit.

Further characters: Anterior median eyes at least as large as the posterior median eyes; male: Epigaster (figs. 580–581) strongly bulging, very large and leathery, ventral margin of the clypeus almost straight, basal cheliceral articles bulging basally (fig. 579), and diverging similar to *Phylloneta*, coxae – especially I–II – projecting similar to *Phylloneta*.

Type species: *Theridium simile* C. L. KOCH 1836; further species in the West Palaearctic: *S. lacuna* WUNDERLICH 1992.

Relationships: In *Phylloneta* – which may be most related – metatarsus III bears a trichobothrium, male chelicerae as well as the pedipalpal femur are different. See also*Theridion*.

Distribution: Holarctic.

***Takayus* YOSHIDA 2001** (figs. 589–593)

Diagnosis (based on *palmgreni*): Sequence of the tibial bristles 2/2/1/2, trichobothrium on metatarsus III present, its position on I–II in ca. 0.43–0.5, cheliceral teeth 1/0; ♂-pedipalpus: Figs. 589–590, ♀: Epigyne (figs. 591–592): A flat pit which has a strongly sclerotized posterior margin; vulva: Fig. 593.

Further characters (based on *palmgreni*): The coxae IV are widely spaced, the ♂-epigaster is not bulging, the patella of the ♂-pedipalpus bears 3 dorsal bristles, the embolus is relatively thick (it may be more slender than in the fig.)

Type species: *Theridion takayense* SAITO 1939. Further species: See below.

The relationships of *T. palmgreni* are unsure, see BLICK et al. (2006: 122–123; I do not want to exclude close relationships to *Achaearanea*. Acording to the structures of the ♂-pedipalpus *T. lyricum* WALCKENAER 1841 and *T. tigrae* ESYUNIN & EFERNIK 1996 may be congeneric with *palmgreni*.

Distribution: The distribution of the genus is at least Holarctic. In NE-Europe and Poland occurs at least *T. palmgreni* (MARUSIK & TSELLARIUS 1986) (sub *Theridion p.*), see BLICK et al. (2006) and above (relationships).

***Theridion* WALCKENAER 1805 s. str.** (figs. 594–597)

Theridion melanurum- (sub *Theridium denticulatum*-) group sensu WIEHLE (1937),
except *blackwalli* O. PICKARD-CAMBRIDGE 1871 (= *Sardinidion*).
Allotheridion ARCHER 1947.

Diagnosis: Sequence of the tibial bristles 2/2/1/2, trichobothrium on metatarsus III present (its position usually in the second quarter), cheliceral teeth: 0–1/0. The opisthosoma bears usually dorsally a variable “undulating” longitudinal band (fig. 594). Male epigaster strongly bulging (fig. 595), ♂-pedipalpus (e. g. as in fig. 597): Internal paracymbium hood-shaped, median apophysis large and widely standing out, embolus (fairly) large, most often describing at least half a circle and not widely enclosed by the conductor, epigyne usually a single larger pit.

Further characters: Shape of the opisthosoma usually globular (female) or oval (males of most species), a dorsal hump does never exist. The ventral margin of the clypeus is usually not convex (fig. 596). *Theridion* sensu stricto is the most diverse genus of the family Therididae in Europe.

Type species: *Aranea picta* WALCKENAER 1802.

Relationships: See *Sardinidion*. In *Simitidion* the chaetotaxy, the cheliceral teeth as well as shape and colour of the opisthosoma, and the bulging male epigaster all are as in *Theridion*, and both may be most related, but in *Simitidion* a trichobothrium on metatarsus III is absent, the male chelicerae and gnathocoxae are bulging (see above), the smaller median apophysis stands not widely out, and the conductor encloses most parts of the embolus. In *Keijia* and *Macaridion* bear all tibiae a single bristle only, the position of the metatarsal trichobothrium is in 0.9–0.95 in *Keijia*. See also *Anatolidion* and *Canilidion*. – *Achaearanea* and *Neottiura* are not closely related to *Theridion*, the pattern of their opisthosoma is different, their male epigaster is not bulging, the structures of the bulbus are different.

Remarks: (1) The genus *Theridion* sensu lato was partly split up by ARCHER but numerous genera were synonymized with *Theridion* by LEVI & LEVI (1962). According to the numerous and important genitalic and somatic differences were these synonymizations not jusified, and are not only a matter of opinion: Several genera like *Neottiura, Paidiscura* and *Rugathodes* are not strongly related to *Theridion* s. str., and are even members of different tribus (see above); they were resurrected by the present author, see also KNOFLACH (1999). Now all European groups of *Theridion* s. l. sensu WIEHLE (1937) are regarded as genera of their own. West Palaearctic species of (e. g.) *Achaeridion* n. gen., *Arctachaea*, *Canilidion* n. gen., *Heterotheridion* n. gen., and *Ohlertidion* n. gen. are most often listed under *Theridion* up to now; see the paragraph on new combinations above. UBICK et al. (2004) included still *Keijia, Rugathodes*, *Simitidion* and *Takayus* in the genus *Theridion* s. l. of North America. – (2) The European members of *Theridion* are closely related and build a uniform group of the nominate subgenus. Numerous SE-Asian species – which still are listed under *Theridion* – are members of different subgenera or even of genera of their own; revisions are needed. – (3) *Allotheridion* ARCHER 1947 – type species: *Theridion murarium* EMERTON 1882 – is regarding to the structures of its bulbus doubtless a synonym of *Theridion* s. str. (identic with the opinion of LEVI & LEVI (1962: 15) although these authors refer to *Theridion* sensu lato). ARCHER (1950) erected *Phylloneta* as a subgenus of *Allotheridion* (type species: *Theridion pictipes* KEYSERLING 1884). But according to the structures of the ♂-pedipalpus – e. g. the position of embolus and conductor – I regard *Phylloneta* as a genus of its own, see above.

Distribution: Cosmopolitical.

***Theridula* EMERTON 1882** (figs. 598–603)

Diagnosis (based mainly on *T. gonygaster*): Sequence of the tibial bristles 2/2/1/2, trichobothrium on metatarsus III present, cheliceral teeth: 1–2/0; opisthosoma (figs. 598–599, 601–602) wider than long, fairly flattened, with a pair of lateral lobes in or in front of the middle, and a dorsal-posterior hump (lobes and hump may be more indistinct in the male); ♂-pedipalpus (fig. 603) small and simple (structures reduced), radix, median apophysis and conductor absent, embolus cork-screwed in the Europen species; epigyne: Fig. 600.

Further characters: The colour of the opisthosoma is very variable.

Type species: *Theridion opulenta* WALCKENAER 1841.

Close relationships of the genus are unknown; it is the single member of the tribus Theridulini ARCHER 1950, see above: The tribus of the Theridiinae.

Distribution of the European species *T. gonygaster* (SIMIN 1881): Cosmopolitical.

Thymoites **KEYSERLING 1884** (figs. 604–608)

Diagnosis (based on *T. bellissimus*): Sequence of the tibial bristles 2/2/1/2, trichobothrium on metatarsus III present, cheliceral teeth: 1/0; ♂: Prosoma (figs. 604–605): Area directly behind the eye field slightly raised, short hairs in the field of the median eyes, pedipalpus: Fig. 606, epigyne (figs. 607–608): Especially the posterior margin of the paired openings are strongly sclerotized.

Further characters: The male epigaster is fairly bulging.

Type species: *Thymoites crassipes* KEYSERLING 1884.

The relationships of the European species and even of the genus – which apparently is not monophyletic, see LEVI & LEVI (1962: 48) – are unsure; the European species may be the member of a different genus, a generic revision is needed.

Distribution of the European species *T. bellissimus* (L. KOCH 1879): Northern Europe, Russia.

Tidarren **CHAMBERLIN & IVIE 1934**

Diagnosis: Sequence of the tibial bristles 2/2/1/2, trichobothrium on metatarsus III present, cheliceral teeth: 0–2/0. The sexually dimorphic dwarf adult males possess only a single pedipalpus (the second pedipalpus is lost by self-amputation, see KNOFLACH & VAN HARTEN (2000, 2001), the pedipalpus is compact. ♀: Opisthosoma higher than long, coxa without a spur, the epigyne – see WUNDERLICH (1987: Fig. 546) and (1992: Fig. 505) – is strongly sclerotized and stands out with a smaller scapus similar to *Echinotheridion*.

Further character: Paracymbium hook-shaped.

Type species: *Theridion fordum* KEYSERLING 1884. In the West Palaearctic *T. chevalieri* (BERLAND 1936) (= *T. hagemani* SCHMIDT 1956); see WUNDERLICH (1992: 410, 429).

Relationships: *Echinotheridion* is in my opinion strongly related according to the chaetotaxy, the existence of only a single pedipalpus of the male, their sexual size dimorphism, the shape of the opisthosoma, as well of the epigyne which is strongly sclerotized, and stands out in a scape (figs. 507–508). According to MILLER (2007) *Echinotheridion* and *Tidarren* are not sister groups. The cymbium is very long and distinctly bilobed in the Western Palaearctic species of *Echinotheridion* (fig. 509), the ♀-coxae IV bears a medial-basal spur (fig. 506).

Distribution: Warmer parts of the world, Mediterranean, Canary Islands: *T. chevalieri*.

TYPE MATERIAL OF THE FOSSIL THERIDIIDAE: Most of this type material has just been deposited in the SMF. 5 paratypes (of *Clavibertus prominens, Kochiuridion pecten, Spinitharinus bulbosus*, and *Unispinatoda aculeata*) as well as the holotypes of *Lasaeola larvaque, Succinura ovalis* and *Unispinatoda aculeata* are kept in the GPIUH, the holotypes of *Eolyrifer longitibialis*, *Eomysmena recta, Eoteutana hirsuta, Episinus nasuticymbium, Euryopis araneoides*, *Nanosteatoda breviscutum* and *Protosteatoda gutta* are deposited in the SMNG. Other specimens are kept in the CJW.

REFERENCES: See the papers nos. (4) and (5) in this volume.

INDEX to the fossil and extant West-Palaearctic subfamilies, tribus, and valid subgenera and genera of the family Theridiidae which are most often treated more closely in this paper (and few synonyms) (see the list p. 375!):

page

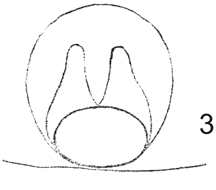
FIGURES 30–613

Remarks to the legends:

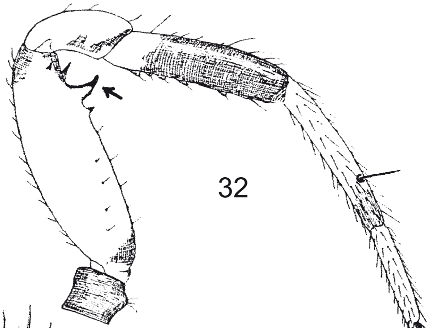
(1) EXTANT TAXA are marked with an asterix (*).
(2) Figs 1-29: See the text.
(3) The scale bars are given in mm.
(4) The MOST FREQUENT ABBREVIATIONS (if not otherwise annotated) are:

B = bubble,
CJW = collection of J. WUNDERLICH of the fossils (F) and their numbers,
C = functional conductor,
E = embolus,
EB = embolic bulb,
M = median apophysis,
P = paracymbium,
R = radix,
S = subtegulum,
T = terminal apophysis (it may be a functional conductor e. g. in *Clya*),
TE = tip of the embolus,
TI = tibia,
TO = tarsal organ/tibial outgrowth,
TTA = theridiid tegular apophysis,
Y = cymbium.

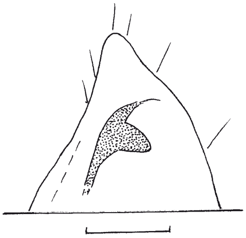
30



31

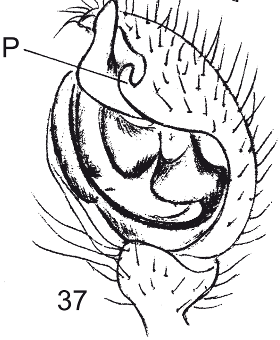


32

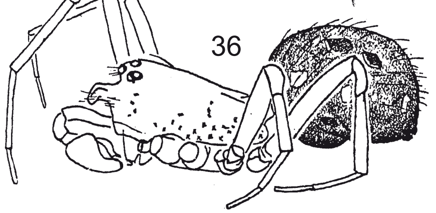


34

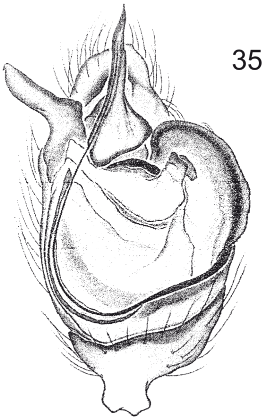
33



37



36



35

Fig. 30) Theridiidae indet. (= "*Theridion*" *alutaceum* KOCH & BERENDT 1854), ♀, holotype, outline of the epigyne which is covered with a white emulsion; scale bar 0.1 mm;

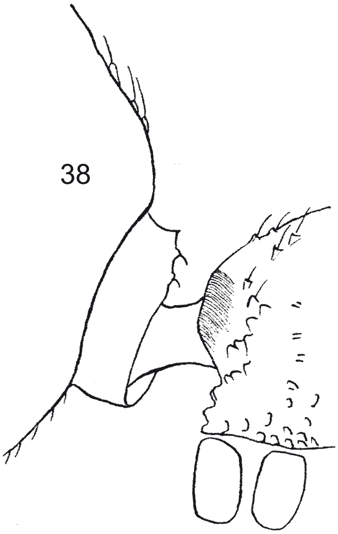
fig. 31) Theridiidae indet., ♀ holotype of *Steatoda succini* PETRUNKEVITCH 1942, epigyne; taken from PETRUNKEVITCH (1942: Fig. 474);

figs. 32–34: *Asagena phalerata* (PANZER 1801), ♂, 32) retrolateral aspect of the r. leg II; the metatarsal trichobothrium has been added by the present author; size and position of the large "clasping spine" (arrow) are variable; 33) ventral aspect of the r. pedipalpus; 34) distal part of the r. cymbium and paracymbium (dark), ventral aspect; the figs. 32–33 are taken from WIEHLE (1937); scale bar 0.2 in fig. 34;

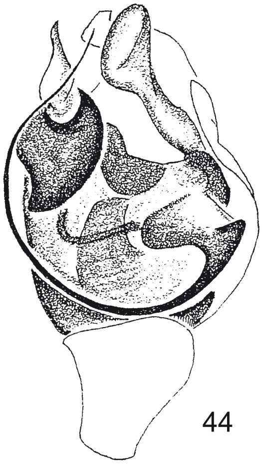
fig. 35) *Asagena americana* EMERTON 1882, ventral aspect of the l. ♂-pedipalpus; taken from PAQUIN & DUPERRE (2003);

fig. 36) *Craspedisia spatulata* BRYANT, ♂, lateral aspect of the body, body length 2.2 mm; taken from LEVI (1963: Fig. 32);

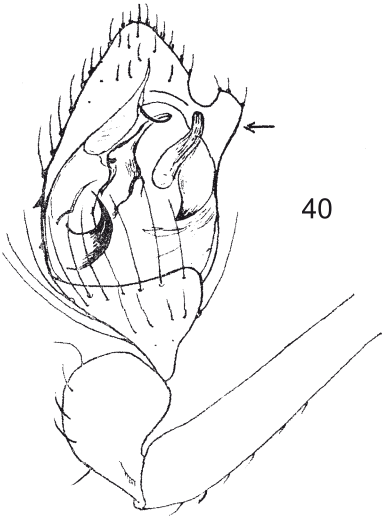
fig. 37) *Craspedisia longiembolia* YIN et al. 2003, retrolateral aspect of the l. ♂-pedipalpus. Taken from YIN et. al. (2003);



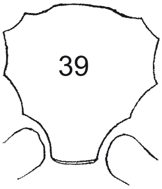
38



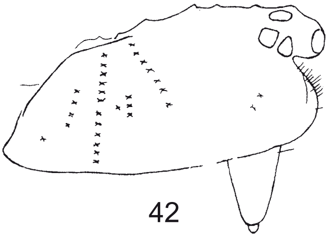
44



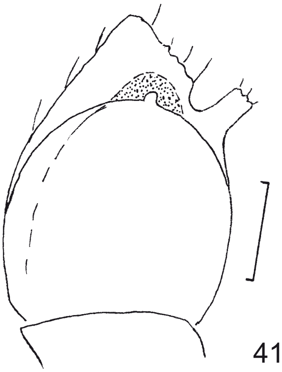
40



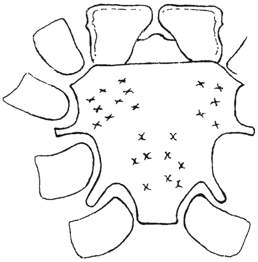
39



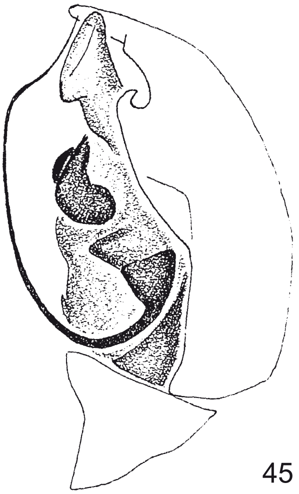
42



41



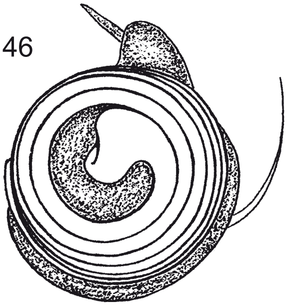
43

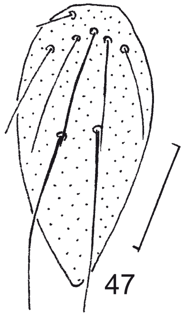


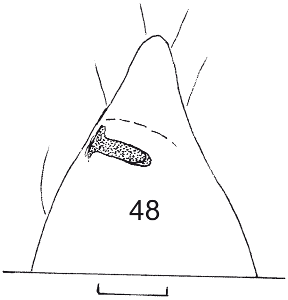
45

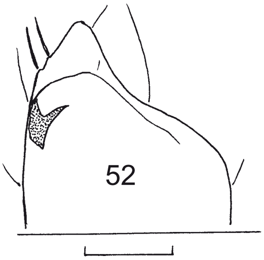
figs. 38–41: **Crustulina guttata* (WIDER 1834), ♂; 38) lateral aspect of the prosomal-opisthosomal stridulatory organ. Note the posterior opisthosomal files and the anterior picks on the sclerotized opisthosomal ring; 39) ventral aspect of the sternum and the posterior coxae which are widely spaced in this genus; 40) retroventral aspect of the r. pedipalpus. Note the proventral outgrowth of the cymbium (arrow); 41) cymbium of the r. pedipalpus, ventral aspect. Note the hood-shaped internal paracymbium (punctuated). Figs. 38–40) are taken from WIEHLE (1937);

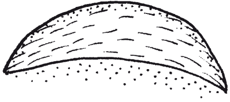
figs. 42–45: **Helvidia scabricula* THORELL 1890, ♂; 42) lateral aspect of the prosoma; 43) ventral aspect of the prosoma; 44–45) ventral and retrolateral aspect of the l. pedipalpus. Taken from LEVI (1972);

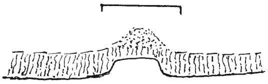


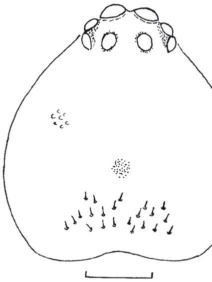


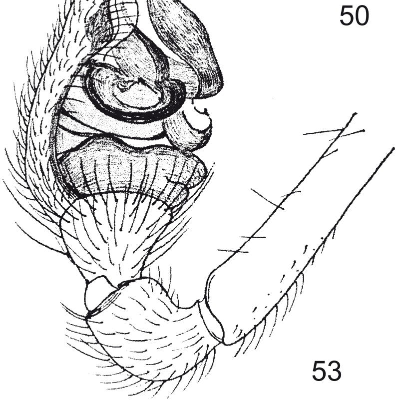












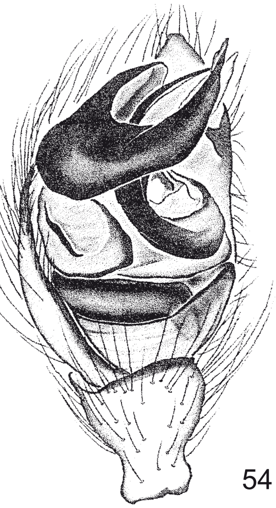


fig. 46) *<u>*Latrodectus rhodesiensis*</u> MACKAY 1972, ventral aspect of the ♂-pedipalpus. Note the long and coiled embolus;

fig. 47) *<u>*Steatoda* (*Steatoda*) *paykulliana*</u> (WALCKENAER 1806), ♀, ventral aspect of the large colulus. The number of hairs is not constant within a species. Scale bar 0.1 mm;

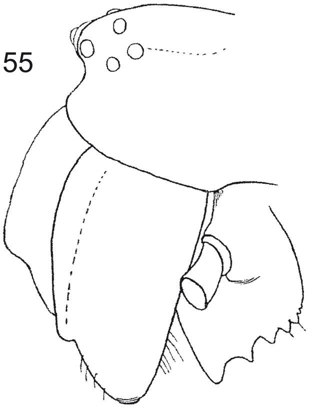
fig. 48) *<u>*Steatoda* (*Steatoda*) *grossa*</u> (C. L. KOCH 1838), distal part of the r. cymbium and paracymbium, ventral aspect. Scale bar 0.2;

fig. 49) *<u>*Steatoda* (?*Steatoda*) *cingulata*</u> (THORELL 1890), hood-shaped paracymbium of the r. ♂-pedipalpus;

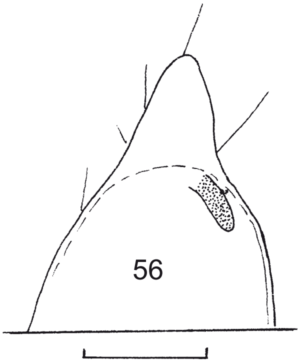
fig. 50) *<u>*Steatoda* (*Steatoda*) *borealis*</u> (HENTZ 1850), anterior aspect of the ventral margin of the male clypeus. Note its medial gap and compare fig. 110. Scale bar 0.2;

figs. 51–54: *<u>*Steatoda* (*Steatoda*) *bipunctata*</u> (LINNAEUS 1778); 51) ♀, dorsal aspect of the prosoma. The short spines in the basal half of the prosoma are unique in this species; 52) distal part of the r. cymbium with the hook-shaped paracymbium; 53) retrolateral aspect of the r. ♂–pedipalpus; 54) ventral aspect of the l. ♂-pedipalpus. Fig. 53) is taken from WIEHLE (1937), fig. 54) from PAQUIN & DUPERRE (2003). Scale bar 0.5 in fig. 51), 0.2 in fig. 53);

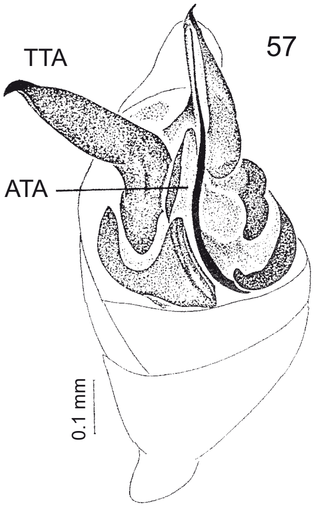
55



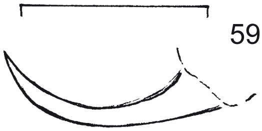
56



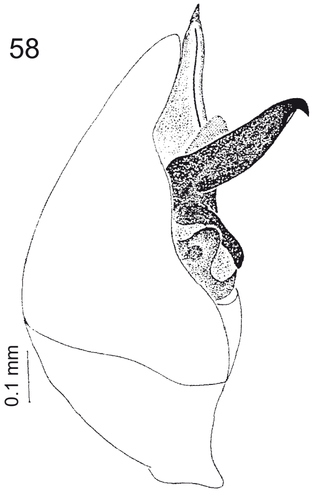
57



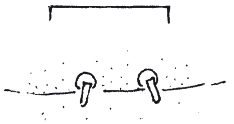
59



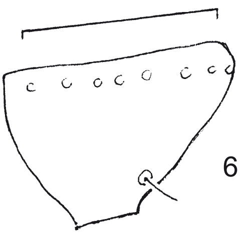
58



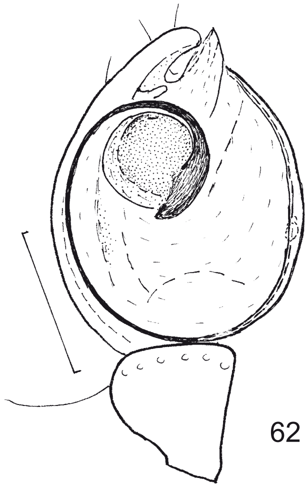
60



61

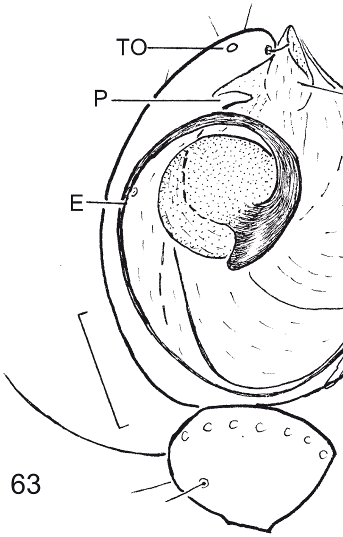


62

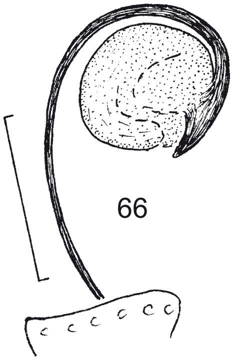


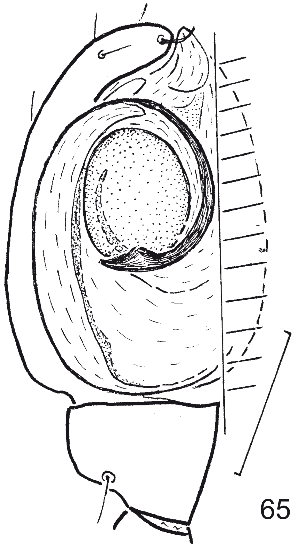
figs 55–58: *<u>*Steatoda* (*Lithyphantes*) *albomaculata*</u> (DE GEER 1778), ♂; 55) lateral aspect of the anterior part of the prosoma, taken from WIEHLE (1937); 56) distal part of the cymbium with the hood-shaped paracymbium, ventral aspect, scale bar 0.2; 57–58) ventral and prolateral aspect of the l. pedipalpus, taken from LEVI (1998);

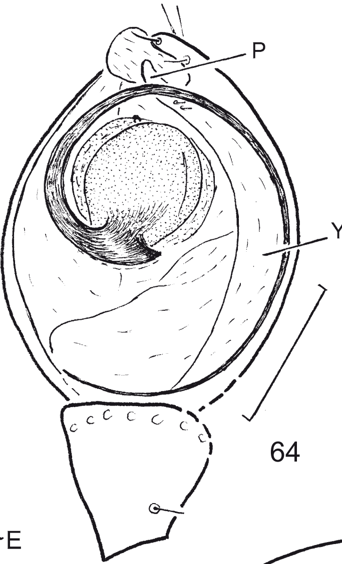
figs. 59–66: <u>*Clya lugubris*</u> KOCH & BERENDT 1854, male; 59) (F1572/CJW), anterior aspect of the l. fang; 60) (F1571/CJW), epiandrous gland spigots; 61) (coll. F. EICHMANN no. 03), ventral aspect of the tibia of the left pedipalpus. The tibia is rather short in this specimen; 62) holotype, ventral aspect of the r. pedipalpus. Specimen with a rather long tibia; 63) (F1569/CJW), ventral aspect of the r. pedipalpus. Specimen with a rather short tibia. The tarsal organ (TO) is well observable; 64) (F1570/CJW), ventral aspect of the l. pedipalpus. Note the unusual position of the embolic point in this specimen; 65) (F1672/CJW), ventral aspect of the r. pedipalpus; the prolateral part is hidden by a leg; 66) (F1580/CJW), embolus and distal part of the tibia of the r. pedipalpus, retroventral aspect. Scale bars 0.1 in fig. 60), 0.2 in the remaining figs.;

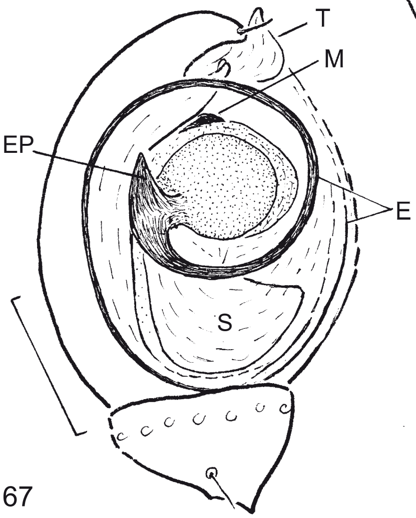


63

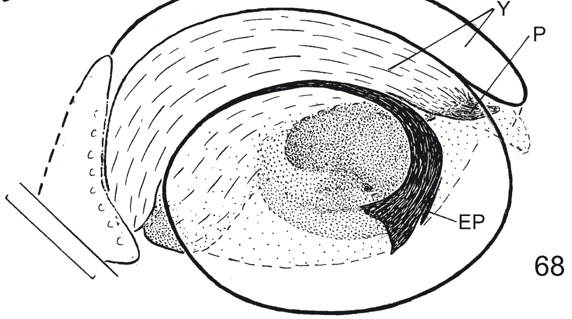








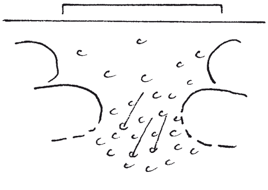
67



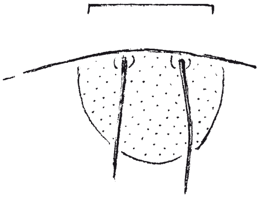
68

fig. 67) <u>*Clya calefacta*</u> **n. sp**., male holotype, ventral aspect of the r. pedipalpus. EP = embolic peak. Scale bar 0.2;

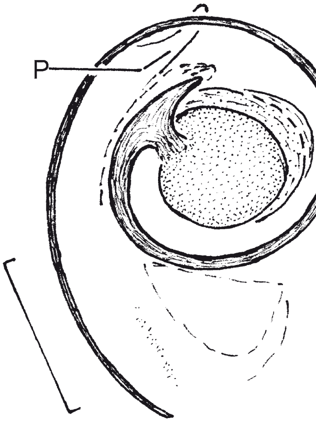
fig. 68) <u>*Clya gracilis*</u> (PETRUNKEVITCH 1958), male holotype, retrodorsal aspect of the r. pedipalpus. The embolus has a circular position. Scale bar 0.2;



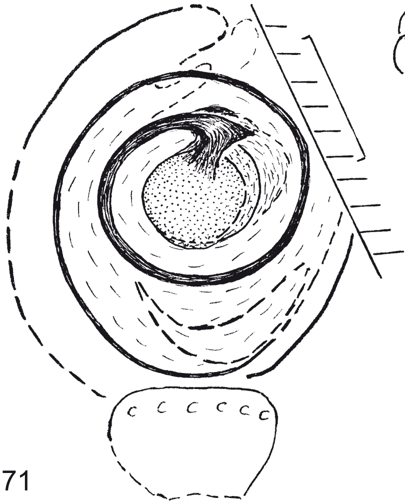
69



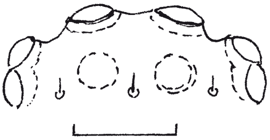
70



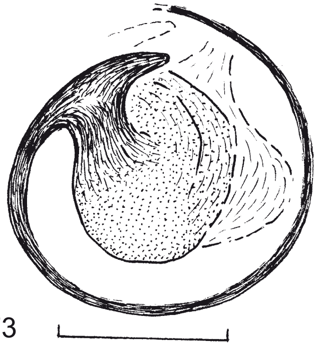
72



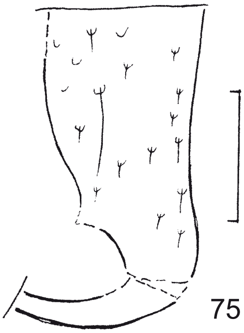
71



74



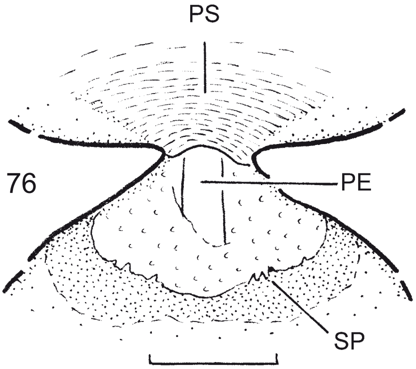
73



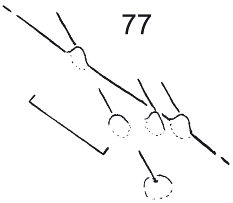
75

figs. 69–73: <u>*Clya supercalefacta*</u> **n. sp.**, male; 69) (GPIUH), posterior part of sternum and coxae; 70) holotype, colulus; 71) holotype, ventral aspect of the r. pedipalpus (parts are hidden); 72) (GPIUH) paracymbium and embolus of the r. pedipalpus, ventral aspect. The tibial margin hides distal parts of th embolus; 73) (coll. M. KUTSCHER, Bitterfeld deposit), paracymbium (dotted) and basal part of the embolus, ventral aspect. The bulbus is partly expanded. Scale bars 0.03 in fig. 70), 0.2 in the remaining figs.;

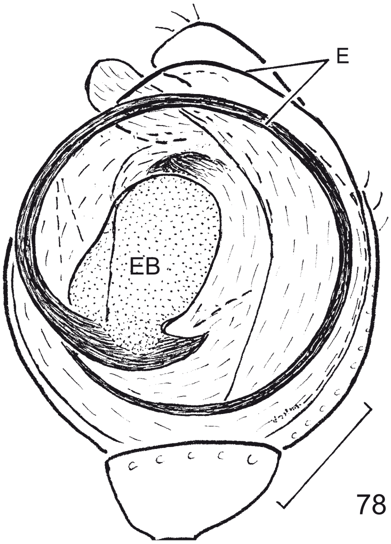
figs. 74–87: <u>*Clya obscura*</u> (KOCH & BERENDT 1854), male; 74) (F1600/CJW), position of the eyes; 75) (F1598/CJW), anterior aspect of the left chelicera; 76) (GPIUH, male a), dorsal aspect of the prosomal-opisthosomal stridulatory organ. PE = petiolus, PS = pars stridulans (files), SP = stridulatory picks on the sclerotized anterior opisthosomal margin; 77) (F1593/CJW), hair-bearing ventral-basal hooks of the anterior femur; 78) (holotype), ventral aspect of the l. pedipalpus. Note the embolic bulb (EB) which is rather long in this specimen. The paracymbium is hidden by the embolus; 79) (holotype), dorsal aspect of the l. pedipalpus; 80) (F1593/CJW), ventral aspect of the l. pedipalpus. The distal loop of the embolus has an unnatural position. Note the droplet (D) at the tip of the embolus; 81) (F1617/CJW), ventral aspect of the l. pedipalpus; 82) (F1587/CJW), ventral aspect of the r. pedipalpus. The paracymbium, the conductor and the tip of the embolus are hidden; 83) (F1589/CJW), dorsal aspect of the l. pedipalpus with the embolus unfolded; 84) (GPIUH), basal part of the l. embolus, ventral aspect; 85–87: basal parts of the r. embolus (ventral aspect) of F1601, 1619 and 1620CJW. Scale bars: 0.5 in fig. 83), 0.2 in the remaining figs.;



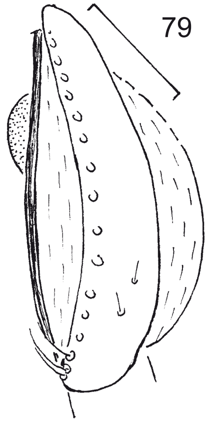
76



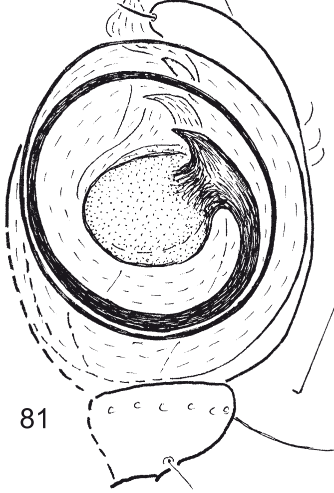
77



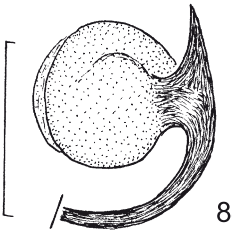
78



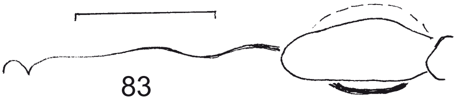
79



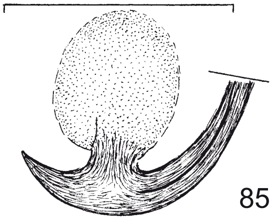
81



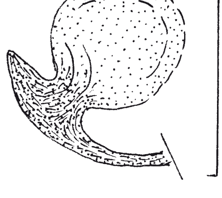
84



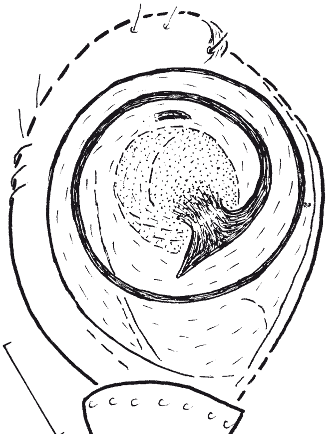
83



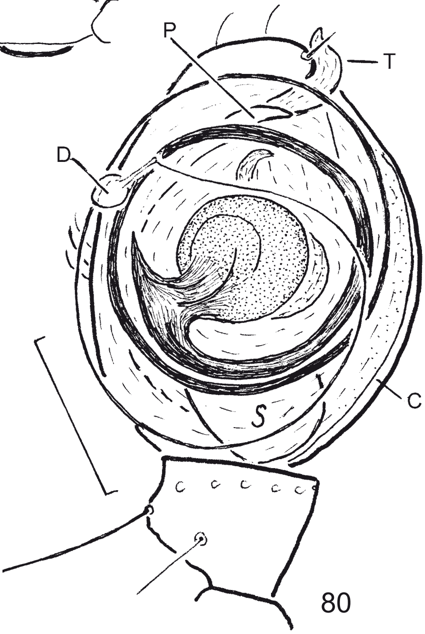
85



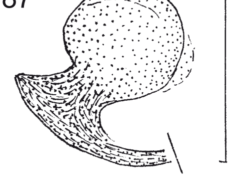
86



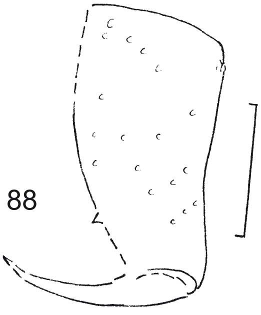
82



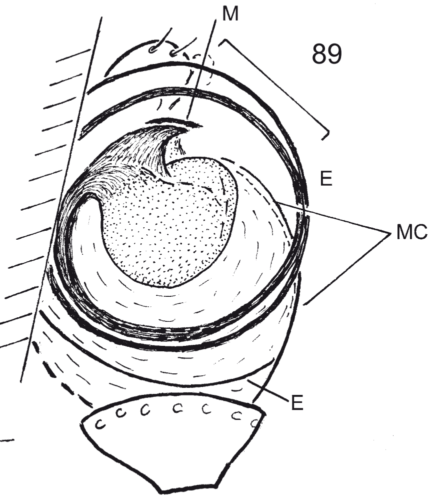
80



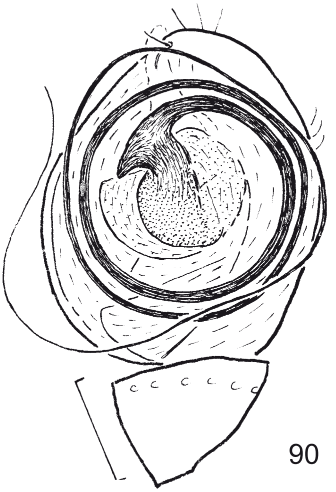
87



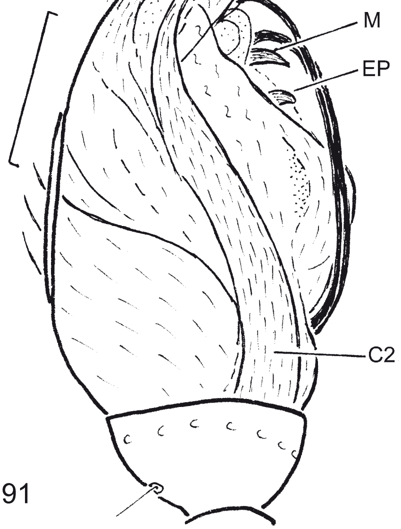
88



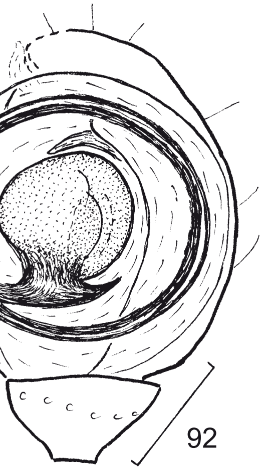
89



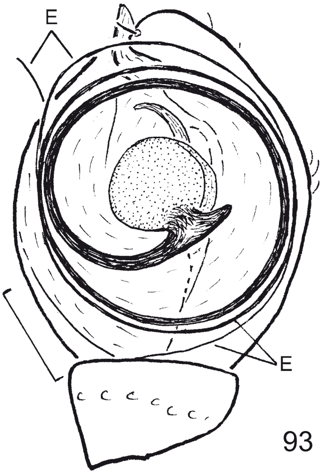
90



91



92

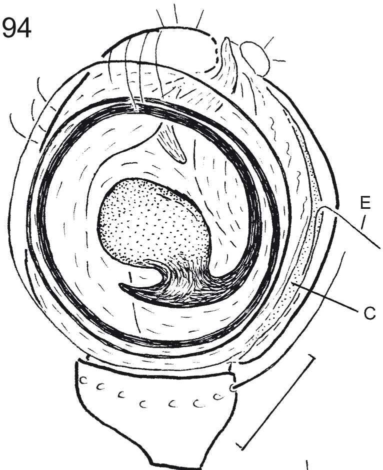


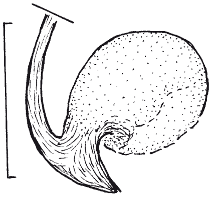
93

figs. 88–91: Clya granulata (KOCH & BERENDT 1854), male; 88) (F1605/CJW), anterior aspect of the l. chelicera; 89) (holotype), ventral (slightly retrobasal) aspect of the r. pedipalpus (parts are hidden). MC = cymbial margin; 90) (F1604/CJW), ventral aspect of the l. pedipalpus. The distal part of the embolus has an unnatural position; 91) (F1630), prolateral aspect of the l. pedipalpus; C2 = questionable subconductor. Scale bars 0.2;

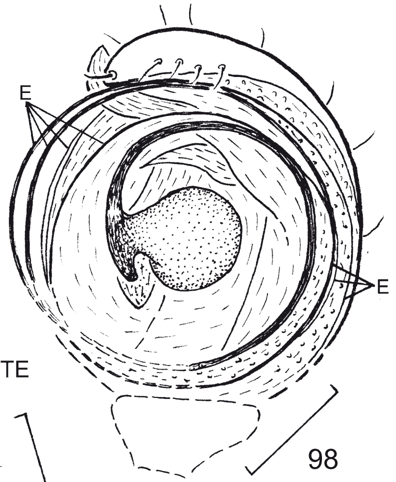
figs. 92–95: Clya tricurvata **n. sp.**, male; 92) (holotype), ventral aspect of the l. pedipalpus. The distal half-circle of the embolus is hidden in this position of the pedipalpus; 93) (paratype F1592/CJW), ventral aspect of the l. pedipalpus. In the right pedipalpus the position of the embolic peak is different, nearer to the next embolic loop; 94) (F1614/CJW), ventral (slightly prodistal) aspect of the r. pedipalpus. The distal part of the embolus (E) has left the long channel of the functional cymbial conductor (C) in this unnatural position; 95) (F1590/CJW), ventral aspect of the basal part of the l. embolus (similar is F1591/CJW). Scale bars 0.2;

94



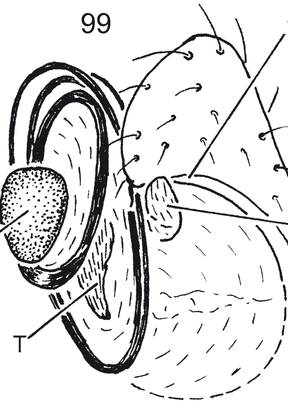


95

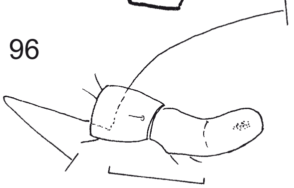


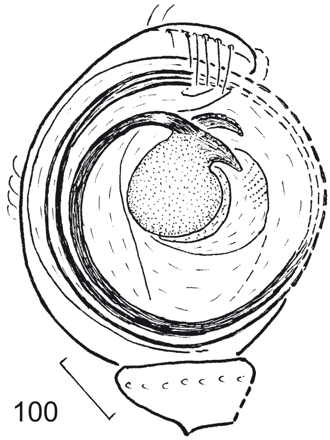
98

99

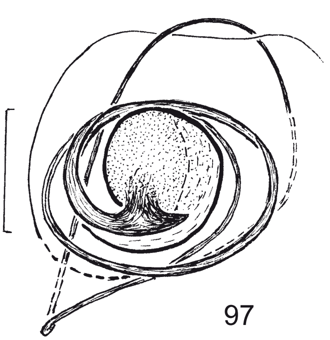


96

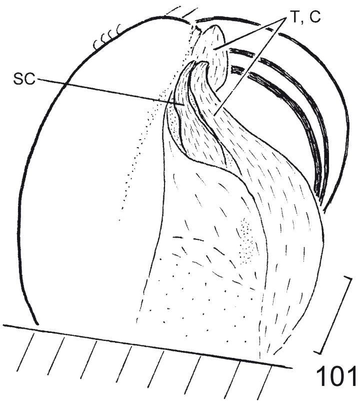




100



97



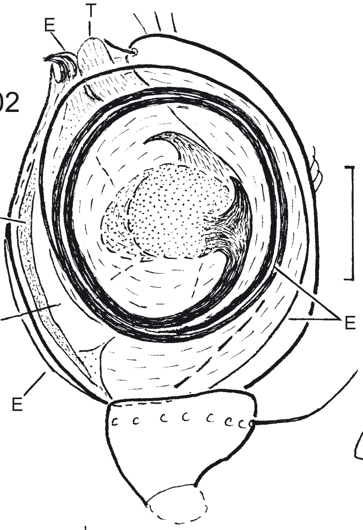
101

figs. 96–97: *Clya ?tricurvata* **n. sp.**, questionable male of this species; 96) regenerated, shortened and bristle-less patella and tibia of the left leg IV and part of a dragline of this spider which runs to its anterior spinnerets; 97) ventral-basal aspect of the l. pedipalpus. Beyond ca. 1 ½ loops (of at least 3 ½ loops) the embolus has left its natural position; its distal half is deposited on a layer in the amber. Scale bar 0.2;

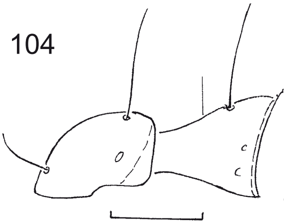
figs. 98–99: *Clya rotata* **n. sp.**, male; 98) ventral aspect of the l. pedipalpus. Basal parts are hidden; 99) apical aspect of the r. pedipalpus. Note the three-dimensional position of the embolus in its last loop (L). Scale bar 0.2;

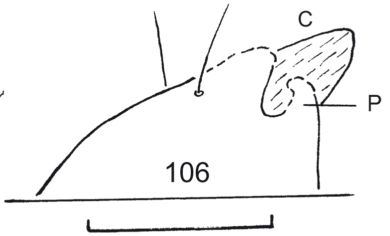
figs. 100–101: *Clya superspiralis* **n. sp.**, male; 100) ventral aspect of the r. pedipalpus which is partly hidden; 101) prodorsal (and fairly distal) aspect of the l. pedipalpus which is basally hidden. SC = questionable subconductor. Scale bar 0.2;

102

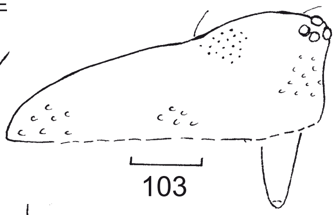


104

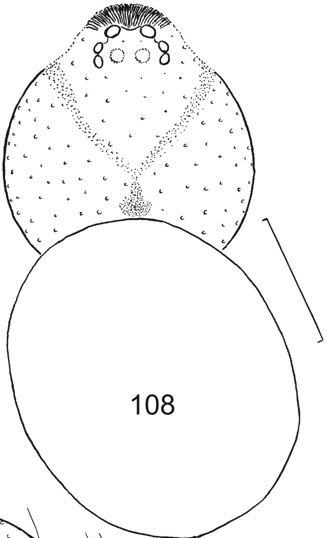




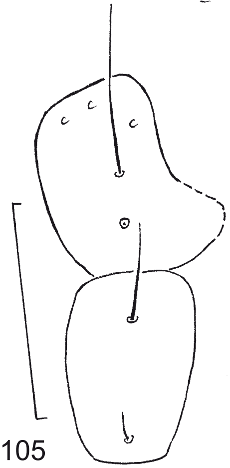
106



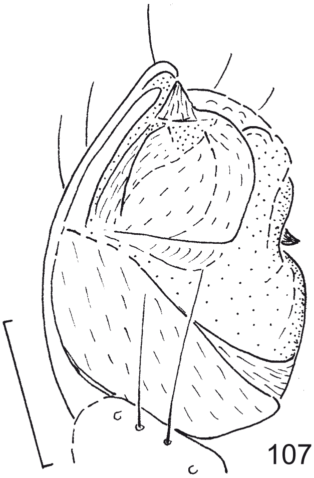
103



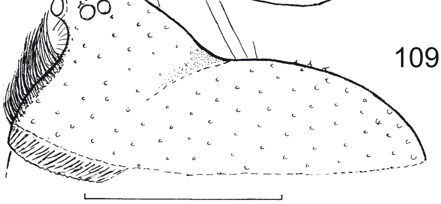
108



105



107



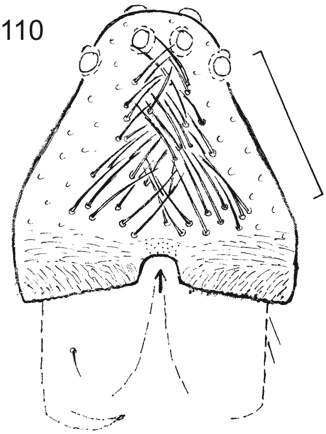
109

fig. 102) *Clya abdita* **n. sp.**, male, ventral aspect of the l. pedipalpus. The long prolateral functional cymbial conductor (C) has been separated in a somewhat unnatural position by a gap (G) from the bulbus by artificial heating. Scale bar 0.2;

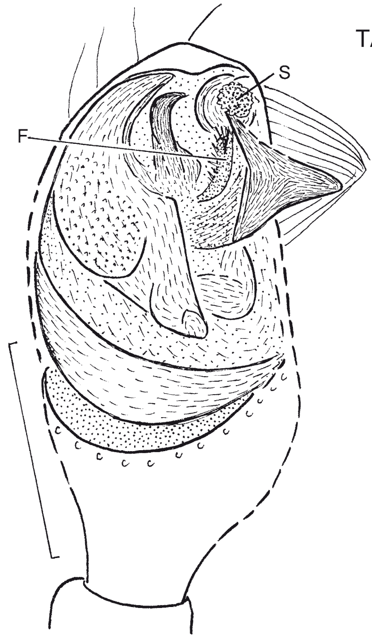
figs. 103–107: *Eoasagena scutata* **n. gen. n. sp.**, male (holotype); 103) outline of the prosoma, lateral aspect. Only few wrinkles are drawn; 104) medial aspect of patella and tibia of the l. pedipalpus; 105) dorsal aspect of patella and tibia of the l. pedipalpus; 106) dorsal aspect of the distal part of the r. cymbium with paracymbium and conductor; 107) ventral aspect of the r. pediplpus. Scale bars: 0.1 in figs. 105–106), 0.2 in the remaining figs.;

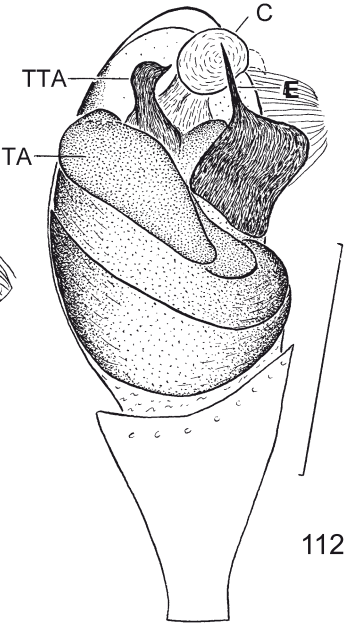
figs. 108–110: *Eomysmena* sp. indet., (F1700, F1700, F1702/CJW), male body/prosoma dorsal, lateral and anterior aspects. The prosomal wrincles are drawn somewhat schematically, they really build partly rows. Note the dense field of hairs on the clypeus, and the medial gap of the ventral clypeal margin (arrow in fig. 110). Parts of the chelicerae in fig.110) are hidden by a white emulsion. Scale bars 1.0, 1.0 and 0.5;

110

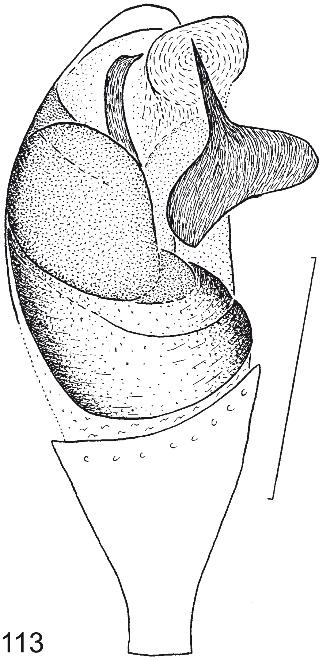


114

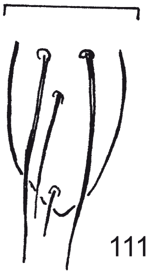




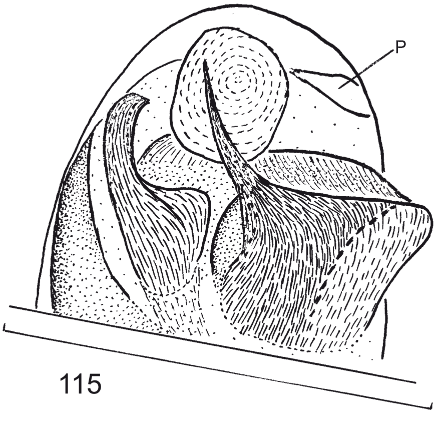
112



113



111



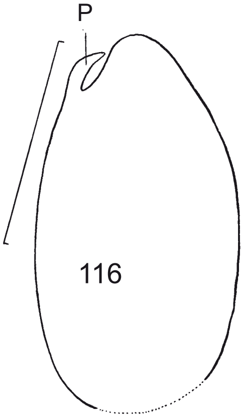
115

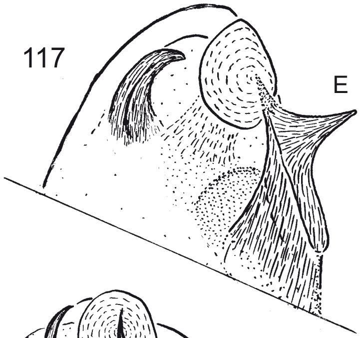
fig. 111) *Eomysmena* sp. indet., male (F1703CJW), colulus. Scale bar 0.05;

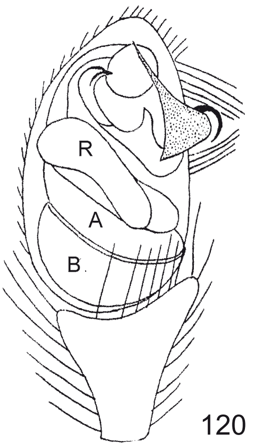
fig. 112. *Eomysmena aviceps* **n. sp.**, male (holotype), proventral aspect of the l. pedipalpus (the fringed apophysis is not drawn). Scale bar 0.5;

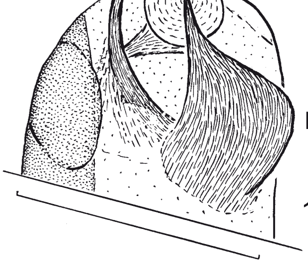
fig. 113) *Eomysmena calefacta* **n. sp.**, male (holotype), proventral aspect of the l. pedipalpus (the fringed apophysis is not drawn). Scale bar 0.5;

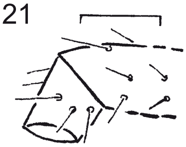
figs. 114–115: *Eomysmena crassa* (PETRUNKEVITCH 1958), male; 114) (coll. H. FLEISSNER), proventral aspect of the l. pedipalpus (F = fringed apophysis); 115) (holotype), distal part of the l. pedipalpus, proventrally-distally (the fringed apophysis is not drawn). Scale bars 0.5;

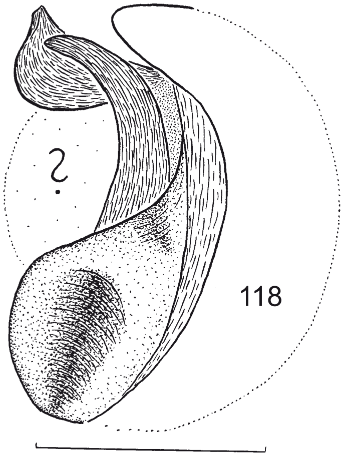

116

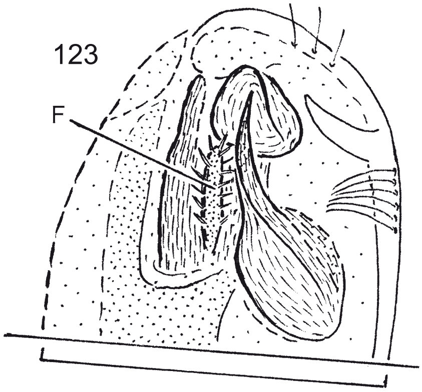

117

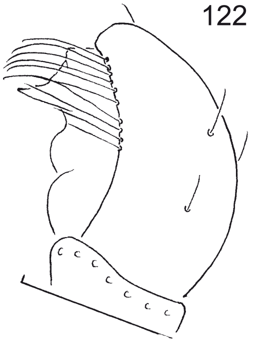

120


119


121


118


123

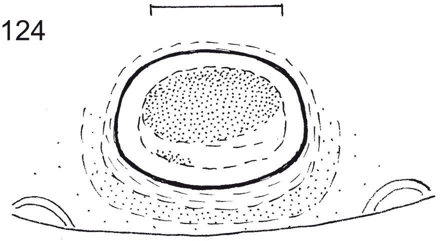

122

figs. 116–118: Eomysmena militaris (KOCH & BERENDT 1854), male (holotype); 116) dorsal aspect of the cymbium of the l. pedipalpus; 117) distal part of the l. pedipalpus, proventral aspect; 118) prolateral aspect of the r. pedipalpus which is partly hidden. Scale bar 0.5;

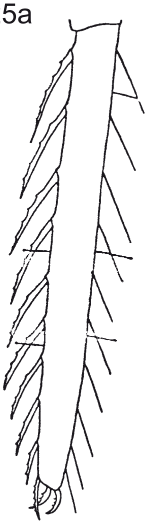
figs. 119–120: Eomysmena moritura PETRUNKEVITCH 1942, male; 119) (holotype), distal part of the l. pedipalpus (redrawn from the r. pedipalpus), proventral aspect (the fringed apophysis is not drawn). Scale bar 0.5; 120) specimen in the coll. of the ZMHUB; taken from PETRUNKEVITCH (1958: Fig. 104);

figs. 121–123: Eomysmena recta **n. sp**., male (holotype); 121) amputation through the l. patella III, retrolateral aspect. Note the stump of the patella which apparently is closed and healed; 122) retrolateral aspect of the l. pedipalpus, outline; 123) proventral aspect of the l. pedipalpus, distal parts; basal parts are hidden by an emulsion. F = fringed apophysis. Scale bars 0.2 in fig. 121, 0.5 in the remaining figs.;

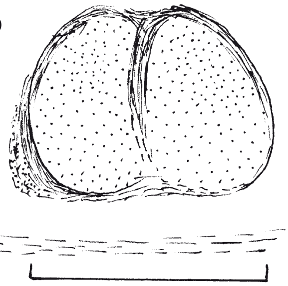
124



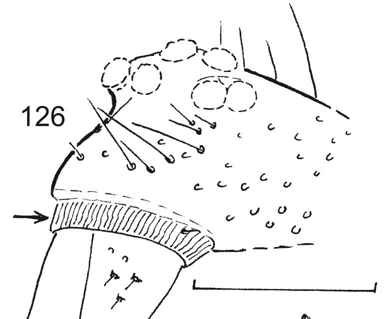
125a

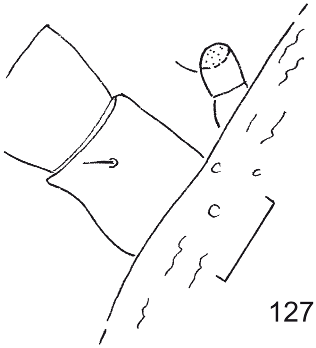


125b

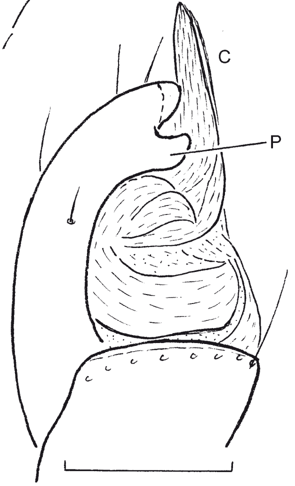


126

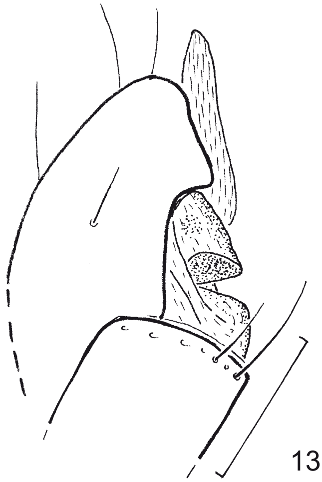




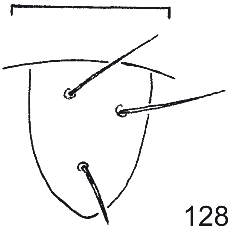
127



129



130



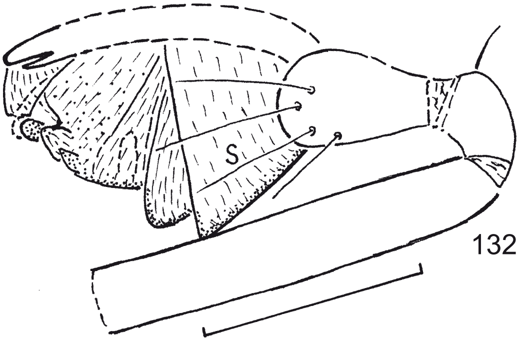
128

fig. 124) Eomysmena sp. indet., female (F1701/CJW), epigyne with a plug in the middle, and partly covered with an emulsion. Scale bar 0.1;

figs. 125a–125b: Eomysmena kaestneri (PETRUNKEVITCH 1958) female (holotype); 125a) lateral aspect of the posterior tarsus with its ventral comb of serrated hairs; 125b) divided groove of the epigyne, ventral aspect, slightly from the right side. The paired large pits werde erroneously called “sperm receptacula” by PETRUNKEVITCH (1958: 188). Scale bar 0.2;

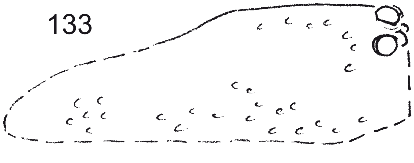
figs. 126–130: Eoteutana hirsuta **n. gen. n. sp**., male (holotype); 126) laeral and slightly anterior aspect of the prosoma. The arrow points to the clypeal furrows. The eyes are covered with emulsions; 127) regenerated stump of the left pedipalpus as well as the first left coxa and trochanter, dorsal aspect, and prosomal margin;128) colulus; 129–130: retroventral and retrolateral aspects of the r. pedipalpus. Scale bars 0.05 in fig. 128), 0.5 in fig. 126), 0.2 in the remaining figs.;

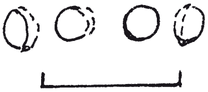
131



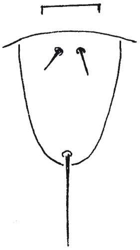
132

133



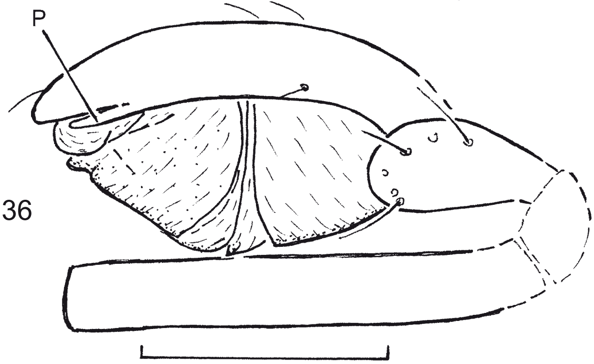


134



135

137



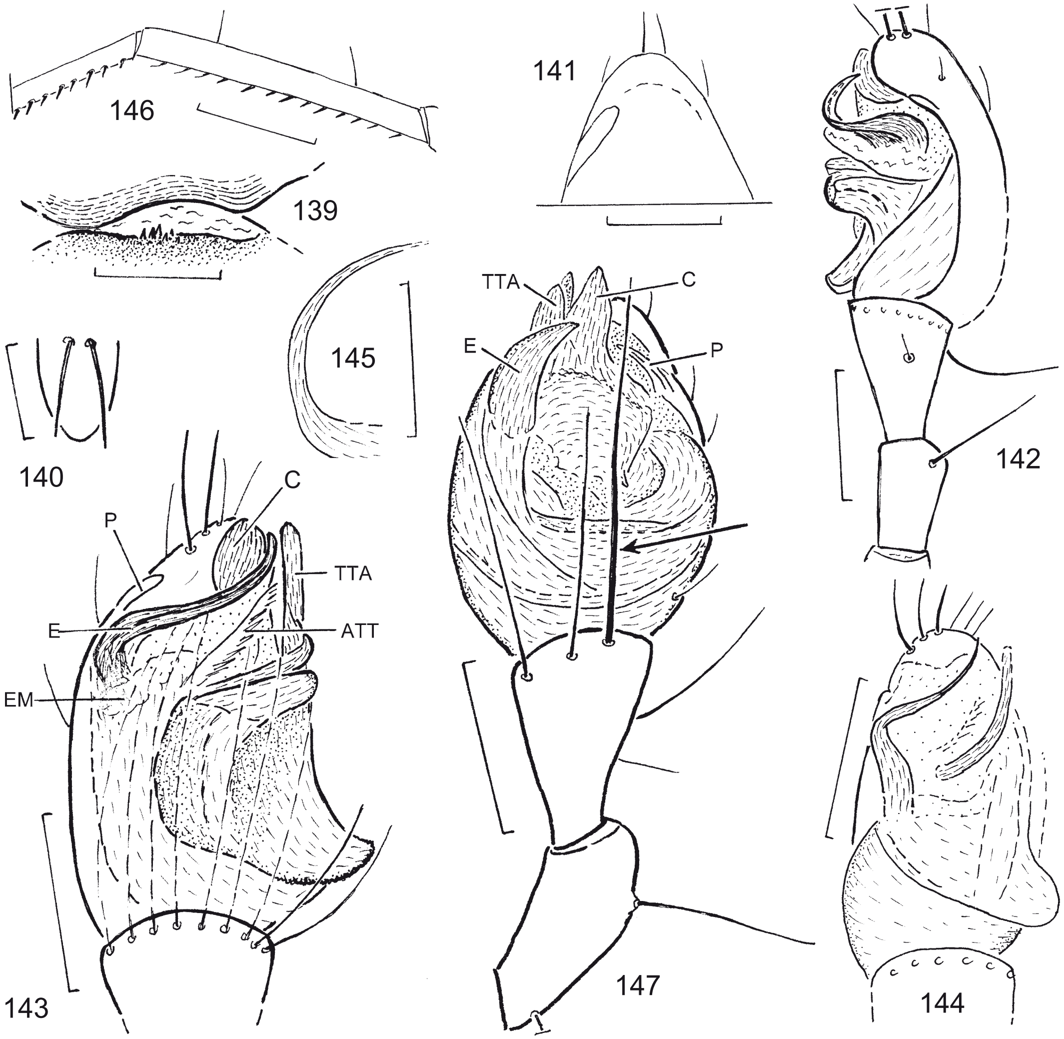
136

138

figs. 131–132: Nanosteatoda breviscutum **n. gen. n. sp**., male (holotype); 131) proventral aspect of the left tibia IV, with a single dorsal bristle (arrow) and three trichobothria; 132) retrolateral aspect of the l. pedipalpus. Scale bar 0.2;

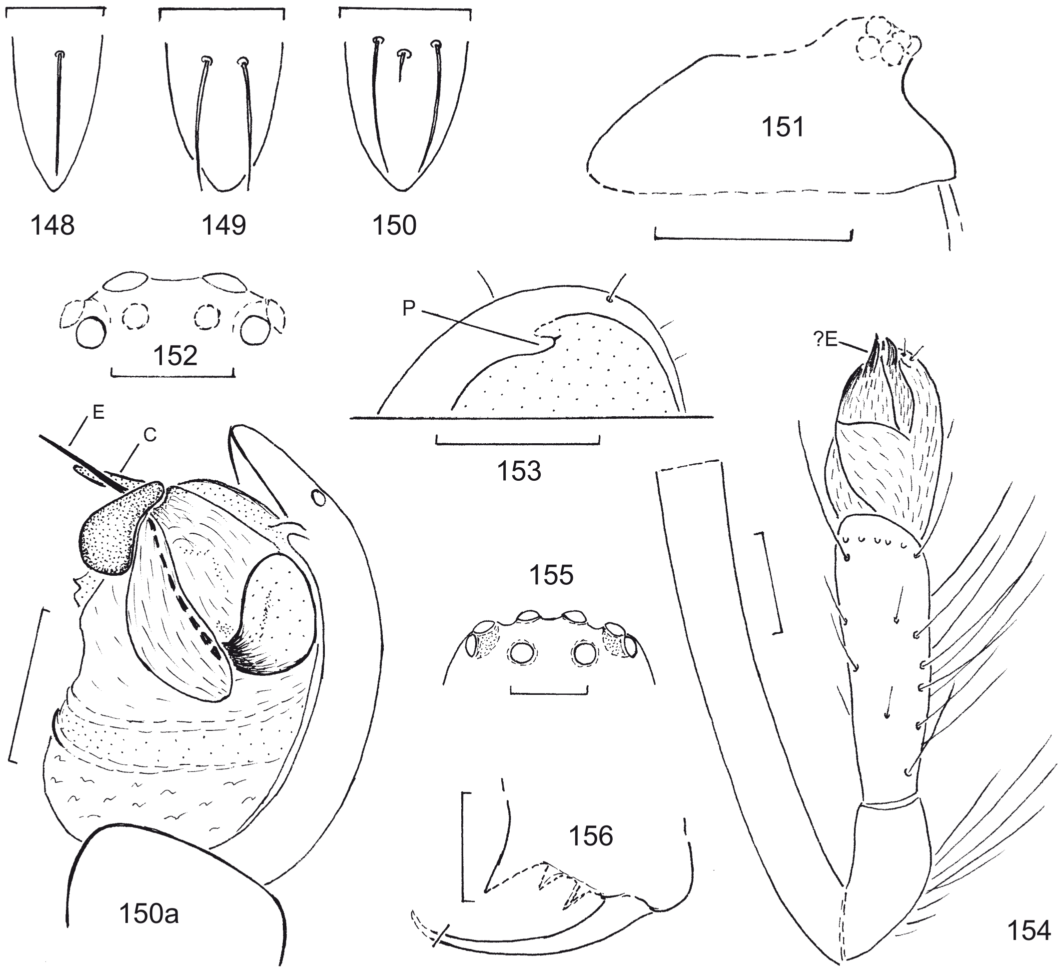
figs. 133–136: Nanosteatoda trisetae **n. gen. n. sp**., male (holotype); 133) outline of the prosoma which is partly hidden, lateral aspect. Only some of the wrincles are drawn; 134) dorsal aspect of the posterior eye row; 135) colulus; 136) retrolateral aspect of the l. pedipalpus. Scale bars 0.02 in fig. 135), 0.2 in the remaining figs.;

figs. 137–138: Protosteatoda gutta **n. gen. n. sp**., male (holotype); 137) anterior-lateral aspect of the chelicerae; 138) retroventral aspect of the l. pedipalpus. Note the hair-bearing outgrowth of the cymbium (arrow). Scale bar 0.2;



figs. 139–145: *Pseudoteutana stigmatosa* (KOCH & BERENDT 1854), male; 139) (GPIUH, coll. HERRLING), prosomal-opisthosomal stridulatory organ. Note the prosomal files and the opisthosomal picks; 140) (F1723/CJW), colulus; 141) (F1717 CJW), distal part of the r. cymbium and paracymbium, central aspect (reconstruction); 142) (F1717/CJW), retrolateral aspect of the l. pedipalpus; 143) (F1722/CJW), retroventral aspect of the r. pedipalpus. Some structures are partly hidden, the basal part of the embolus is hidden by an emulsion. In this figure most of the long tibial hairs are drawn or outlined; 144) (F1728/CJW), ventral aspect of the r. pedipalpus. Some structures are slightly deformed by heating; 145) (F1726/CJW), retrodistal aspect of the left embolus. Scale bars 0.05 in fig. 140), 0.1 in figs. 139) and 145), 0.2 in the remaining figs.;

figs. 146–147: *Unispinatoda aculeata* **n. gen. n. sp.**, male; 146) (GPIUH) prolateral aspect of the r. tibia and the basal part of the r. metatarsus I. Note the ventral cusps/spines from which hairs are partly broken off; 147) ventral aspect of the l. pedipalpus. Note the single long and bristle-shaped tibial hair (arrow). Scale bars 0.5 and 0.2;

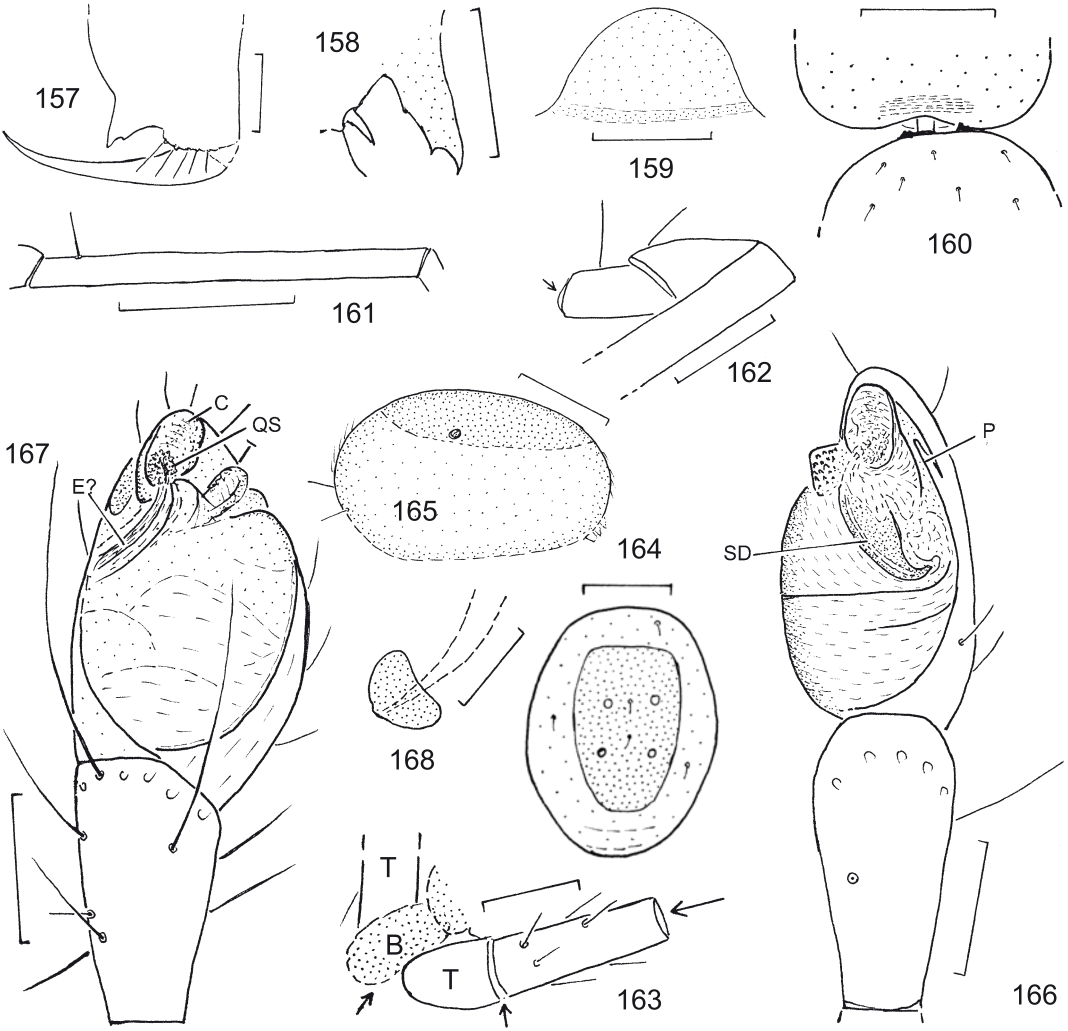


figs. 148–150: *<u>Robertus lividus</u> (BLACKWALL 1836), colulus; 148–149) male and female from Austria (CJW), 150) female from Berlin (CJW). Note the intraspecific variability; most frequent is a pair of hairs (fig. 149). Scale bar 0.05;

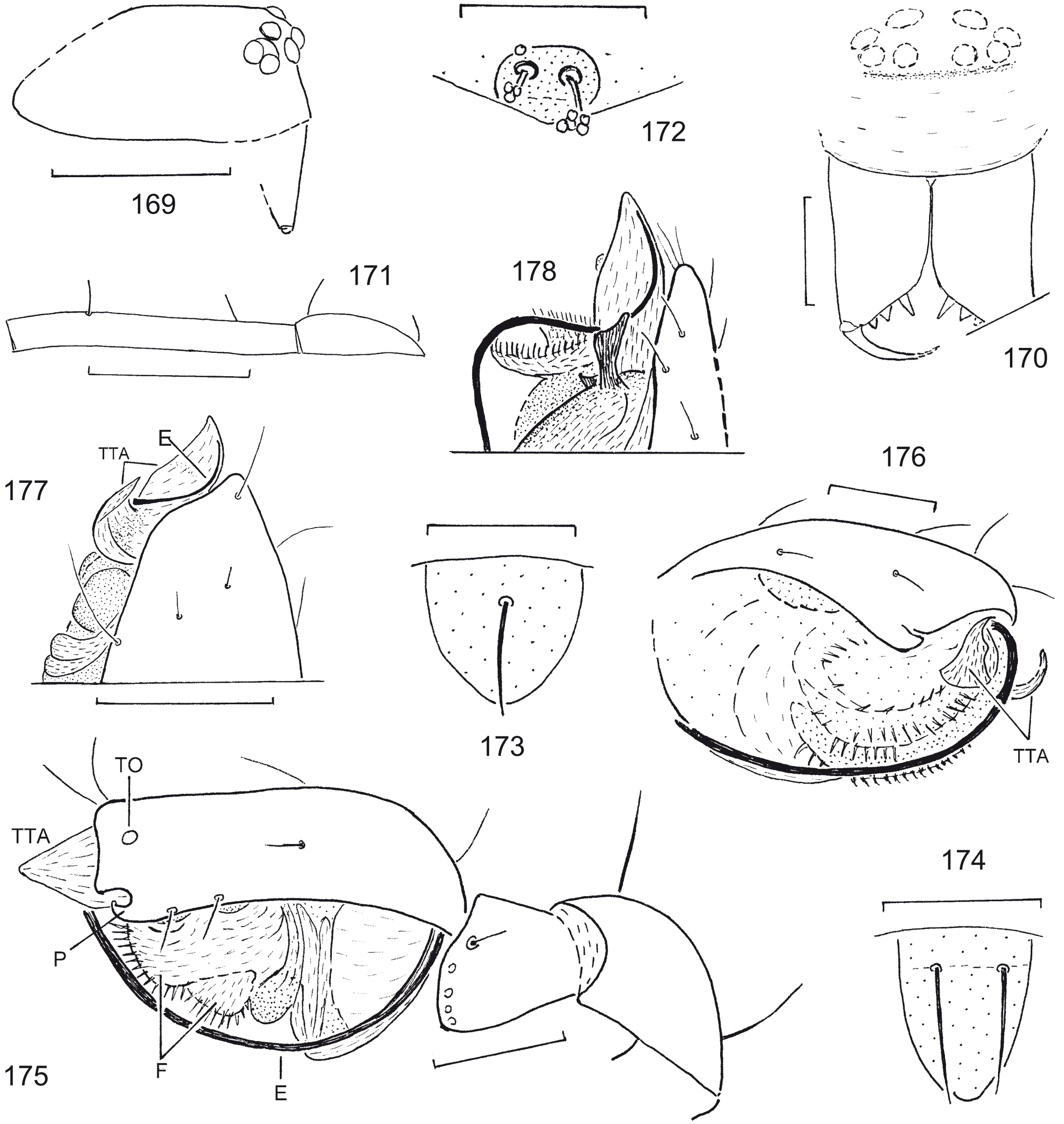
fig. 150a) *<u>Enoplognatha ovata</u> (CLERCK 1757), retrolateral aspect of the left pedipalpus which is partly expanded. The long distal part of the embolus (E) is frequently broken off. Scale bar 0.2;

figs. 151–154: <u>Eolyrifer longitibialis</u> **n. gen. n. sp**., male; 151) (paratype), lateral aspect of the prosoma. Bubbles cover the eye lenses; (paratype), 152) anterior aspect of the eyes; 153) (holotype), cymbium with the paracymbium of the r. pedipalpus, retroapical aspect; 154) (holotype), retrolateral aspect of the l. pedipalpus. Only some hairs are drawn. Scale bars 0.1 in fig. 153), 0.5 in fig. 151), 0.2 in the remaining figs.;

figs. 155–168: <u>Hirsutipalpus varipes</u> **n. gen. n. sp**., male; 155) (paratype F1782/CJW), dorsal aspect of the eyes; 156) (holotype), profrontal aspect of the l. chelicera; 157) (paratype F1783/CJW), distal part of the l. chelicera and fang, anterior and slightly

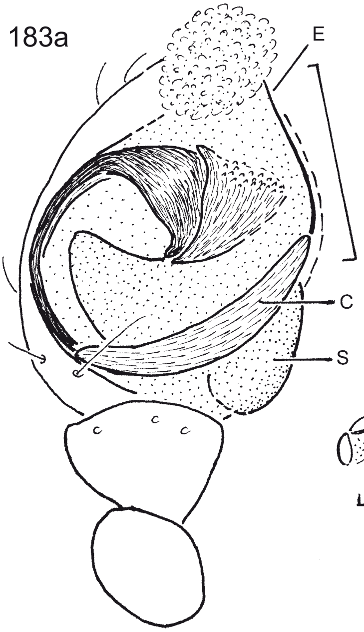


apical aspect; 158) (paratype F1787/CJW), anterior aspect of the largest r. promarginal cheliceral teeth; 159) (F1776/CJW), labium; 160) (paratype F1784/CJW), dorsal aspect of the prosomal-opisthosomal stridulatory organ; 161) (holotype), retrolateral aspect of the r. tibia I with its single dorsal bristle; 162) (paratype F1778/CJW), left leg II, amputation through the base of the tibia (arrow), retrodorsal-basal aspect; 163) (paratype F1782/CJW), broken right leg IV, two times broken tibia (T, short arrows), and amputation through the metatarsus (long arrow); 164) (paratype F1782/CJW), dorsal aspect of the opisthosoma with the scutum and two pairs of sigillae; 165) (paratype 1777/CJW), lateral aspect of the opisthosoma. Note the dorsal scutum. Only one of four sigillae is observable; 166–167) (holotype), retrolateral and ventral aspects of the left and right pedipalpus; 168) (F1780/CJW), anterior aspect of questionable remains of poison at the tip of the left fang. SD = sperm duct within the basal part of the questionable embolus, QS = questionable sperm around the questionable embolus. Only few of the long tibial hairs are drawn. Scale bars 0.5 in figs. 160, 161, 164 and 165), 0.2 in figs. 155–158, 162–163, and 168), 0.1 in the remaining figs.;

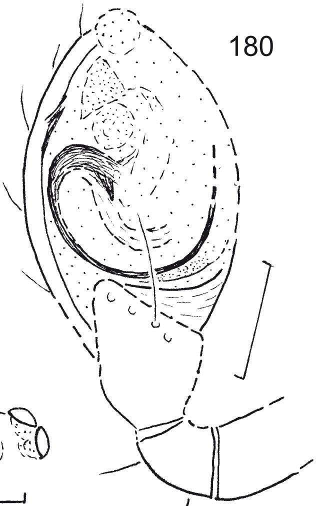


figs. 169–178: *Succinobertus adjacens* **n. gen. n. sp.**, male; 169) (paratype F1766/CJW), lateral aspect of the prosoma; 170) (paratype F1765/CJW), anterior and slightly dorsal aspect of the prosoma. The eye lenses are covered with bubbles; 171) (holotype), retrolateral aspect of the l. patella and tibia with their dorsal bristle (hairs are not drawn); 172) (F1766/CJW), epiandrous gland spigots with secretions just in front of the epigastral furrow; 173) (coll. KUTSCHER, Bitterfeld deposit), colulus; 174) (F1766/CJW), colulus; 175) (holotype), retrodorsal aspect of the l. pedipalpus. F = fringed conductor; 176) (holotype), retrodorsal and slightly apical aspect of the r. pedipalpus. Basal parts (on the left) are partly hidden by a white emulsion; 177) (holotype), prodorsal aspect of the distal part of the r. pedipalpus; 178) (paratype F1768/CJW), proventral aspect of the distal part of the r. pedipalpus. Scale bars 0.5 in figs. 169 and 171), 0.05 in figs. 173–174), 0.2 in figs. 170, 172 and 177), 0.1 in the remaining figs.;

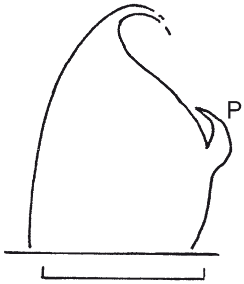
183a



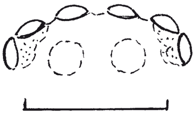
180



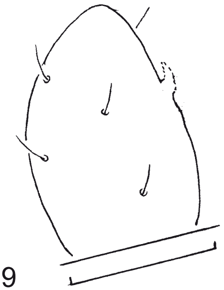
182



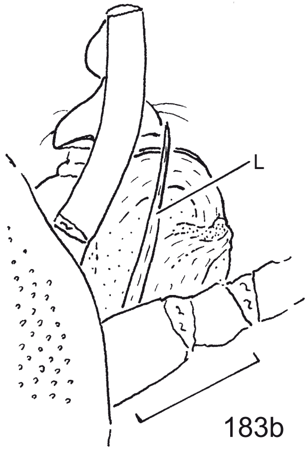
181



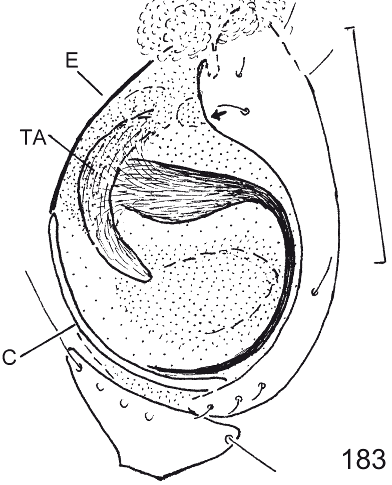
179



183b



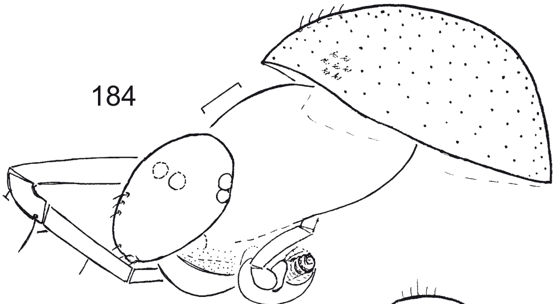
183

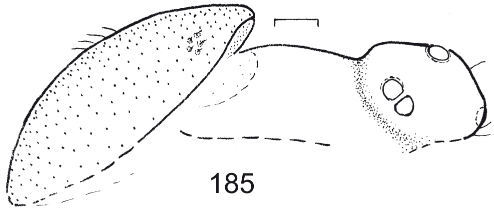


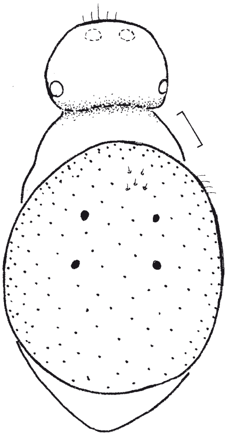
figs. 179–180: *Balticpholcomma scutatum* **n. gen. n. sp**., male (holotypus); 179) retrodorsal aspect of the r. cymbium. The paracymbium is covered by an emulsion; 180) retrolateral aspect of the r. pedipalpus. Parts of the bulbus and embolus are hidden by a white emulsion and a leg article. Scale bar 0.1;

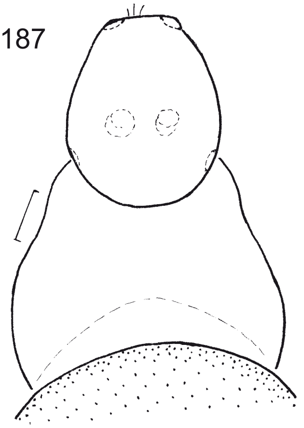
figs. 181–183: *Cymbiopholcomma dudum* **n. gen. n. sp**., male; 181) (holotype), dorsal aspect of the eyes; 182) (paratype), retrodistal aspect of the distal part of the cymbium with the paracymbium; 183) (holotype), ventral and slightly distal aspect of the l. pedipalpus. Mainly distal parts are hidden by bubbles and emulsions. Scale bars 0.1 in fig, 182, 0.2 in the remaining figs;

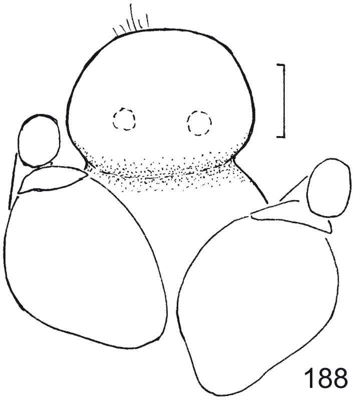
figs. 183a–183b: *Cymbiopholcomma spiculum* **n. gen. n. sp**., male (holotype); 183a) ventral and slightly basal aspect of the r. pedipalpus. Distal parts are hidden; 183b) dorsal aspect of the prosomal margin, basal articles of the r. leg I and the r. pedipalpal femur as well as the ventral aspect of the bulbus. L = lanceolate bulbus apophysis. Scale bar 0.2;

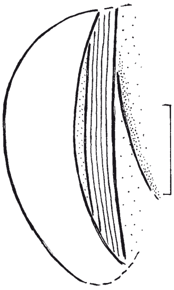

184

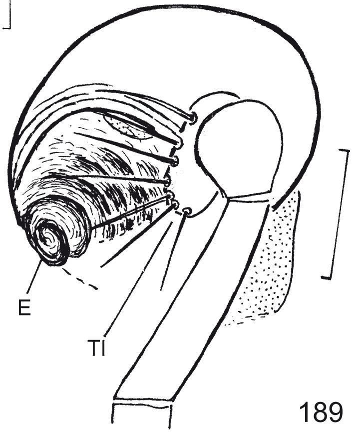

185


186

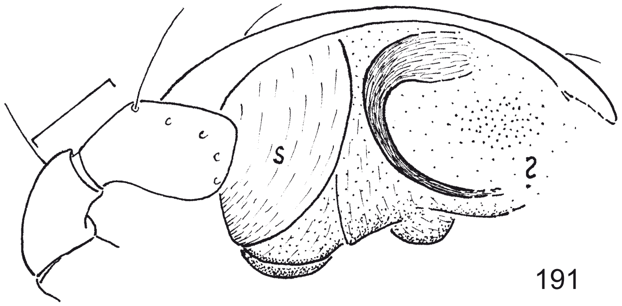

187


188


190



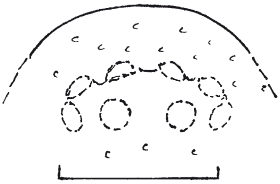
189

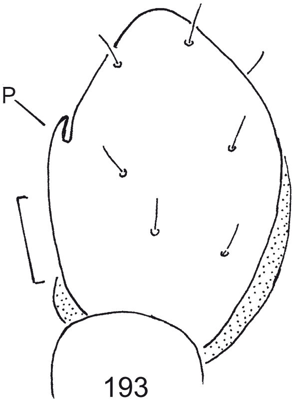


191

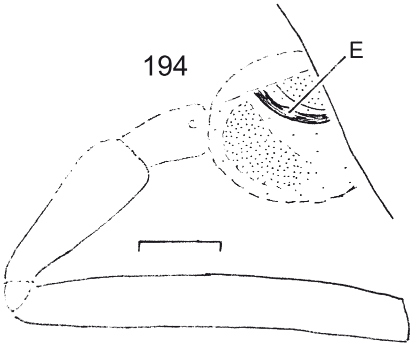
figs. 184–190: *Globulidion spiralis* **n. gen. n. sp**., male (holotype); 184) anterior-left aspect of body, pedipalpi and the anterior right leg. The r. anterior leg bears a single bristle near the base; a longer trichobothrium exists in the distal half. Only few hairs are drawn; 185–186: Lateral and dorsal-posterior aspect of the body; 187) dorsal aspect of the prosoma (the eyes are partly hidden); 188) anterior aspect of prosoma and pedipalpi (most eyes are hidden); 189) anterior-dorsal aspect of the l. pedipalpus; 190) dorsal part of the l. pedipalpus, retrolateral aspect. Note the long and coiled embolus. Scale bar 0.1;

fig. 191) *Obscurpholcomma tegens* **n. gen. n. sp**., male (holotype), retroventral aspect of the r. pedipalpus. Distal parts of the bulbus are hidden. Scale bar 0.1;

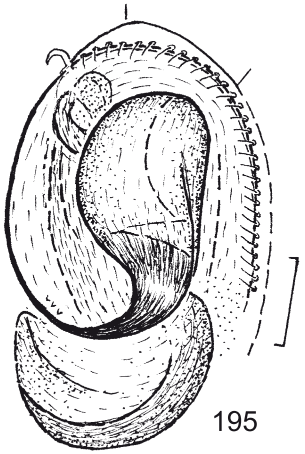

192

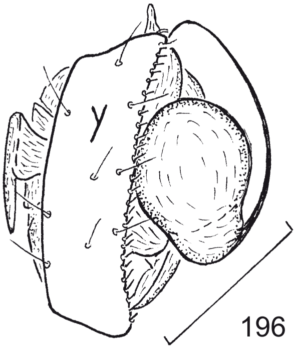


193

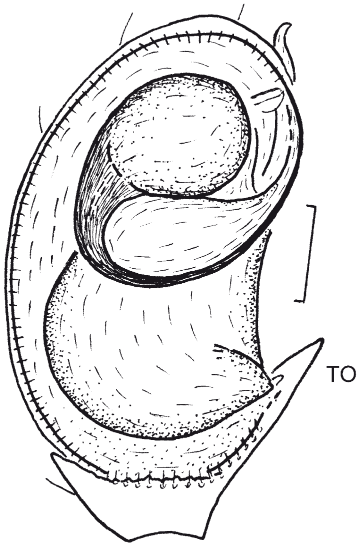


194


195

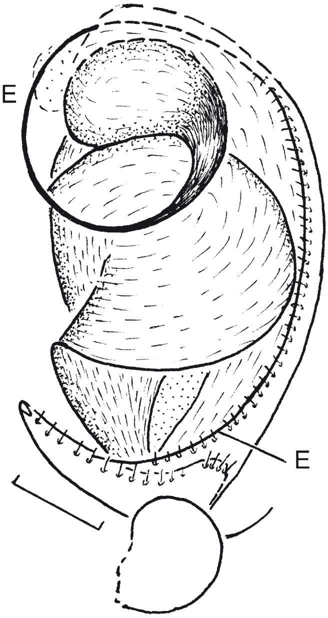


196



197

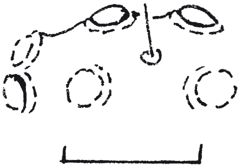
198

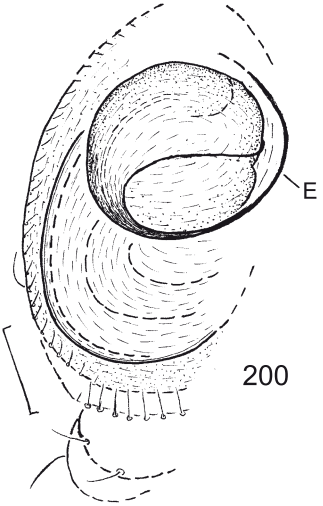


figs. 192–194: <u>*Rugapholcomma patellaris*</u> **n. gen. n. sp.**, male (holotype); 192) dorsal aspect of the anterior part of the prosoma; 193) dorsal aspect of the l. cymbium; 194) retrolateral aspect of the r. pedipalpus (femur retrodorsal, bulbus retroventral). The bulbus is distally hidden by the r. femur II. Scale bars 0.4 in fig. 192) 0.1 in fig. 193), 0.2 in fig. 194);

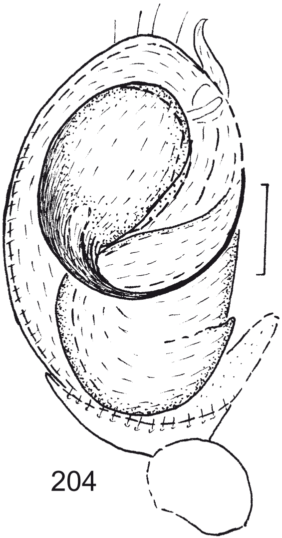
figs. 195–196: <u>*Succinura aciesaeta*</u> **n. gen. n. sp.**, male (holotype); 195) ventral aspect of the l. pedipalpus; 196) retrodorsal-apical aspect of the r. pedipalpus. The bulbus is slightly expanded. Note the slender cymbium (Y). Scale bars 0.1 and 0.2;

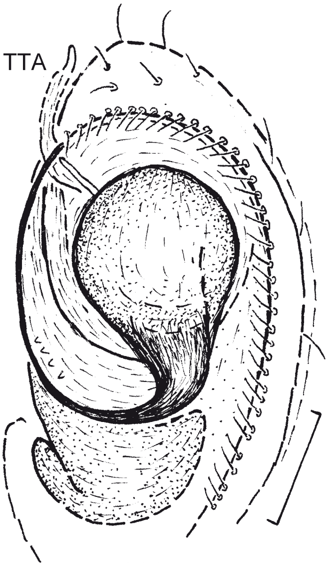
figs. 197–198: <u>*Succinura bellavista*</u> **n. gen. n. sp.**, male (holotype); 197) “ventral” (retrolateral) aspect of the r. pedipalpus; 198) retroventral-basal aspect of the l. pedipalpus. Note the tibial outgrowth (TO). Scale bar 0.1;


199

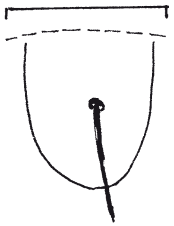


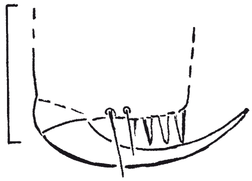
200

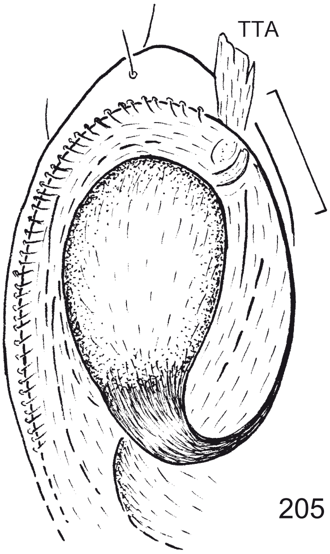

204



203


202


201



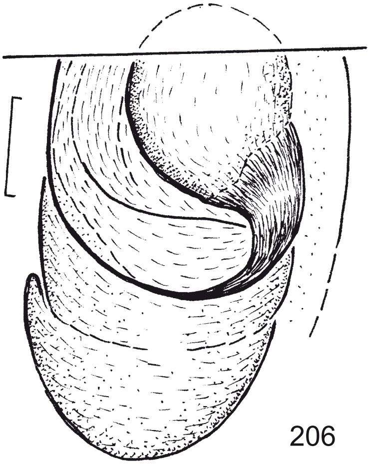
205

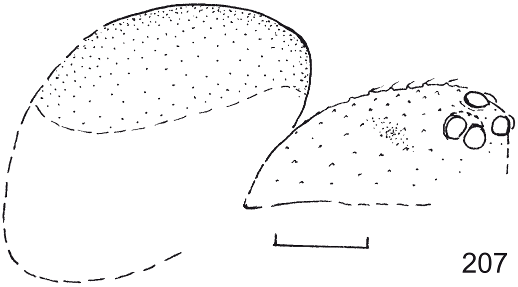
figs. 199–200: Succinura circuita **n. gen. n. sp**., male (holotypus); 199) position of the eyes (the right eyes are hidden); 200) ventral aspect of the r. pedipalpus (distal parts are hidden, the embolus is most probably not in its natural position). Scale bar 0.1;

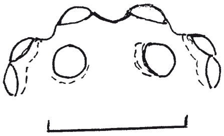
figs. 201–203: Succinura dubia **n. gen. n. sp**., male (holotype); 201) anterior aspect of the distal part of the right chelicera; 202) colulus; 203) ventral aspect of the l. pedipalpus. Scale bars 0.1, 0.02 and 0.1;

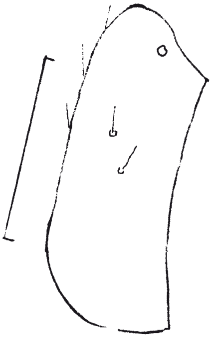
fig. 204) Succinura fuscoruber **n. gen. n. sp**., male (holotype), ventral aspect of the r. pedipalpus. Scale bar 0.1;

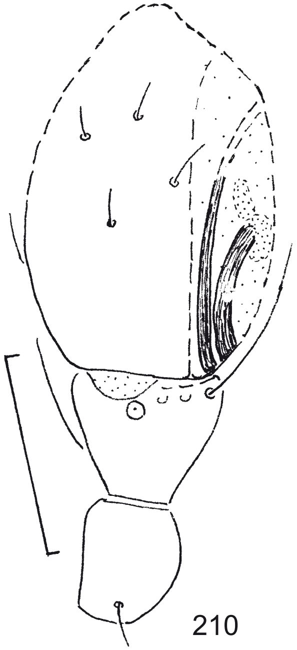
fig. 205) Succinura ovalis **n. gen. n. sp**., male (holotype), ventral aspect of the r. pedipalpus (the basal part is hidden). Scale bar 0.1;

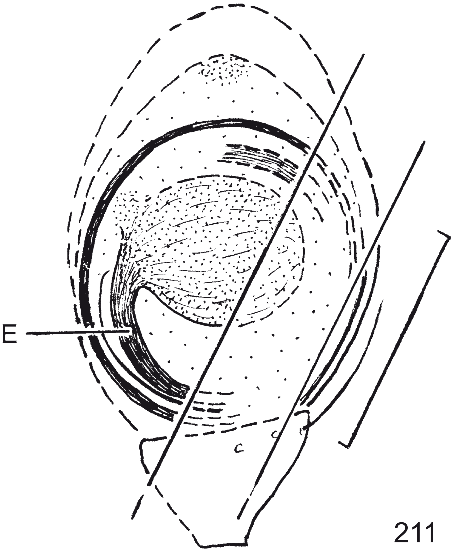

206


207


208


209

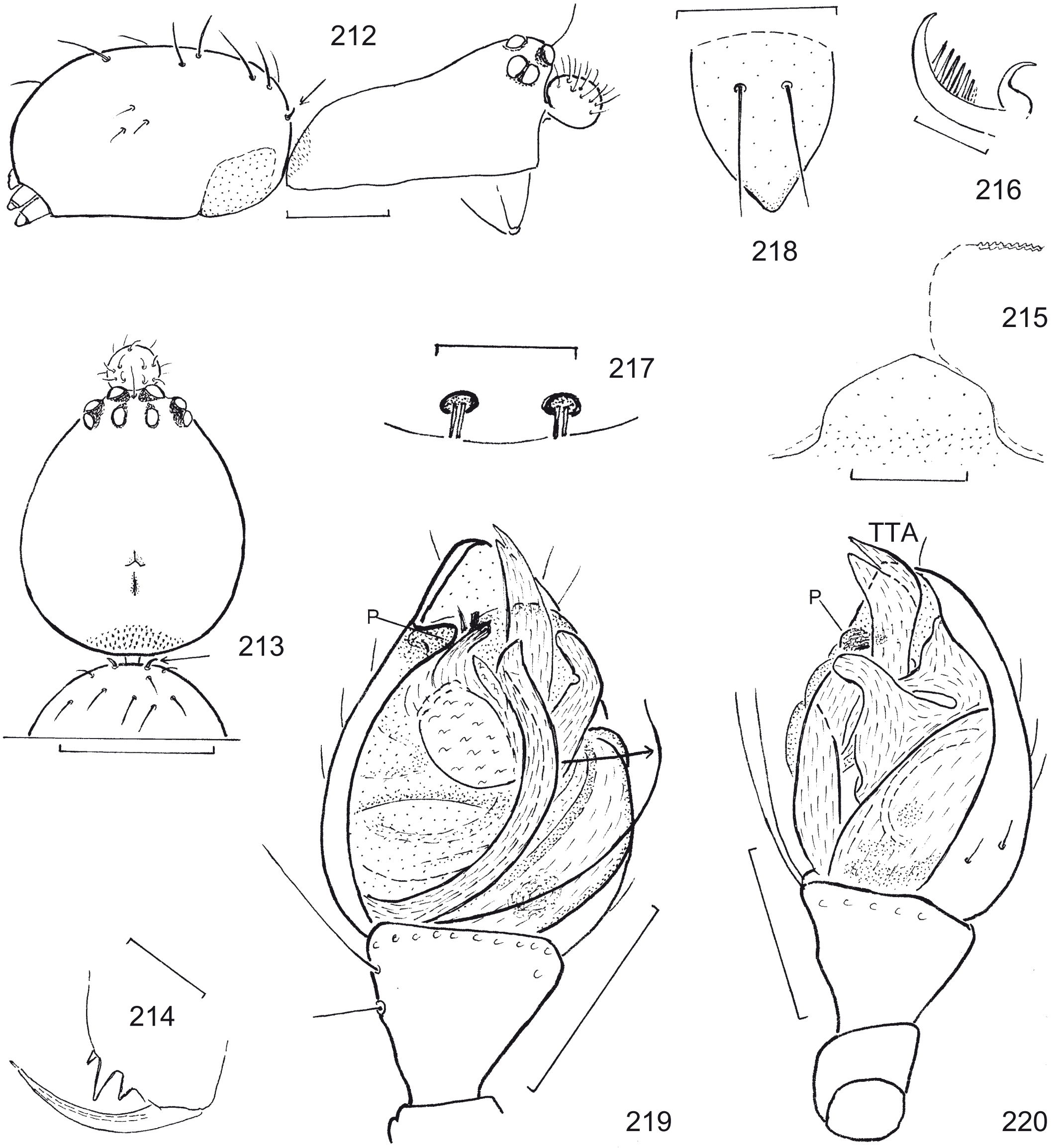

210



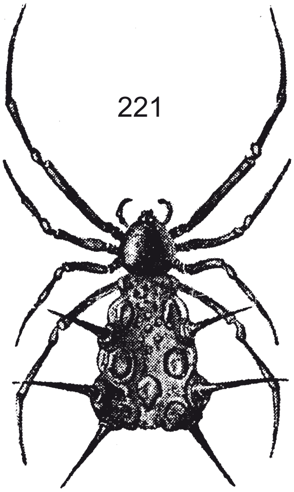
211

fig. 206) <u>*Succinura*</u> (**n. gen.**) sp. indet., male (F1818/CJW), ventral aspect of the l. pedipalpus (the distal part is hidden). Scale bar 0.1;

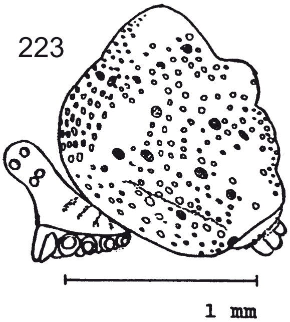
figs. 207–211: <u>*Vicipholcomma spiralis*</u> **n. gen. n. sp**., male (paratype fig. 209, holotype: The remaining figs.); 207) lateral aspect of the body. (Parts of the body – e. g. the spinnerets and the ring around the spinnerets – are hidden by a white emulsion or leg articles); 208) dorsal aspect of the eyes; 209) retrolateral aspect of the r. cymbium; 210) retrodorsal aspect of the r. pedipalpus. (Parts are hidden by a white emulsion); 211) ventral aspect of the r. pedipalpus which is partly hidden by a white emulsion, the r. pedipalpal tibia and distally by a bubble. Scale bar 0.2;



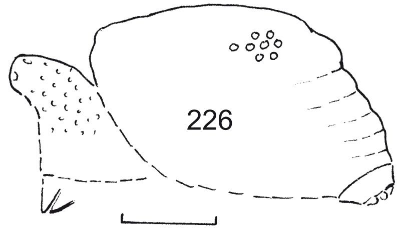
figs. 212–220: *<u>Magnopholcomma globulus</u> **n. gen. n. sp**., male (holotypus); 212) lateral aspect of the body. The arrow points to the right opisthosomal stridulatory bristle. (Only few hairs are drawn); 213) dorsal aspect of the prosoma and the anterior part of the prosoma. The arrow points to the r. stridulatory bristle; 214) anterior-dorsal aspect of the distal part of the l. chelicera; 215) ventral aspect to the labium which is fused to the sternum, and of parts of the left gnathocoxa; 216) prolateral aspect of the unpaired and prolateral paired claw of the l. tarsus IV; 217) epiandrous gland spigots. There are two pairs which have a sclerotized base; 218) colulus; 219) ventral aspect of the r. pedipalpus. The embolus is taken off from the conductor in an artificial position (arrow); 220) prolateral aspect of the r. pedipalpus. Scale bars 0.05 in figs. 217–218), 0.1 in fig. 217), 0.2 in figs. 214–215), 0.5 in the remaining figs.;

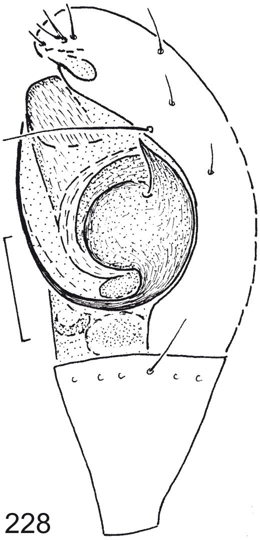

221

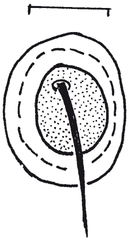

222

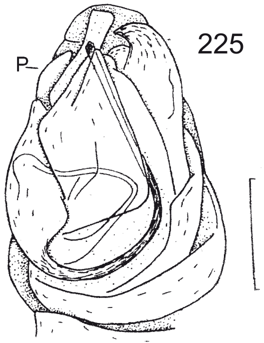

223


224


226


228


227


225

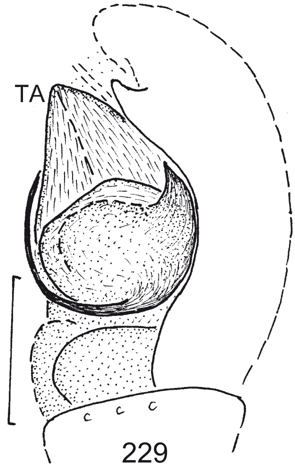
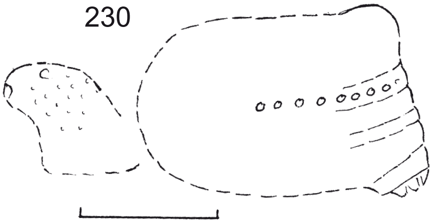

229

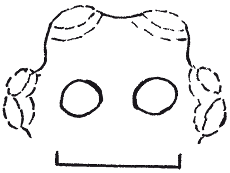
fig. 221) *Phoroncidia lygeana (WALCKENAER 1841), dorsal aspect of a female; taken from SIMON;

figs. 222–225: *Ulesanis paradoxa (LUCAS 1846); 222) male from France (CJW), prolateral aspect of the r. tarsus II; scale bar 0.1. Note the bristle-shaped hair in the middle (claws and hairs – except two ones – are not drawn); 223–224) lateral aspect of the body; taken from VANUYTVEN (1991); 225) ventral aspect of the l. pedipalpus; taken from THALER & NOFLATSCHER (1990);

figs. 226–29: Ulesanis antecessor **n. sp**. male; 226) paratype F1802/CJW, lateral aspect of the body; 227) paratype F1803/CJW, hair on a sclerotized plate of the dorsal part of the opisthosoma; 228) holotype, retrolateral aspect of the l. pedipalpus; 229) F1803/CJW, retrolateral aspect of the l. pedipalpus. Scale bars 0.5 in fig. 226), 0.01 in fig. 227), 0.1 in the remaining figs.;

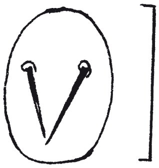
230

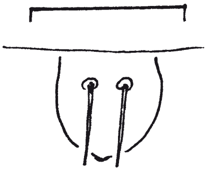




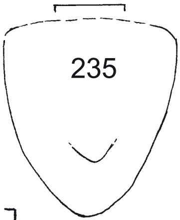
231

232

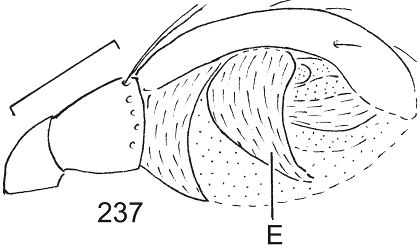




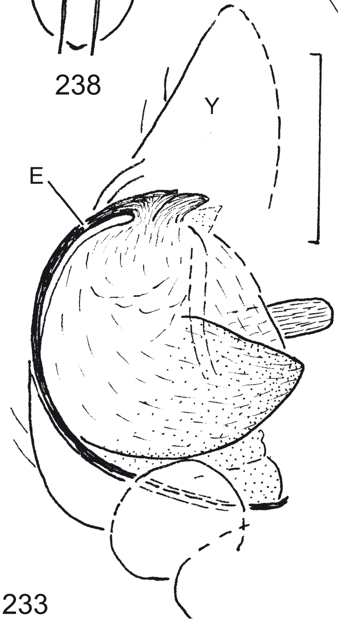
238



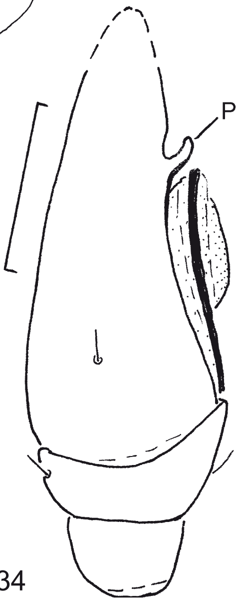
235



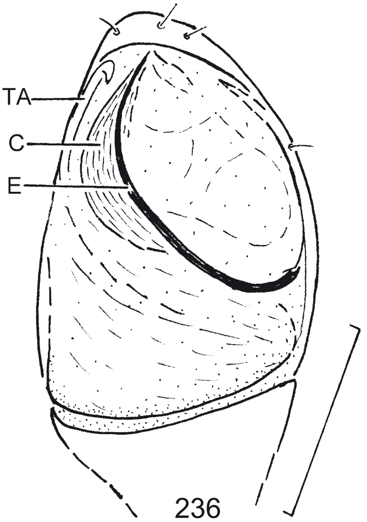
237



233



234



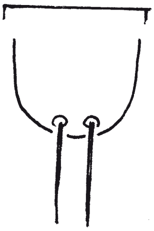
236

figs. 230–235: *Ulesanis longicymbium* **n. sp**.; 230) male paratype F1808/CJW, lateral aspect of the body (parts are hidden or absent); 231) male holotype, dorsal aspect of the eyes; 232) male holotype, colulus; 233) male holotype, ventral and slightly basal aspect of the r. pedipalpus (parts are hidden by emulsions and leg articles); 234) male holotype, retrodorsal aspect of the r. pedipalpus; 235) female paratype F1804/CJW, dorsal-posterior aspect (outline) of the opisthosoma. Note the dorsal hump. Scale bars 0.5 in figs. 230) and 235), 0.02 in fig. 233), 0.2 in the remaining figs.;

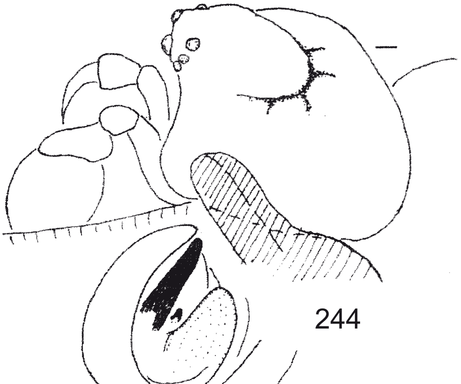
fig. 236) *Ulesanus ovalis* **n. sp**., male (holotype), ventral aspect of the l. pedipalpus (parts of the bulbus are hidden by emulsions). Scale bar 0.2;

fig. 237) *Ulesanis parvus* **n. sp**., male (holotype), retrolateral aspect of the r. pedipalpus (ventral parts are hidden). Scale bar 0.1;

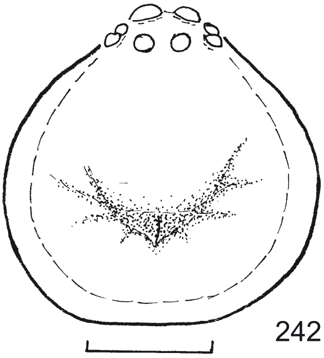
fig. 238) **Dipoena melanogaster* (C. L. KOCH 1837), female (Europe, CJW), colulus. Scale bar 0.05;



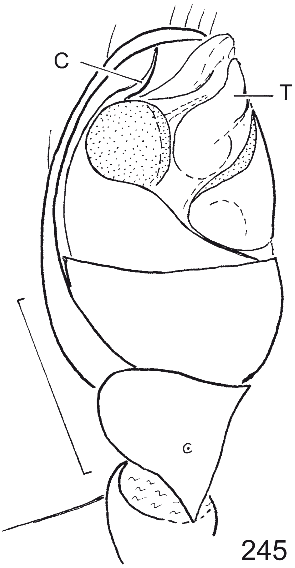
239



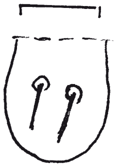
244



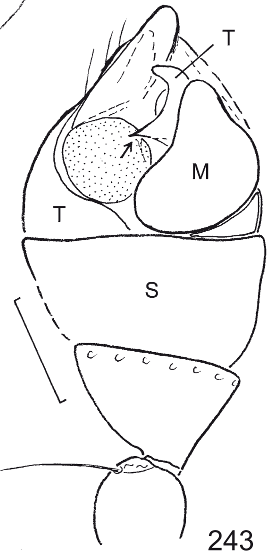
242



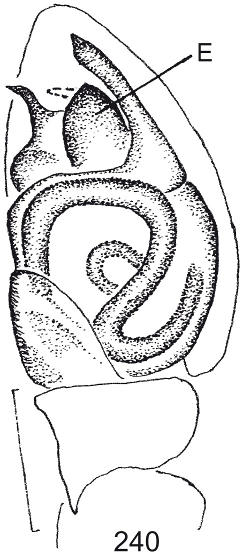
245



241



243



240

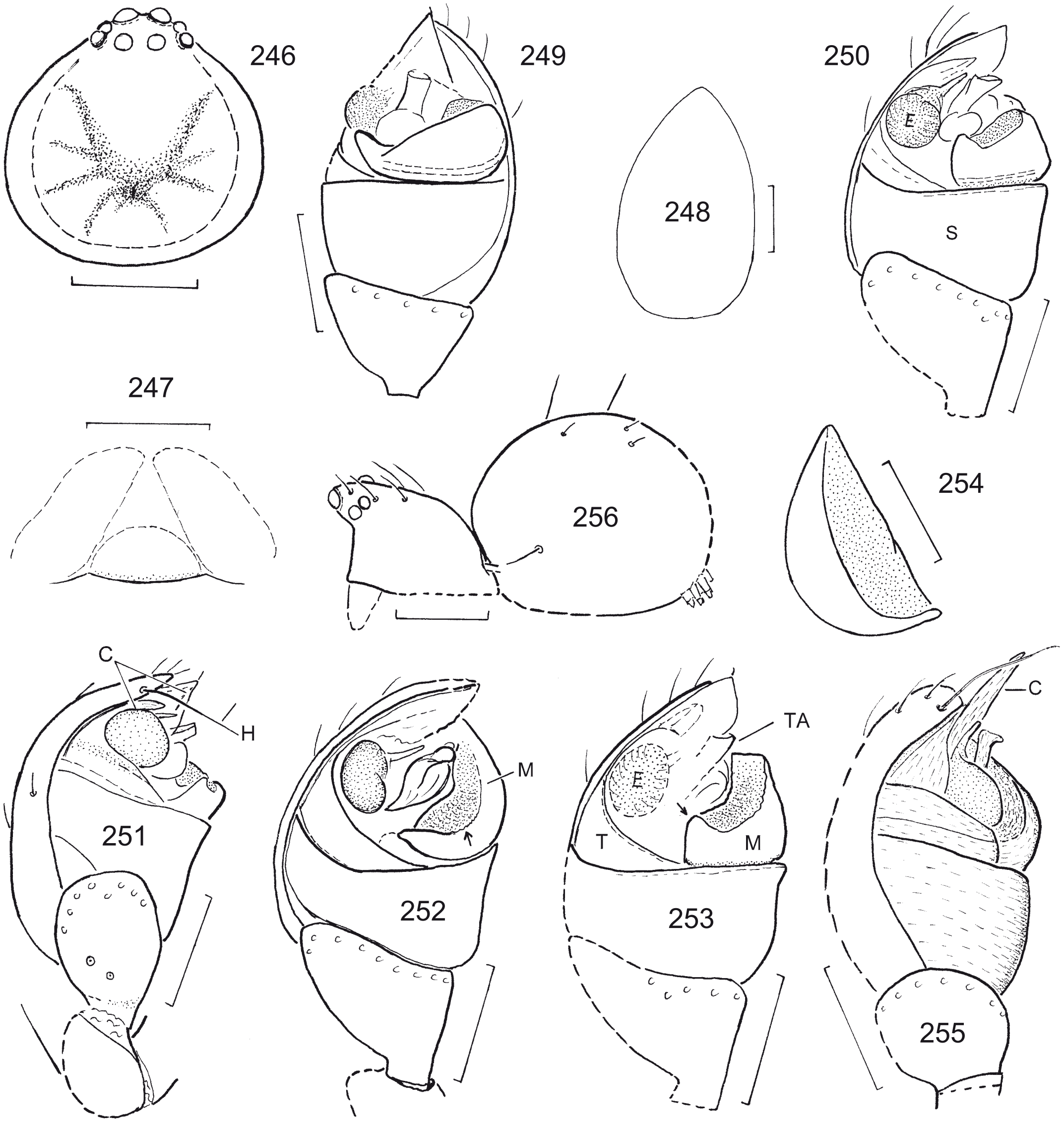
figs. 239–240: *<u>Lasaeola</u> (<u>Yaginumena</u>) <u>mutilata</u> (BOESENBERG & STRAND 1906) from Japan, 239) female, ventral aspect of the colulus; 240) ventral aspect of the l. ♂-pedipalpus; taken from YOSHIDA (2003: Fig: 461), slightly modified; scale bars 0.03 and 0.1;

fig. 241) <u>Lasaeola</u> (<u>Lasaeola</u>) sp. indet., male F1534/CJW, colulus. Note the paired hairs. Scale bar 0.02;

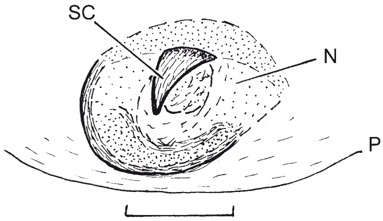
figs. 242–243: <u>Lasaeola</u> (<u>Lasaeola</u>) <u>acumen</u> **n. sp.**, male holotype; 242) dorsal aspect of the prosoma (hairs are not drawn); 243) ventral and slightly basal aspect of the r. pedipalpus. The embolus is hidden; the arrow points to the tegular apophysis. Scale bar 0.2;

fig. 244) <u>Lasaeola</u> (?<u>Lasaeola</u>) <u>baltica</u> (MARUSIK & PENNEY 2005) (sub “*Euryopis*”), male holotype, prosoma and pedipalpi. Taken from MARUSIK & PENNEY(2993);

fig. 245 <u>Lasaeola</u> (<u>Lasaeola</u>) <u>bitterfeldensis</u> **n. sp.**, male holotype, retroventral aspect of the r. pedipalpus. Scale bar 0.2;

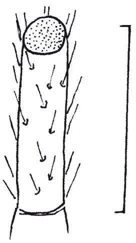


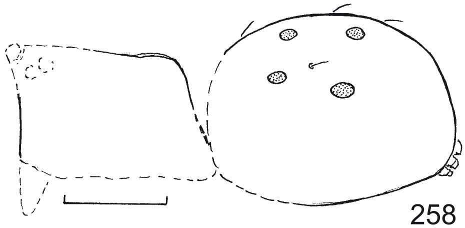
figs. 246–257: Lasaeola (Lasaeola) communis **n. sp.**, male types in figs. 246–255; 246) F1483/CJW, dorsal aspect of the prosoma (hairs are not drawn); 247) F1511/CJW, ventral aspect of labium and gnathocoxae (parts are hidden by a white emulsion); 248) F1475/CJW, dorsal aspect of the l. cymbium; 249) F1474/CJW, ventral aspect of the r. pedipalpus; 250) holotype, ventral and slightly retrolateral aspect of the r. pedipalpus; 251) F1541/CJW, retrolateral aspect of the r. pedipalpus. Note the tibia which appears longest in this position. A bristle-shaped cymbial hair (H) exists also in other species but is not always drawn; 252) F1491/CJW, retroventral aspect of the r. pedipalpus; 253) F1474/CJW, retroventral aspect of the r. pediplpus (parts are hidden); 254) F1492/CJW, retroventral aspect of the median apophysis of the l. pedipalpus; 255) coll. H. GRABENHORST, Bitterfeld deposit, retroventral (and fairly basal) aspect of the r. pedipalpus. The conductor appears very long in this position; 256–257: Fe-



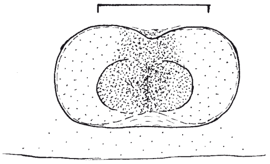
257

261

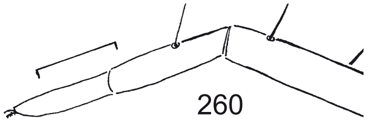




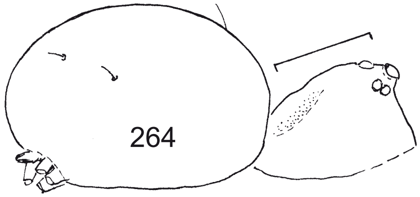
258



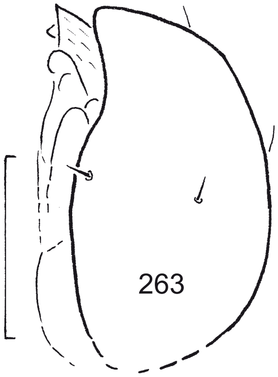
265



260

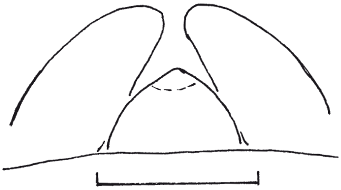


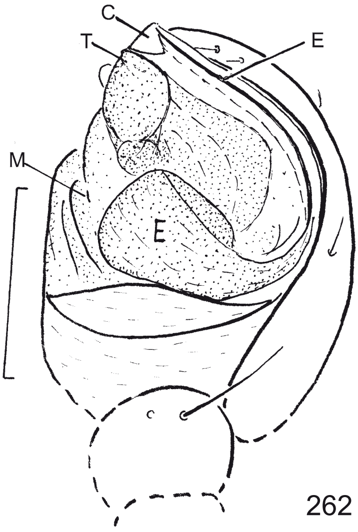
264



263

259

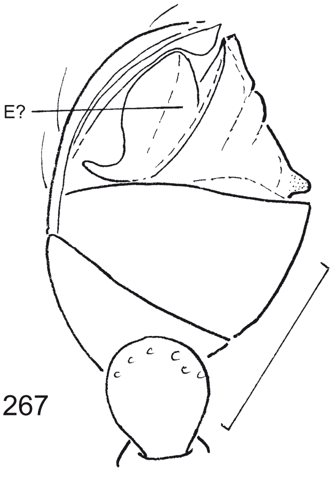




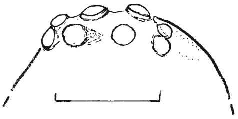
262

male paratype F1476/CJW; 256) lateral aspect of the body (only few hairs are drawn); 257) ventral-left aspect of the epigyne (slightly from behind). N = plug or emulsion, P = epigastral furrow, SC = scape of the epigyne. Scale bars 0.5 in fig. 256), 0.1 in figs. 246), 254) and 257), 0.2 in the remaining figs.;

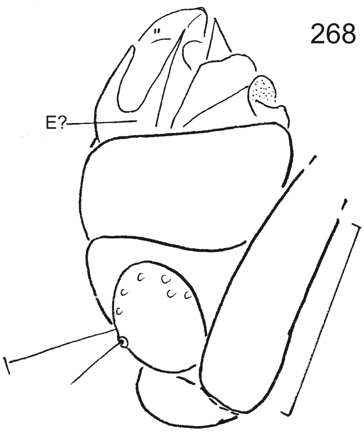
figs. 258–265: Lasaeola (Nactodipoena) dunbari (PETRUNKEVITCH 1858), male: Figs. 258–263, female: Figs 364–265; 258) F1519/CJW, body, lateral aspect of the prosoma, retrodorsal aspect of the opisthosoma; the eyes are hidden; 259) F1515/CJW, ventral aspect of labium and gnathocoxae; 260) F1519/CJW, prolateral aspect of the right leg I. Note the long metatarsal trichobothrium (hairs are not drawn); 261) F1515/CJW, ventral-apical aspect of the l. anterior metatarsus which was amputated – probably by an ant – between this article and the tarsus. The stump looks healed, the spider was apparently preserved alive in the resin; 262) F1519/CJW, retroventral aspect of the l. pedipalpus; 263) prolateral aspect of the r. pedipalpus; 264) ♀ F152/CJW, lateral aspect of the opisthosoma (the opisthosomal sigillae are not drawn); 265) ♀ F1521/CJW, epigyne. Scale bars 0.5 in figs. 258) and 264), 0.1 in figs. 259) and 265), 0.2 in the remaining figs.;



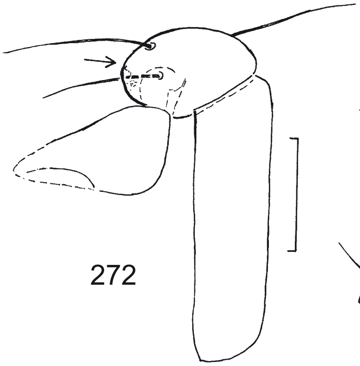
267



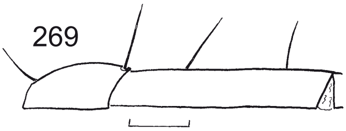
266



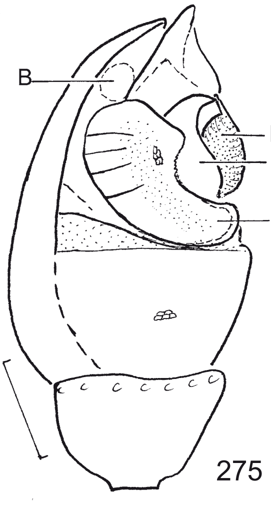
268



272

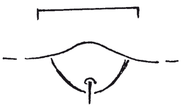


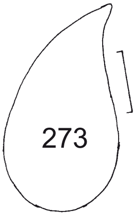
269



275

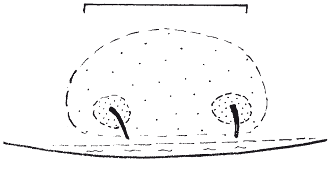
271

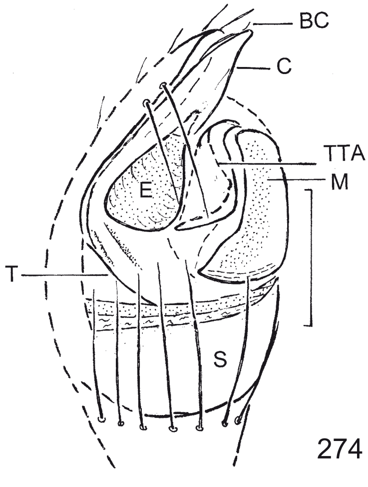




273

270



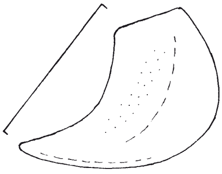


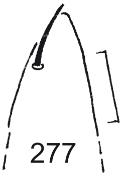
274

figs. 266–268: ?<u>*Lasaeola furca*</u> **n. sp.**, male holotype; 266) dorsal-right aspect of the anterior part of the prosoma with eyes; 267) retrolateral aspect of the r. pedipalpus; 268) ventral and slightly basal aspect of the r. pedipalpus. Scale bar 0.2;

figs. 269–279: <u>*Lasaeola*</u> (<u>*Lasaeola*</u>) <u>*germanica*</u> (PETRUNKEVITCH 1958), male; 269) F1466/CJW, prolateral aspect of the left patella and tibia; 270) F1470/CJW, paired epiandrous gland spigots in front of the epigastral furrow; 271) F1470/CJW, colulus; note its single hair; 272) holotype, retrolateral aspect of the left pedipalpal femur, patella and tibia. The arrow points to the elevated patella; 273) F1468/CJW, dorsal and slightly apical aspect of the cymbium of the l. pedipalpus; 274) F1466/CJW, retroventral aspect of the r. pedipalpus (BC = distal bristle of the conductor); 275) F1470/ CJW, proventral aspect of the l. pedipalpus. Note the four furrows of the median apophysis, the scaly structure (only few scales are drawn) of the subtegulum and the median apophysis;

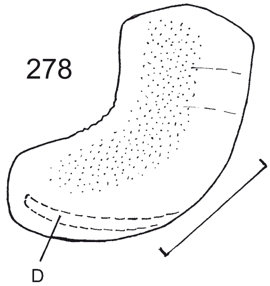
276

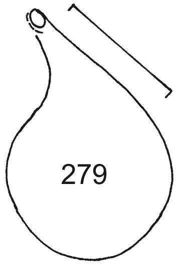




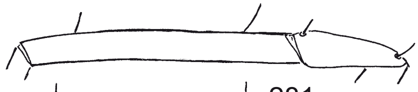
277

278



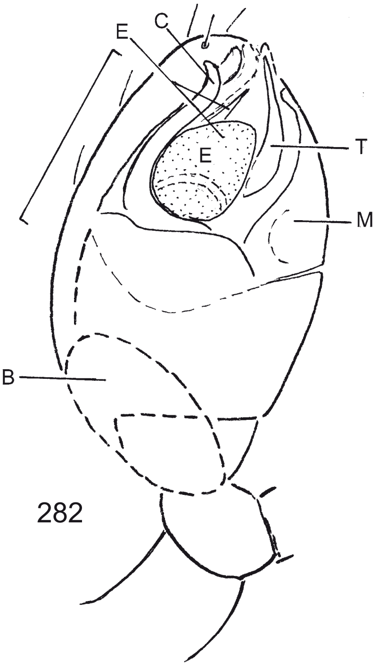


279



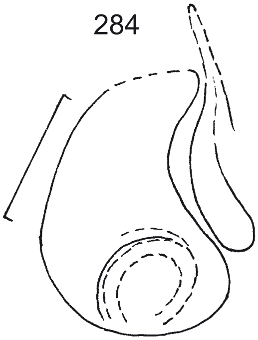
281

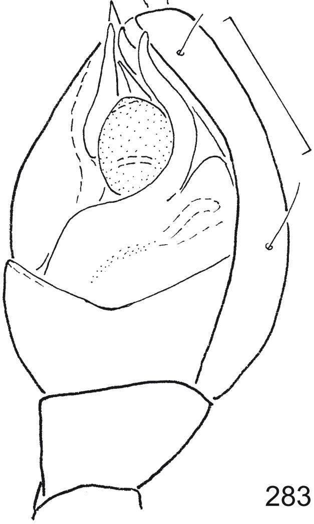
280



282

284

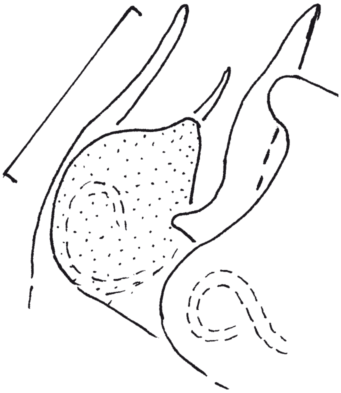




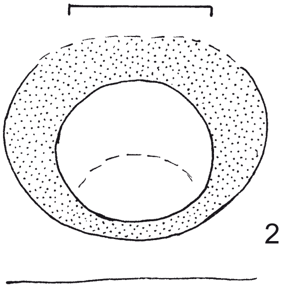
283

276) F1566/CJW, ventral aspect of the short median apophysis of the r. pedipalpus; 277) F1467/CJW, dorsal aspect of the r. conductor with its distal bristle; 278) F1466/CJW, ventral aspect of the median apophysis of the r. pedipalpus. Note the low depression and the sperm duct (D); 279) ventral aspect of the embolus of the left pedipalpus. Note the apical opening of the sperm duct. Scale bars 0.05 in figs. 271) and 277), 0.1 in fig. 279), 0.2 in the remaining figs.;

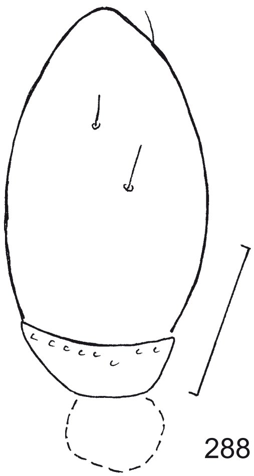
figs. 280–284: <u>Lasaeola</u> (<u>Lasaeola</u>) <u>infulata</u> (KOCH & BERENDT 1854), male; 280) F1528/CJW, lateral aspect of the body (only few hairs are drawn); 281) prolateral aspect of the r. tibia and patella I with bristles; 282) holotype, retroventral aspect of the r. pedipalpus (some basal parts are hidden); 283) F1532/CJW, retroventral aspect of the l. pedipalpus; 284) F1529/CJW, median apophysis (note the sperm duct) and tegular apophysis of the l. pedipalpus. Scale bars 0.5 in figs. 280–281), 0.1 in fig. 284), 0.2 in the remaining figs.;



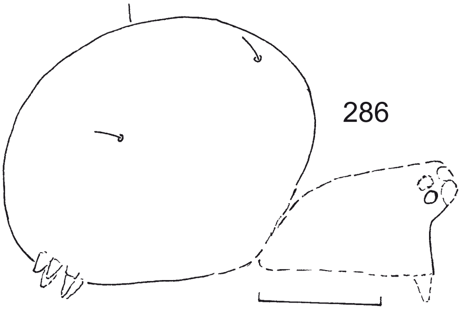
285



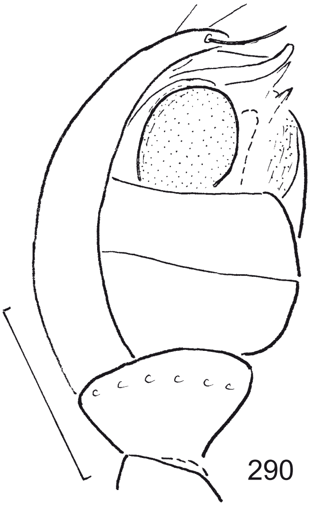
287



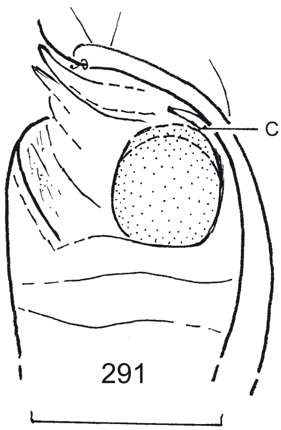
288



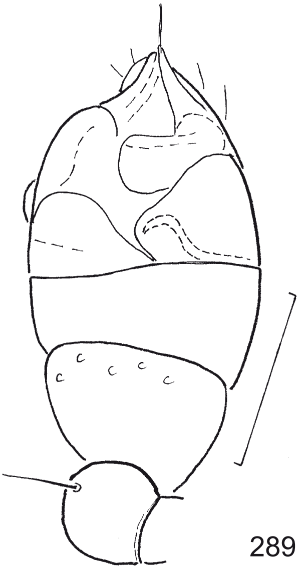
286



290



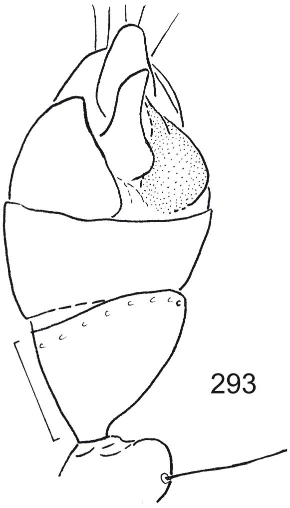
291



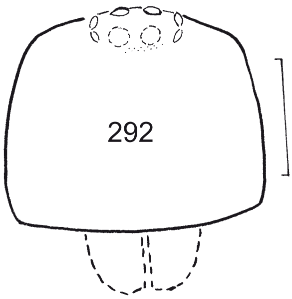
289

figs. 285–287: Lasaeola (Lasaeola) ?infulata (KOCH & BERENDT 1854); 285) male, Mus. Ziemi no. 19356, ventral aspect of the distal structures of the r. pedipalpus; 286) female F1537/CJW, lateral aspect of the body (parts are covered by a white emulsion); 287) female F1539/CJW, epigynal pit which is surrounded by a sclerotized ring. Scale bars 0.1, 0.5 and 0.05;

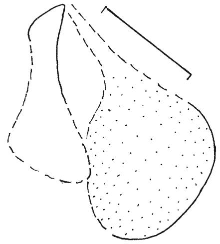
figs. 288–291: Lasaeola (Lasaeola) larvaque **n. sp.**, male; 288) paratype, dorsal aspect of the r. pedipalpus; 289) holotype, ventral aspect of the r. pedipalpus; 290) holotype, retrolateral aspect of the r. pedipalpus; 291) paratype, retroventral aspect of the l. pedipalpus (parts are hidden). Scale bar 0.2;



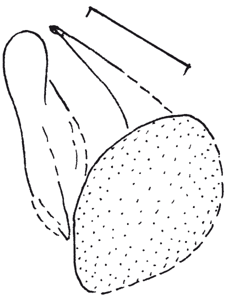
293



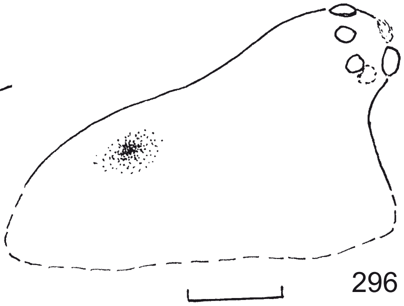
292



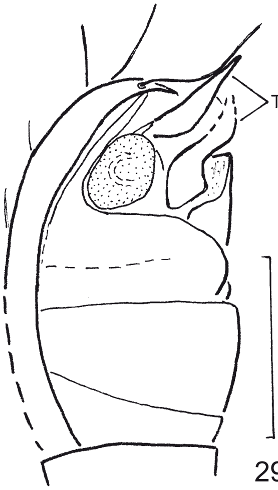
294



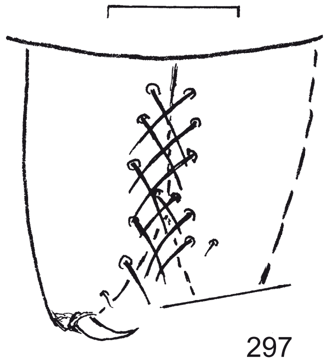
295



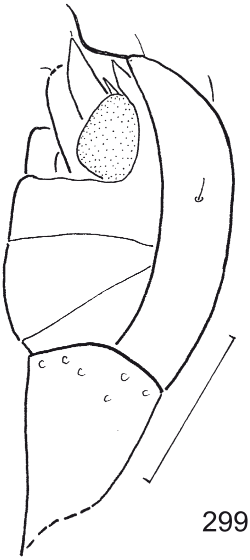
296



298



297

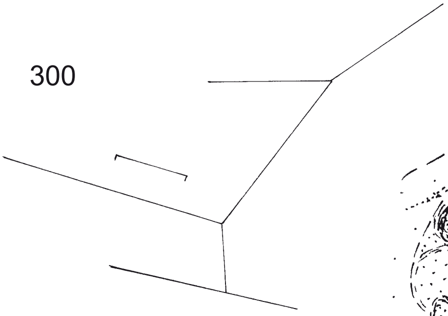


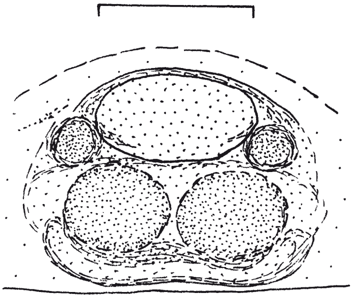
299

figs. 292–295: Lasaeola (Lasaeola) latisulci **n. sp.**, male; 292) paratype F153/CJW, anterior aspect of the prosoma; 294) paratype 1495/CJW, ventral aspect of tegular apophysis and embolus of the l. pedipalpus; 293) holotype, ventral aspect of the l. pedipalpus; 295) paratype F1497/CJW, retrolateral aspect of embolus and tegular apophysis of the l. pedipalpus. Scale bars 0.5 in fig. 292), 0.1 in fig. 295), 0.2 in the remaining figs.;

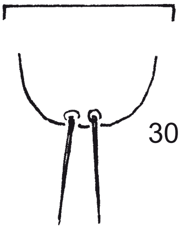
figs. 296–299: Lasaeola (Lasaeola) sexsaetosa **n. sp.**, male; 296) paratype F1546/CJW, lateral and slightly dorsal aspect of the prosoma; 297) holotype, anterior aspect of the chelicerae (parts are hidden); 298) holotype, retroventral aspect of the r. pedipalpus; 299) holotype, retrolateral aspect of the l. pedipalpus. Note the strongly bent apical cymbial hair. Scale bars 0.1 in fig. 297), 0.2 in the remaining figs;

300

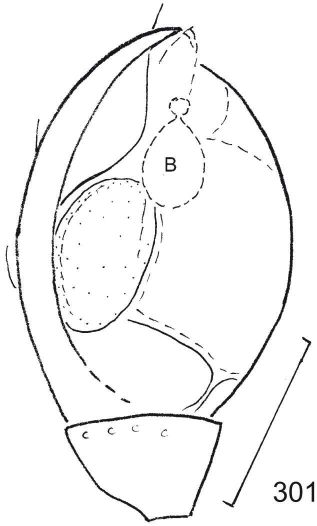




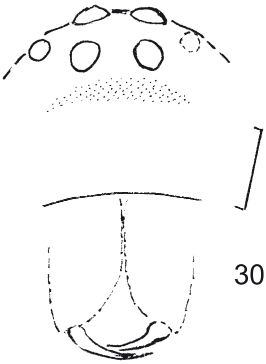
304



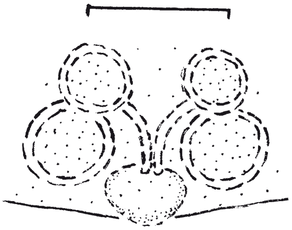
306



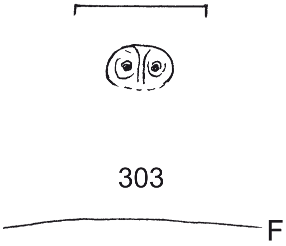
301



305



302



303

fig. 300) Part of an almost two-dimensional spiders web with the paratype F1544/CJW of Lasaeola (Lasaeola) sexsaetosa **n. sp**.. Scale bar 1.0;

fig. 301) Lasaeola (Lasaeola) sigillata **n. sp**., retroventral aspect of the r. ♂ -pedipalpus (parts are hidden). Scale bar 0.2;

fig. 302) Lasaeola sp. indet., ♀ F1675/CJW, dorsal aspect of the vulva. Scale bar 0.2;

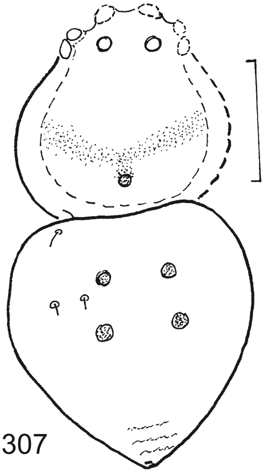
fig. 303) ?Lasaeola sp. indet. 2, ♀, coll. H. GRABENHORST AR-156 (Bitterfeld deposit), epigyne far in front of the epigastral furrow (F). Scale bar 0.1;

fig. 304) Lasaeola sp. indet., ♀, coll. C. GRÖHN no. 5910, epigyne. Note the two pairs of translucent receptacula seminis. Scale bar 0.2;

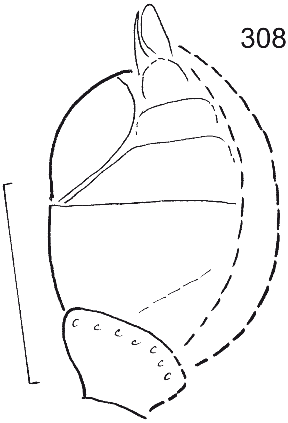
fig. 305) Lasaeola sp. indet., 1681/CJW, anterior aspect of the prosoma (parts are hidden). Scale bar 0.2;

fig. 306) *Euryopis laeta WESTRING 1851) (Germany), ♀, ventral aspect of the colulus. Scale bar 0.05;

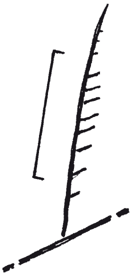
307



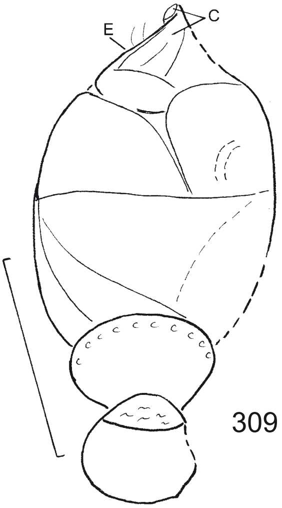
308



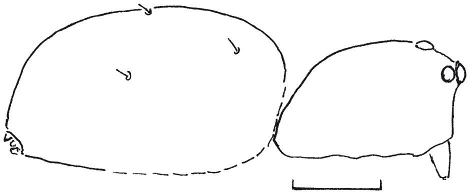
311



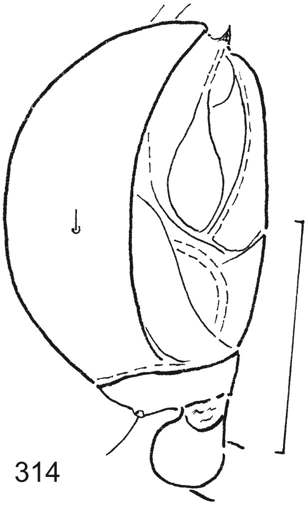
309



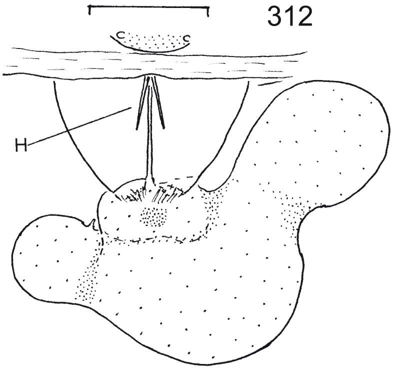
310



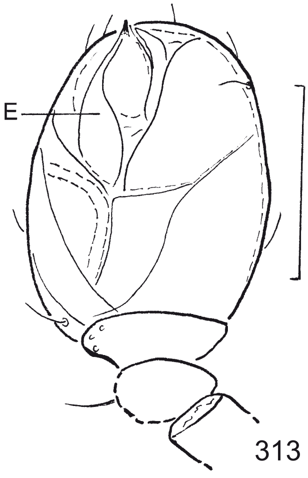
314



312

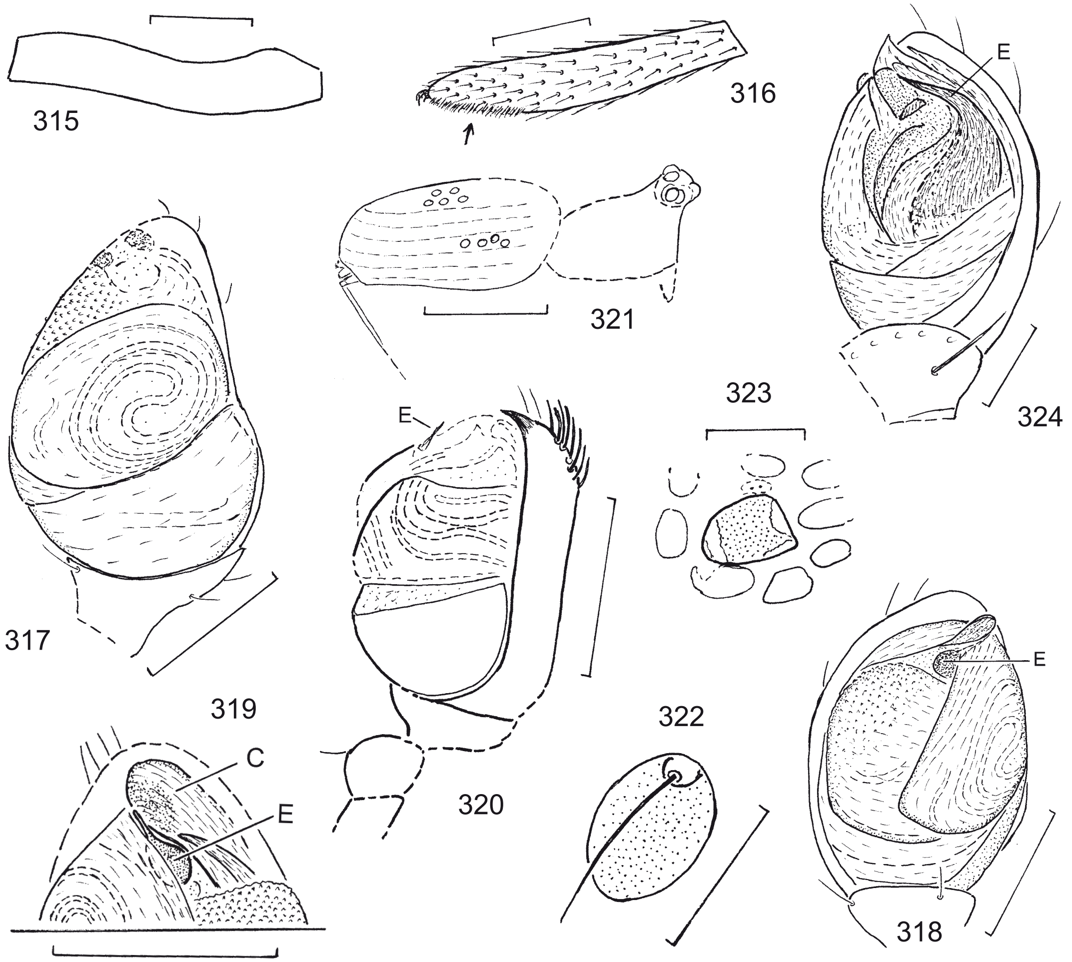


313



figs. 307–309: ?*Euryopis araneoides* **n. sp.**, male holotype; 307) dorsal aspect of the body; 308) retrolateral aspect of the l. pedipalpus; 309) ventral aspect of the r. pedipalpus. Scale bar 0.5 and 0.2;

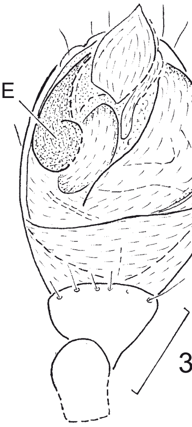
figs. 310–314: *Euryopis bitterfeldensis* **n. sp.**, male; 310) paratype coll. H. GRABENHORST, lateral aspect of the body. Only three eyes are visible; 311) paratype coll. GRABENHORST, trichobothrium on the r. metatarsus **I**, prodistal aspect; 312) paratype coll. GRABENHORST, a pair of "colular hairs" (H) (a colulis is probably absent) behind the tracheal spiracle, and questionable remains of excrements behind the anterior spinnerets; 313) paratype coll. GRABENHORST, ventral aspect of the r. pedipalpus; 314) paratype F1558/CJW, retroventral aspect of the r. pedipalpus. Scale bars 0.05 in fig. 311), 0.1 in fig. 312), 0.2 in the remaining figs.;



figs. 315–319: *Euryopis nexus* **n. sp**., male holotype; 315) prolateral aspect of the r. femur I. Note the strong dorsal concavity in the basal half; 316) prolateral aspect of the thickened r. tarsus I. Note the short ventral specialized typical “hadrotarsine hairs” (arrow) which look similar to a scopula in this magnification; 317) ventral aspect of the r. pedipalpus (which is turned to the dorsal side). The distal structures are partly hidden); 318) retroventral aspect of the r. pedipalpus. Note the long and coiled sperm duct within the tegulum; 319) ventral part of the distal part of the l. pedipalpus (most parts of the cymbium are hidden). Scale bars 0.1 in fig. 316), 0.2 in the remaining figs.;

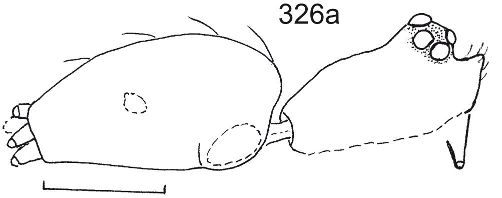
fig. 320) *Euryopis streyi* **n. sp**., male holotype, prolateral aspect of the r. pedipalpus. Note the long and coiled sperm duct within the tegulum. Cymbium and bulbus are distorted by 180° in an unnatural position. Scale bar 0.2;

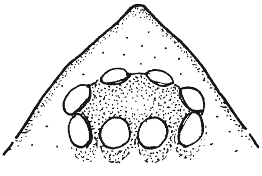
figs. 321–325: *Praetereuryopis phoroncidoides* **n. gen. n. sp**., male; 321) paratype coll. VELTEN, lateral aspect of body and dragline. Only few of the lateral opisthosomal plates are drawn; most parts of the chelicerae and parts of the eye lenses are hidden;



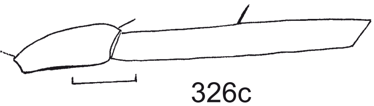
325

326a

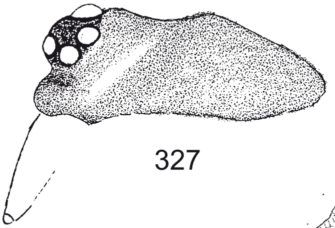




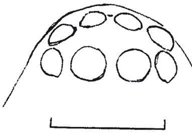
326b



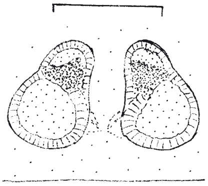
326c



327

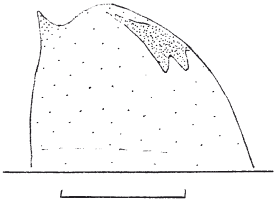


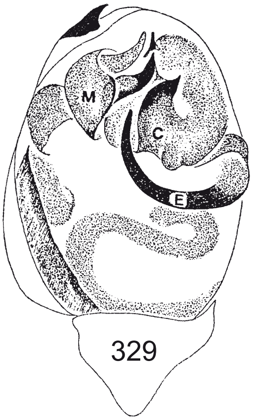
328



332

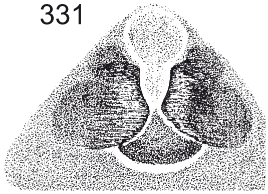
330

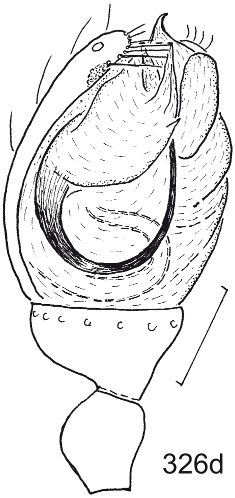




329

331





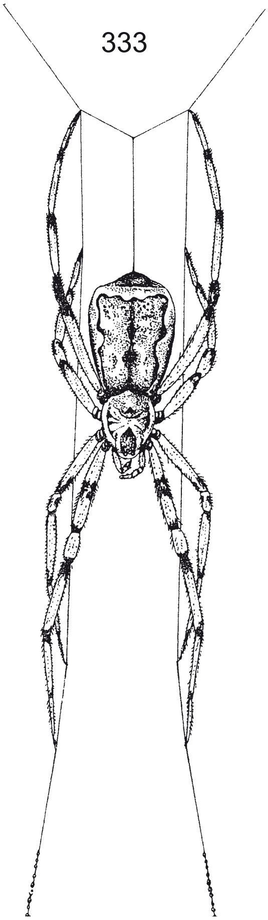
326d

322) paratype F1793/CJW, sclerotized hair-bearing plate of the of the dorsal margin of the opisthosoma; 323) paratype F1792/CJW, questionable bite mark (centre) surrounded by sclerotized plates just right in front of the spinnerets; 324) holotype, retroventral aspect of the l. pedipalpus; 325) paratype coll. VELTEN, proventral aspect of the r. pedipalpus which is turned by 180° to the dorsal side. Scale bars 0.5 in fig. 321), 0.05 in figs. 322–323), 0.2 in figs. 324–325);

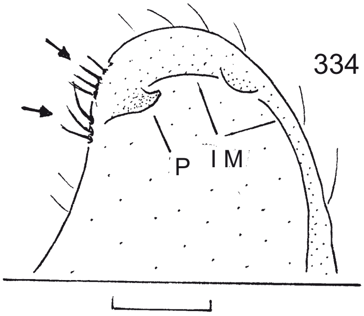
figs. 326a–d: *<u>Coscinida asiatica</u> ZHU & ZHANG 1992 (Indonesia, CJW), male; a) lateral aspect of the body; b) dorsal aspect of the anterior part of the prosoma; c) retrolateral aspect of the r. patella and tibia IV; d) ventral aspect of the r. pedipalpus. Scale bars 0.5 infig. a), 0.2 in the remaining figs.;

figs. 327–332: *<u>Coscinida tibialis</u> SIMON 1895 (Mediterranean); 327) lateral aspect of the prosoma (both sexes); 328) dorsal aspect of the anterior part of the prosoma (note the large posterior medin eyes); 329) ventral aspect of the l. pedipalpus; 330) distal part of the left cymbium, ventral aspect. Note its pointed apical outgrowth and the internal paracymbium; 331) ♀ epigyne; 332) dorsal aspect of the vulva. Figs. 327) (slightly modified) and 331) are taken from LEVY (1998). Scale bars 0.2 in fig. 328), 0.1 in the remaining figs.;

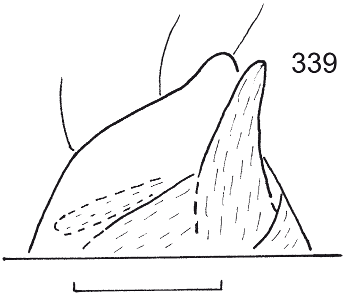
333



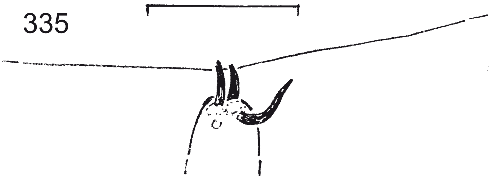
334



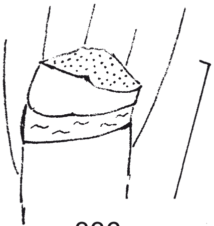
339



335



336



337

338

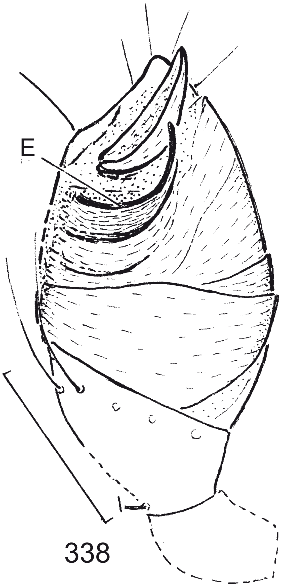
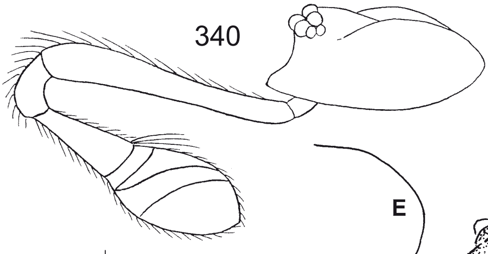


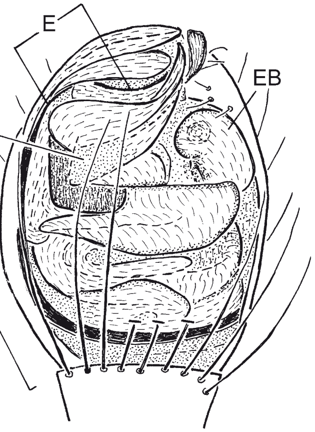
fig. 333) *<u>Episinus</u> sp., ♀, hanging in its reduced capture web which consists of only few threads which partly bear sticke droplets (below). Taken from HEIMER (1988);

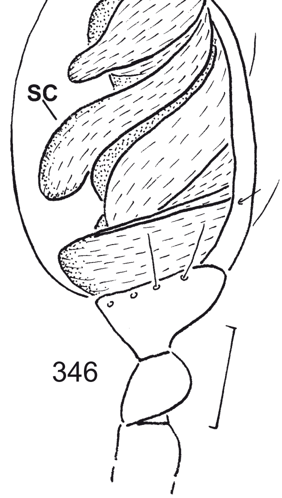
fig. 334) *<u>Episinus truncatus</u> LATREILLE 1809 (Europe), male, distal part of the r. cymbium, ventral aspect, with the hook-shaped internal paracymbium (P), the intracymbial margin (IM), and two groups of tiny prodistal cymbial bristles (arrows). Scale bar 0.2;

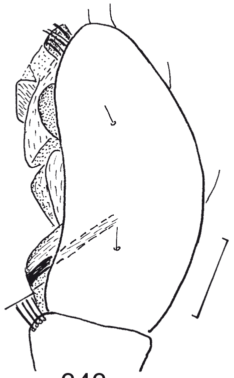
figs. 335–338: <u>Episinus nasuticymbium</u> **n. sp.**, male holotype; 335) a thread of the capture web at the tip of the left posterior tarsus (compare fig. 333), dorsal aspect. Hairs are not drawn; 336) prolateral and slightly apical aspect of the artificial “tip” of the l. anterior leg. Note the short metatarsus which has been amputated at its base. Blood is not preserved. Only few hairs are drawn; 337) dorsal aspect of the distal part of the l. cymbium; only few hairs are drawn; 338) ventral aspect of the r. pedipalpus. Scale bars 0.2 in fig. 338), 0.1 in the remaining figs.;

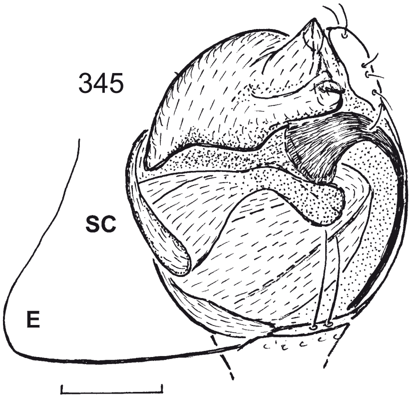
fig. 339) <u>Episinus mutilus</u> PETRUNKEVITCH 1958), male holotype, ventral aspect of the deformed distal part of the r. pedipalpus. The darkened structures are only roughly recognizable. Scale bar 0.2;

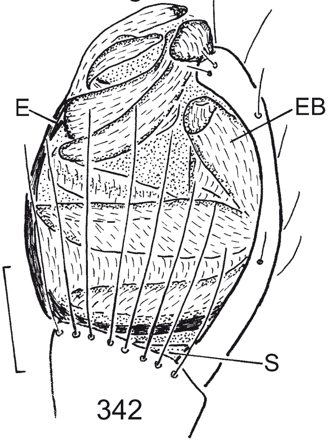


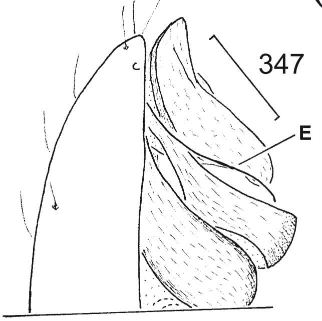


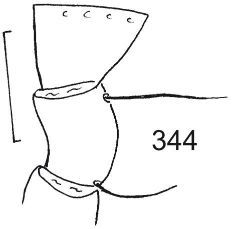






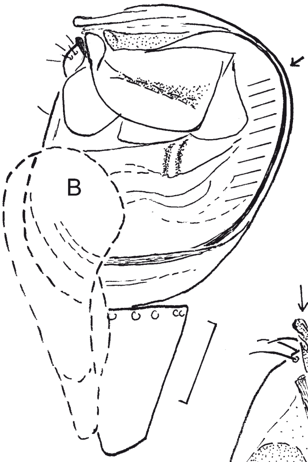






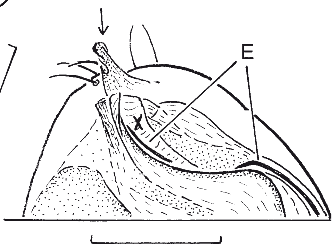
figs. 340–343: *Episinus longimanus* (KOCH & BERENDT 1854), male; 340) subad. male, lateral aspect of the prosoma and the left pedipalpus; taken from PETRUNKEVITCH (1950: Fig. 5); note the long pedipalpal articles; 341) male F1429/CJW, ventral aspect of the l. pedipalpus (EB = questionable base of the embolus); 342) coll. H. GRABENHORST, ventral and slightly retrolateral aspect of the l. pedipalpus; 343) F1428/CJW, retrolateral aspect of the l. pedipalpus. Scale bar 0.2;

figs. 344–347: *Episinus latus* **n. sp.**, male; 344) holotype, proventral aspect of patella and tibia of the l. pedipalpus; 345) holotype, ventral and slightly apical aspect of the l. pedipalpus (the distal part of the embolus is not in its natural position); 346) holotype, prolateral aspect of the l. pedipalpus (twisted to the retrolateral side); 347) paratype, distal part of the l. pedipalpus, prolateral aspect. (S = spoon-shaped conductor). Scale bar 0.2;

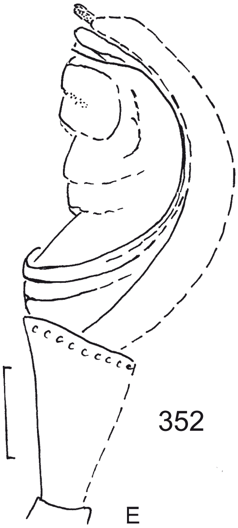


348

349

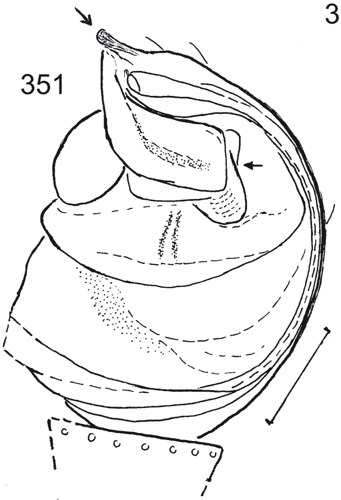


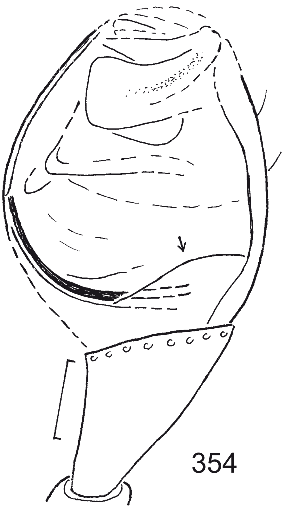
350



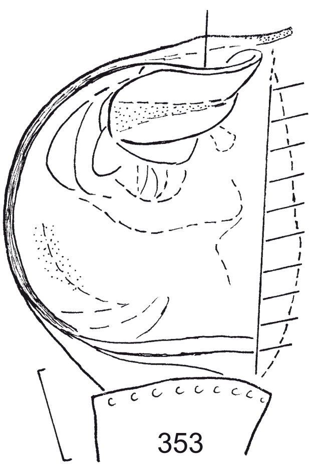
352

351





354



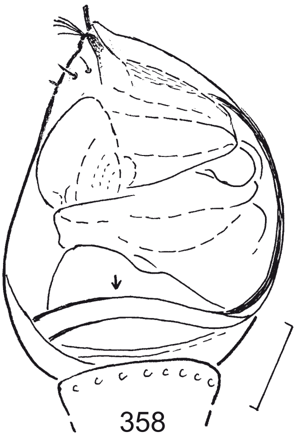
353

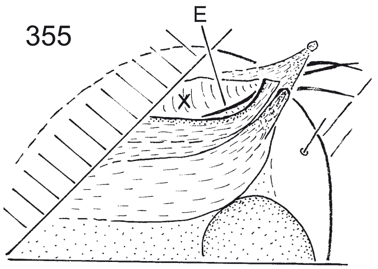
fig. 348) *Episinus dimidius* **n. sp**., male holotype, ventral aspect of the r. pedipalpus (parts are hidden). Scale bar 0.2;

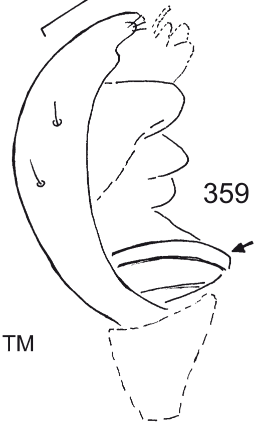
figs. 349–350: *Episinus anapidaeque* **n. sp**., male holotype; 349) ventral aspect of the r. pedipalpus (Y = cymbial margin); 350) ventral aspect of the distal part of the r. pedipalpus (X = conductor near the tip of the embolus). Scale bars 0.2 and 0.5;

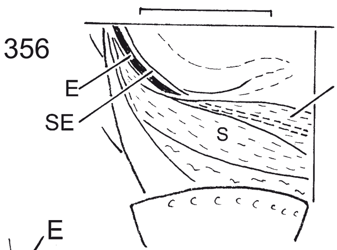
figs. 351–353: *Episinus appendix* **n. sp**., male; 351) holotype, ventral and slightly medial aspect of the r. pedipalpus; 352) holotype, medial aspect of the r. pedipalpus (parts are hidden by a white emulsion); 353) probably conspecific specimen (F1440/ CJW), ventral aspect of the l. pedipalpus (the structures on the right side are hidden). Scale bar 0.2;

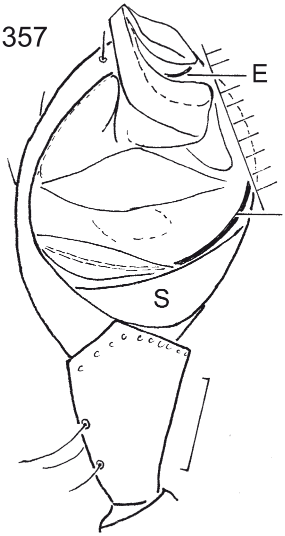
fig. 354) *Episinus bulla* **n. sp**., male holotype, ventral aspect of the l. pedipalpus (parts of the bulbus structures are hidden). Scale bar 0.2;

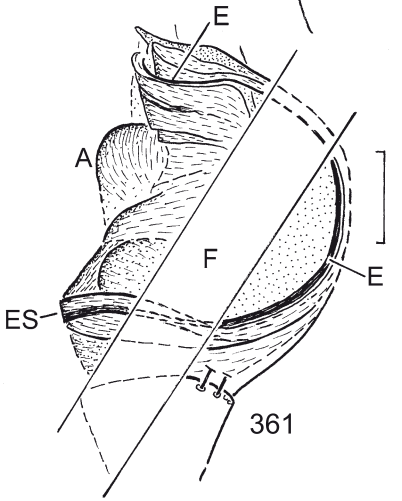


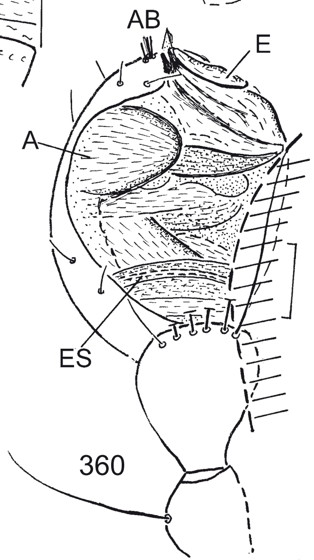










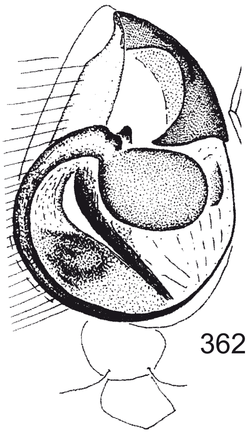


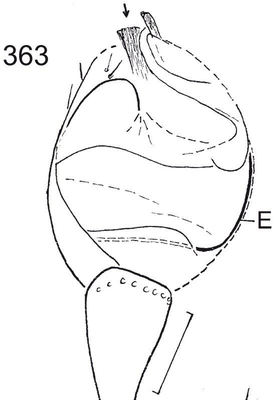
figs. 355–356: _Episinus cochlear_ **n. sp**., male holotype; 35) distal part of the l. pedipalpus, ventral aspect (parts are hidden); 356) basal section of the l. pedipalpus, ventral-prolateral aspect (SE = seam of the embolus, TM = tegular margin).Scale bar 0.2;

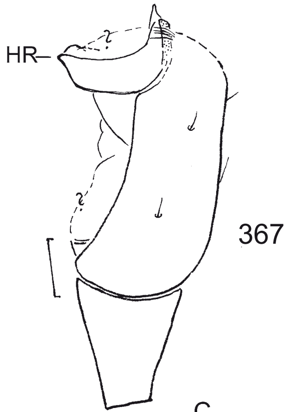
fig. 357) _Episinus cymbialis_ **n. sp**., male holotypus, ventral aspect of the r. pedipalpus (a lateral part is hidden). Scale bar 0.2;

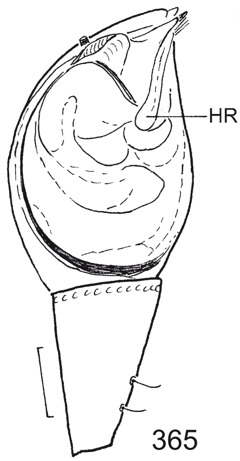
figs. 358–359: _Episinus isopteraque_ **n. sp**., male holotype; 358) ventral aspect of the r. pedipalpus (the distal part of the embolus is hidden); 359) retrolateral aspect of the r. pedipalpus (the tibia is partly hidden). Scale bar 0.2;

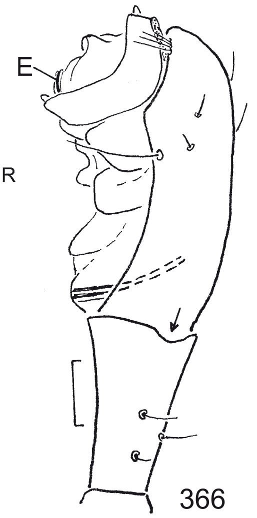
figs. 360–361: _Episinus_ sp. indet near _isopteraque_ n. sp., male (F1433/CJW); 360) ventral aspect of the r. pedipalpus (parts are hidden by a white emulsion); 361) retroventral aspect of the r. pedipalpus (parts are hidden by the r. femur (F) or by white emulsions). (ES = embolus with its seam, A = tegular apophysis, AB = apical cymbial bristles). Scale bar 0.2;

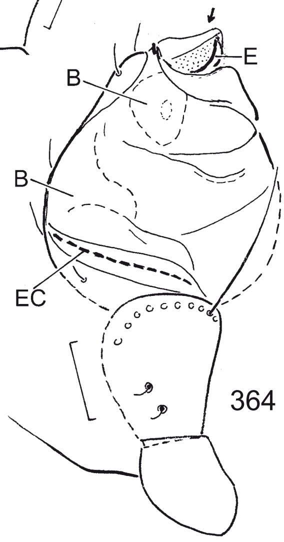

362


363









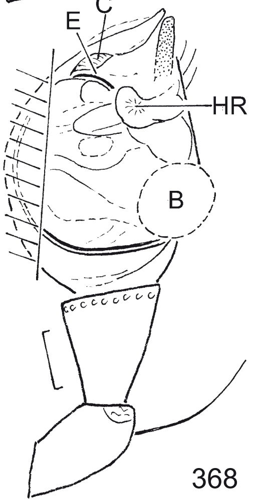


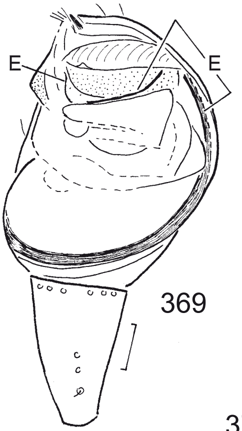
fig. 362) *Episinus eskovi* MARUSIK & PENNEY 2005, male holotype, ventral aspect of the l. pedipalpus. Scale bar 0.1. Taken from MARUSIK & PENNEY (2005: Fig. 14);

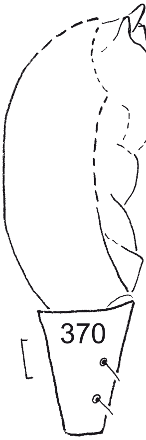
fig. 363) *Episinus mordellidaeque* **n. sp.**, male holotype, ventral aspect of the r. pedipalpus (the distal part of the embolus is hidden, parts of the bulbus are covered by a white emulsion). Scale bar 0.2;

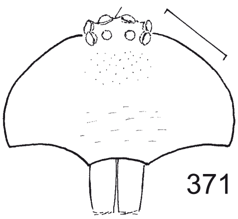
fig. 364) *Episinus musculus* **n. sp.**, male holotype, ventral aspect of the r. pedipalpus (white emulsions and bubbles (B) hide parts of the pedipalpus). (EC = embolus/ conductor). Scale bar 0.2;

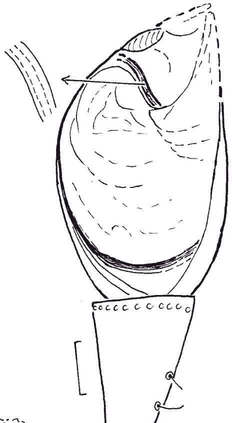
figs. 365–366: *Episinus arrodens* **n. sp.**, male holotype; 365) ventral and slightly prolateral aspect of the l. pedipalpus; 366) retrolateral aspect of the l. pedipalpus (HR = hook of the retrolateral sclerite). Scale bar 0.2;

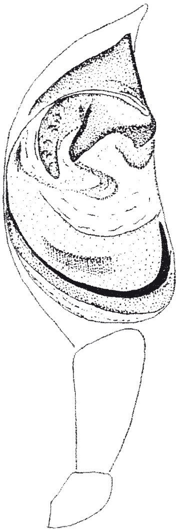
figs. 367–368: *Episinus clunis* **n. sp.**, male holotype; 367) retrolateral aspect of the l. pedipalpus (some parts are hidden, the tibial trichobothria are not drawn); 368) ventral aspect of the l. pedipalpus (the left side is partly hidden). (HR = hook of the retrolateral sclerite). Scale bar 0.2;

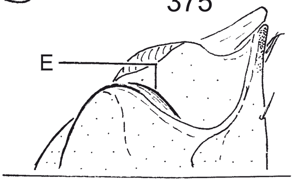

369

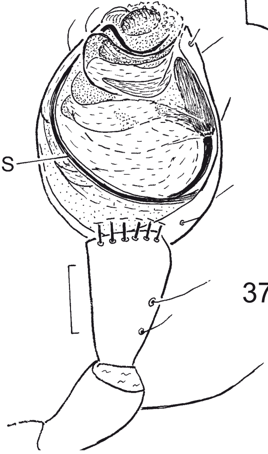

370

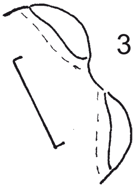

371


374


373


375


377


372

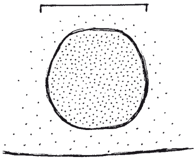

376

fig. 369) _Episinus longisoma_ **n. sp**., male holoype, ventral and slightly proapical aspect of the r. pedipalpus (parts are hidden by a white emulsion). Scale bar 0.2;

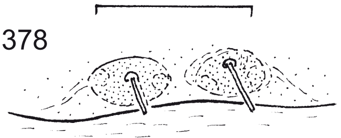
fig. 370) _Episinus_ ?_longisoma_ **n. sp**., male, outline of the r. pedipalpus, retrolateral aspect (parts are hidden by a white emulsion). Scale bar 0.2;

figs. 371–375: _Episinus balticus_ MARUSIK & PENNEY 2005, male; 371) F1457/CJW, anterior aspect of the prosoma (the fangs are hidden); 372) F1457, dorsal aspect of the right lateral eyes; 373) holotype, ventral aspect of the l. pedipalpus (taken from MARUSIK & PENNEY (2005: Fig. 17); 374) F1457, ventral aspect of the l. pedipalpus (some distal parts are hidden). Note the sperm duct in the enlarged part of the embolus (left); 375) F1459/CJW, distal part of the l. pedipalpus, ventral aspect. Note the distal part of the embolus which is widely hidden by structures of the bulbus. Scale bar 0.2;

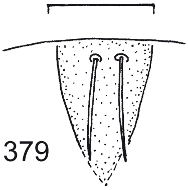
fig. 376) _Episinus_ ?_balticus_ MARUSIK & PENNEY 2005, ♀, epigyne. A plug coveres probably its pit. Scale bar 0.2; see fig. 381;

fig. 377) _Episinus transversus_ **n. sp**., male holotype, ventral aspect of the l. pedipalpus. Parts (e. g. apically) are hidden by a white emulsion. ES = embolic seam. Scale bar 0.2;

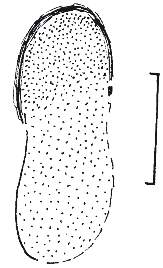
378



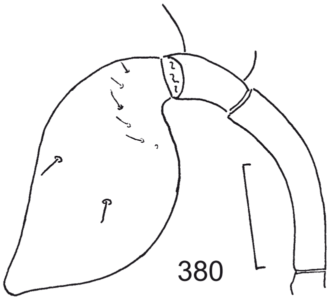
379



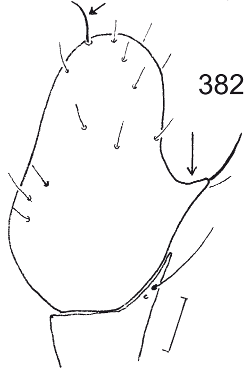
381



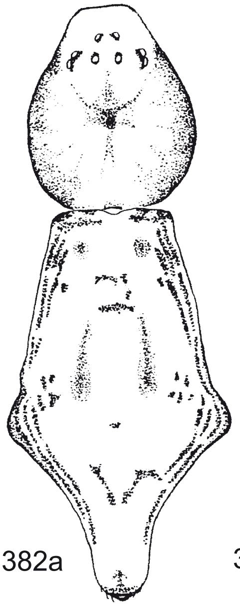
380



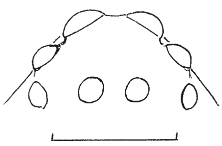
382



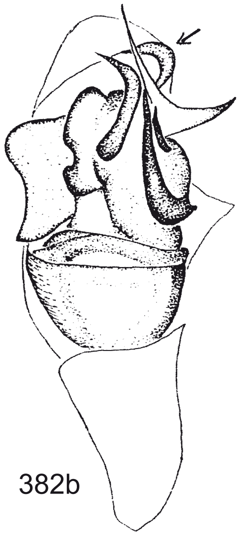
382a



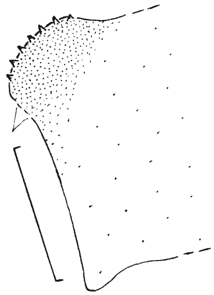
383



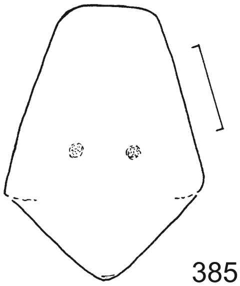
382b



384



385



figs. 378–379: *Episinus* sp. indet. 1 male F1442/CJW, 378) paired epiandrous gland spigots just in front of the epigastral furrow; 379) colulus. Scale bars 0.1 and 0.05;

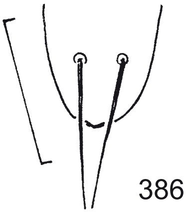
fig. 380) ?*Episinus* sp. indet. 2, subad. male F1447/CJW, retrolateral aspect of the l. pedipalpus. Note the absence of a free tibia which border to the cymbium is indicated by the row of hairs. Scale bar 0.2;

fig. 381) *Episinus* sp. indet. 5, ♀, ventral-right aspect of the epigyne which partly may be filled with a secretion (a plug); see fig. 376;

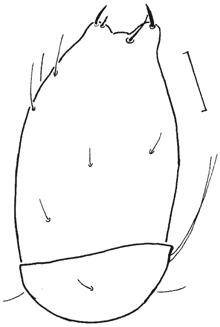
fig. 382) *Moneta sp. indet. male (Australia), dorsal aspect of the r. cymbium.Note the apical bent bristle (short arrow), and the retrolateral “paracymbium” (long arrow). Scale bar 0.1;

figs. 382 a–b: *Moneta mirabilis (BOESENBERG & STRAND 1906) (Taiwan), taken from YOSHIDA (2001: Figs. 13 and 15); a) ♀, dorsal aspect of the body; b) ventral aspect of the l. ♂-pedipalpus;

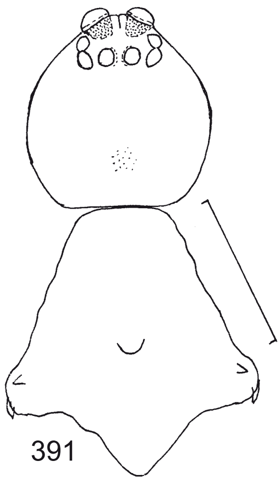
figs. 383–390: *Pycnoepisinus kilimandjaroensis **n. gen. n. sp**. (Africa), male holotype; 383) dorsal aspect of the eye region; 384) dorsal aspect of the basal part of the right



386

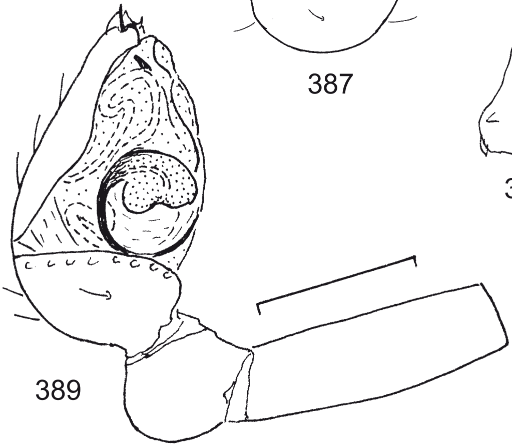


387

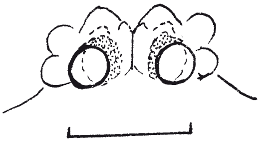


391

390

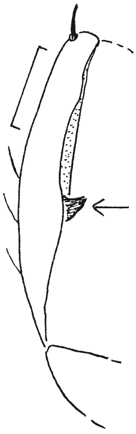


389

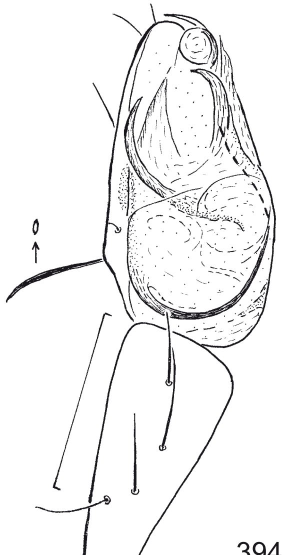


393

392



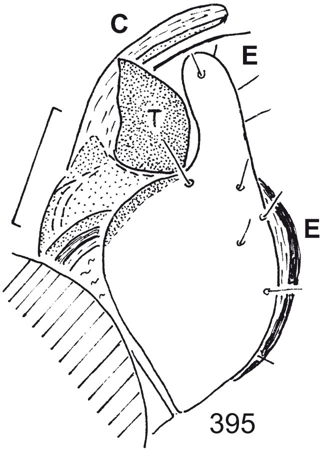
388



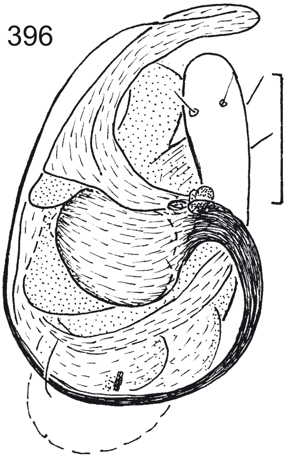
394

femur II with toothed and strongly sclerotized stridulatory ledge; 385) outline of the opisthosoma, dorsal aspect; 386) colulus; 387) dorsal aspect of tibia and cymbium of the r. pedipalpus. The tibia is very close to the basally shortened cymbium; 388) retroventral aspect of the cymbium with the internal hooked paracymbium (arrow); 389) retroventral aspect of the r. pedipalpus; 390) ventral aspect of the r. pedipalpus. Scale bars 1.0 in fig. 385), 0.5 in fig. 389), 0.05 in fig. 386), 0.2 in the remaining figs.;

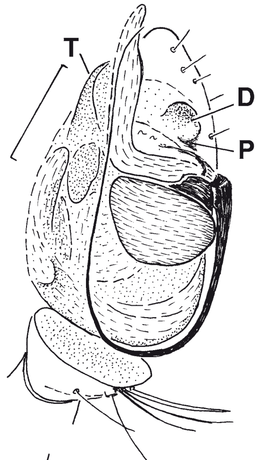
figs. 391–394: *<u>*Monetoculus parvus*</u> **n. gen. n. sp**. (SE-Asia), male holotype; 391) dorsal aspect of the body; 392) lateral aspect of the body; 393) anterior aspect of the eye region with the paired dorsal humps; 394) ventral aspect of the r. pedipalpus. Note the flattened cross section (arrow) of the retrolateral cymbial bristle. Scale bars 0.5 in figs. 391–392), 0.2 in figs. 393–394);



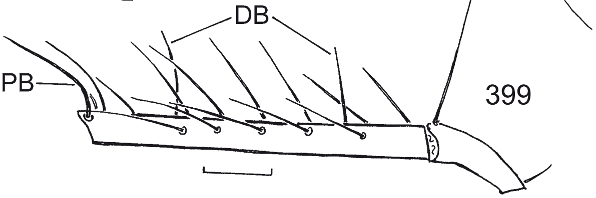
395



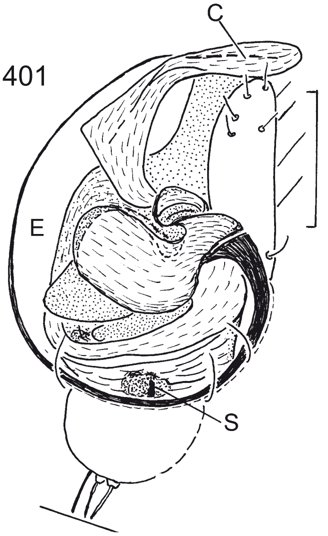
396



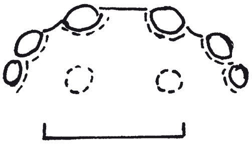
397



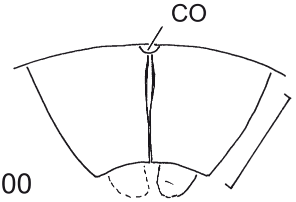
399



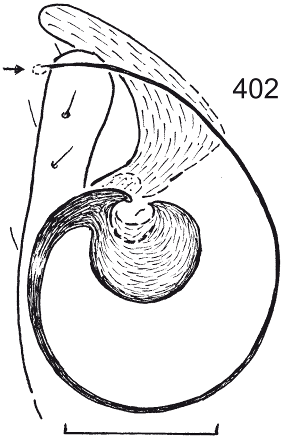
401



398



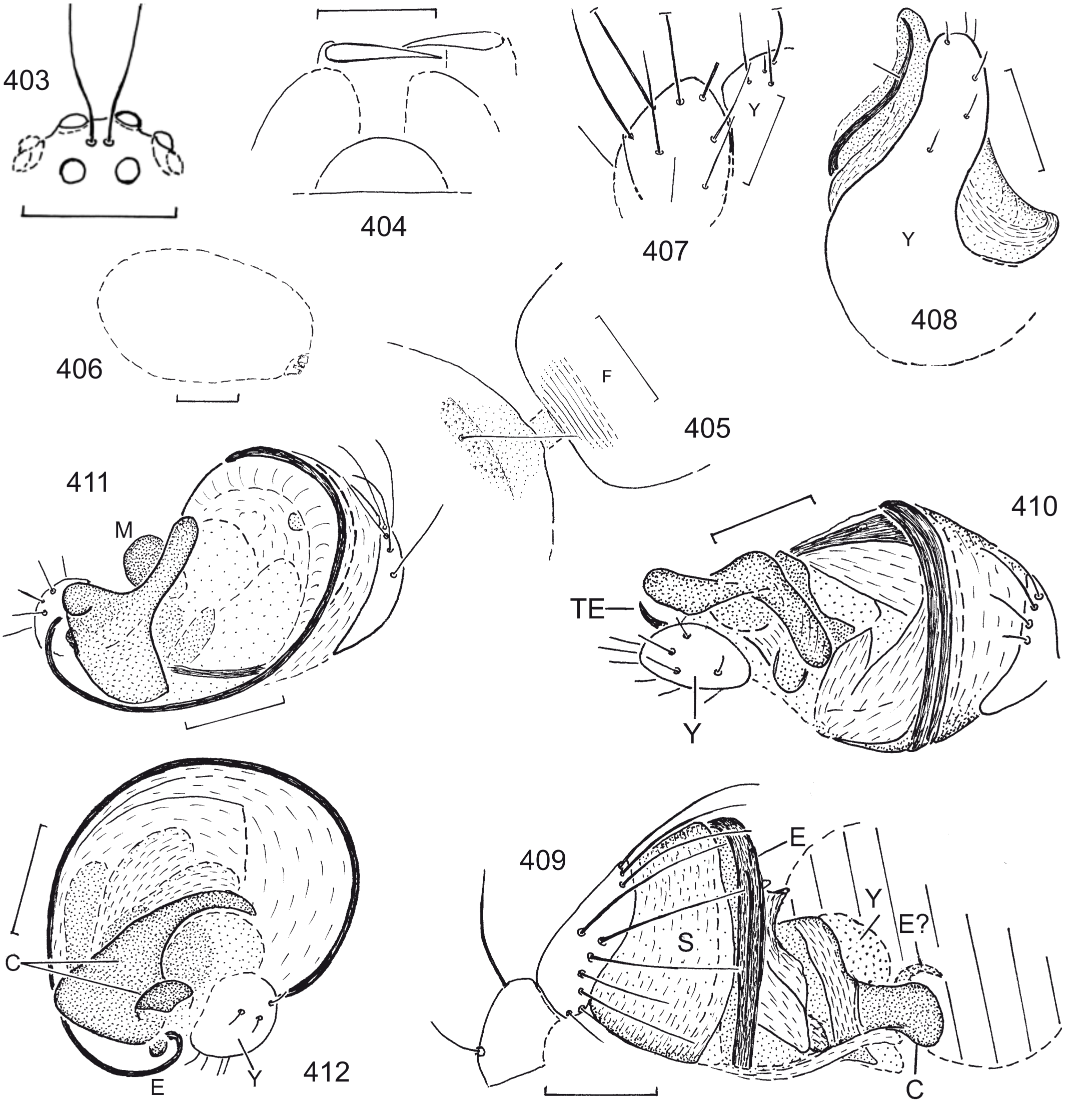
400



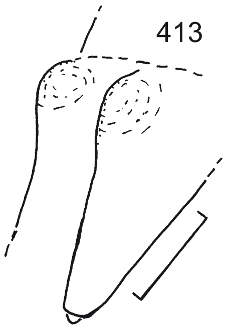
402

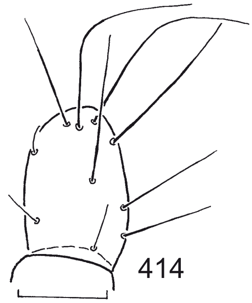
figs. 395–397: <u>*Spinisinus splendidus*</u> **n. gen. n. sp**., male holotype; 395) dorsal aspect of the r. pedipalpus (basal parts are hidden); 396) retrolateral aspect of the l. pedipalpus; 397) retroventral aspect of the l. pedipalpus (D = distal sclerite). Scale bar = 0.2;

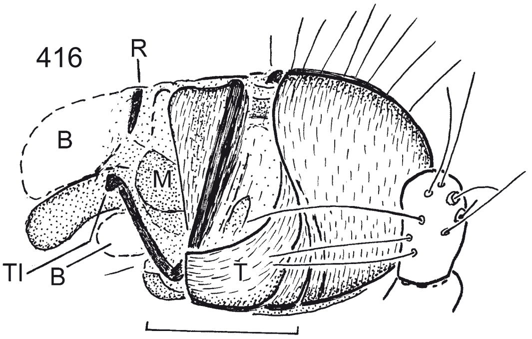
figs. 398–402: <u>*Spinisinus parvioculi*</u> **n. gen. n. sp**., male, 398–401) holotype; 398) dorsal aspect of the eyes; 399) prolateral aspect of the r. tibia and patella I. Only two rows of the prolateral long hairs are drawn. (DB = dorsal tibial bristles, PB = proapical tibial bristle); 400) colulus (CO) and outline of the anterior spinnerets, ventral aspect; 401) retrolateral aspect of the l. pedipalpus; 402) paratype, ventral aspect of cymbium, embolus and conductor of the right pedipalpus. Note the tiny droplet of secretion at the tip of the embolus; the distal part of the embolus lies not in its natural position on the conductor. (S = tooth-shaped sclerotized structure of the subtegulum). Scale bars 0.1 in fig. 400), 0.2 in the remaining figs.;

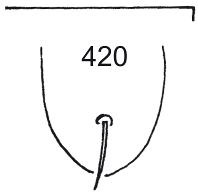


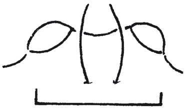
figs. 403–412: Spinitharinus bulbosus **n. gen. n. sp**., male; 403) holotype, dorsal aspect of the eye field. Note the pair of long hairs in the field of the median eyes; 404) paratype b, ventral aspect of the mouth parts; 405) holotype, dorsal aspect of the prosomal-opisthosomal stridulatory organ. Note the prosomal stridulatory files (F) and some of the opisthosomal stridulatory picks which enclose a long proprioreceptorical hair; 406) paratype b, outline of the opisthosoma, lateral aspect (parts are covered with a white emulsion); 407) paratype a, tibia of the l. pedipalpus and basal part of the cymbium, dorsal aspect. (Basal parts are hidden by a white emulsion); 408) paratype a, dorsal aspect of the r. pedipalpus (parts are hidden); 409) holotype, retrolateral aspect of the r. pedipalpus. (Distal parts are partly hidden by a large bubble); 410) paratype, prolateral-ventral aspect of the r. pedipalpus; 411) paratype b, retrolateral-distal aspect of the l. pedipalpus. (Parts of the bulbus are hidden by a white emulsion); 412) ventral-distal aspect of the r. pedipalpus. Scale bars 0.5 in fig. 406), 0.2 in the remaining figs;

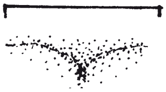

413

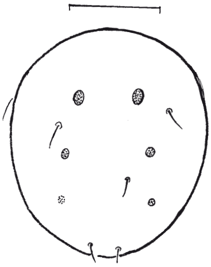

414


416

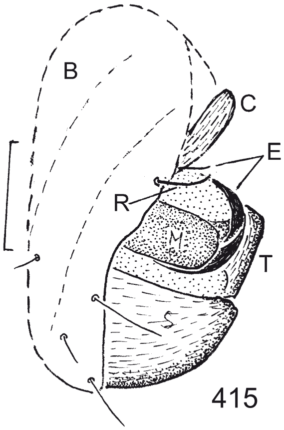

420

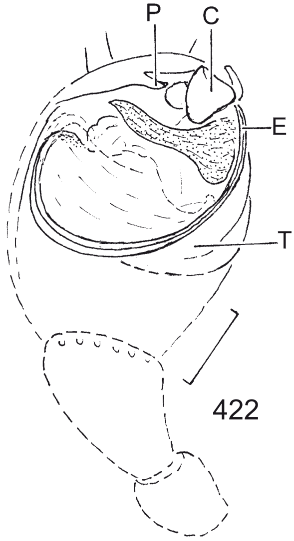

417

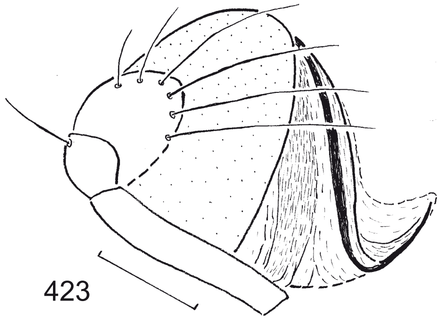

418


419


421

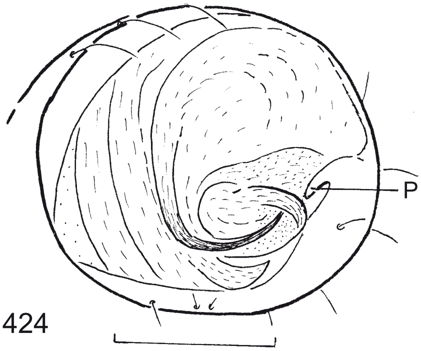

415

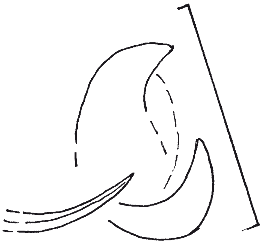

422

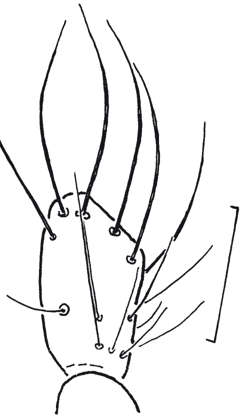

423

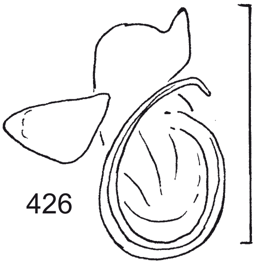
figs. 413–416: <u>*Spinitharinus cheliceratus*</u> **n. gen. n. sp**., male holotype; 413) anterior-left aspect of the chelicerae. Note the anterior-basal humps which probably are enlarged by emulsions; 414) dorsal aspect of the tibia of the r. pedipalpus; 415) retrodorsal aspect of the r. pedipalpus. (A large bubble and emulsions cover large parts of the cymbium; 416) retrolateral aspect of the l. pedipalpus. (Only few hairs are drawn). (R = cymbial bristle). Scale bar 0.2;

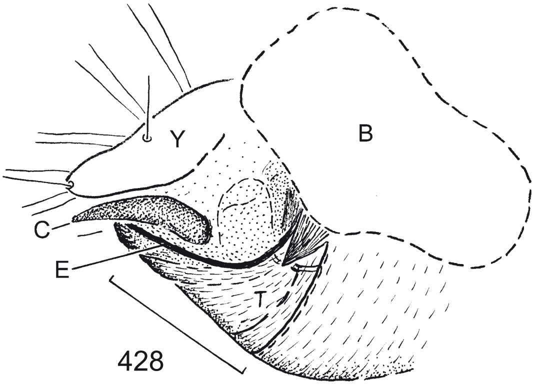
figs. 417–426: <u>*Spinitharinus curvatus*</u> **n. gen. n. sp**., male holotype if not otherwise annotated; 417) paratype, thin hairs in the field of the median eyes; 418) fovea, 419) dorsal aspect of the opisthosoma which bears three pairs of sigillae (only few hairs are drawn); 420) paratype, colulus; 421) distal part of the left cymbium with paracymbium, retrolateral aspect; 422) retrolateral-ventral aspect of the r. pedipalpus. (Parts are hidden by an emulsion); 423) paratype F1461/CJW, retrobasal aspect of the r. pedipalpus (the conductors are not observable); 424) paratype F1556/CJW, retroapical aspect of the r. pedipalpus. (Note the strongly sclerotized distal part of the embolus); 425) tip of

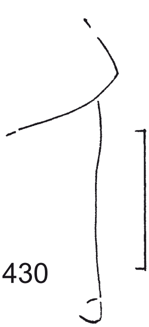

424

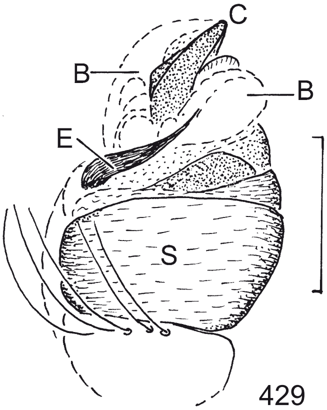

425

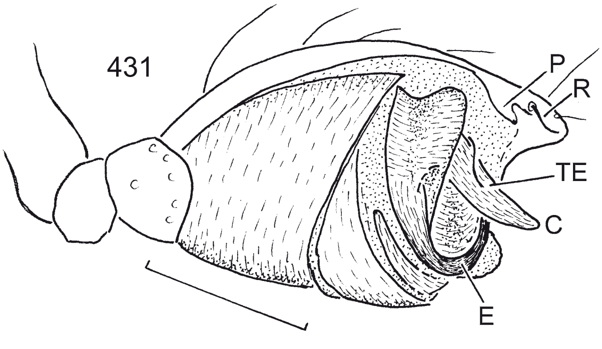

427


426


428


430


429


431

the embolus and two parts of the conductor of the l. pedipalpus, retroventral-distal aspect; 426) embolus and two parts of the conductor of the l. pedipalpus, prolateral-distal aspect. Scale bars 0.05 in fig. 420), 0.1 in fig. 421), 0.3 in fig. 418), 0.5 in fig. 419), 0.2 in the remaining figs.;

figs. 427–429: *Spinitharinus coniectens* **n. gen. n. sp**., male holotype; 427) dorsal aspect of the tibia of the r. pedipalpus; 428) retrolateral aspect of the l. pedipalpus (T = tegulum); 429) ventral aspect of the r. pedipalpus. Scale bar 0.2;

figs. 430–431: *Spinitharinus cymbioseta* **n. gen. n. sp**., male holotype; 430) retrolateral aspect of the r. chelicera; 431) retrolateral aspect of the r. pedipalpus. (R = bristle-shaped cymbial hair). Scale bar 0.2;

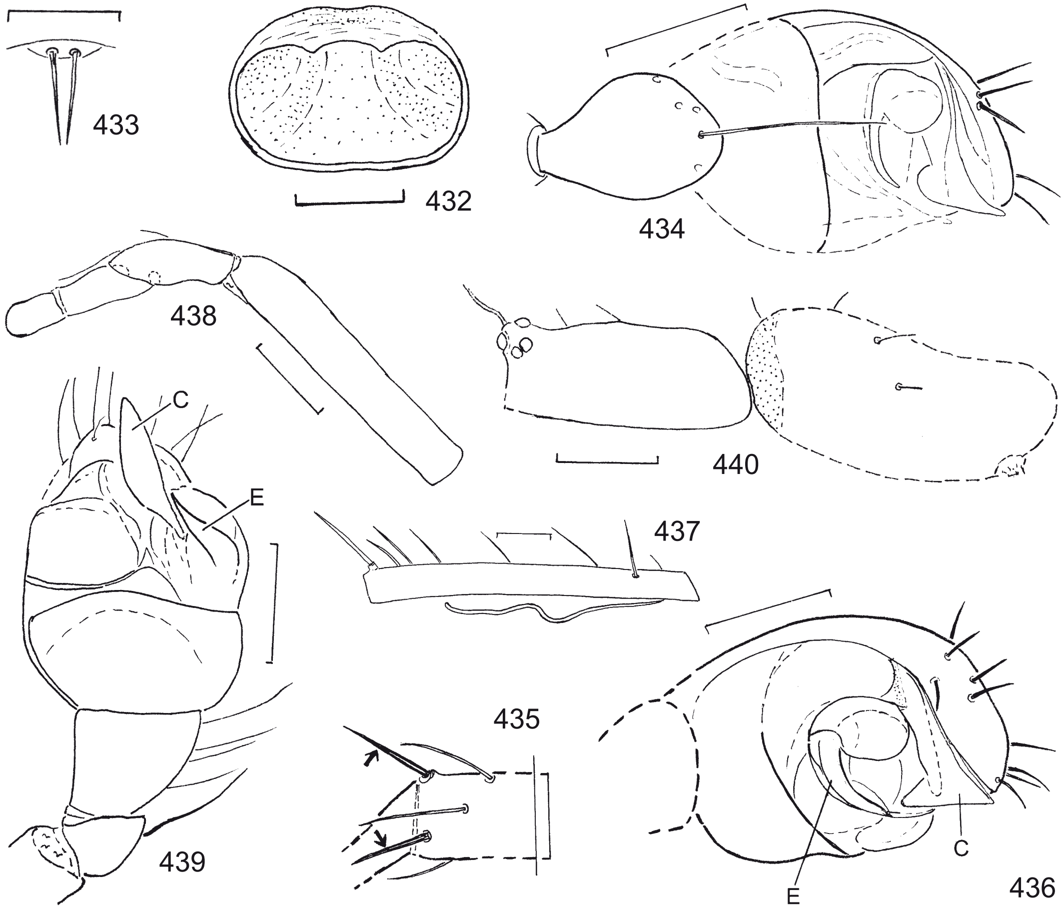


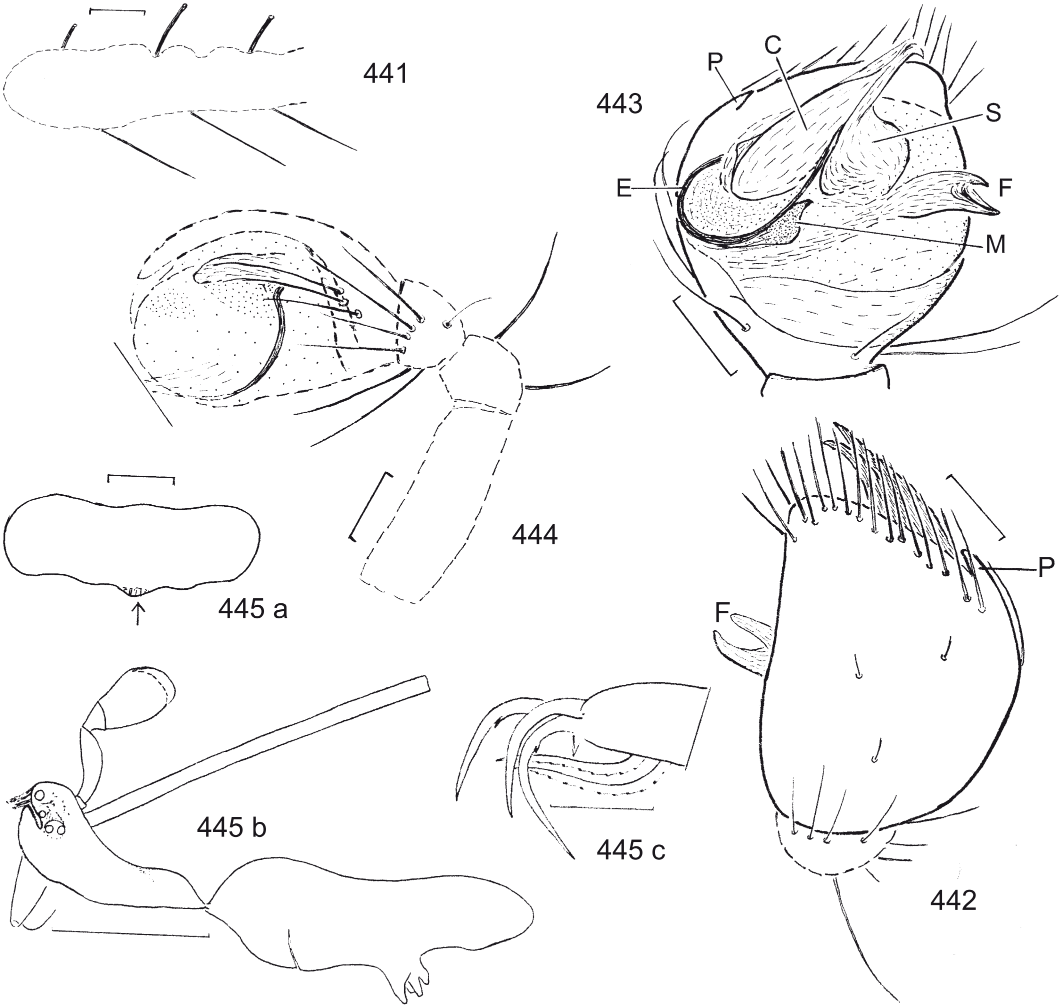
fig. 432) ?<u>*Spinitharinus*</u> sp. indet, ♀, epigyne. Scale bar 0.1;

figs. 433–434: <u>*Caudasinus caudatus*</u> **n. gen. n. sp**., male holotype; 433) colulus; 434) retrolateral aspect of the r. pedipalpus. Scale bars 0.02 and 0.2;

figs. 435–436: <u>*Caudasinus bispinosus*</u> **n. gen. n. sp**., male holotype; 435) distal part of the left tibia I, retrodorsal aspect, with paired apical bristle (arrows) and three hairs; 436) retrolateral and slighly dorsal aspect of the r. pedipalpus. Scale bar 0.2;

figs. 437–439: <u>*Caudasinus regeneratus*</u> **n. gen. n. sp**., male holotype; 437) retrolateral aspect of the l. anterior tibia with a phoretic Nematoda: Rhabditida indet. below of it. (Only few hairs of the tibia and two bristles are drawn; 438) prolateral aspect of the left leg III which has been partly regenerated; the tarsus is absent, tibia and metatarsus are strongly shortened, patellar bristles are absent; 439) retroventral aspect of the l. pedipalpus. Scale bar 0.2;

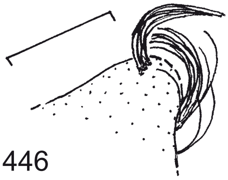
fig. 440) <u>*Caudasinus*</u> sp. indet., male F1423/CJW, outline of the body, lateral aspect. (A white emulsion covers most parts of the opisthosoma; only few hairs are drawn). Scale bar 0.5;

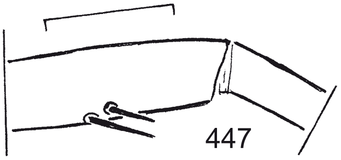


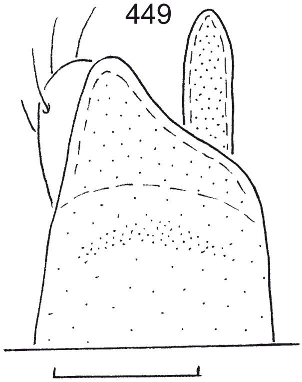
figs. 441–444: Mimetidion furca **n. gen. n. sp**., male holotype; 441) basal part of the r. metatarsus I, dorsal aspect. (The dorsal half and the distal parts of the three prolateral bristles/spines are cut off; only three long ventral hairs are drawn; 442) dorsal aspect of the r. pedipalpus. (Only few hairs are drawn); 443) ventral aspect of the r. pedipalpus; 444) retrolateral aspect of the l. pedipalpus. (Parts are covered with a white emulsion). (S = sickle-shaped apophysis. The identity of the median apophysis is questionable). Scale bar 0.2;

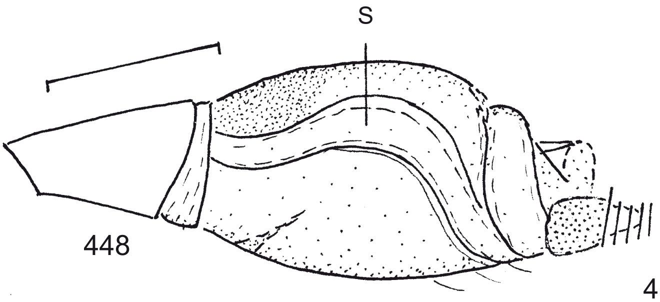
fig. 445 a) Argyrodes sp. indet., ♀, dorsal-right aspect of the deformed opisthosoma, outline, most probably a fake which has been annotated as “Baltic amber”, Mus. Copenhagen. The piece of amber was heated. Note the position of the spinnerets (arrow). Scale bar 0.5;

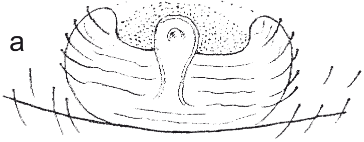
figs. 445 b–c: Argyrodes (Argyrodes) crassipatellaris WUNDERLICH 1988, male in Dominican amber; b) lateral aspect of the body; c) prolateral aspect of the claws of the r. tarsus I. Note the long unpaired claw (below). Scale bars 1 and 0.05;

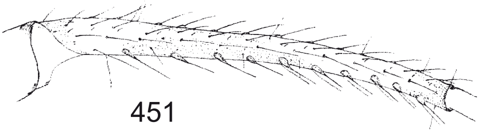


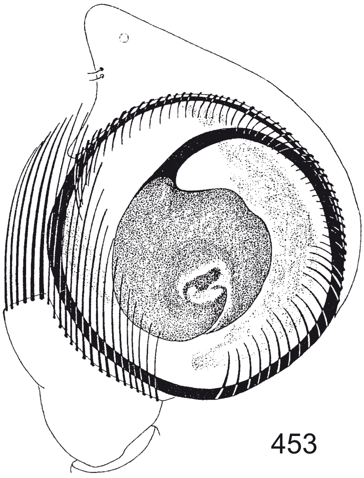


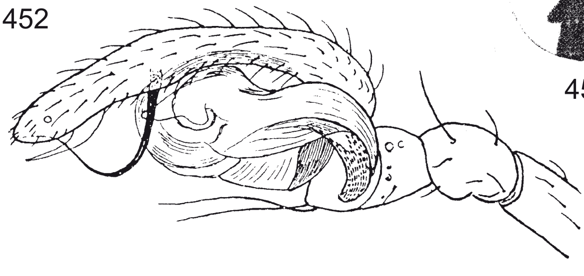








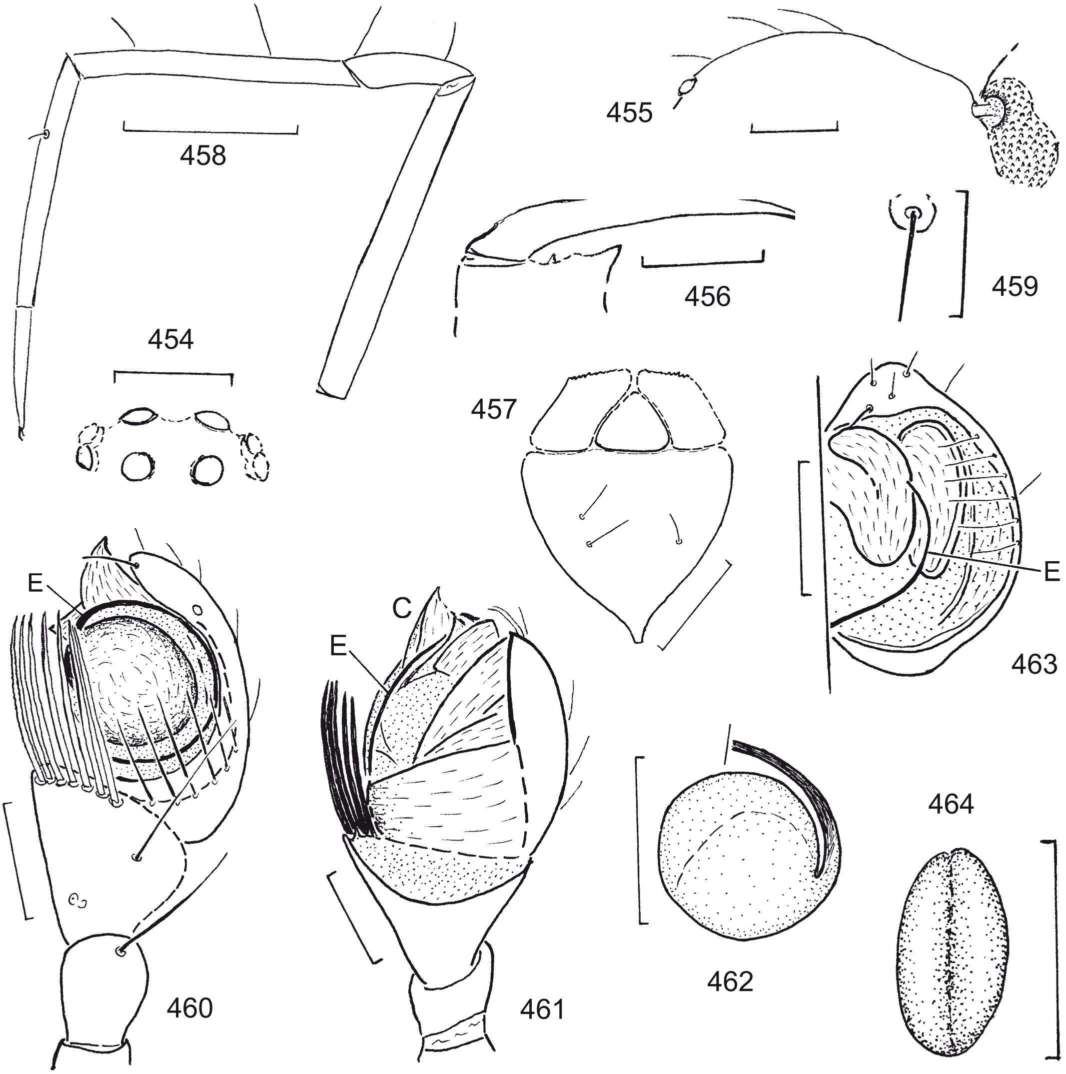




figs. 446–449: Argyrodes (Ariamnes) copalis **n. sp.**, male holotype; 446) lateral and slightly dorsal aspect of the cephalic part with two hairy areas (eyes are not drawn); 447) distal part of the r. tibia and basal part of the metatarsus II, retroventral-distal aspect. Note the two short ventral tibial bristles; 448) retrolateral aspect of the r. pedipalpus. (The distal part is hidden). Note the thick sperm duct (S); 449) distal part of the l. pedipalpus, prodorsal aspect. Scale bars 0.1 in fig. 447), 0.2 in the remaining figs.;

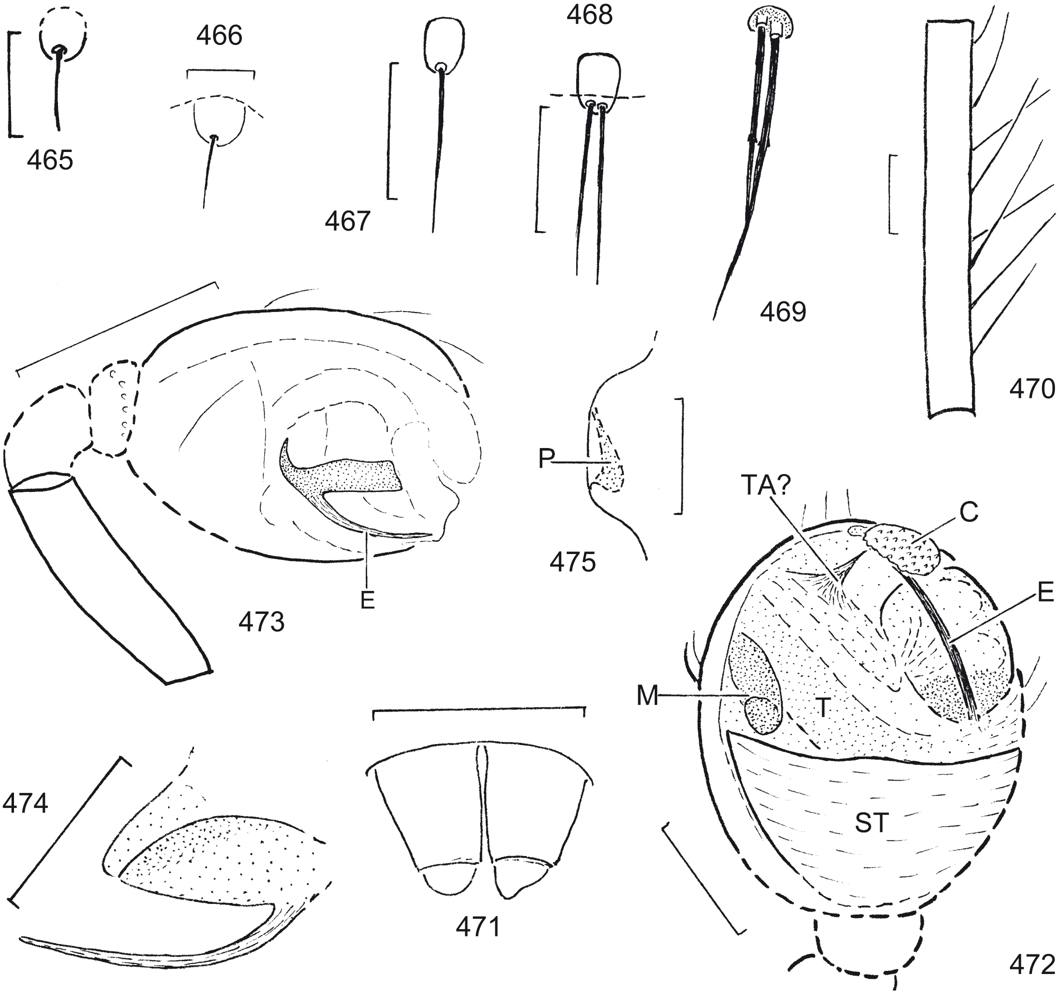
figs. 450–452 a: *Selimus vittatus (C. L. KOCH 1836) (specimens from Europe); 450) ♀, dorsal aspect of the body; 451) lateral aspect of the r. ♂-metatarsus I; 452) retrolateral aspect of the l. ♂-pedipalpus; 452 a) ♀, epigyne. Taken from WIEHLE (1937);

fig. 453) *Kochiura aulica (C. L. KOCH 1838) (specimen from Europe), retrolateral/ventral aspect of the l. ♂-pedipalpus. Taken from LEVY (1998: Fig. 257). Note the remarkable convergence to the the Eocene *Kochiuridion pecten*, fig. 460!;



figs. 454–463: Kochiuridion pecten **n. gen. n. sp.**, male; 454) paratype F1823/CJW, position of the eyes; 455) holotype, anterior part of the opisthosoma (on the right) with a rugose and most probably stridulatory field, and the profile of the prosoma (only a single eye is drawn); 456) paratype F1823/CJW, posterior aspect of the r. fang and base of the basal cheliceral article, posterior-apical aspect; 457) paratype F1822/CJW, ventral aspect of the prosoma; 458) paratype F1823/CJW, retrolateral aspect of the l. leg I; 459) paratype, colulus; 460) holotype, ventral and slightly basal aspect of the l. pedipalpus; 461) holotype, prolateral aspect of the r. pedipalpus; 462) holotype, basal part of the r. embolus, ventral aspect; 463) paratype F1821/CJW, ventral-apical aspect of the r. pedipalpus. (A part is hidden by a leg). Scale bars 0.02 in fig. 459), 0.5 in fig. 458), 0.2 in figs. 454–456 and 460–463, 0.2 in the remaining figs.;

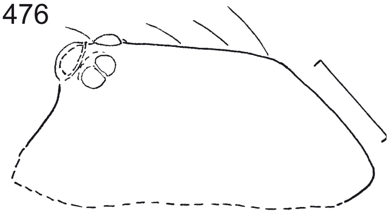
fig. 464) A coffee-bean shaped pollen grain, probably originating from an oak (Fagaceae) near the holotype of *Kochiuridion pecten*. Scale bar 0.05;

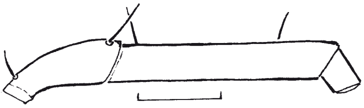


figs. 465–469: Coluli of extant females of the subfamily Analosiminae. 465) *Kochiura aulica* (C. L. KOCH 1836) (Europe, CJW); 466) *Anelosimus chonganicus* ZHU 1998 (Australia, Cairns, CJW); 467–468) *Anelosimus jucundus* (O. PICKARD-CAMBRIDGE 1896) (Venezuela, CJW), variability of the number of the colular hairs. The cover of the opisthosomal fold has been dissected; 469) *Anelosimus studiosus* (HENTZ 1859) (America), hairs of the hidden tiny colulus. Redrawn from from AGNARSSON (2004: Fig. 25E, REM photo). Scale bars 0.05;

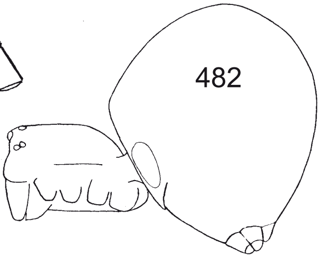
figs. 470–475: *Balticoridion dubium* **n. gen. n. sp**., male; holotype: Figs. 470) and 473), paratype F163/CJW: The remaining figs.; 470) dorsal aspect of the l. tibia I. (Only the long prolateral hairs are drawn); 471) ventral aspect of the anterior spinnerets with the colular area; 472) apical aspect of the translucent part of the left cymbium and the hood-shaped internal paracymbium; 473) retrolateral aspect of the r. pedipalpus (large parts are hidden by leg articles and emulsions); 474) retrolateral aspect of the left embolus (the hook at the right side is hidden in this specimen); 475) ventral aspect of the l. pedipalpus. Scale bars 0.2 in figs. 470–471, 473), 0.1 in the remaining figs.;

476

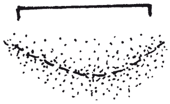


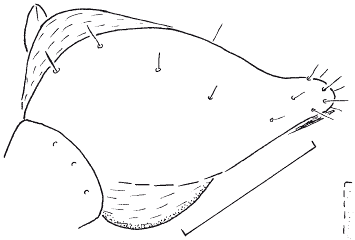


477



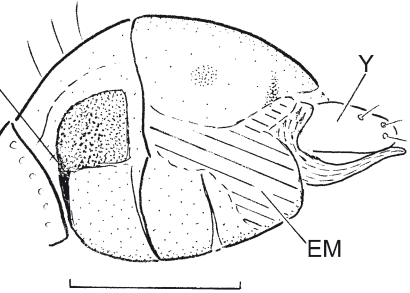
480

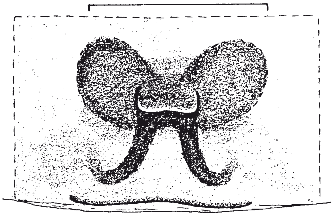




478

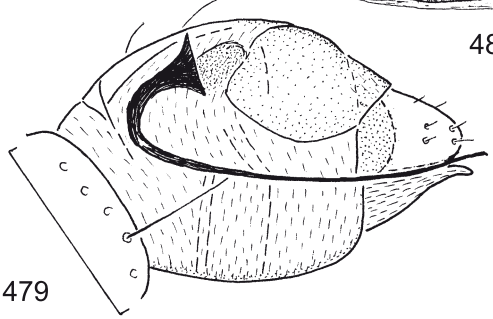
481



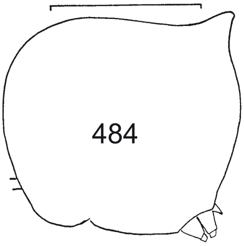


484 a

483



479



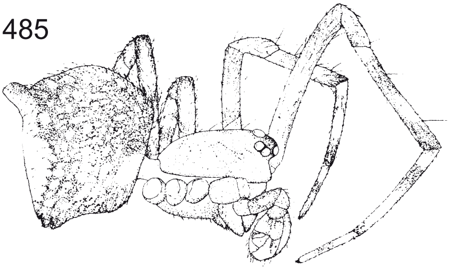
figs. 476–479: *Clavibertus prominens* **n. gen. n. sp**., male; 476) paratype F1771/ CJW, lateral aspect of the prosoma. The lense of the anterior median eye is artificially enlarged by a bubble; 477) paratype 1773/CJW, prolateral aspect of the patella, tibia and the stump of the amputated metatarsus II which apparently is healed; 478) paratype F1772/CJW, dorsal aspect of the l. pedipalpus; 479) holotype, ventral aspect of the r. pedipalpus. Scale bar 0.2;

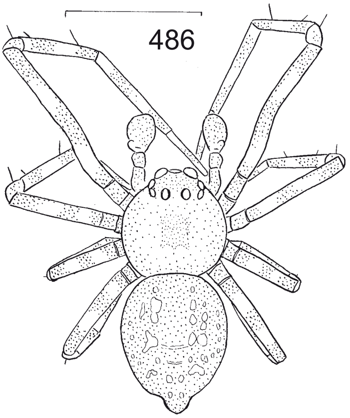
figs. 480–481: *Clavibertus parvus* **n. gen. n. sp**., male holotype; 480) fovea; 481) retrolateral aspect of the r. pedipalpus. (EM = emulsion). Scale bar 0.2;

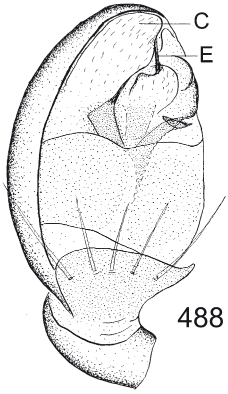
figs. 482–483: **Achaearanea lunata* (OLIVIER 1789), (specimen from Europe), ♀, lateral (outline) and dorsal aspects of the body. Taken from WIEHLE (1937) (sub *Theridion*);

figs. 484–484 a: **Achaearanea dubitabilis* WUNDERLICH 1987 (specimen from the Canary Islands), ♀; 484) outline of the opisthosoma, lateral aspect; 484 a) epigyne. Scale bars 1.0 and 0.1;

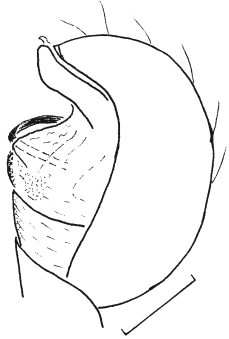
485

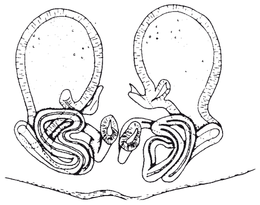



486

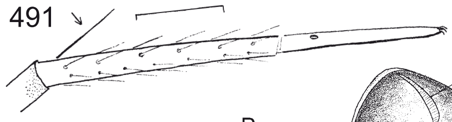


488

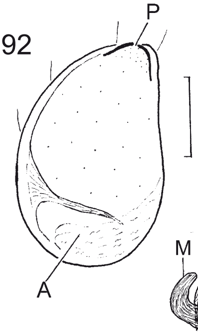

494

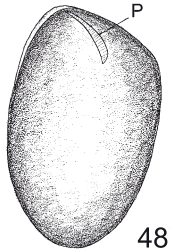

490

491

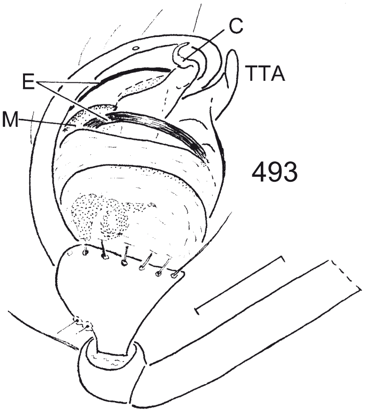


492

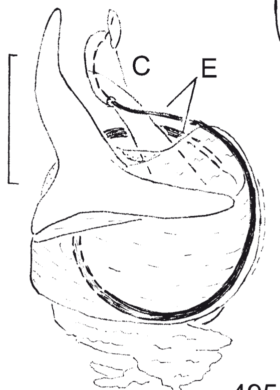




487



493

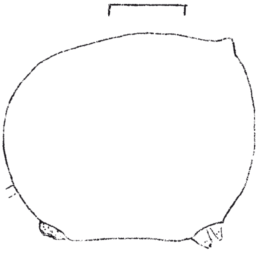


495

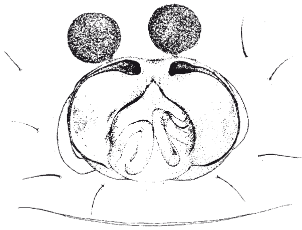
489

figs. 485–490: *<u>*Achaeridion conigerum*</u> (SIMON 1914) (specimens from Europe); 485) male, lateral aspect of the body (taken from HOLM (1977); 486) dorsal aspect of the male; 487) ventral aspect of the cymbium, 488) retroventral aspect of the r. ♂-pedipalpus; 489) bulbus, expanded; 490) ♀, ventral aspect of the vulva, taken from KNOFLACH (1993). Scale bar 0.1 in figs. 486) and 490), 0.5 in fig. 486);

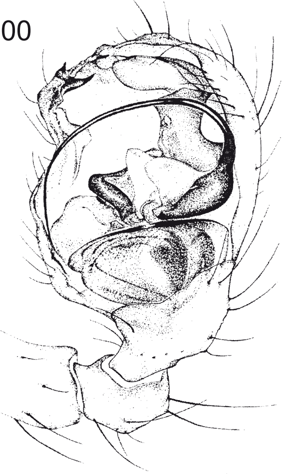
figs. 491–495: *<u>*Anatolidion osmani*</u> **n. gen. n. sp**., male holotype from Turkey; 491) prolateral aspect of the l. metatarsus and tarsus IV. Note the long basal metatarsal bristle-shaped hair (arrow). (Tarsal bristles are not drawn); 492) ventral aspect of the r. cymbium with the paracymbium (P) and the basal alveolus (A); 493–494) ventral and retrolateral aspects of the r. and l. pedipalpus; 495) dorsal aspect of the r. bulbus. Scale bar 0.2;



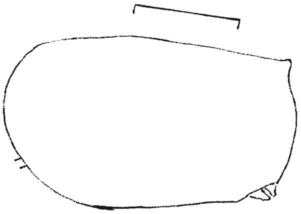
496



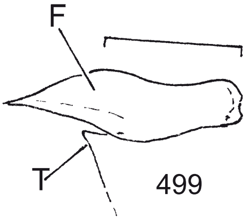
497



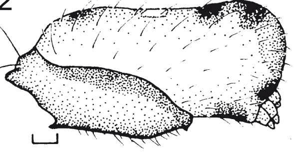
500



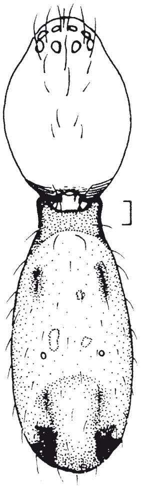
498



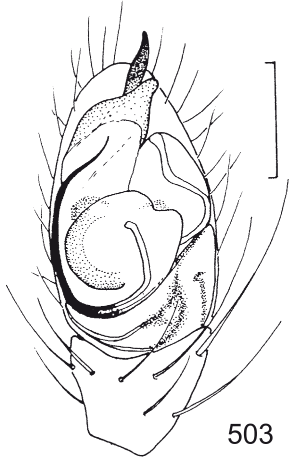
499



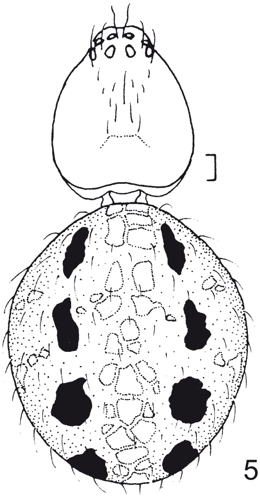
502



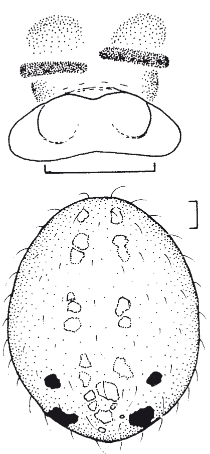
501



503



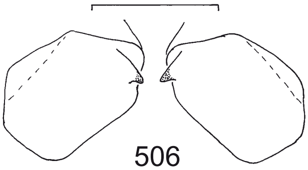
504

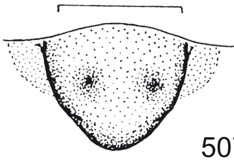


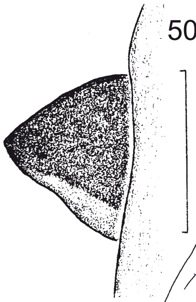
505

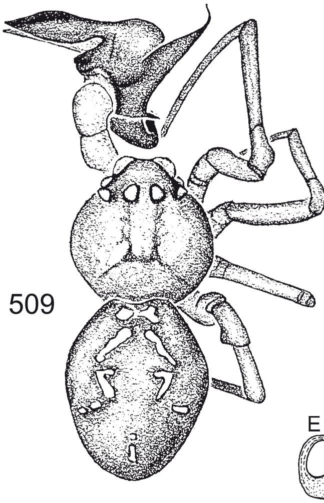
figs. 496–500: **Arctachaea nordica* (CHAMBERLIN & IVIE 1947) (specimen from N-Europe); 496) outline of the ♀-opisthosoma, lateral aspect; 497) ♀, epigyne; 498) outline of the male opisthosoma, lateral aspect; 499) ventral aspect of the very thick left ♂-fang (F) and the large tooth (T) of the posterior cheliceral margin; 500) proventral aspect of the l. ♂-pedipalpus. Figs. 497) and 500) are taken from SZINETAR et al. (2004). Scale bar 0.5 in figs. 496) and 498), 0.2 in fig. 499);

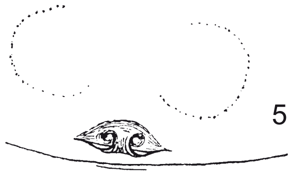
figs. 501–505: **Coleosoma floridanum* BANKS 1900 (specimens from Japan); 501) and 504) body of the female and the male-opisthosomoa (on the right), dorsal aspect; 502) lateral aspect of the ♂-opisthosoma; 503) ventral aspect of the ♂-pedipalpus; 505) ♀, epigyne. Scale bar 0.1. Taken from TANIKAWA (1991);

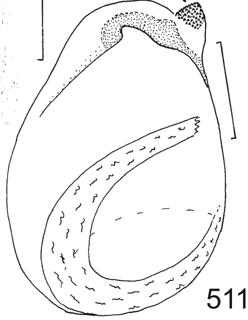

506

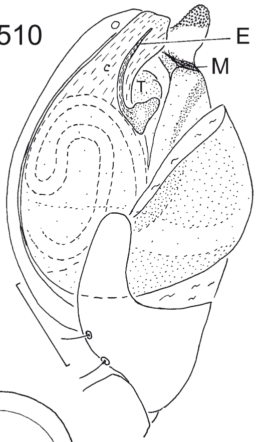

507

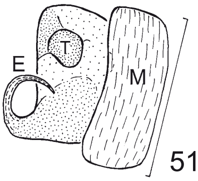

508

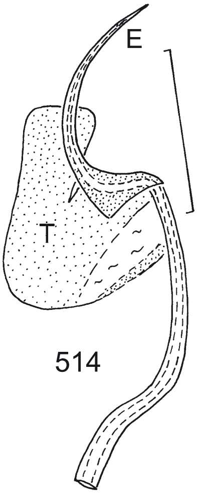

509

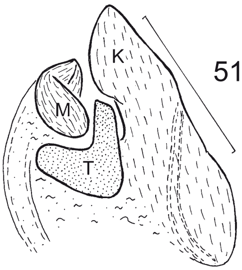

515

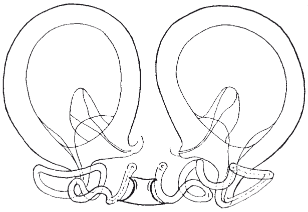

511


510


513


514


512

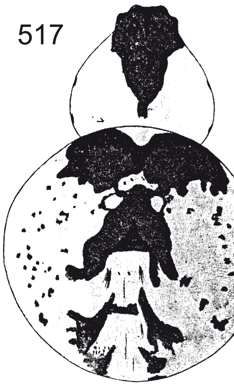

516

figs. 506–508: *<u>*Echinotheridion gibberosum*</u> (KULCZYNSKI 1899) (Madeira), ♀; 506) coxae IV, 507–508) ventral and lateral aspect of the epigyne. Scale bars 0.5 in fig. 506), 0.2 in figs. 507–508);

fig. 509) *<u>*Echinotheridion cartum*</u> (LEVI 1963) (America), dorsal aspect of a male. Taken from LEVI (1981). Scale bar 1 mm;

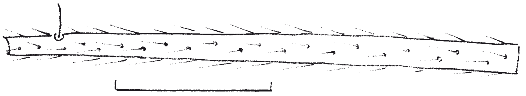
figs. 510–516: *<u>*Heterotheridion nigrovariegatum*</u> (SIMON 1873) (specimens from Europe); 510) retroventral aspect of the r. ♂-pedipalpus; 511) ventral aspect of the cymbium of the r. pedipalpus. The arrow points to the field of tiny cusps on an apical outgrowth; 512) distal part of the bulbus of the r. ♂-pedipalpus, prolateral and slightly apical aspect; 513) apical aspect of the distal sclerites of the r. bulbus; 514) r. embolus and terminal apophysis, proventral aspect; 515–516) epigyne and vulva, taken from WIEHLE (1937). Scale bar 0.2;

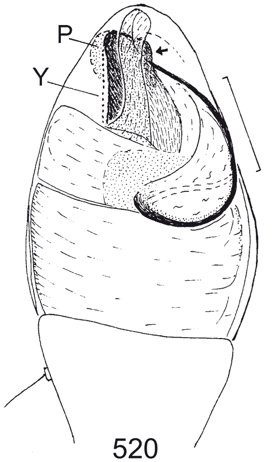
517



518

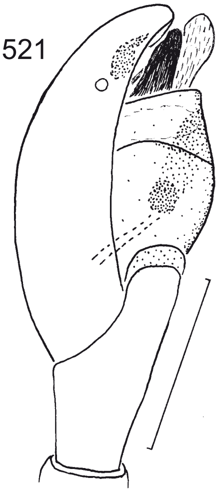
519

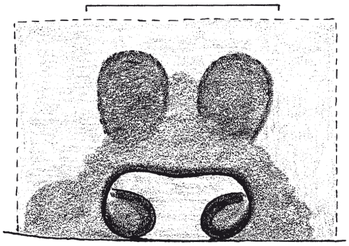




520

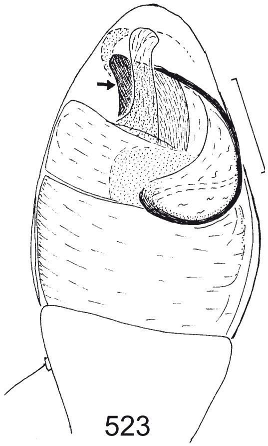
521



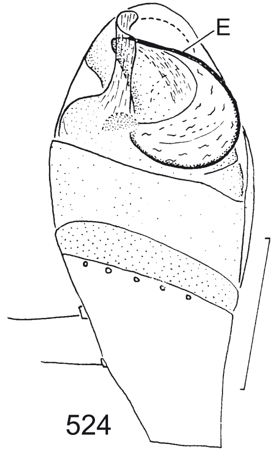


526

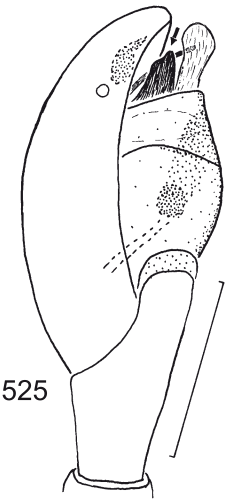
522



523



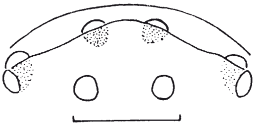
524

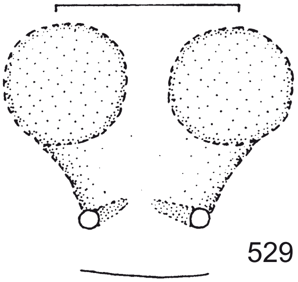


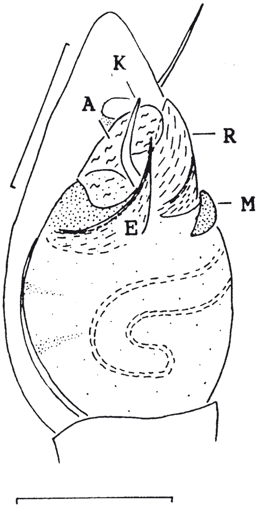
525

figs. 517–521: *<u>Keijia tincta</u> (WALCKENAER 1802) (specimen from Europe), male and female (fig. 517); 517) dorsal aspect of the body, taken from WIEHLE (1937); 518) ventral aspect of femur I, typical colouration; 519) prodorsal aspect of the right metatarsus I. Note the distal position of the erect trichobothrium; 520–521) ventral and retrolateral aspects of the r. pedipalpus (V = variability of the terminal apophysis). Scale bars 0.5 in fig. 519); 0.2 in figs. 520–521;

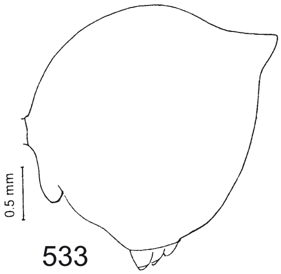
figs. 522–526: *<u>Keijia nigropunctata</u> (LUCAS 1846) (specimens from the Mediterranean); 522) ventral aspect of the r. femur I, typical colouration; 523–524) ventral aspect of the r. ♂-pedipalpus; 525) retrolateral aspect of the r. ♂-pedipalpus; 526) ♀, epigyne. Scale bar 0.2;


527

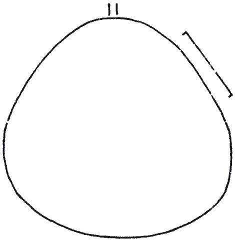

529

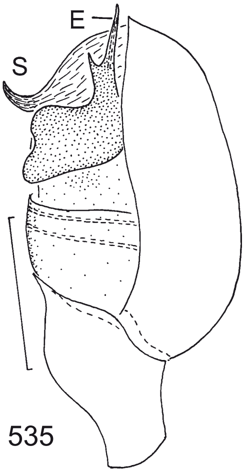


530

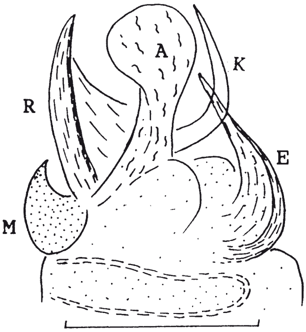


533

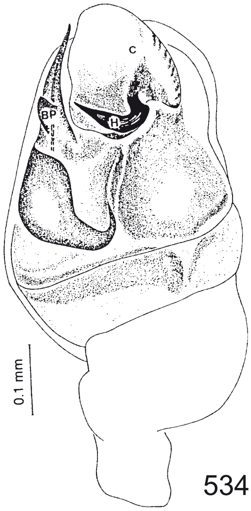

528



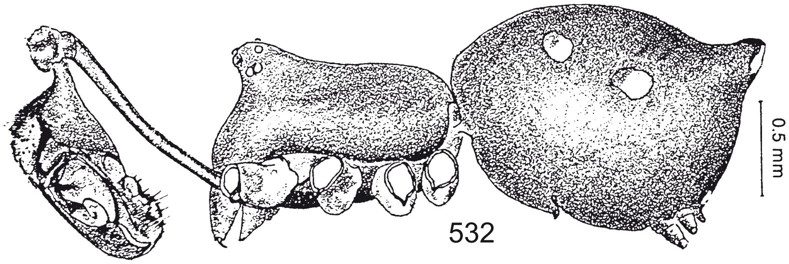
535



531



534

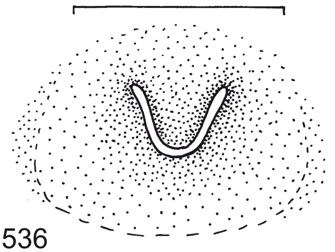


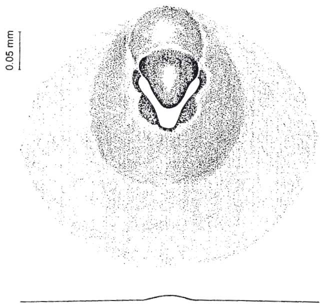
532

figs. 527–531: *Macaridion barretti (KULCZYNSKI 1899) (specimens from Madeira); 527–529) ♀; 527) position of the eyes, 528) dorsal aspect of the opisthosoma; 529) epigyne; 530) ventral aspect of the r. ♂-pedipalpus; 531) dorsal aspect of the distal bulbus apophyses. (A = transparent tegular apophysis, K = conductor). Scale bar 0.2 in fig. 527), 0.1 in the remaining figs.;

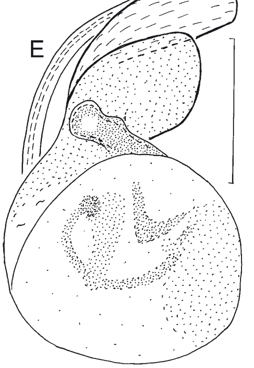
figs. 532–533: *Neottiura uncinata (LUCAS 1846) (specimens from the Mediterranean); 532) male, lateral aspect of the body; 533) female, lateral aspect of the opisthosoma; taken from LEVY (1998);

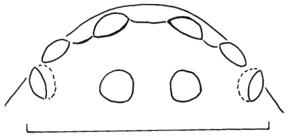
figs. 534–538: *Nesticodes rufipes (LUCAS 1846) (Mediterranean specimens); 534) ventral aspect of the l. ♂-pedipalpus; 535) retrolateral aspect of the r. ♂-pedipalpus;

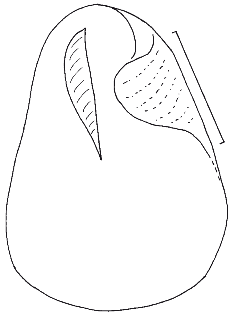

536

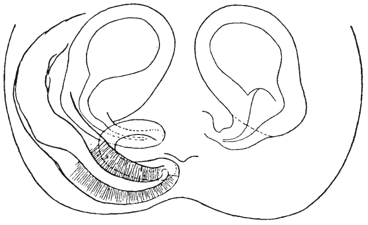


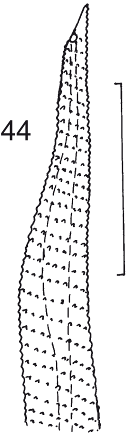
537


542

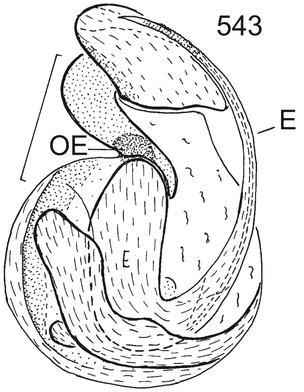

539

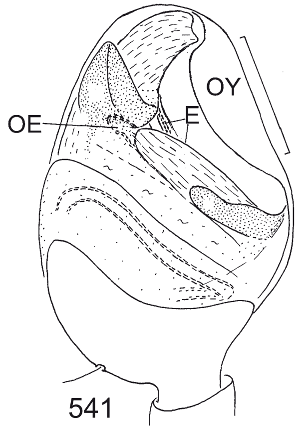

540

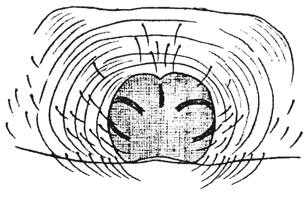

546


544


538


543

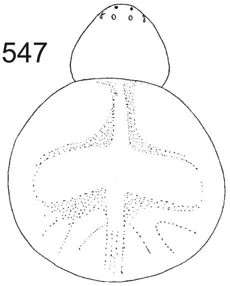

541

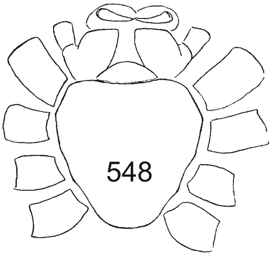

545

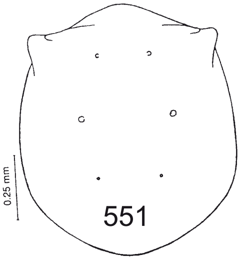
536–537) ♀, ventral aspect of the epigyne; 538) lateral aspect of the epigyne with a plug?; figs. 534) and 537) are taken from LEVY (1998). S = sickle-shaped (terminal) apophysis. Scale bars 0.2 if not otherwise annotated;

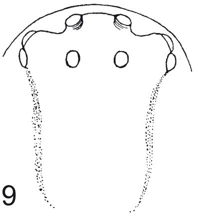
figs. 539–546: *<u>*Ohlertidion ohlerti*</u> (THORELL 1870) (Europe); figs. 540–544: r. ♂-pedipalpus; 539) position of the eyes; 540) ventral aspect of the cymbium with its outgrowth and paracymbium; 541) ventral aspect; 542–543) retroventral and dorsal aspects of the bulbus; 544) distal part of the embolus, prolateral aspect; 545–546) ♀, epigyne and vulva, taken from WIEHLE (1937). OE = basal outgrowth of the embolus OY = outgrowth of the cymbium. Scale bars 0.5 in fig. 539), 0.2 in the remaining figs.;

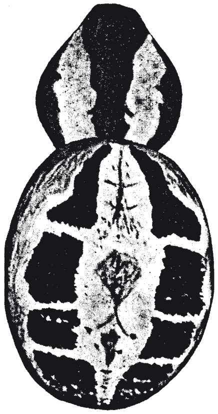
547

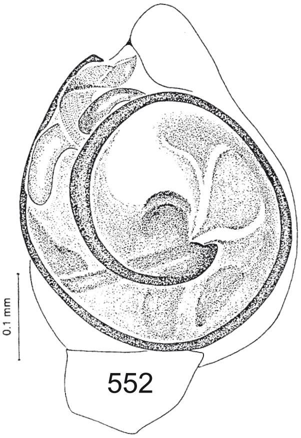


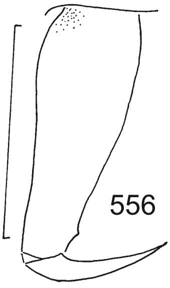




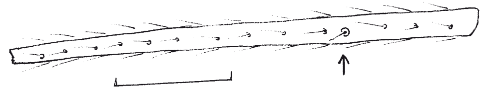

549

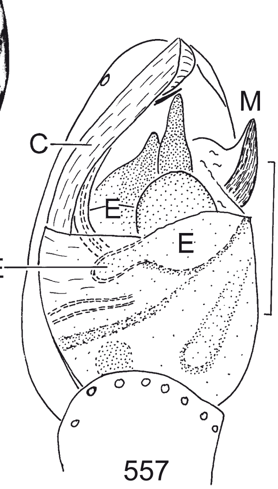

554





555



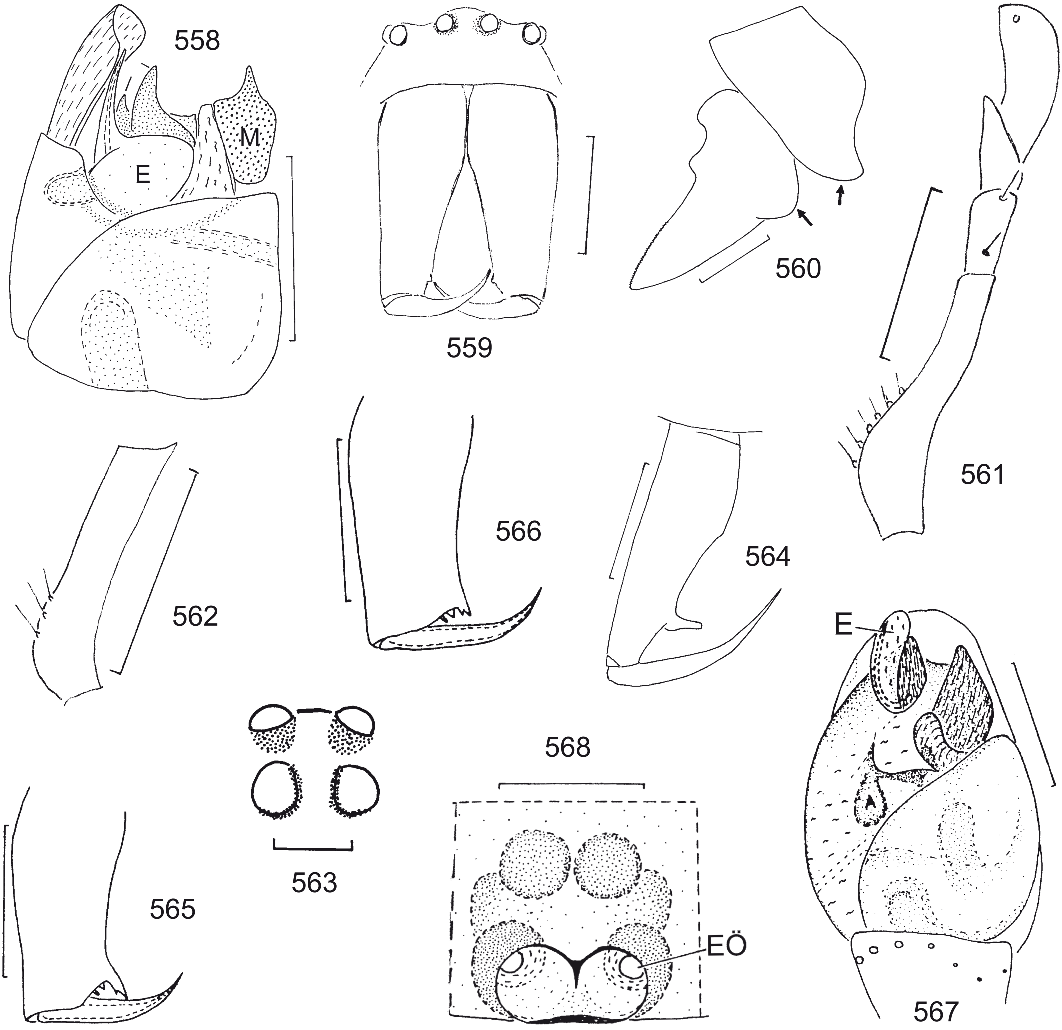


figs. 547–550: **Paidiscura pallens* (BLACKWALL 1834) (Europe); 547) ♀, dorsal aspect of the body; 548) sternum, mouth parts and leg coxae; 549) anterior part of the prosoma; 550) ventral aspect of the r. ♂-pedipalpus; taken from WIEHLE (1937);

figs. 551–552: **Paidiscura dromedaria* (SIMON 1880) (Mediterranean specimens); 551) dorsal aspect of the ♀-opisthosoma; 52) ventral aspect of the l. ♂-pedipalpus; taken from LEVY (1998);

fig. 553) **Phylloneta pictipes* (KEYSERLING 1884) (USA), anterior aspect of the r. ♂-chelicera. Scale bar 0.5;

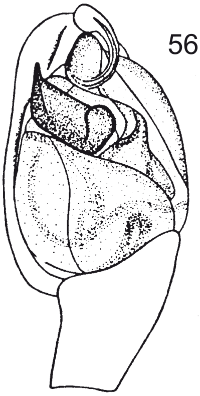
figs. 554–557: **Phylloneta impressa* (L. KOCH 1881) (Europe); 554) ♀, dorsal aspect of the body; 555) retrodorsal aspect of the left metatarsus I. Note the basal position of the small trichobothrium in ca. 0.25; 556) anterior aspect of the r. ♂-chelicera; 557) ventral aspect of the r. ♂-pedipalpus. Fig. 554) is taken from WIEHLE (1937). Scale bars 0.5 in figs. 555–556), 0.2 in fig. 557);



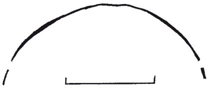
figs. 558–562: *Phylloneta sisyphia (CLERCK 1757) (Europe), male; 558) ventral aspect of the bulbus of the r. pedipalpus (slightly expanded); 559) anterior aspect of the prosoma; 560) l. anterior coxa and basal cheliceral article, retrolateral aspect. Note the distinct humps (arrows); 561) dorsal aspect of the l. pedipalpus (the structures of the bulbus are not drawn); 562) proventral aspect of the r. pedipalpal femur. Scale bars 0.2 in figs. 558) and 560), 0.5 in the remaining figs;

fig. 563) *Rugathodes sp. indet. (Europe), area of the median eyes. Scale bar 0.1; fig. 564) *Rugathodes instabilis (O. PICKARD-CAMBRIDGE 1871) (Europe), anterior aspect of the r. ♂-chelicera. Scale bar 0.5;

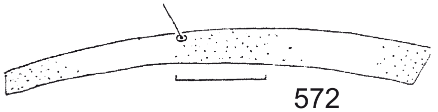
figs. 565–568: *Rugathodes acoreensis WUNDERLICH 1992 (Acores); 565–566) anterior aspects of the r. ♂-chelicera, variability of the large tooth; 567) ventral aspect of the r. ♂-pedipalpus (A = basal outgrowth of the embolus); 568) ♀, epigyne (EÖ = introducing opening). Scale bars 0.2 in figs. 565–566), 0.2 in figs. 567–568);



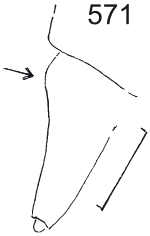
569



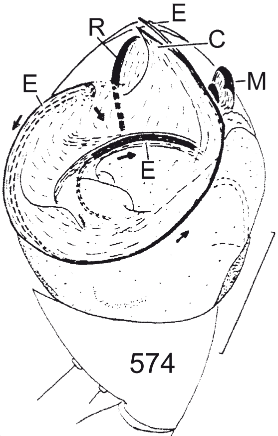
570



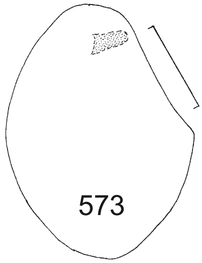
572



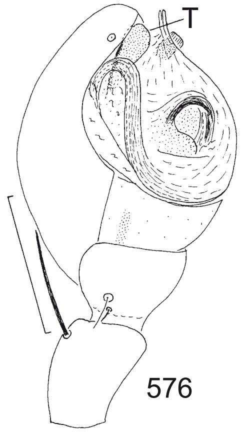
571



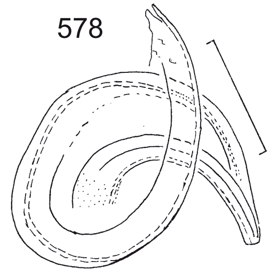
574



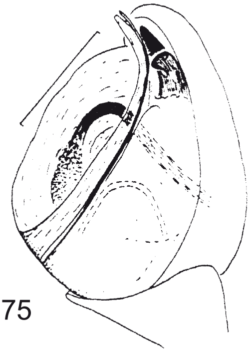
573



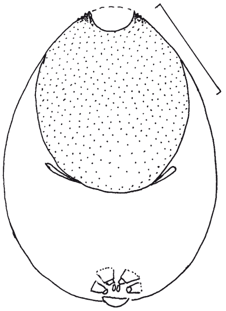
576



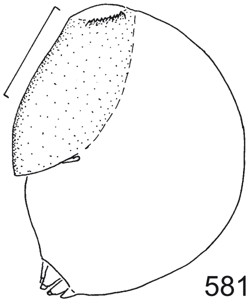
578



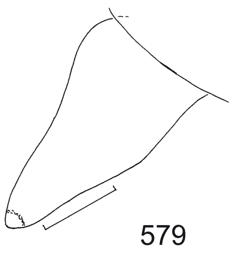
575



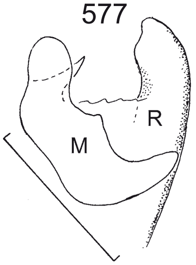
580



581



579

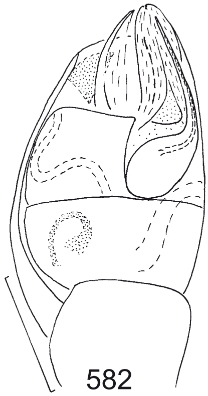


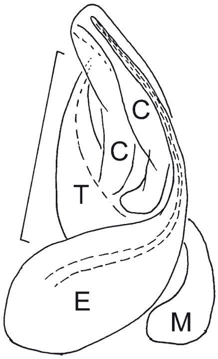
577

fig. 569) **Rugathodes pico* (MERRETT & ASHMOLE 1989) (Acores), ventral aspect of the l. ♂-pedipalpus;

figs. 570–578: **Sardinidion blackwalli* (O. PICKARD-CAMBRIDGE 1870) (Europe), male; 570) dorsal aspect of the clypeus; 571) lateral aspect of the l. chelicera (the arrow indicates to the basal hump); 573) dorsal aspect of the r. cymbium with the translucent paracymbium; 574–576: ventral, prolateral and retrolateral aspects of the r. pedipalpus; 577) dorsal aspect of the right median apophysis and radix (terminal) apophysis; 578) ventral-prodorsal aspect of the right embolus. Scale bar 0.2;

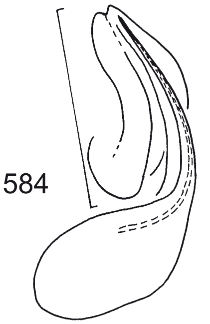
figs. 579–587: **Simitidion simile* (C. L. KOCH 1836) (Europe), male figs. 579–586), female fig. 587); 579) lateral aspect of the l. chelicera; 580–581) ventral and lateral


582

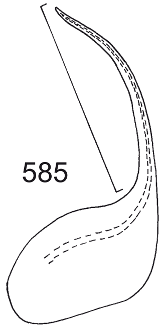


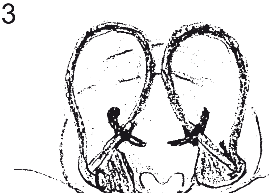
583

584

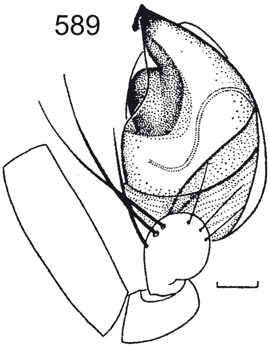


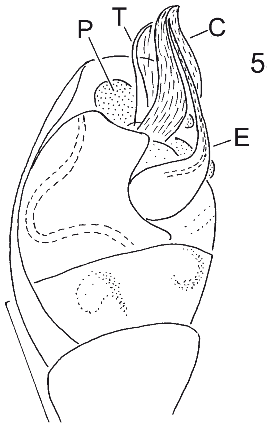
585



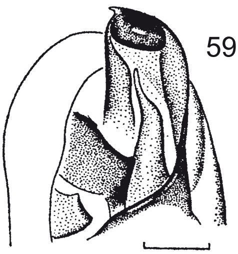

593

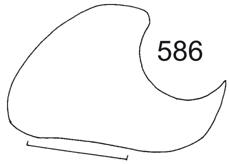
589



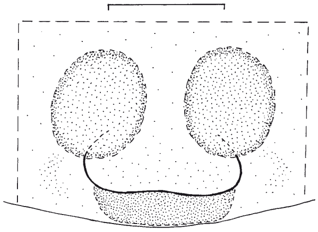


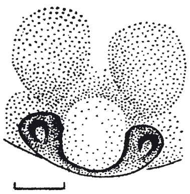
588

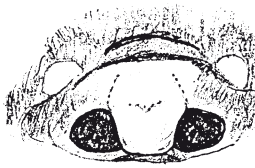

590


586

587



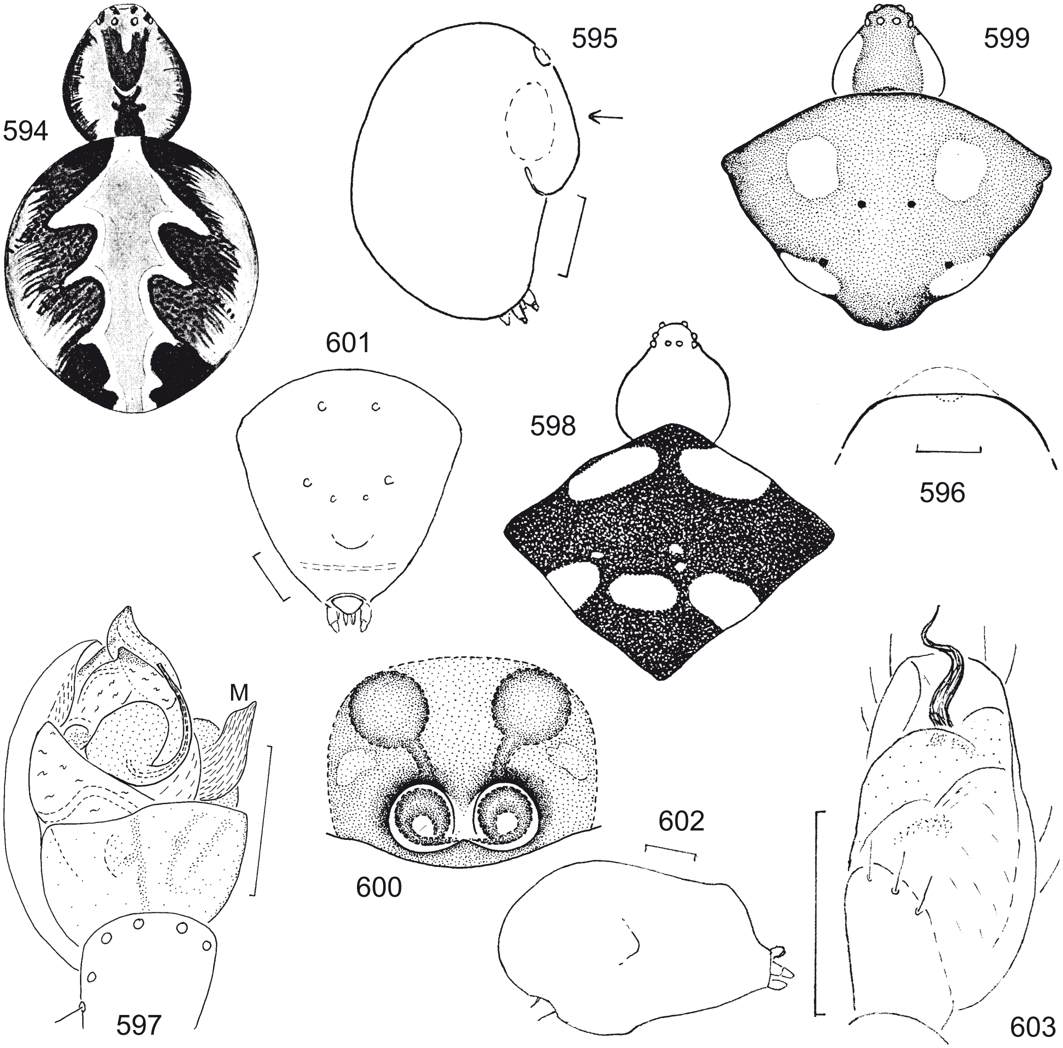

591


592

aspects of the opisthosoma; 582) ventral aspect of the r. pedipalpus; 583) ventral aspect of the sclerites of the r. bulbus; 584) proventral aspect of embolus and conductor; 585) ventral aspect of the embolus; 586) r. median apophysis, prolateral aspect; 587) ♀, epigyne. Scale bars 0.05 in fig. 586), 0.2 in fig. 579), 0.5 in figs. 580–581), 0.1 in the remaining figs.;

fig. 588) *Simitidion lacuna WUNDERLICH 1992 (Mediterranean), ventral aspect of the r. pedipalpus. Scale bar 0.1;

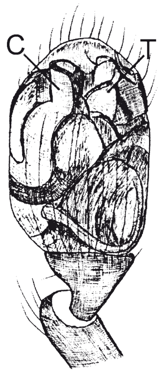
figs. 589–593: *?Takayus palmgreni (MARUSIK & TSELLARIUS 1986) (specimens from Russia and Poland); 589–590) ♂-pedipalpus; 591–592) ♀, epigyne, 593) ♀, vulva. Figs. 589–591) are taken from MARUSIK & TSELLARIUS (1986) (sub *Theridion p.*), figs. 592–593) are taken from BLICK et al. (2006). Scale bar 0.1;



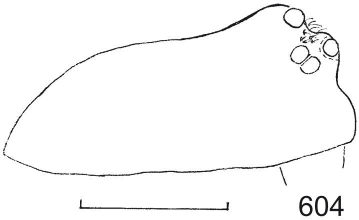
figs. 594–596: *Theridion pictum (WALCKENAER 1802) (Europe); 594) ♀, dorsal aspect of the body; 595) lateral aspect of the ♂-opisthosoma (the arrow points to the bulging epigaster); 596) dorsal aspect of the ventral margin of the ♂-clypeus. Dark line: Most frequent shape which may be inclined medially; the clypeus is rarely protruding like in *Theridion nasutum* WUNDERLICH. Scale bars 0.5 in fig. 595), 0.2 in fig. 595);

fig. 597) *Theridion hemerobium SIMON 1881 (Corsican specimen), retroventral aspect of the r. ♂-pedipalpus. Scale bar 0.2;

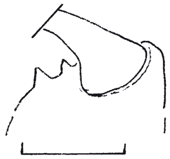
figs. 598–603: *Theridula gonygaster (SIMON 1873) (Mediterranean specimens); 598–599) dorsal aspect of the ♀-opisthosoma; 600) ♀, epigyne; 601–602) dorsal and lateral aspects of the ♂-opisthosoma; 603) ventral aspect of the r. ♂-pedipalpus (note the simple bulbus and the spiral embolus). Scale bars 0.2 in figs. 601–603). Fig. 598) is taken from BRIGNOLI (1969), figs. 599–600) from ZHU (1998);



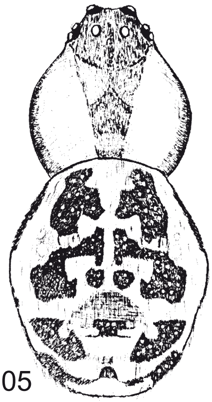
606



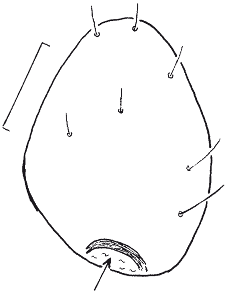
604



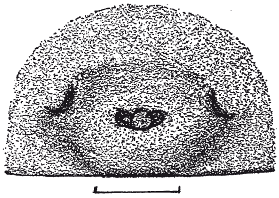
609



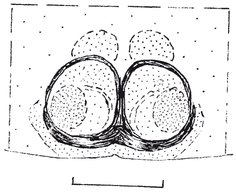
605



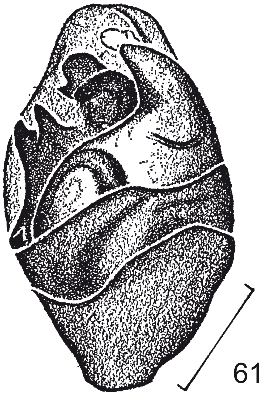
610



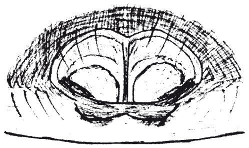
613



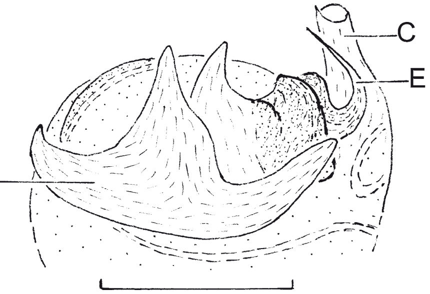
608



612



607



611

figs. 604–608: *<u>*Thymoites bellissimus*</u> (C. L. KOCH 1879) (N-Europe); 604) lateral aspect of the ♂-prosoma; 605) dorsal aspect of the body; 606) ventral aspect of the l. ♂-pedipalpus; 607–608) ♀, epigyne. Figs. 605–607 are taken from ALMQUIST (2006). Scale bars 0.5 in fig. 604), 0.2 in fig. 608,

figs. 609–613: *<u>*Canalidion montanum*</u> (EMERTON 1882); 609) ♂♀ from Finland, posterior aspect of the distal part of the left chelicera. Note the two teeth of the anterior cheliceral margin; 610–611 male from Finland, 610) dorsal-basal aspect of the cymbium of the r. pedipalpus. Only few hairs are drawn. Note the basal inclination (depression) which encloses a scinny area; 611) dorsal and slightly apical aspect of the structures of the r. bulbus; 612) male from the USA, ventral aspect of the l. pedipalpus; 613) ♀, epigyne. Figs. 612–613) are taken from LEVI (1957), fig. 613) is slightly modified after a ♀ from Finland. Scale bars 0.1 in fig. 609), 0.2 in the remaining figs.

BEITR. ARANEOL., 5 (2008)

ON EXTANT AND FOSSIL SPIDERS (ARANEAE) OF THE RTA-CLADE IN EOCENE EUROPEAN AMBERS OF THE FAMLIES BORBOROPACTIDAE, CORINNIDAE, SELENOPIDAE, SPARASSIDAE, TROCHANTERIIDAE, ZORIDAE S. L., AND OF THE SUPERFAMILY LYCOSOIDEA

JOERG WUNDERLICH, 69493 Hirschberg, Germany.

Abstract: The following spider taxa (Araneae of the RTA-clade) of the Eocene Baltic amber forest and extant are described or revised: *Eohalinobius scutatus* **n. gen. n. sp**. (questionable Lycosoidea) with notes on this superfamily and some families of the "Trionycha", *Ablator niger* (PETRUNKEVITCH 1942) and *Ablator felix* (PETRUNKEVITCH 1958) (**n. comb**., from *Abliguritor*) (Corinnidae), *Thereola petiola* (KOCH & BERENDT 1854) (Trochanteriidae?); *Succiniraptor radiatus* (KOCH & BERENDT 1854) (**n. comb**.) (= *Succiniraptor paradoxus* WUNDERLICH 2004 (**n. syn**.), is revised, and a revised diagnosis of the family Borboropactidae WUNDERLICH 2004 is given, the first sure members (juveniles) of the family Sparassidae in Baltic amber are described but not named. – Liocranidae and Zoridae are united in the single family Zoridae; Zoridae s. l. (**n. defin**.) is regarded in a wide sense, including – in Europe – 6 tribus of at least 2 subfamilies: Cybaeoinae (incl. the tribe Liocranini which is downgraded from the family rank), and Zorinae; selected taxa are treated: Agroecini **n. trib**., Apostenini **n. trib**., Cybaeoini, *Cybaeodes mallorcensis* **n. sp**., Liocranini, *Liocranum variabilis* **n. sp**., Succinomini **n. trib**. (in Baltic amber) with *Succinomus* **n. gen**. and *S. duomammillae* **n. sp**., *Zorapostenus raveni* **n. gen. n. sp**. (in Baltic amber), and Zorini; *Sagana* THORELL 1875 (**gen. resurr**.) is removed from the synonymy with *Liocranum* KOCH 1866; *Cryptoplanus* PETRUNKEVITCH 1958 is transfered from the Corinnidae to the Zoridae with some hesitation (**quest. n. relat**.), *Prochora* SIMON 1897 is transferred from the Miturgidae to the Zoridae s. l.. – There is no proof of the family Selenopidae in Eocene ambers, see the paragraph "Erroneous determinations" in the paper (no. 5) on Cretaceous spiders in this volume.

Most **material** is kept in the collection of J. WUNDERLICH (CJW) in the Laboratory of Arachnology in 69493 Hirschberg, some fossils are deposited in the Geol. Palaeont.

Inst. of the University Hamburg (GPIUH), in the Mus. Nat. Hist. Paris (MNHNP), and the SMF.

In this paper I report on fossil taxa of seven families of the RTA-clade – see WUNDERLICH (2004) – which mainly are preserved in Baltic amber, including extant and fossil members of the Zoridae s. l..

(1) Superfamily LYCOSOIDEA s. l., with notes on some families of the "Trionycha" and the new description of a remarkable extinct taxon in Baltic amber: *Eohalinobius scutatus* n. gen.

The **superfamily Lycosoidea s. l**. comprises families of the "Trionycha" like Agelenidae, Amaurobiidae, ?Dictynidae s. l., Lycosidae, Pisauridae, and Zoropsidae s. l., as well as probably Phyxelididae and Titanoecidae, see WUNDERLICH (2004); the exact number of families is still unknown. I regard Lycosoidea in a wide sense (incl. Amaurobioidea sensu LEHTINEN (1967) and probably Dictynoidea sensu WUNDERLICH (2004: 253). A revision of this superfamily, its families and their relationships (sister groups) is urgently needed. Amaurobiidae s. l., Dictynidae s. l. and Zoropsidae s. l. sensu WUNDERLICH (2004) probably have to be split up.

Remark on the synonymy and priority: The older names Lycosoidea (Lycosidae SUNDEVALL 1833) and Argyronetidae THORELL 1870 – have priority over Amaurobioidea (Amaurobiidae BERTKAU 1878) and Cybaeidae BANKS 1892. Similar cases of priority are Archaeoidea KOCH & BERENDT 1854 (= Palpimanoidea O. PICKARD-CAMBRIDGE 1871). Some families of the Mygalomorpha are also still not accepted by their oldest name in PLATNICK's Catalog of Spiders.

The superfamily Lycosoidea s. l. is the most diverse taxon of the classical "Trionycha" ("Trionycha": See WUNDERLICH (2004: 296–296)). It is characterized by the combination of several characters: The existence of an unpaired tarsal claw, tarsal trichobothria (their number and/or length is reduced in some Dictynidae, Titanoecidae and Amaurobiidae s. l., e. g. in the Phryxelidinae) and tiny furrows (not scales) of the cuticula of prosoma and legs; cribellum and calamistrum are present in most Amaurobiidae s. l., Dictynidae s. l. and Zoropsidae s. l. of the families which are listed above. The sister group of the Lycosoidea s. l. is unknown; in the Zodariidae s. l. ("Zodarioidea") a scaly cuticula of prosoma and legs exists. – According (e.g.) to their tarsal trichobothria and the tibial apophyses of their male pedipalpi Phyxelididae and Titanoecidae may be taxa outside the RTA-clade and not closely related to the Lycosoidea.

Up to now only a single fossil specimen of the subfamily Amaurobiinae has been reported from Baltic amber, a dubious juvenile spider, see WUNDERLICH (2004: 1377–1379). Members of *Eomatachia* PETRUNKEVITCH 1942 in Baltic amber are conspicuously similar to Amaurobiinae; they were erroneously published sub *Amaurobius* by KOCH & BERENDT (1854) and MENGE in KOCH & BERENDT (1854) – see WUNDERLICH (2004: 1499) – but are apparently not strongly related to the Amaurobiine.
In this paper I describe sub *Eohalinobius* n. gen. a taxon in Baltic amber whose combination of characters is so unusual – and whose relationships are so unsure – that I place it as a questionable "Lycosoidea s. l. incertae sedis". In my opinion it is probably a member of an undescribed suprageneric taxon; a better preserved conspecific specimen – in which the bulbus structures are visible more closely – is needed for finding out its real relationships. Related extant genera may still exist in the tropics which are not well-studied.

***Eohalinobius* n. gen.** (figs. 1–10, photos 352–353)

Diagnosis and description (♂; ♀ unknown): Thoracal part higher than cephalic part (fig. 1), very small anterior median eyes (fig. 2); legs (figs. 4–5): Tibia I distinctly bent and ventrally bristle-less, tibia and metatarsus II with long paired ventral bristles (their "normal" position is close to their articles), tarsus I–III with a single trichobothrium only (not drawn); spinnerets short; pedipalpus (figs. 6–10): Tibia dorsally-basally with a long erect and hook-shaped modified bristle and a bristle on an outgrowth, apically with four apophyses including a folded dorsal apophysis (similar to some *Titanoeca*-species, Titanoecidae) and a large ventral apophysis; terminal apophysis, median apophysis and embolus as well are long.

Further characters: Ecribellate, unpaired tarsal claw present, posterior eye row distinctly recurved, opisthosoma with a dorsal scutum (photo), tibial sutures absent, metatarsus I with only two long trichobothria (fig. 4), leg scopulae, tarsal claw tufts, pseudoannulations and spines of the tarsi are absent.

Behaviour and ecology: Due to the absence of tarsal claw tufts and leg scopulae – and probably also because of the short leg III – I suggest that members of *Eohalinobius* may have been capture web building spiders but the short spinnerets may contradict this suggestion.

Type species: *Eohalinobius scutatus* n. sp. (the only known species of the genus).

The **relationships** are quite unsure. The combination of characters – short spinnerets, the low number of trichobothria and the short cymbium – exclude a membership of Agelenidae, Argyronetidae and Dictynidae. Argyronetidae possesses furthermore a higher number of tarsal and metatarsal trichobothria than *Eohalinobius*, a low thoracal region, strong basal cheliceral articles and a long cymbium. Amaurobiidae and Dictynidae possess a lower posterior part of the prosoma, they are frequently cribellate and the male chelicerae are often larger in the Dictynidae. Amaurobiinae are cribellate and have a larger number of tarsal and metatarsal trichobothria than *Eohalinobius*; in the Zoropsidae s. l. a suture exists on the male tibia. – The Titanoecidae possess a short cymbium like *Eohalinobius* – as well as certain Amaurobiinae like *Amaurobius* –, frequently reduced tarsal trichobothria and reduced ventral bristles of the male anterior tibia but they are cribellate, their posterior eye row is not distinctly recurved, the anterior part of their prosoma is higher than their posterior part and an opisthosomal scutum is absent. Is *Eohalinobius* a ecribellate taxon of the Titanoecidae? – The Phyxelididae are cribellate spiders, ground-living as probably were members of *Eohalinobius*, tarsal trichobothria are absent, and the male metatarsus I bears a clasping spine (compare fig. 4). The modified anterior male leg in *Eohalinobius* (fig. 4) may be a hint of relationships to the Phyxelididae in which the anterior male METATARSUS is modified contrarily to the bent tibia in *Eohalinobius*. Titanoecidae and Phyxelididae may be most releted to *Eohalinobius* although both are – extant! – cribellate, and their posterior eye row is not strongly recurved. Thus *Eohalinobius* may even be the member of an unknown extinct family. – The eye position, the high number of leg trichobothria, the absence of a tibial apophysis of the male pedipalpus and the long cymbium in the Lycosidae exclude a membership of this family. – The presence of a tarsal pseudo-segmentation, the large number of leg trichobothria, as well as the – usually – long cymbium in the Pisauridae (= Halidae) exclude a membership of this family.

Distribution: Early Tertiary Baltic amber forest.

***Eohalinobius scutatus* n. gen. n. sp**. (figs. 1–10, photos 352–353)

Material: Holotypus ♂ in Baltic amber and a large separated piece of amber, F1661/BB/AR/CJW.

Preservation and syninclusions: The spider is fairly well preserved in a piece of amber which was heated. Ventral parts of prosoma, opisthosoma and ventral parts of pedipalpi and legs are thickly covered with a white emulsion, pyrite is present on and around the spider except of its front, the right tarsi I and IV as well as the tips of the left tarsus IV and the right tarsus II are cut off, the dorsal surface of the opisthosoma is strongly depressed artificially so that the scutum is pressed into the opisthosoma. – A Diptera, few particles of detritus and 3 tiny eggs of an insect are also preserved in the large piece of amber (5 cm long) but no stellate hairs. A tiny Nematoda: Rhabditida is preserved 5 mm to the left behind the spider, a larger bubble is present between the right chelicera and the left bulbus.

Diagnosis: See above.

Description (♂):
Measurements (in mm): Body length 3.5, prosoma: Length 1.8, width 1.55; leg I: Femur 2.0, patella 0.8, tibia 2.0, metatarsus 1.9, tarsus 0.55, tibia II 1.95, tibia III ca. 1.2, tibia IV ca. 1.8; the opisthosomal scutum is ca. 0.5 long and 0.8 wide; pedipalpus: Patella ca. 0.55, tibia ca. 0.55.
Colour: The spider's body and most legs are darkened by heating and the inclusion of pyrite. – Prosoma (figs. 1–3) slightly depressed in the middle, thoracal part higher than cephalic part, longer than wide, with a large fovea and indistinct hairs. The cuticula has probably a fine scaly structure but because of the preservation this fine structure cannot surely be recognized. Eye field fairly wide, posterior row strongly recurved, posterior median and lateral eyes separated by ca. their radius, anterior median eyes small, posterior median eyes largest. Clypeus longer than the diameter of the anterior median eyes. Basal cheliceral articles fairly long (partly hidden), fangs long and slender; gnathocoxae, labium and sternum are hidden by a white emulsion. – Legs (figs. 4–5, photos) prograde, fairly slender, covered with indistinct smooth hairs (I did not find feathery hairs) and thin bristles (except some ventrals which are stronger); order of length I/II/IV/III, tarsi much shorter than metatarsi, pseudo-segmentation absent, metatarsus IV straight and without calamistrum, leg I modified: Tibia distinctly and metatarsus slightly bent, tibia I ventrally bristle-less (in contrast to tibia II). All femora 1 dorsal-basal bristle, patellae dorsally 1/1 (the basal one weak), all tibiae dorsally with 1/1 (weak on I–II), tibia II ventrally with 5 pairs of long bristles close to the article, tibiae III–IV bear similar ventral bristles close to their articles, metatarsus I bears a single long ventral-basal one, metatarsus II bears at least 3 pairs of long ventral bristles, tarsal bristles are absent. Metatarsus I bears 1/1 long trichobothria, the tarsi bear a single one in the basal half near the middle. Three tarsal claws, paired claws with long teeth which are situated in a normal position (not medially as in Zodariidae), teeth of the unpaired claw unknown (most unpaired claws are cut off or hidden). Claw tufts, scopulae and preening hairs of metatarsus III are absent. – Opisthosoma (photo) egg-shaped, artificially depressed dorsally, with short hairs and a distinct dorsal scutum which has a length of about one third of the opisthosomal length. Area of the spinnerets hidden by a white emulsion; as far as visible the spinnerets are short and close together. (The anterior spinnerets should be widely spaced if a cribellum would exist). – Pedipalpus (see also above, the genus diagnosis): The femur bears a long prolateral bristle, the long patella is thickened in the middle, the tibia bears a long and modified (thickened) erect probasal bristle which is bent in a right angle in the distal half as well as a retrobasal outgrowth which bears a short apical bristle and apically with 4 apophyses; cymbium short, the long and strongly bent embolus originates prolaterally, a long and bent apophysis may be the median apophysis, distally exists a large and divided terminal apophysis, a conductor is not recognizable.

Relationships and ecology: See above.

Distribution: Early Tertiary Baltic amber forest.

(2) Family CORINNIDAE

(a) ***Ablator niger*** (PETRUNKEVITCH 1942) (figs. 11–12)

Material: Holotypus ♂ in Baltic amber, British Museum In. no. 18119.

The monotypic genus *Abligurito*r PETRUNKEVITCH has been regarded as synonym of *Ablator* by WUNDERLICH (2004: 1641). Although strongly darkened the holotype of *Abligurito*r *niger* PETRUNKEVITCH 1942 shows all characters of *Ablator*, e. g. the outgrowth of the gnathocoxae and the strongly bent pedipalpal femur (figs. 11–12). PETRUNKEVITCH (1942: 387) erroneously noted differences in the length of the legs, and the spination of the posterior metatarsus as different in *Ablator* and *Abligurito*r but leg IV is longer than leg III in *Ablator* as well in *Abligurito*r and ventral bristles of metatarsus IV are also present in *Ablator*, e. g. in *splendens* WUNDERLICH 2004. In *niger* the bulbus is strongly protruding in the basal half (fig. 11), and the ventral bristles of tibia I are ca. 0.2mm long as in *biguttatus* WUNDERLICH 2004 but in *biguttatus* exists a tegular apophysis which stands distinctly out, and the tibial apophysis – which is long in both species – is more pointed in *niger*.

(2) *Ablator felix* (PETRUNKEVITCH 1958) (**n. comb**., from *Abliguritor*): In the male holotype (Zool. Mus. Copenhagen) the pedipalpi are darkened and badly preserved; the typical single pair of stout anterior spinnerets is well preserved.

(3) Family TROCHANTERIIDAE: A questionable taxon in Baltic amber

Trochanteriidae in Baltic amber have been described by WUNDERLICH (2004).

Thereola petiola (KOCH & BERENDT 1854) sensu PETRUNKEVITCH 1958

Material: “Hypotype” (juv. ♀): Geol. Miner. Mus. Copenhagen no. 10 008.

Thereola PETRUNKEVITCH 1955 (type species *Therea petiola* KOCH & BERENDT 1854) is a member of the family Zodariidae, see WUNDERLICH (2004: 679).

PETRUNKEVITCH (1958) regarded a juvenile female from the Mus. Copenhagen "tentatively" as *Thereola petiola* (= *Therea petiola*) and as a member of the family Dysderidae but according to my investigation it may be a member of the family Trochanteriidae.

Because of darkenings, an emulsion and tiny bubbles the eyes of the spider – which is in a bad condition – are difficult to recognize. PETRUNKEVITCH (1958: Fig. 575) recognized 6 eyes but in fact there are most probably 8 eyes in two rows, the anterior medians largest. The tarsi bear only two tarsal claws, there is a dense tarsal and metatarsal scopula. According to the absence of retroventral bristles of tibia and metatarsus I–II (two proventral tibial bristles are present), the protruding basal cheliceral articles, the roughly equal length of patellae and metatarsi and the length of leg I which are shorter than leg II (in contrast to the measurements of PETRUNKEVITCH (1958: 354) the specimen in question is surely not a member of the Dysderidae but probably of the Trochanteriidae (**quest. nov. relat**.).

(4) Family SPARASSIDAE (= HETEROPODIDAE) (figs. 13–16, photos 377–379)

Below I describe the first fossil spiders in Baltic amber which are surely members of the family Sparassidae, see WUNDERLICH (2004: 1694–1698). The determination of sp. 1 was confirmed by PETER JÄGER (SMF, person. commun.). I am grateful that this specimen was sold to me by WALTER LUDIWG in Berlin.

Fossil Sparassidae are extremely rare. The reasons may be (1) their usually large body size – larger animals could more easily escape from the sticky resin – and (2) their mainly nocturnal hunting behaviour: The resin is less sticky at colder night time and could hardly capture a member of this family. Because of the – really? – absence of small juvenile Sparassidae in Baltic amber these spiders (3) may have lived away from resin-producing trees within the Eocene forest, and were (4) probably not dwellers of higher strata of the vegetation.

The juvenile spiders which are described below have a body length of 7.2 and 9.3mm and – according to its fairly swollen pedipalpi – at least the larger one may have been two moultings before being adult; as an adult spider it could well have been almost 2cm long, having a leg span of about 6cm, and is one of the largest known spider species in amber. – Similar large spiders – which also had laterigrade legs – are members of the family Trochanteriidae, e.g. of the genus *Sosybius* KOCH & BERENDT 1854, which possess a stronger flattened body, an oval shape of the posterior median eyes and only a single row of ventral bristles of the anterior tibiae.

Sparassidae indet. sp. 1 (figs. 13–15, photos 377–378)

Material: 1 juv.♂ (probably two moultings before being adult) in Baltic amber, F2103/BB/AR/CJW, ex coll. WALTER LUDWIG in Berlin.

Preservation and syninclusions: The spider is fairly well but incompletely preserved in a piece of amber which is up to 3cm long and was slightly heated. It is partly covered with a white emulsion and with hyphae. Its opisthosoma is deformed, the spider has been injured and has apparently already been died when is was captured. The spider's legs are bent under the body, the left leg III is missing beyond the coxa by autotomy, several distal parts of the legs are cut off, a white emulsion covers parts of body and legs, hyphae – few ones as well as brushes – are preserved on several parts of body and legs. A large bubble, parts of plants, detritus and excrement of insects are preserved in the same piece of amber, stellate hairs are absent.

Description (juv. ♂):
Measurements (in mm): Body length ca. 9.3, prosomal length and width ca. 4.5, opisthosomal length/width ca. 5.5/3.5; leg I: Femur 6.0, patella 2.3, tibia 5.5, metatarsus ca. 6.0 (tarsus hidden), tibia II 5.5, femur III ca. 4.3, IV: Metatarsus ca. 4.6, tarsus 1.6; pedipalpus: Length ca. 2.0, width 1.0.
Colour: Light to medium (prosoma) brown.
Prosoma as wide as long, fairly flattened, covered with short hairs, fovea well developed, 8 large eyes in a wide field (fig. 13), anterior medians largest, field of the median eyes longer than wide, posterior row slightly procurved. Clypeus as long as the diameter of an anterior median eye, basal cheliceral articles robust and hairy, no condylus, teeth hidden, fangs long, labium, gnathocoxae and sternum hidden. – Legs in a laterigrade position (although most articles are bent under the body in an unnatural position in the dead spider), fairly long, I, II and IV about equal in length, III distinctly shorter, tarsi and metatarsi with a dense scopula, tarsal claws hidden or cut off, bristles long and numerous on tibiae and metatarsi, leg I (fig. 14): Femur 1 dorsal, 2 lateral pairs, 1 prodorsal and 1 retrodorsal-apical (short); tibia 2 ventral pairs, 2 lateral pairs, 2 ventral-apical (short); metatarsus 2 ventral pairs and 2 lateral pairs. Trilobate metatarsal membrane (fig. 15) with a weakly developed median part – Opisthosoma long, soft, covered with short hairs; spinnerets short. – Pedipalpal tarsus fairly thickened, less than in a subadult male.

Close **relationships** are unknown; an adult specimen is needed. See the Sparassidae indet. sp. 2 below.

Destribution: Eocene Baltic amber forest.

Sparassidae indet. sp. 2 (fig. 16, photo 379)

Material: 1 juvenile spider in Baltic amber, F 1883/BB/AR/CJW.

Remark: The spider is juvenile, probably three moultings before being adult. I do not want to exclude that it is a juvenile female.

Preservation and syninclusions: The spider is well and almost completely preserved in a piece of amber which was slightly heated; the distal part of the right tibia and the basal part of the right metatarsus I are cut off, ventral parts of body and legs are covered with a white emulsion. – A large "brush" of numerous tiny white bubbles is preserved left of the spider, 2 large remains of leafs are preserved below the spider, a tiny ant, a small Diptera, 2 Psocoptera (one is partly covered with hypae and partly cut off) and several particles of insect's excrement are also present but no stellate hairs.

Description (juv.):
Measurements (in mm): Body length 7.2, prosomal length and width 3.3; leg I: Femur 4.4, patella 1.7, tibia 3.8, metatarsus 3.8, tarsus 1.5.
Colour light brown.
Prosoma (photo) as wide as long, fairly flattened, densily covered with short hairs, fovea long and deep, 8 eyes in a wide field, fairly small, posterior row slightly procurved, posterior median eyes separated by slightly more than their diameter, anterior median eyes separated by slightly more than their radius, clypeus short, chelicerae slightly protruding, stout and hairy, fangs fairly long, remaining mouth parts hidden. – Pedipalpus with slender articles, a tarsal claw may be hidden. Legs laterigrade, similar to sp. 1, III shortest, I, II and IV not much different in length, scopulae and claw tufts dense, claws with numerous long teeth (fig. 16), trilobate metatarsal membrane (well recognizable on the left metatarsus II) as in sp. indet. 1; tarsus I bears about 8 trichobothria in two irregular rows. Opisthosoma fairly slender, soft, 1.5 times longer than wide, covered with short hairs, in the basal half distinctly wider than posteriorly, spinnerets stout. – Pedipalpus with long articles, tarsus slightly thickened.

Relationships: I do not want to exclude that Sparassidae indet. sp. 1 and 2 are conspecific; the chaetotaxy of both is very similar and probably even identical. In the larger sp. indet. 1 are the anterior median eyes larger and separated by less than their diameter, and the posterior median eyes are separated only by their diameter; the differences may be a result of allometric growth in this species.

Distribution: Eocene Baltic amber forest.

(5) **Family BORBOROPACTIDAE** (figs. 17–23, photos 380–382)

Introductory remarks: Borboropactidae WUNDERLICH 2004 (German name: Ur-Krabbenspinnen) has been separated from the Thomisidae: Stephanopinae. It is a tropical relict family – only the genera *Borboropactus* SIMON 1884 and *Angaeus* THORELL 1871 are known today – which occurs in the Oriental Region and in Africa. Nowadays the family is extinct in Europe and in the whole Holarctic Region. The only known fossils are preserved in Early Tertiary Baltic amber, see WUNDERLICH (2004: 1737–1746).
The rarity of these tropical spiders in Baltic amber – 4 specimens among 100 000 – may be a consequence (a) of their preference of tropical regions and (b) of their occurrence on the ground, in leaf litter etc., away from the resin of trees; see below.

Fossil material in Baltic amber: Up to now only two fossil specimens of two nominal species have been described: A female of *Syphax radiatus* KOCH & BERENDT 1854 and a male of *Succiniraptor paradoxus* WUNDERLICH 2004 in a bad condition. To this material I now add a juvenile specimen and a further adult male which is very well preserved and shows a remarkable leg position.

Synonymy: *Syphax radiatus* is not congeneric with the type species of *Syphax* KOCH & BERENDT 1854 which is a member of the family Thomisidae; see WUNDERLICH (2004: 1752). – The newly discovered material leads me to a revision of the fossil taxa and to the conclusion that members of only a single subfamily exist: Borboropactinae SIMON 1884; Succiniraptorinae WUNDERLICH 2004 is a junior synonym, and I now regard the male of *Succiniraptor paradoxus* as the hitherto unknown female of *Syphax radiatus* and *paradoxus* as a junior synonym of *radiatus*. *Syphax radiatus* is not a member of *Borboropactus* (that placement was not excluded by me (2004: 1741)); so *radiatus* has to be included in *Succiniraptor*. A single fossil genus is known – *Succiniraptor* WUNDERLICH 2004 – which is related to the tropical genus *Borboropactus* SIMON 1884, and most probably only a single species: *Succiniraptor radiatus* (KOCH & BERENDT 1854).
The conspecificy of the males and the juvenile spider with the holotype female of *radiatus* is based on morphological characters but is not quite sure because the spiders are preserved in different pieces of amber; furthermore only in one of the two males the bulbus is observable in the ventral aspect. In numerous other fossil genera we basicly have the same situation, e.g. in *Spatiator* PETRUNKEVITCH 1942 (Spatiatoridae) and in the monotypic genus *Anniculus* PETRUNKEVITCH 1942 (Zodariidae) in which the holotypes are females.

What is the function of the powerful anterior legs in the Borboropactidae (photos, figs. 17, 22)? As the consequence of the existence of powerful legs in BOTH sexes I exclude a connection with mating behaviour. – In contrast to my earlier opinion (2004: 1738–1739) I now question a digging behaviour at least in the fossil spiders of the Borboropactidae; in contrast to the Borboropactidae almost all digging spiders possess stout anterior legs. According to BARRION & LITSINGER (1995: 203) the body of extant *Borboropactus* is coated with mud (not so in the fossil specimens) but a digging behaviour is not mentioned. As shown by the SYNINCLUSIONS – flying insects, a Diptera, a Hymenoptera: Pompilidae and a Coleoptera: Cleridae with partly enfolded wings as well as the large leg of a probably bark-dwelling spider and stellate hairs – at least one specimen of the four known fossils – the holotype male of *Succiniraptor paradoxus* – has been trapped by the resin in a higher stratum of the vegetation, on the bark of a tree, but not by a fallen drop of resin on the ground. If these spiders occurred – occasionally? – on bark: Why are they so rare in amber? Did they not occur on or near amber-producing trees or were they very rare or probably restricted to a small area within the amber forest? I suppose that the fossil spiders lived on the ground like their extant kin, probably in more open habitats.

In the fossil male F1654/CJW the powerful anterior legs are stretched out forewards (fig. 17, photo) and the remaining legs are not so strongly bent under the body as in most fossil spiders which are preserved in amber. This leg positon – a kind of camouflage? – may be similar to the natural position of members of this species and is similar to (a) *Borboropactus* sp. indet., fig. 22; see MURPHY & MURPHY (2000: Plate 26.5–6) and (b) to the walking position of leg I in ground-living members of the genus *Palpimanus* DUFOUR 1820 (Palpimanidae) which feed on spiders and which raise and stretch their anterior “tactile/detecting legs” foreward. The existence of tarsal and metatarsal sense organs of the anterior legs in the Borboropactidae (fig. 18) may be a hint that they function as “tactile/detecting legs”, detecting prey similar to members of the Palpimanidae. – In respect to the special shape of the anterior femora of Borboropactidae – which are strongly thickened, bulging prolaterally in the middle and bearing some stout spines in this position – the first leg pair may well have a further function, namely as raptorial legs similar to spiders of the genus *Palpimanus*. The stout femoral spines are the only lateral leg spines in the Borboropactidae; if they would be longer one would suppose them to be used for fixing their prey. Probably the strong ventral bristles/ spines of the anterior tibia and metatarsus (fig. 17) are used to capture prey.

The Thomisidae possess raptorial legs, too, but their legs are laterigrade, their leg II is powerfully developed, not much smaller than leg I and distinctly larger than III and IV. Special sensory modifications of tarsi and metatarsi are unknown to me in the Thomisidae.

Remark on the leg position in the fossil material: In the original description the holotype of *Syphax radiata* has been drawn in an incorrect leg position (and the absent anterior pair of legs has been added), see the photo fig. 16 in the book of WUNDERLICH (1986: 153). Apparently the holotype of *Succiniraptor paradoxus* is preserved in an unnatural leg position at the corner of the amber piece; the leg position is clearly not laterigrade.

Remark on extant spiders: In extant spiders of several families exist also raptorial anterior legs, e. g. in Mimetidae, Palpimanidae, Salticidae, Thomisidae. Palpimanidae – as well as most members of related families –, and most Mimetidae possess small male pedipalpi similar to Borboropactidae. Additionally in numerous Mimetidae the pedipalpal articles are lengthened so that their pedipalpi are not in their way of their anterior capture legs. In contrast to Borboropactidae, Salticidae and Thomisidae there are modifications on the prolateral side of the anterior legs in Palpimanidae (hair brushes) and Mimetidae (special strong “mimetid bristles”) and some Araneidae (special strong bristles in *Arcys*). In members of these families strong VENTRAL bristles are absent on the anterior legs.

Why do such small male pedipalpi and a prolateral depression of the anterior femora in the Borboropactidae exist? In members of this family the male pedipalpus is only about as voluminous as the anterior coxa (photos, fig. 17). Straight thickened anterior femora and normally large male pedipalpi would hinder each other during the procedure of prey catching and fixing it by putting together the large anterior legs. The enlarged femora possess a prolateral depression exactly sidewards to the pedipalpi and basally to their stout spines – see the photo (ventral aspect) and fig. 17 –, and so the pedipalpi are (a) not in the legs way and (b) they furthermore are protected from a prey's attack – e. g. an ant – by the large femora (fig. 17).

Camouflage: Apparently the shape of body and legs – they may be largely stretched out foreward (figs. 17, 22, photo 380) – as well as the very small male pedipalpi and the behaviour of *Borboropactus* – often daubed with mud particles – are a kind of camouflage; see fig. 22 and the photos of living spiders in the book of MURPHY & MURPHY (2000: Plate 26.5–6). In fossil spiders I found no mud. – The connection with camouflage in a resting position may be a third function of the stretched out anterior legs in all fossil and extant members of the family Borboropactidae. A similar camouflage – to and on the bark of trees (mimesis) – exists e. g. in several Philodromidae and Thomisidae like *Pandercetes, Runcinia, Sidymella* and *Stephanopis* as well as in *Cryptothele* (Zodariidae) (see below), and Tetragnathidae. This kind of camouflage has evolved convergently several times in spiders and in numerous families.

Evolution: (1) It is of interest to compare the pits/grooves of tarsi and metatarsi in the extinct *Succiniraptor* of the Baltic amber forest with the extant members of *Borboropactus*: In *Succiniraptor* low grooves (furrows) exist which bear two trichobothria (figs. 18–19); the trichobothria may be modified; in *Borboropactus* we find – besides "feathery" or "plumose" trichobothria – additionally several thickened sensory hairs in a pit on the tarsi, see WUNDERLICH (2004: Figs. 4–9). According to their shape these may be olfactory hairs. The trichobothria-bearing furrow of the anterior tarsus of the fossil *Succiniraptor* (fig. 18) may well be a first step, and in this respect the model of an evolutionary precursor of *Borboropactus*. To my knowledge such a derived "tarsal pit organ" did still not exist in the Eaerly Tertiary Borboropactidae (*Succiniraptor*). With regard to the only slightly modified tarsi *Succiniraptor* may be a "missing link" between its unknown ancestor and the advanced extant members of the genus *Borboropactus* which possess a large and highly modified "tarsal pit organ". ("Missing links" – connecting structures – in fossil spiders: See WUNDERLICH (2004: 265–266)).

Remark on similar sensory hairs in a different spider family: In at least one species of *Cryptothele* (Zodariidae) tarsi and metatarsi are modified – bearing conspicuous sensory hairs – in an apparently similar way convergently to the Borboropactidae; see MURPHY & MURPHY (2000: 146, fig. 1): "These sensory hairs are probably used to detect prey." In a congeneric species from Africa such modification is absent; R. JOCQUE (person. commun.), and in a male from Singapore (CJW) such modifications are absent, too. Has *Cryptothele* to split up?

(2) The body length of extant Borboropactidae (usually 6–10 mm) is about twice as in the extinct spiders (3–4.2 mm). The tendency to evolve larger spiders within certain families/genera during the Tertiary is discussed by WUNDERLICH (2004: 260–261); see also above, and the paper on Therididae in this volume (no. 3).

Revised diagnosis of the family Borboropactidae WUNDERLICH 2004 (*) (figs. 17–23; see also WUNDERLICH (2004: Figs. 1–13)): Eye field narrow, lateral eyes small and not situated on large tubercles, tarsi and metatarsi with a trichobothria-bearing groove (in *Succiniraptor*, figs. 18–19) or even a large and modified "tarsal pit organ" on leg I (in *Borboropactus*). The raptorial powerful leg I distinctly longest (II much shorter (**)), femur I distinctly bulging prolaterally, bearing some spines in this area and with a prolateral depression in front of the thickening, patellar bristles absent, lateral and dorsal leg bristles absent, male pedipalpal articles unusually small.

(*) See the remarks on the taxonomy and the opinion of LEHTINEN (2007) in the paper "Differing views in the taxonomy of spiders (Araneae)..." in this volume (no. 13).

(**) *Borboropactus mindoroensis* BARRION & LITSINGER 1995 from the Philippines (female, fig. 116a) has leg I not much longer than II (see below: *Isala*), femur I is not bulging and prolateral femoral spines are absent; this specimen may have leg I regenerated or is probably the member of another genus.

Further characters (see WUNDERLICH (2004: 1739)): Ecribellate two-clawed spiders of medium size (body length usually 3–10 mm), body flattened and rugose, prosoma narrowed anteriorly, thoracal fissure/fovea absent or strongly reduced, clypeus of medium length, chelicerae hairy apically, toothed on both margins and with teeth within its furrow, basal cheliceral articles long, fangs fairly long, labium free, opisthosoma armoured, colulus reduced (or even absent?); leg position prograde, autotomy between coxa and trochanter, most leg articles modified/depressed, club-shaped hairs present (probably rare in the fossils – rubbed off? – short, thick hairs are present in the fossils), paired ventral tibial and metatarsal bristles present on legs I–II, few ventral bristles on tibia and metatarsus III–IV, claw tufts and false tarsal and metatarsal scopula (thin hairs) present, a field of ventral "preening hairs" is present on metatarsus III. Male pedipalpus: Retrolateral tibial apophysis present, ventral tibial apophysis absent, the strongly convex cymbium may distally be scopulate, bulbus/tegulum prominent, median apophysis sickle-shaped, embolus probably enclosed by a "conductor" at least in *Borboropactus* (questionable in *Succiniraptor*); epigyne: See below (*Borboropactus*). At least the extant spiders are ground-living animals and are often covered with mud.

Type genus: *Borboropactus* SIMON 1884. *Angaeus* THORELL 1871 is a second extant genus. The extinct genus *Succiniraptor* WUNDERLICH 2004 is a further – the only known extinct – genus. According to the shape of the body and the position of the legs – see HAWKESWOOD (2003: Plate 81) – I will not exclude that *Isala* L. KOCH 1876 (extant, Australia) may be a further genus of this family (I did not yet have the opportunity to study members of this genus). In contrast to *Borboropactus* and *Succiniraptor* leg II is not much shorter than leg I in *Isala*.

Remark: The single male of the genus *Succiniraptor* on which I based the diagnosis of the Succiniraptorinae is incomplete and partly badly preserved and led me (2004: 1742–1743) to some erroneous conclusions. The material which I studied recently is much better preserved.

Subfamily: Only Borboropactinae (= Succiniraptorinae) (**n. syn**.).

Relationships (compare WUNDERLICH (2004:1739) and above (*): Claw tufts, tarsal scopulae, toothed cheliceral margins and apically hairy chelicerae are also characters of plesiomorphic Thomisidae s. l.: Stephanopinae s. l., and apparently Thomisidae is strongly related to Borboropactidae. In the Thomisidae the legs are laterigrade (less distinct in the Stephanopinae), and leg II is almost as powerful as leg I, usually patellar and lateral leg bristles are present, special tarsal/metatarsal sense organs are not known, the eye field is wide with the lateral eyes situated on humps, a ventral tibial apophysis of the male pedipalpus is usually present, the bulbus is more or less disc-shaped. Stephanopinae O. PICKARD-CAMBRIDGE 1871 may be a family of its own, and is probably not monophyletic; at least *Epidius* THORELL 1877 and related genera in which conductor and tutaculum are absent – may represent a further family of its own; see WUNDERLICH (2004: 1750). – I do not want to exclude relationships of the Borboropactidae to the Zodariidae. In all the three families a capture web has been lost, powerful anterior raptorial legs are present and probably a similar behaviour exist at least in the ancient taxa: Digging behaviour, covering with mud – which probably evolved in parallel ways –, and numerous spiders feed on ants.

Distribution: Extant: Tropical Africa and Oriental Region (*Borboropactus* and *Angaeus* THORELL 1881 according to LEHTINEN); fossil: Early Tertiary Baltic amber forest (*Succiniraptor*).

<u>The genera of the Borboropactidae</u> (the extant genus *Angaeus* is not treated here):

(a) ***<u>Borboropactus</u>*** SIMON 1884 (figs. 22–23)

Diagnosis: Tarsus I with a large dorsal-distal “<u>pit organ</u>” which bears few trichobothria and numerous special thickened sensory hairs; see WUNDERLICH (2004: 1745, REM-photos 4–9); embolus: Most parts are hidden/enclosed by a long “conductor”, distal embolic part <u>spiral</u>; see WUNDERLICH (2004: 1744, fig. 3). Female genital organs: The epigyne bears – in all species? – anteriorly a helmet-shaped sclerotized structure (fig. 23).

Relationships: See *Succiniraptor*.

Distribution: Tropical regions of Africa and the Oriental Region.

(b) *Succiniraptor* WUNDERLICH 2004 (figs. 17–21, photos 380-382))

Diagnosis: All tarsi and metatarsi possess a longitudinal dorsal groove which bears two trichobothria each (fig. 17); ♂-pedipalpus (figs. 17, 22): Conductor probably present (*), the embolus is stragiht; see WUNDERLICH (2004: 1746, fig. 12); female genital organs unknown.

(*) The “embolus” in fig. 12 – see WUNDERLICH (2004: 1746) – is partly covered by a white emulsion and may in fact be part of a “conductor”, an only the tip of the embolus is observable, see fig. 21.

Type species: *Syphax radiata* KOCH & BERENDT 1854, the only known species of this genus. (*Succiniraptor paradoxus* WUNDERLICH 2004 is a synonym).

Relationships: The shape of body and legs (including the powerful leg I and modified sense organs of tarsi and metatarsi), eyes and pedipalpal articles are comparable or very similar to – the extant genus *Borboropactus* but in *Borboropactus* a large and modified “tarsal pit organ” is present on leg I (only a low groove/furrow exists in this position in *Succiniraptor*, figs. 18–19), and the distal part of the embolus has a spiral shape. Spiders of *Borboropactus* are larger than members of *Succiniraptor*, see above (evolution) and the number of spines on their femur I is – probably in all species – higher than two.

Distribution: Early Tertiary Baltic amber forest.

Succiniraptor radiatus (KOCH & BERENDT 1854) (**n. comb**.) (figs. 17–21, photos 380–382)

1854 *Syphax radiatus* KOCH & BERENDT, in BERENDT (ed.): Die im Bernstein befindlichen Organischen Reste der Vorwelt, 1 (2): 81, t. 17, fig. 148 (♀) (**n.comb**.).
1986 *Syphax radiatus*, – WUNDERLICH, Spinnenfauna gestern und heute: 28, figs. 16–17 (♀) (**n. comb**.).
2004 ?*Borboropactus radiatus*, – WUNDERLICH, Beitr. Araneol., 3: 1741 (♀) (**n. comb**.).
2004 *Succiniraptor paradoxus* WUNDERLICH, Beitr. Araneol., 3: 1742, figs. 10–13, photos 397–398 (♂) (**n. syn**.).

Acknowledgements: I thank JONAS DAMZEN in Vilnius (Lithunia) very much for making the male F1654/CJW available to scientific study.

Material (in Baltic amber): Holotypus of *Syphax radiatus* (adult ♀): PMHUB; holotypus of *Succiniraptor paradoxus* (♂): F609/CJW; further material: 1♂ F1654/CJW (later on GPIUH), 1 juv. ♂ F1653/CJW.

Synonymy and conspecifity of the spiders: See above.

Diagnosis: See the diagnosis of the genus and WUNDERLICH (2004: 1742–1746, figs. 10–13); femur I bears only two prolateral spines (fig. 1), the pedipalpal tibia bears a long retrolateral apophysis.

Preservation and syninclusions of the new material: The adult male F1654 (photos) is well preserved in a piece of amber which has a size of 2.5 x 2 x 0.8 cm, few parts of the ventral side are covered with a white emulsion, the mouth parts are hidden, larger hairs of body and legs were probably rubbed off, the distal parts of the right legs II–IV and of the left leg IV are cut off, some bubbles cover the sternum and some ventral parts of both anterior legs. The anterior legs of the spider are stretched out foreward (see above), the remaining legs are only slightly bent. Because of their position the ventral aspect of both pedipalpi is not recognizable. Stellate hairs are absent. – The juvenile male F1653 is almost completely preserved, the left leg I is missing beyond the coxa by autotomy. Most parts of its body and legs – especially dorsally – are covered by a white emulsion. The apical pedipalpal article is not strongly thickened. Numerous stellate hairs and the part of the wing of a Diptera are preserved in the same small piece of amber.

Description (see also above: the genus *Succiniropsis* and the family Borboropactidae):
Measurements (adult spiders, in mm): Body length ♂ ca. 3–3.5, ♀ 4.2; prosoma (male F1654): Length 1.65, width 1.65; leg I (male F1654): Femur 2.1 (width 0.7), patella 0.9, tibia 1.7, metatarsus ca. 0.9, tarsus ca 0.6, tibia II ca. 1.0, femora: II 1.1, III 0.85, IV 1.1; length of the cymbium 0.38.
Colour usually silvery but in F609 dark brown (the amber piece was probably heated, some parts of body and legs are cut off so that the fossil has been in contact with oxygenium). Male (figs. 17–21): Body flattened and rugose; the posterior eye row is distinctly recurved, the median eyes are smaller than the lateral ones, a thoracal fissure is absent, the coxae IV are close together. Legs as in the genus, rugose and partly depressed. Apparently all metatarsi and tarsi possess a low longitudinal dorsal furrow which bears 1/1 trichibothria which may be thickened (a "tarsal pit" as in *Borboropactus* is absent), tibia I bears ca. 5 pairs of thick ventral bristles, metatarsus I bears 3 strong proventral and 4 strong retroventral bristles and a pseudoscopula (thin hairs), tibia II bears 3, metatarsus II 2 pairs of strong ventral bristles; tarsus I stout, with a well developed claw tuft, a pseudoscopula and a pair of strongly bent claws. Metatarsus III bears ventrally along its whole length a large and well developed field of “preening hairs”. Leg I is distinctly the longest, IV about as long as II. The opisthosoma is armoured dorsally and ventrally, with lateral furrows and two pairs of dorsal sigillae. Spinnerets short and in a rosette-shaped position, the medians are hidden (or absent?), a tiny colulus may exist, the anal tubercle is large and bears a bent row of stout hairs in a half-circle. The ♂-pedipalpus is small, the short tibia bears a long and bent retrolateral apophysis (fig. 17), the cymbium is convex and bears probably an apical scopula. The epigyne is unknown (hidden in the holotype). – In the juvenile male leg I is not so strongly elongated as in the adult male but femur I is distinctly thickened, tibia I is ca. 1mm long, tibia II ca. 0.75 mm.

Relationships: See the genus. – MENGE in KOCH & BERENDT (1854: 81) listed sub *Syphax* n. sp. three fossil species in Baltic amber – *hirtus, fuliginosus and thoracica* –

which I regard as nomina nuda, and which are most probably members of the Thomisidae. Only *hirtus* is very shortly and insufficiently characterized as "rough-haired and short-legged". Most probably the type material is lost. Other fossil species which were described in Baltic amber sub *Syphax* by KOCH & BERENDT (1854) (sub Thomisidae): See WUNDERLICH (2004).

Distribution: Early Tertiary (Eocene) Baltic amber forest.

(6) Family ZORIDAE s. l. (LIOCRANIDAE)

Introductory remarks: In this paper I will start with the study of the 13 to 15 extant and fossil European genera of the family Zoridae s. l. in a REVISED SENSE; half a dozen genera are known from fossils in Baltic amber; with the exception of *Apostenus* they are extinct. The relationships of *Cryptoplanus* – a member of the Corinnidae? – are unsure, see WUNDERLICH (2004) and remark (c) at the key below. The number of nearctic genera of this family is much lower, in SE-Asia members of the Zoridae s. l. are extremely rare, the probably related taxa of the Australian Region and of South America are waiting for a revision. I suppose that Europe – especially the Mediterranean area – has been a "hot spot" of evolution of the Zoridae, comparable with the condition of the family Dysderidae in the same region.

Zoridae s. l. in the sense of this paper may be a monophyletic taxon or not. I propose herewith to unite the families Liocranidae and Zoridae to a single family, the Zoridae s. l. (*) (**), six tribus to (a) the Cybaeodinae (including the tribe Liocranini which is ranked down from the family level), and (b) Zorinae (formerly Zoridae s. str.). The relationships of certain tribus remain unsure; they may be members of a third subfamily.

Fossil spiders of the family Zoridae s. l. in Baltic amber – of the genera *Apostenus* WESTRING 1851 and *Palaeospinisoma* WUNDERLICH 2004 – have been described by WUNDERLICH (2004: 1623–1635) sub Liocranidae; they are transferred here to the Zoridae s. l.. In this paper I will add the fossil taxa *Succinomus duomammillae* n. gen. n. sp. of the Succinomini n. trib., and *Zorapostenus raveni* n. gen. n. sp. (Apostenini) as well as two extant species of the genera *Cybaeodes* and *Liocranum*. I also discuss the interfamiliar and the intrafamiliar relationships of the Zoridae s. l..

The male of the remarkable fossil species *Zorapostenus raveni* is an example of fossils which may provide important conclusions on the relationships even on the family level. The presence of bristles/spines on the posterior male coxae in this genus (fig. 29) allows also conclusions on the behaviour of these extinct spiders: The bristles/ spines may have had a stridulatory function, and were probably used during courtship. Similar structures exist in certain extant members of the genus *Zora* C. L. KOCH 1847. Such hairs/bristles/spines are unknown to me in other taxa of the whole RTA- (= retrolateral tibial apophysis-) clade of the higher spiders. The actually stridulatory function of the hairs in males of *Zora* is unknown to me, and is only suggested here.

According to their powerful femora III and IV (fig. 28) the spiders of the new fossil genus *Zorapostenus* were apparently fast sprinters or even jumpers; their extreme rareness indicates that they were not bark dwellers but ground spiders like other Zoridae which are wandering hunters and most often forest spiders.

The existence of half a dozen extinct genera of the Zoridae (there may be one or two further undescribed genera in Baltic amber) indicate that this family was quite diverse in the Early Tertiary. Fossil species of the genus *Apostenus* are not too rare in Eocene Baltic amber, and they probably occasionally climbed the bark of trees. *Apostenus* is the only known zorid genus which survived from the Eocene.

(*) Remarks on the family name: The oldest suprageneric names within the Zoridae s. l. – in the new sense of the present author – are Cybaeodinae SIMON 1893 (sub Cybaeodeae) and Zorinae F. O. PICKARD-CAMBRIDGE 1893. Liocraninae SIMON 1897 is younger but was used by SIMON although this author (1932) included the genus *Zora* in his Liocraninae (!), and ignored the upgraded family rank of Zoridae which was proposed already by DAHL in 1912. Zoridae has been more in use than Cybaeodinae, but – if Zoridae would be shown as NOT related to the remaining taxa in question (being and independent family) – the family name Cybaeodidae has to replace the name Liocranidae, although – in a paper on *Cybaeodes* – PLATNICK & DI FRANCO (1992) inconsequently used the name Liocranidae.

(**) The change of a common family name in spiders happens rarely today; two recent examples are the change of Cybaeidae to Argyronetidae (questionable) and of Heteropodidae (Eusparassidae) to Sparassidae. Controversely discussed are the names Anapidae and/or Symphytognathidae if this taxon is used in a wide sense.

Taxonomy (questionable taxa/subfamilies see below): Limits and **diagnosis** of the Zoridae s. l. are not sure (*); this family can best be characterized by a combination of typical characters: A narrow anterior part of the prosoma with usually a narrow field of the eyes (figs. 24–26), a finely furrowed (never scaly or distinctly corniculate) prosomal cuticula, a short labium, and most often relatively short gnathocoxae (they are not depressed ventrally) (fig. 33), as well as long paired and overlapping ventral bristles of the anterior tibiae (similar to fig. 34) (**), patellar bristles are usually reduced or absent (at least on I–II, see *Succinomus* n. gen.); a colulus is either strongly reduced/ absent or wide and flat (not “fleshly”, see *Liocranum variabilis* n. sp., fig. 45b).

(*) The diagnoses and the limits – in a strict or in a wide sense – of several other spider (sub-) families are insufficient/subjective, too; examples are the Amaurobiidae (limits?), Dictynidae (incl. Copaldictyninae and Hahniinae?), Malkaridae (?= subfamily of the Mimetidae?), Micropholcommatidae (?= subfamily of the Anapidae?), Miturgidae auct. (apparently not monophyletic), Pisauridae (including the extinct Insecutoridae?), Sicariidae (including the Loxoscelidae?), Synotaxidae (monophyletic?), and Zodariidae (limits?).

(**) More weak and only slightly overlapping bristles exist e. g. in *Cybaeodes* and in male *Liocranum variablis* n. sp.. – Long ventral bristles occur in numerous genera of related and non-related families, too, but are absent in the Nearctic genus *Hesperocranum* UBICK & PLATNICK 1991, see below (j); see also *Macedoniella* DRENSKY 1935 below.

Further characters and variability (see also below) of selected structures; evolutionary "trends": Ecribellate, unpaired tarsal claw absent, clypeus usually short (long in *Cryptoplanus*), posterior eye row procurved (e.g. in *Agroeca, Scotina*, fig. 48), straight or slightly recurved (e. g. in *Cybaeodes*, fig. 32 and *Succinomus*) to distinctly or strongly recurved (e. g. in *Apostenus* and *Zora*, figs. 24–26), anterior median eyes usually being the smallest (figs. 26, 48, 49), posterior median eyes usually circular (but see below, e), labium usually not longer than wide, praecoxal triangles of the sternum (arrow in fig. 33) exist in *Cybaeodes* and the Liocranini (see below, g), intracoxal triangles are well developed in *Zora*; legs: IV most often longest, but I and IV almost equal in length e. g. in *Liocranum variabilis* n. sp., or I even longer than IV in *Succinomus* n. gen., mediograde in Apostenini, Liocranini, and probably in *Succinomus*, trochantera not or only fairly notched, tarsi with two irregular rows of trichobothria, at least the posterior tarsi may be more or less distinctly pseudosegmented (more distinct in the males), leg scopulae usually absent or indistinct, see below (j); spatulate hairs of the claw tufts most often present (absent e. g. in the Liocranini, see below, (f); feathery hairs: See below, (i); opisthosoma: scuta usually absent (a small dorsal-basal leathery structure exists e.g. in the male of *Cryptoplanus*, *Sagana rutilans,* and probably in *Succinomus duomammillae*), anterior spinnerets usually short/stout and conical (but sexually dimorph in *Cybaeodes*, fig. 35 and probably in *Succinomus*, fig. 51 in which only the anterior spinnerets are well developed in the male sex), enlarged piriform gland spigots on these spinnerets are present in the Apostenini and in males of *Cybaeodes* (fig. 35), see below (d) (in the Gnaphosidae they exist in both sexes), female median spinnerets frequently (!) modified (see the tribus below), enlarged or depressed (e. g. fig. 36); embolus in most taxa abruptly bent in the distal half (not in Apostenini and Zorini, unknown in the Succinomini), epigyne most often anteriorly with a single or a pair of helm-shaped structure(s) (fig. 41) (not in *Agraecina*, Apostenini and Zorini). The colour of body and legs is most often brown but pale yellow in *Liocranus variabilis*, grey in *Cybaeodes* and light yellow with conspicuous dark patches/bands in *Zora*. A capture web is absent, the spiders are hunting and ground-dwelling animals usually of forests. – In the Apostenini and in the Zorini a "tendency" (disposition) to the evolution of ventral stridulatory bristles/spines on (a) the male opisthosoma (*) or on (b) the male coxae IV (*Zora* and *Zorapostenus*, fig. 29) (sexual dimorphism) exists. Such stridulatory bristles/spines exist in extant taxa of *Apostenus* and several species of *Agroeca*, one kind of them exists in all (!) known fossil zorid members, of *Apostenus*, *Palaeospinisoma* and *Zorapostenus*. (See below, a and b).

(*) See WUNDERLICH (2004: 1626, figs. 7, 12 p 1634–1635, photos 360–362). These bristles/spines probably play a role during courtship and may produce stridulatory vibrations when rubbed e. g. at dry leaves; I still do not know a single study of such a behaviour in these spiders. The spines on the male coxa IV of *Zora* and *Zorapostenus* (fig. 29) – which are situated in the basal half of the coxa – stand out from the article and have probably a stridulatory function, too. – "Tendency" in this sense means the disposition of the multiple convergent evolution of structures or behaviour – which have a similar function – in related taxa.

Remarks: In the newest edition of "Spider Families of the World" (2007) by JOCQUE & DIPPENAAR the subfamily Phrurolithinae is still included in their Liocranidae instead in the Corinnidae, the posterior median spinnerets are erroneously noted as generally flattened in the female sex as a diagnostic character of the Liocranidae, and the colulus is noted as present, "unpaired, with setae" although in fig. 54c a colulus is absent (actually the colulus is strongly reduced or even absent in – almost? – all taxa of this family).

Variability of certain structures and possible convergences within the Zoridae s. l.:

The taxonomical value of certain structures has largely been overestimated in my opinion, e. g. the position of the posterior eye row, see figs. 25–26 of two related ge-nera. The enormous variability of the spinnerets – their size, shape and spigots – within the Zoridae s. l. – down to the intraspecific sexual dimorph variability, see e.g. the genera *Cybaeodes* (figs. 35–36) and *Succinomus* – indicates not an important taxonomical value; they are simply quite variable. The well or weakly developed notches of the trochantera posses apparently also only a low taxonomical value at least in the family Zoridae. Feathery hairs exist in most European Zoridae (fig. 29a) but are absent in certain taxa like *Zora* as well in the Nearctic genus *Hesperocranum*, and probably in the fossil genus *Succinomus*. Their occurrence is quite variable within different families, see e. g. Agelenidae (they exist in *Tegenaria* LATREILLE 1804) and below. As an "old" apomorphic pattern of the Araneomorpha these hairs have been lost numerous times, see LEHTINEN (1967: 283, fig. 1), and apparently numerous reversals exist. The – probably low – suprageneric value of the "coxal window" is still unclear to me; see DEELEMAN-REINHOLD (2001: 401).

(a) Ventral male coxal IV bristles/spines seem to be extremely rare within the RTA-clade; they are known to me from *Zora* and similar in *Zorapostenus* (fig. 29). Based on a common "disposition" or not, this structure may have evolved two times independently within the Zoridae, and therefore I am quite unsure about close relationships of these genera in which (e. g.) the structures of sternum and male pedipalpus are quite different.

(b) Ventral stridulatory bristles/spines of the male opisthosoma in Zoridae s. l. are known from *Apostenus*, *Palaeospinisoma* – see WUNDERLICH (2004: Photos 363, 365) and some (!) species of *Agroeca.* Such bristles may have been evolved independently at least two times within *Agroeca*. But what about the absence of such bristles in *Agraecina*, *Liocranoeca* and *Scotina* which are usually regarded as well related? It seems not likely to me that the absence of such bristles within certain Zoridae is the result of several losses. – Such opisthosomal bristles evolved convergently several times within the family Lycosidae.

(c) Size and shape – especially of the anterior and median spinnerets – are quite variable within the Zoridae s. l., and frequently a sexual dimorphy exists, see e. g. *Cybaeodes*, the Liocranini, and the Succinomini (reduction in the ♂). Laterally flattened median spinnerets exist in the fossil genus *Zorapostenus* (in the males; females are unknown) as well as in females – not in males – of *Liocranum* and *Sagana* of the Liocranini and in the Cybaeodini. *Zorapostenus* is not regarded here as sister group to *Liocranum* + *Sagana*; in my opinion flattened median spinnerets developed convergently at least three times within the Zoridae. In *Mesiotelus* the median spinnerets are not flattened although the genus is considered as closely related to *Liocranum*, see e. g. BOSSELAERS & JOCQUE (2001: 256); in *Prochora* they are also not flattened.

(d) Is the existence of enlarged piriform gland spigots of the anterior spinnerets (fig. 35) a plesiomorphic character of the Zoridae s. l.?

(e) In *Cybaeodes* the lenses of the posterior median eyes are usually oval (fig. 32) (similar to Gnaphosidae), in constrast to other Liocranidae (but compare *Macedoniella* below); their oval shape is probably nothing else than the result of the reduction of the eye lenses in spiders of this genus.

(f) Spatulate hairs of the claw tufts (fig. 28a) exist in the Apostenini (few hairs; their number may have been reduced in this taxon), *Cybaeodes*, *Zora* and *Sagana* of the Liocranini (unknown in the Succinomini), and are frequent in taxa of related families. Such hairs evolved probably several times independently within the Zoridae s. l., but it seems not unlikely to me that they were lost two times: (1) In the ancestor of the Agroecini and (2) within the Liocranini: the ancestor of *Liocranum* + *Mesiotelus*.

(g) Praecoxal sternal triangles (fig. 33) exist in *Cybaeodes* and the Liocranini; they are also known from the Nearctic genus *Hesperocranum* UBICK & PLATNICK 1991 (as well as from *Argistes* SIMON 1897 – Sri Lanka – which is probably not related).

(h) A mediograde leg position and a fairly flattened body exist in the fossil taxa in Baltic amber (indistinct in *Cryptoplanus* which relationships are unsure), and in several extant taxa of the Liocranini.

(i) I found feathery leg hairs (fig. 29a; not all genera were studied) in *Agroeca, Cybaeolus, Liocranum, Mesiotelus*, *Sagana* and *Zorapostenus* but not in *Zora,* and probably they do not exist in *Succinomus*, too; their absence in the Nearctic genus *Hesperocranum* has been reported by UBICK & PLATNICK (1991);

(j) A dense and undivided scopula exists on metatarsi and tarsi in *Sagana rutilans*, a distinct and longitudinally divided scopula exist e. g. in females of *Liocranum* (it is weakly developed in males of this genus). According to their different shape these scopulae may have evolved convergently. (Small bristles – reminding of a pseudoscopula – exist on tibia, metatarsus and tarsus I–II in members of the Nearctic genus *Hesperocranum*, see UBICK & PLATNICK (1991)),

(k) A proventral-distal cymbial bristle (rarely two bristles) exist in *Cybaeus* and in the Liocranini (arrows in figs. 39, 45) but is absent in the remaining European taxa of the Zoridae s. l.. A retrolateral cymbial groove exists in some genera, e.g. fig. 31a) a furrow exists in *Prochora*.

(l) The number of the paired ventral bristles of tibia and metatarsus I–II (fig. 50) may be intrageneric and even intraspecific distinctly variabel, e. g. in *Agraecina* and *Liocranoeca*, see the keys.

Relationships of the Zoridae s. l. (see also Zorini below): The related family Clubionidae – probably the sister group to Zoridae – possesses also a furrowed prosomal cuticula, but they are pale spiders (most often exist an almost white opisthosoma which is rare in the Zoridae, similar e. g. in *Cybaeodes* and in *Zora* which possesses dark markings; their legs are not darkened or annulated in contrast to several Zoridae), possess a wide clypeus, a wide eye field (not in most Systariinae with the exception of *Systaria drassiformis* SIMON 1897, the generotype(!)), as well as a long labium and long gnathocoxae which are usually distinctly widened distally and inclined laterally. To my knowledge ventral stridulatory bristles/spines are absent in all members of the Clubionidae and related families (I know solely retroventral – not ventral! – spines on the male trochanter I in *Clubiona inquilina* DEELEMAN-REINHOLD 2001, Clubionidae, and a ventral opisthosomal brush of hairs (!) in *Otacilia parva* DEELEMAN-REINHOLD 2001 (Corinnidae: Phrurolithinae). (Ventral OPISTHOSOMAL bristles evolved convergently in certain taxa of the non-related Lycosidae, e. g. in several groups of *Pardosa* C. L. KOCH 1847). – Members of the family Corinnidae possess a scaly or corniculate prosomal cuticula and – usually – opisthosomal scuta in contrast to the Zoridae (and to almost all members of the Clubionidae). Furthermore the Corinnidae are frequently ant-shaped (such spiders have usually a slender body, a saddle-shaped opisthosomal inclination, iridescent hairs, and light dorsal opisthosomal spots), members of several taxa possess a long clypeus, large to powerful basal cheliceral articles, oval posterior median eyes, ventral depressions of the gnathocoxae, and a well developed colulus (Castianeirinae). Ventral stridulatory bristles/spines in Corinnidae are unknown to me. – In contrast to most Zoridae (but see *Liocranum variabilis*, fig. 42!) are the basal cheliceral articles – at least in the male sex – enlarged in most Corinnidae and protruding in most Clubionidae.

A well developed colulus exists at least in the Corinnidae: Castianeirinae like in certain Clubionidae (not e. g. in Cheiracanthinae WAGNER 1888 (= Eutichurinae LEHTINEN 1967). Spatulate hairs of the claw tufts and distinctly sexually dimorphic developed spinnerets are not rare in members of the three families. – Miturgidae are larger spiders which possess a body length of 5–28 mm; the shape of their prosoma, their spinnerets and spigots are different. – In summary: Mainly the narrow eye field, as well as – usually – the not protruding mouth parts of the Liocranidae are different from the Clubionidae, and mainly the structure of the furrowed cuticula and the non-armoured opisthosoma are different to the Corinnidae which furthermore frequently are ant-shaped.

Remark on the prey in fossils: According to the fossil material in Baltic amber (CJW; paper in prep.) certain members of the Zoridae were hunters of ants.

Distribution of the Zoridae s. l.: Cosmopolitical; most taxa occur apparently in the Northern Hemisphere, the Holarctic Region; probably occur most of the true zorid genera in the mediterranean area. In Eocene European amber forests existed more than half a dozen genera (CJW) of which only four or five are described up to now. DEELEMAN-REINHOLD (2001: 399) placed the SE-Asian genera *Argistes* and *Paratus* – in respect to the absence of a “retrocoxal window” – only with hesitation in her Liocraninae.

List of the extant and fossil European Zoridae s. l. in alphabetic order of the tribes:

Remark: In his catalogue of Araneae – Advances in Spider Taxonomy 1992–1995 – PLATNICK (1998: 698, 699) trasferred – apparently based on spinneret spigots solely – the genera *Liophrurillus* WUNDERLICH 1992 and *Phrurolinillus* WUNDERLICH 1995 from the family Corinnidae – where they were originally placed well founded – erroneously (?) and in my opinion incorrectly to the Liocranidae (Zoridae).

(1) Agroecini **n. trib**.: *Agroeca* WESTRING 1861, *Agraecina* SIMON 1932 (= *Lascona* GEORGESCU 1989), *Liocranoeca* WUNDERLICH 1999 (*striata*), and probably *Scotina* MENGE 1873.

(2) Apostenini **n. trib**.: *Apostenus* WESTRING 1851 (fossil and extant), *Palaeospinisoma* WUNDERLICH 2004 (extinct), and – most probably – *Zorapostenus* **n. gen.** (extinct).

(3) Cybaeodini SIMON 1893: *Cybaeodes* SIMON 1878 (= *Cerrutia* ROEWER 1960).

(4) Liocranini SIMON 1897: *Liocranum* L. KOCH 1866, *Mesiotelus* SIMON 1897, and *Sagana* THORELL 1875 (**gen. restit**.) (*rutilans*).

(5) Succinomini **n. trib**.: *Succinomus* **n. gen**. (*duomammillae* **n. sp**.).

(6) Zorini F. O. PICKARD-CAMBRIDGE 1893: *Zora* C. L. KOCH 1847 (**rev. relat**.).

(7) Dubious taxa of the Zoridae s. l.: *Macedoniella* DRENSKY 1935 (*karamani* DRENSKI), *Cryptoplanus* PETRUNKEVITCH 1958, and *Prochora* SIMON 1885 see below.

Intrafamiliar pattern, subfamilies, tribes, and on the genera *Macedoniella* (no. 7), *Prochora* (no. 7) and *Sagana* (Liocranini, under no. 4):

Remarks: (a) I focus here on the type genera of the suprageneric taxa which all are known from Europe. – (b) *Cybaeodes* and *Zora* have been regarded as related to – or even members of five – (!) different families of spiders, and the family Liocranidae in the current Araneae catalogue of PLATNICK may be only an assembly of (partly) non-related taxa, such genera which fit not well in Clubionidae, Corinnidae and Miturgidae. – (c) I am still unable (1) to present a plausible cladogram and (2) to unite the tribes with certainty to subfamilies, but I suppose – according to the distinctly recurved position of their posterior eye row (fig. 24–26), their spatulate hairs of the claw tufts, and their ventral stridulatory structures (fig. 28; WUNDERLICH (2004: Figs. 362–263)) – that Apostenini and Zorini may probably be regarded as members of a monophyletic taxon, Zorinae (but I do not want to exclude that Apostenini may be related to the Agroecini), and – according to their praecoxal sternal triangles (arrow in fig. 33) as well as their cymbial bristle – Cybaeodini and Liocranini MAY BE considered as members of a second monophyletic taxon, Cybaeodinae (= Liocraninae). Close relationships of the Agroecini remains unclear; I do not want to exclude that it may be part of the Cybaeodinae or be regarded as a third subfamily.

Most extant European genera are treated by GRIMM (1986) (with few exceptions like *Cybaeodes*, *Mesiotelus* and *Prochora*); *Agroeca striata* KULCZYNSKI has been transferred from *Agraecina* to *Liocranoeca* WUNDERLICH 1999, and *Sagana* THORELL (gen. resurr.) is split off here again from *Liocranum* L. KOCH, see below. The five Nearctic genera are shortly treated by UBICK et al. (2006: 162–163); two of these – *Hesperocranum* and *Neoanagraphis* – are absent from Europe, *Apostenus, Agroeca*, and *Liocranoece* are shared with Europe.

(1) Agroecini **n. trib**., type genus *Agroeca* WESTRING 1861, further genera *Agraecina, Liocranoeca* and probably *Scotina*. Diagnosis: Leg position prograde, posterior eye row almost straight (e. g. as in fig. 48); absent are spatulate hairs under the tarsal claws (few thin hairs are present), enlarged piriform gland spigots of the anterior spinnerets, and praecoxal sternal triangles; ventral stridulatory bristles/spines of the male opisthosoma exist in certain species of *Agroeca* as in Apostenini. – The relationships are unsure; in the Apostenini – which may be most related according to their ventral bristles on the ♂-opisthosoma – and in the Zorini the posterior eye row is distinctly to strongly recurved and spatulate hairs of the claw tufts are present, in the Cybaeodini and the Liocranini praecoxal sternal triangles exist and the median spinnerets are modified in the female sex.

(2) Apostenini **n. trib.**, type genus *Apostenus* WESTRING 1851, further the genera *Palaeospinisoma* WUNDERLICH 2004 and most probably *Zorapostenus*, see below, Zorini. – Diagnosis: Apostenini posseses ventral stridulatory bristles/spines on the male opisthosoma – see WUNDERLICH (2004: Fig. 363) – or on the posterior coxae (*Zorapostenus*, fig. 29), in which ventral opisthosomal bristles are absent), enlarged piriform gland spigots of the anterior spinnerets, and only few spatulate hairs of the claw tufts. The posterior eye row is fairly to strongly recurved (figs. 25–26), their leg position is mediograde, the embolus is fairly stout, the epigyne has a pair of grooves, a helm-shaped structure is absent. – Relationships: Apostenini and Zorini may be most related.

(3) Cybaeodini SIMON 1893, type genus *Cybaeodes* SIMON 1878 (= *Cerrutia* ROEWER 1960) (figs. 32–41). – Diagnosis (based on *Cybaeodes*): Posterior median eyes oval (fig. 32) (unique within the Zoridae s. l.), male anterior spinnerets long, almost cylindrical, and bearing piriform gland spigots (fig. 35) in contrast to the sexual dimorph female anterior spinnerets (fig. 36) which are short, conical, and in which enlarged piri-

form gland spigots are absent. Furthermore characteristic are the sexually dimorphic median spinnerets, which are oval in the cross-section and widened apically in the female (fig. 36) but long, slender and not flattened in the male (fig. 35), the presence of spatulate hairs of the claw tufts and of feathery hairs, the existence of a prolateral/ventral cymbial bristle (fig. 39), the pale colour of body and legs, the small to tiny eyes (they are fairly large in *C. mallorcensis* n. sp., fig. 32), and the unpaired or paired, usually strongly sclerotized and helm-shaped anterior structure of the epigyne (fig. 41). – Relationships: *Cybaeodes* was originally assigned to the family Clubionidae s. l. by SIMON 1878, regarded as a member of the family Gnaphosidae by SIMON 1914, as a taxon of the "Zodarioidea" by LEHTINEN (1967: 292), but – well founded in my opinion – as a member of the Liocranidae (here = Zoridae s. l.) by PLATNICK & DI FRANCO (1992), and finally as related to Miturgidae and Ctenidae by DAVILA (2003). – According to the existence of praecoxal sternal triangles and a prolateral cymbial bristle Liocranini may be most related, see below. – *Andromma* SIMON 1893 may be not related to *Cybaeodes*, see JOCQUE & BOSSELAERS (2001), SIMON (1893) contra LEHTINEN (1967: 214). I disagree with the opinion of BOSSELAERS & JOCQUE (2002) that Cybaeodinae is the sister group to Castianeirinae, which I regard as a member of the Corinnidae, see WUNDERLICH (2004: 1638). – Praecoxal sternal triangles exist also in the genera *Hesperocranum* UBICK & PLATNICK 1991 (USA), which has a quite different chaetotaxy, and in *Argistes* SIMON 1897 (Liocranidae?) from Sri Lanka, which has very large anterior median eyes, see DEELEMAN-REINHOLD (2001: Fig. 634); the posterior median eyes are circular in these genera which close relationships are unsure.

(4) Liocranini SIMON 1897, type genus *Liocranum* L. KOCH 1866, further genera in Europe: *Mesiotelus* SIMON 1897 and *Sagana* THORELL 1875 (see below). – Diagnosis: Sternum provided with praecocal triangles (as in fig. 33), cymbium with a proventral bristle (arrow in fig. 45) and – except in *Mesiotelus* – are the median spinnerets sexually dimorphic distinctly flattened in the female sex. Leg scopulae are present, spatulate hairs of the claw tufts exist in *Sagana*; see below (the genus *Sagana*) and above (variability; sexual dimorphism in *Liocranum*). – Remark: There is an enormous variability of the body size in *Liocranum*, see below. – Relationships: According to the existence of praecoxal sternal triangles and a prolateral/ventral cymbial bristle (arrow in fig. 39) Cybaeodini may be most related. In the Cybaeodini the shape of the eyes and of the spinnerets are quite different.

Sagana THORELL 1875 (= *Drapeta* MENGE 1875) was regarded as a synonym of *Liocranum* L. KOCH 1866 by SIMON (1878). In the type species by monotypy – *Sagana rutilans* THORELL 1875 – the sternum bears praecoxal triangles (as in fig. 33) and the cymbium bears a single (rarely two) prolateral/ventral bristle(s) (similar to figs. 39 and 45) like *Liocranum* and *Mesiotelus*; tibiae I–II bear 6 pairs of ventral bristles, metatarsi I–II bear a singl pair. According to the dense and **UNDIVIDED** metatarsal and tarsal scopula in both sexes, the numerous spatulate hairs of the claw tufts, the more slender embolus, and the strongly pigmented body and legs – in contrast to *Liocranum* (and *Mesiotelus*) – I regard *Sagana* as a genus of its own (**gen. restit**.); see the remark of BERTKAU (1880: 276). – Remark: In a questionable specimens of *Liocranum* (CJW) I found a distinct tarsal and metatarsal scopula which is clearly divided longitudinally in contrast to *Sagana*. See the key below, no. (1),
(5) Succinomini **n. trib**., only *Succinomus* in Baltic amber (♀ unknown). – Diagnosis:

Leg I longest, only the anterior spinnerets are well developed (fig. 51), articles of the ♂-pedipalpus very long and slender (fig. 52). – Further characters and the relationships – which are unsure – see below (description of the new tribus).

(6) Zorini F. O. PICKARD-CAMBRIDGE 1893, type genus *Zora* C. L. KOCH 1847. – Diagnosis (based on *Zora*): Posterior eye row strongly recurved (looking like three eye rows, fig. 24), a brush of ventral stridulatory bristles/spines of the male coxae IV exists (similar to fig. 29 but a single group only) as well as a ventral hair brush of the male anterior spinnerets (fig. 47) (which is absent in *Zorapostenus* which more likely is a member of the Apostenini, see above and below), numerous spatulate hairs of the claw tufts, and posterior intercoxal sternal triangles, epigyne a single groove, helm-shaped structe(s) absent, embolus long, fairly but not abruptly bent, median apophysis usually very long. – Further characters and remarks: Feathery and scale-shaped leg hairs, enlarged piriform gland spigots of the median and posterior spinnerets are absent, the tibial apophysis of the male pedipalpus is widened basally (similar to *Apostenus fuscus* and *Neoanagraphis* GERTSCH & MULAIK (1936)); a ventral hair brush of the male anterior spinnerets (fig. 47) exists apparently only in *Zora*, body and legs light coloured, having conspicuous dark patches. – Relationships: *Zora* C. L. KOCH 1847, the type genus of the family Zoridae, was included already by SIMON (1932) in his Liocraninae (within the Clubionidae s. l.), and considered as related to *Apostenus* WESTRING 1851. Ventral stridulatory bristles/spines exist in both taxa, but in the Apostenini occur ventral bristles/spines of the ♂-opisthosoma and A PAIR of grooves of the epigyne; intercoxal sternal triangles are absent. Other authors believed in relationships of *Zora* to Ctenidae, Lycosidae, Miturgidae or Zoropsidae.

I do not find weighty differences of *Zora* to the pattern of other taxa which are treated here; the colouration and the ventral hair brush of the anterior spinnerets in the male sex (fig. 47) are differing. A distinctly to strongly recurved posterior eye row (fig. 24) exist also within the tribus Apostenini, in *Apostenus*, *Palaeospinisoma* and especially in *Zorapostenus* (figs. 25–26), a tibial apophysis of the ♂-pedipalpus which is widened basally, exist in *Zora* and in *Apostenus fuscus* as well. Founded on these arguments – and based on the type genus – I propose here to regard the Zorini (**revid. relat**.) as related to the Liocranini and *Cybaeodes*, but most related to the Apostenini as already considered by SIMON (1937).

According to the coxal stridulatory bristles/spines (fig. 29) and the position of the eyes (figs. 24, 26) the Eocene genus *Zorapostenus* n. gen. is similar to *Zora*, but its leg position is mediograde, its sternum is different, its median spinnerets are flattened laterally, there are only few spatulate hairs of the claw tufts, and the tegulum is strongly protruding basally. According to these characters *Zorapostenus* may be more likely a member of the Apostenini (and the coxal bristles evolved convergently to *Zora*), although ventral opisthosomal bristles/spines are absent in *Zorapostenus*. – Extant genera which are probably related to *Zora* are listed in the book of JOCQUE & DIPPENAAR-SCHOEMAN (2006: 270); according to R. RAVEN (person. commun. in XI 2006) in Australia exist genera which may be related to *Zora*.

(7) Remarks on two dubious genera:

(a) *Macedoniella* DRENSKY 1935 from Macedonia (♂ unknown), type species by monotypy: *Macedoniella karamani* DRENSKY 1935: Measurements unknown, paired ventral tibial and metatarsal bristles of the legs I–II are absent according to DRENSKY, the four eyes of the posterior row are oval, the female anterior spinnerets are long and almost oval, the shape of labium and gnathocoxae is unknown. DRENSKY compared *Macedoniella* with *Cybaeodes* SIMON, but the chaetotaxy and the female median spinnerets are quite different to members of this genus. Were legs and spinnerets really correctly described and figured by DRENSKY? I regard even the family relationships of this genus as unsure (Gnaphosidae?).

(b) *Prochora* SIMON 1885 from Sicily and Israel has been regarded as a member of the Liocraninae by SIMON (1887), and was transferred to the Miturgidae by LEHTINEN (1967: 260). During the print of this volume I got the loan of a pair of *P. lycosiformis* (O. P.-C. 1872) from G. LEVY (Jerusalem). According mainly to the helm-shaped anterior structure of the epigyne, the structures of the male pedipalpus, and the leg spination I regard *Prochora* as a member of the Zoridae s. l., due to the absence of a gnathocoxal serrula and a long distinct retrolateral furrow of the cymbium *Prochora* is the member of an undescribed tribus which is related to the Agroecini, no. 3 in the tab. below.

Key to the extant and fossil European genera of the family Zoridae s. l.:
and taxonomical remarks on the extinct genera *Succinomus* and *Cryptoplanus* (b, c)

Remarks: **(a)** The dubious genera *Macedoniella* and *Prochora* (see above of this key) are not included. – **(b)** The single male of the extinct genus *Succinomus* (figs. 49–54) is only incompletely preserved, therefore it is not included in the key. *Succinoma* possesses certain unique intrafamiliar generic characters: Only the anterior spinnerets are well developed at least in the male sex (fig. 51), the anterior leg is longer than the posterior leg, the pedipalpal articles are very long, and a prolateral pedipalpal tibial apophysis exists (fig. 52). – **(c)** The extinct genus *Cryptoplanus* PETRUNKEVITCH 1958 has been regarded with hesitation as a member of the family Corinnidae by WUNDERLICH (2004: 1659) but – in contrast to the Corinnidae – a dorsal opisthosomal scutum may be indistinct or even absent in this genus, and the prosomal cuticula is smooth or almost smooth. Therefore I include now *Cryptoplanus* with some hesitation in the Zoridae. Special characters of *Cryptoplanus* are: Leg III about as long as I and II, clypeus longer than the field of the median eyes, pedipalpal tibia with a large apophysis which stands widely out, cymbium with spines, a basal outgrowth and a retrobasal depression. – **(d)** The genera *Agraecina, Cybaeodes* and *Mesiotelus* are known from S-Europe but they do not occur in Central or North Europe. – **(e)** A mediograde leg position exists in *Sagana* (1), *Liocranum, Mesiotelus* (2), in the tribus Apostenini (4); not in *Zora*, probably in *Cryptoplanus*, and apparently in *Succinomus*. – **(f)** Ventral bristles on the male opisthosoma exist in most members of the tribus Apostenini (no. 4) (not in *Zorapostenus*) and in some species of *Agroeca* (no. 3). – **(g)** The extinct genera in Baltic amber – with the exception of *Succinomus* – are listed within no. 4 together with the extant genus *Zora*; members of *Apostenus* are known from Baltic amber and extant as well.

	spatulate (*) hairs under the tarsal claws, cymbium with a proventral bristle, fig. 39		thin hairs under the tarsal claws	
	praecoxal sternal triangles present arrow in fig. 33 (**)	praecoxal sternal triangles absent	praecoxal sternal triangles present arrow in fig. 33	praecoxal triangles absent
posterior eye row slightly procurved or slightly re-curved (fig. 32)	(1) *Cybaeodes* *Sagana*	*Cryptoplanus?*	(2) *Liocranum* *Mesiotelus*	(3) *Agraecina* *Agroeca* *Liocranoeca* *Scotina*
posterior eye row distinctly to very strongly recurved (figs. 24-26)		(4) *Apostenus* *Palaeospinisoma* *Zorapostenus* *Zora*		

(*) See fig. 28a).

(**) They may be indistinct in juvenile, small and weakly sclerotized spiders.

(1)

Posterior median eyes oval (fig. 32) (unique in European Zoridae), eyes most often tiny to small; gnathocoxae without depression (in contrast to members of the Gnaphosidae), metatarsi and tarsi bear only a weak scopula, spinnerets strongly sexual-dimorph as in the figs. 35–36, anteriors in the male long and almost cylindrical, medians in the female enlarged apically. Pale spiders . . . . Cybaeodes

- Posterior median eyes circular, eyes not reduced, metatarsi and tarsi with dense, undivided scopula (a scopula which is distinctly divided longitudinally exist in at least one species of *Liocranum* of the Mediterranean), spinnerets different, the medians flattened medially. Spiders medium to dark brown. *S. rutilans*, see above . . . . . . Sagana

(2)

Tibia I bears usually 4–11 pairs of ventral bristles; ♀: Median spinnerets strongly flattened laterally (as in *Sagana*) . . . . .Liocranum

- Tibia I bears usually 2 pairs of ventral bristles; ♀: Median spinnerets not or only slightly flattened. . . . . <u>*Mesiotelus*</u>

(3)

1 Smallest European Zoridae, body length usually 2.0– 3.5 mm (♀). Distance between the posterior median eyes larger than to the lateral eyes (fig. 48) . . . . <u>*Scotina*</u>

- Body length usually > 3.5mm. Eyes of the posterior row aequidistant 2

2(1) Metatarsi I–II bear usually 3 (rarely 2) pairs of ventral bristles. The ♂-opisthosoma of certain species bears ventral bristles/spines. Tegulum with longitudinally folds, median apophysis with a long and slender distal half which tip points medially, epigyne with a pair of strongly sclerotized introducing openings and a large v-shaped medial field . . . . <u>*Agroeca*</u>

- Metatarsi I–II bear usually 2 (rarely 3) pairs of ventral bristles. Ventral bristles/spines of the ♂-opisthosoma absent. Tegulum without folds, median apophysis and epigyne different 3

3(2) ♂: Median apophysis very long, bulbus with an additional long and thin tegular apophysis. ♀: Epigyne with a median septum, without helm-shaped anterior structure. Southern Europe. *A. lineata* . . . . <u>*Agraecina*</u>

- ♂: Median apophysis stout, additional spine-shaped tegular apophysis absent. ♀: Epigyne with a shallow median furrow and an anterior helm-shaped structure. *L. striata* . . . . <u>*Liocranoeca*</u>

(4)

<u>Remarks</u>: *Apostenus* is the only genus of the family Zoridae which is known extant and fossil in Baltic amber as well. *Palaespinisoma* and *Zorapostenus* are extinct genera in Baltic amber; their females are unknown. Two other extinct genera – *Cryptoplanus* and *Succinomus* – are treated above, see the remarks (b) and (c) above the key.

1 Mainly light coloured spiders which bear conspicuous black patches/stripes on body (fig. 1) and legs. Sternal praecoxal triangles present between coxae. ♂: Anterior spinnerets with a ventral brush of hairs (fig. 47); in most species bear the posterior coxae hairs/bristles similar to *Zorapostenus* (fig. 29). Extant . . . . <u>*Zora*</u>

- Spiders medium to dark brown (unknown in the fossils), without conspicuous black patches. Sternal praecoxal triangles absent. ♂: Hair brush of the anterior spinnerets absent, posterior coxae with bristles only in the extinct genus *Zorapostenus*. Extinct (Baltic amber) but *Apostenus* is known extant, too 2

2(1) ♂ (♀ unknown): The posterior coxae bear ventral stridulatory bristles/spines (fig. 29) similar to *Zora*; ventral opisthosomal bristles are absent. Femora III AND IV very thick (high) (fig. 28) . . . . *Zorapostenus*

- Bristles/spines of the posterior coxae absent, ventral opisthosomal bristles present, see WUNDERLICH (2004: Figs. 262–263). Femur III very thick in *Palaeospinisoma* 3

3(2) ♂ (♀ unknown): Femur III very thick (similar to fig. 28), posterior eye row strongly recurved, anterior median eyes probably absent. . . . . *Palaeospinisoma*

- Femur III (compared with the remaining femora) not thickened, posterior eye row fairly recurved (fig. 25), anterior median eyes well developed. . . . .*Apostenus*

DESCRIPTIONS OF NEW FOSSIL TAXA IN BALTIC AMBER:

(1) *Zorapostenus* n. gen. (figs. 26–31, photos 367–371)

Diagnosis (♂; ♀ unknown): Femora III and especially IV very thick (high) and laterally flattened (fig. 28), posterior eye row strongly recurved (fig. 26), coxae IV ventrally with – probably stridulatory – bristles/spines in two groups (fig. 29), pedipalpus (figs. 30–31a) with a basally strongly protruding tegulum and a long embolus.

Further characters: Prosoma fairly flattened, median spinnerets flattened laterally, leg position probably mediograde (photos).

Type species by monotypy: *Zorapostenus raveni* n. sp.

Relationships: According to the narrow anterior part of the prosoma, the long overlapping paired ventral bristles of the tibiae and metatarsi I–II, and the (questionable) stridulatory bristles/spines of the posterior coxae I regard *Zorapostenus* as a member of the family Zoridae; the median spinnerets are flattened laterally, the posterior eye row is strongly recurved. *Zorapostenus* is a “morphological connecting link” between two tribes or even subfamilies: It has a basally not widened ♂-pedipalpal tibial apophysis which is similar to *Apostenus* and related genera (“Liocraninae”), but on the other hand exist the coxal IV bristles/spines similar to *Zora* (“Zorinae”); the eye position is intermediate, similar recurved as in *Zora*, see figs. 24–26 and WUNDERLICH (2004: Figs. 3 and 11, p. 1633 and 1635). Concerning the fairly flattened prosoma, the only few spatulate hairs of the claw tufts, and the shape of the slender pedipalpal tibial apophysis I regard *Zorapostenus* as more related to *Apostenus,* and as a member of the Apostenini. In the type genus of the Zorini – *Zora* – the anterior prosomal part is still more narrow, the anterior median eyes are larger, the median spinnerets are not flattened, and the anterior spinnerets bear a ventral brush of hairs in the male sex. Because of so many differences in these genera I suppose that the coxal stridulatory bristles/spines evolved convergently in *Zora* and *Zorapostenus*, and both may be members of different tribes. – The depression of a retrobasal cymbial hump of *Zorapostenus* – in which the pedipalpal tibial apophysis may fit, see fig. 30 – is like in *Apostenus, Cybaeodes, Palaeospinisoma*, and in numerous related – and non-related – genera; it evolved apparently several times convergently, and this is surely not an important taxonomical character. The position of the strongly recurved posterior eye row of *Zorapostenus* is similar to *Palaeospinisoma* WUNDERLICH 2004 in Baltic amber, which is most probably six-eyed, and which may be related, but opisthosomal spines are absent in *Zorapostenus* and coxal bristles are present in contrast to *Palaeospinisoma*. Extremely thick femora III and/or IV are absent in most other Zoridae s. l.; *Palaeospinisoma,* which has strongly thickened femora III like *Zorapostenus* but contrarily to *Zorapostenus* thickened femora IV are absent.

Distribution: Eocene Baltic amber forest.

***Zorapostenus raveni* n. gen. n. sp**. (figs. 26–31, photos 367–371)

Derivatio nominis: The species is dedicated to ROBERT RAVEN in Brisbane, who published, e.g., on mygalomorph spiders and prepares a paper on Australian zorid spiders.

Material: 2♂ in Baltic amber; holotypus F1892/BB/AR/CJW; paratypus and 6 separated pieces of amber, F1906/BB/AR/CJW, GPIUH.

Preservation and syninclusions: Holotype: The spider is very well but incompletely preserved in a piece of amber which was slightly heated; the left legs I, III and IV are lost beyond their coxae by autotomy, prolateral parts of the left tibia and metatarsus I as well as dorsal parts of the right femur I (distally) and the right patella I (basally) are cut off, a bubble covers dorsally the right tibia and metatarsus IV, the dorsal-anterior part of the opisthosoma is darkened by heating (photo), a white emulsion is absent. – Syninclusions: An indistinct part of a dragline is running near to the right side of the spider's opisthosoma. Also preserved are some thin spider's threads, at least a single air-bag pollen grain, stellate hairs as well (not prey) remains of 5 Diptera, a tiny insect larva, an ant and a small juvenile spider. Two mms left of the spider the larva of a beetle is preserved, which is 3mm long and has a pair of probable bite marks at its end (photo) which are filled with the fossil resin. This larva may well have been a prey of the spider, lost within the fossil resin or just before the animals were captured. – Paratype: The spider is well preserved in a piece of amber which was heated, the body is darkened, the right leg IV is missing beyond the coxa by autotomy. – Syninclusions are a juvenile spider, 2 Diptera and stellate hairs.

Diagnosis (♂; ♀ unknown): Pedipalpus as in figs. 30–31; see the diagnosis of the genus.

Description (♂):
Measurements (in mm): Holotype/paratype: Body length 3.1/3.1, prosoma: Length 1.45/1.4, width 1.15/1.2; leg I: Femur ca. 1.1 (hight 0.4)/1.2, patella 0.48, tibia 1.0/1.1, metatarsus > 0.6, tarsus 0.55, tibia II 0.85, tibia III 0.7, leg IV: Femur 1.3 (hight 0.65), tibia 1.1.
Colour: Body and legs dark brown, opisthosoma light brown.
Cuticula not scaly; prosoma almost smooth, legs finely furrowed.
Prosoma (photos, fig. 26) flattened, 1.26 times longer than wide, covered with indistinct hairs. Thoracal fissure distinct. 8 eyes, anterior medians smallest, posterior laterals largest, posterior medians separated by slightly more than their diameter, posterior row strongly recurved. Clypeus as long as the diameter of an anterior median eye. Basal cheliceral article fairly stout, bearing a small condylus, teeth of their furrow unknown (hidden), fangs long and slender, labium free, as long as wide, gnathocoxae long, serrula present, a depression is absent, sternum small prolongated between the posterior coxae, intercoxal and praecoxal triangles are absent. – Legs (photos, figs. 27–29a) fairly slender, apparently mediograde, order IV/I/II/III (II and III may be equal in length), with feathery hairs (fig. 29a), femora III and especially IV strongly thickened (see the measurements above, compare I and IV). Bristles long on femora, tibiae (overlapping) and metatarsi; femora dorsally 1/1 or 1/1/1, I additionally with a prolateral one in the middle, patellae dorsally 1/1 (thin), tibia I–II 5 ventral pairs, metatarsi I–II 2 ventral pairs; tibia III bears 2 dorsal bristles, tibia IV bears at least 2 ventral pairs, 2 prolaterally and 1 dorsally. The tarsi bear several trichobothria in 2 irregular rows. Scopulae and dense claw tufts are absent, the claw tufts consists of only about 3 pairs of spatulate hairs. Metatarsus III without apical cleaning hair brush but with an apical ring of about 5 strong bristles. The paired tarsal claws bear long teeth. Coxae not notched. The coxae IV (photo, fig. 29) bear ventral stridulatory bristles/spines in two groups of about a dozen each in the holotype, ca 18/13 in the paratype; the basal group consists of short spines which stand more out from the article, the distal group is bristle-shaped. – Opisthosoma (photo) 1.7 times longer than wide, soft, covered with shorter hairs, dorsally with 3 pairs of small sigillae; spinnerets stout, partly hidden, the medians flattened, colulus hidden or absent. – Pedipalpus (figs. 30–31): Femur straight and fairly slender, patella short, tibia also short, bearing at least 4 trichobothria, some strong hairs and a slender retroapical apophysis. Cymbium with a retrobasal hump which bears a shallow depression, scopulate distally; tegulum retrobasally protruding, median apophysis fairly small, conductor probably bipartite, embolus long and bent.

Relationships: See above.

Distribution: Eocene Baltic amber forest.

(2) SUCCINOMINI n. trib.

Diagnosis (♂; ♀ unknown): Only the anterior pair of spinnerets is well developed (photo 374, fig. 51), anterior legs longer than posterior legs, pedipalpus (photo 375, figs. 52–54) with very long articles (the femur almost as long as the prosoma), tibia with a dorsal, a retrolateral and a prolateral (!) apophysis.

Further characters: Prosoma wide and flat, its cuticula apparently furrowed, shape of the posterior median eyes circular (photo 373, fig. 49), posterior eye row fairly recurved, basal cheliceral articles in a vertical position, leg scopulae absent, tibiae and metatarsi I–II with long ventral bristles (fig. 50), feathery and scale-shaped hairs are most probably absent, opisthosoma dorsally probably leathery, colulus and enlarged piriform gland spigots absent (fig. 51).

Close **relationships** are unknown to me. According to the combination of characters – the furrowed prosomal cuticula, the low caput, the relatively narrow field of the eyes, the circular shape of the posterior median eyes, the shape of the slender basal cheliceral articles which are not protruding, the long paired ventral bristles of tibia and metetarsus I–II as well as the absence of a (distinct) dorsal opisthosomal scutum – I regard the Succinomini as a taxon of the Zoridae s. l.. In contrast to most Zoridae the anterior legs are longer than the posterior legs, the ♂-spinnerets – except the anteriors – are strongly reduced, and the pedipalpal articles are distinctly elongated.
Remark: The posterior – and probably median – spinnerets are reduced in a similar way in the extinct genus *Ablator* PETRUNKEVITCH (family Corinnidae) in Baltic amber, see above and WUNDERLICH (2004). Both genera are surely not confamiliar, and I consider the reduction of the spinnerets as a case of convergence. A female of *Ablator* in Baltic amber – unpublished, F1839/CJW – possesses three pairs of spinnerets which are not reduced in contrast to the male sex. I do not want to exclude that in the unknown female of *Succinomus* the spinnerets are also not reduced in contrast to the condition in the male sex; this would be a further case of sexual dimorphism within the Zoridae.

Type genus (by monotypy): *Succinomus* n. gen.

Distribution: Eocene Baltic amber forest.

***Succinomus* n. gen.** (figs. 49–54, photos 372–375)

The gender of the name is masculine.

Diagnosis, **relationships** and **distribution**: See above.

Type species (by monotypy): *Succinomus duomammillae* n. sp.

***Succinomus duomammillae* n. gen. n. sp.** (fig.s 49–54, photos 372–375)

Material: Holotypus ♂ in Eocene Baltic amber and two separated pieces of amber, F2046/BB/AR/CJW.

Preservation and syninclusions: The spider is incompletely preserved in a piece of amber which was heated, some leg articles are darkened; a white emulsion covers ventral parts of the spider; the dorsal side is partly hidden by a layer within the amber; most distal articles of the legs and most parts of the left pedipalpus are cut off, the ventral side of both bulbi is directed to the spider's body and therefore hidden, the ventral side of the opisthosoma is strongly depressed and bears a smaller bubble; a large ventral bubble – originating probably from decomposing gas – is comming out from the body and is partly cut off, see the photo. Remains of a Diptera are situated right below the spiders body. A tiny mite and remains of a questionable Collembola as well as different kinds of pollen grains – including air-bags – are preserved in the larger separated piece of amber, a ballet of questionable insect's excrement is preserved in the smaller piece of amber; stellate hairs are absent.

Diagnosis (♂; ♀ unknown): See above.

Description (♂):
Measurements (in mm): Body length 2.9, prosoma: Length ~1.2, width ~1.1, tibia I ~1.75, tibia III 1.0; leg IV: Tibia 1.3, metatarsus 1.6, tarsus ~ 0.8; length of a basal cheliceral article 0.6; pedipalpus: Femur 1.1, patella 0.7, tibia without apophyses 0.37, cymbium ~0.55.
Colour mainly light brown, some leg articles are darkened by heating.
Prosoma (fig. 49) flat, not much longer than wide, cuticula almost smooth, hairs indistinct, feathery hairs apparently absent, area of the fovea hidden, eyes in two rows, posterior row fairly recurved, anterior median eyes smallest, posterior median eyes circular, separated by almost their radius. Clypeus fairly short, basal cheliceral articles slender, distally with few plumose hairs, teeth of the furrow and fangs are hidden. Labium, gnathocoxae and most parts of the sternum are also hidden, praecoxal triangles are absent. – Legs long and slender, their position probably mediograde, I longest, III distinctly the shortest, metatarsus IV longer than tibia IV, hairs indistinct, plumose and feathery hairs are apparently absent, preening bristles of metatasus III–IV are also absent. The trochantera are not notched, the tarsi are probably pseudosegmented. Bristles: At least some of the femora bear a dorsal one in the distal half, at least IV bears some shorter distal bristles, prolateral bristles on femur I are absent. A stronger dorsal-basal bristle exist at least on patella IV, tibiae I and II bear 4 pairs of long ventral bristles (fig. 50) as well as a thin dorsal-basal one but none laterally, tibiae III–IV

bear several ventral and lateral bristles. Metatarsi I–II are incompletely preserved; they bear at least 2 (probably 3 or 4) pairs of ventral bristles. Scopulae are absent. The trichobothria are apparently indistinct, tarsal trichobothria and tarsal claws are unknown. – Opisthosoma (photo, fig. 51) deformed (artificially dorsoventrally depressed), oval, probably flattened originally, apparently soft but probably hardened dorsally (mainly medially) in the anterior half; the hairs are very short, the epigaster is hidden, ventral stridulatory spines and a colulus are absent. Spinnerets – most probably sexually dimorphic – strongly reduced: Only the anteriors are well developed, stout and with a short apical article which bears short spinules but no enlarged piriform gland spigots; remains of small posterior spinnerets are recognizable, the median spinnerets – if existing – are hidden. – Pedipalpus (figs. 52–54; both bulbi are bent to the spider's body and are hidden): Articles slender and very long, femur spiny, tibia dorsally-basally with a bent bristle and a prolateral, a dorsal as well as a retrolateral apophysis; the dorsal apophysis is partly hidden by an emulsion; cymbium (it is partly hidden) most probably without a prolateral bristle, bulbus prominent, with two tegular sclerites (the median apophysis and the questionable conductor) which stand widely out from the tegulum; embolus long, recognizable at the retrolateral margin of the cymbium, and probably originating in a basal position.

Relationships and **distribution**: See above.

Description of new European extant species and remarks on the synonymy:

(1) *Cybaeodes* SIMON 1878

See the tribus Cybaeodini above. Members of *Cybaeodes* are pale spiders and have usually tiny or small eyes, the posterior medians are oval (fig. 32), but the species which is described below has relatively large eyes. The spiders of this mediterranean genus are usually epigean spiders, some are cavernicolous, several species of this genus are apparently island endemics, known e. g. from Mallorca, Sardinia and Sicily.
See *Macedoniella* p. 496.

***Cybaeodes mallorcensis* n. sp.** (figs. 33–41)

Material: 2♂1♀ Spain, Mallorca; holotypus ♂ South of the Lake Cuba, under a stone, JW leg. in VIII, CJW; 1♀ paratypus, Valdemossa, JW leg. in VII, CJW; 1♂ paratype near Soller, at the mountain L'Ofre, JW leg. in V, CJW.

Diagnosis: Eyes (fig. 32) fairly large, shape of the posterior medians distinctly oval, tibia I–II bears 4 pairs of ventral bristles (fig. 34). ♂-pedipalpus: Figs. 38–40, epigyne (fig. 41) anteriorly with a single sclerotized helm-shaped structure.

Description:

Measurements (in mm): Body length ♂ 3–4, ♀ 4.5, prosoma: Length ♂ 1.5–1.8, ♀ 1.8, width 1.2–1.3; leg I (♂): Femur 1.7, patella 0.95, tibia 1.55, metatarsus 1.4, tarsus 1.0, tibia IV 1.5, metatarsus IV 1.8; ♀: Tibia I 1.25, tibia IV 1.3, diameter of the posterior median eyes ~0.07.

Colour: Prosoma and legs light brown, opisthosoma light yellow grey.

Prosoma (figs. 32–33) fairly slender, thoracal fissure distinct, eyes fairly large, field narrow, posterior row slightly recurved, posterior median eyes oval, chelicerae fairly large, slender and protruding, fangs slender, anterior margin of the furrow with 3 large, posterior margin with 2 small teeth. Labium free, slightly longer than wide, gnathocoxae fairly converging, serrula present, sternum not elongated between the coxae IV, with praecoxal triangles. – The ♀-pedipalpus bears a slender and tooth-less claw. – Legs fairly long and slender, IV longest, III relatively long, I in the male with long ventral hairs, bristles long and numerous, absent on patellae, tibiae I–II with 4 ventral pairs, metatarsi I–II with a single ventral pair in the basal half, tarsi III–IV with a ventral-distal brush of cleening hairs, tibiae with 2 long and some short trichobothria, metatarsi with 2 irregular rows of partly long trichobothria. Feathery hairs present, metatarsi and tarsi I–II bear a quite weak scopula; a tarsal pseudosegmentation is absent. Tarsal claws toothed, the claw tufts consist of few (more than two pairs) spatulate hairs. – Opisthosoma slender, covered with hairs of medium length. Male genital area (fig. 37) anteriorly slightly sclerotized, bearing a single pair of widely spaced epiandrous gland spigots. Spinnerets (figs. 35–36) with enlarged piriform gland spigots on medians and posteriors, strongly sexual-dimorph; ♀: Anteriors short and conical, medians slightly flattened, short, distinctly widened apically and bearing 4 pairs of enlarged priform gland spigots; ♂: Anteriors long and almost cylindrical, bearing 5 enlarged spigots medians slender, not flattened or widened. – ♂-pedipalpus (figs. 38–41): Patella short, tibia longer than wide, with a retroventral outgrowth (hump), a retrolateral apophysis and numerous dorsal trichobothria, cymbium with 5 bristles (one in a proventral-distal position), distally fairly scopulate; median apophysis fairly long, embolus long, with a basal claw-shaped hook, strongly bent in the distal part and directed medially. – Epigyne/vulva (fig. 41) anteriorly with a sclerotized helm-shaped structure; receptacula seminis small and globular, a pair of glands exists in a medial position.

Relationships: In the remaining congeneric species – see DI FRANCO (1988), PLATNICK & DI FRANCO (1992) – the eyes are distinctly smaller, embolus, median apophysis and epigyne are different. *C. marinae* DI FRANCO 1988 from Italy – which may be most related – bears a retrolateral hair-brush of the pedipalpal tibia and the helm-shaped structure of the epigyne is nearer to the receptacula seminis which are larger.

Distribution: Spain, Mallorca.

(2) *Liocranum* L. KOCH 1866

The genus has a mediterranean distribution and is strongly related to *Mesiotelus* SIMON 1897, see above. The species which is described below has a remarkable variability which is probably only partly caused by allometric growth.

***Liocranum variabilis* n. sp**. (figs. 42–46, photos 363–365)

Material: Spain, Mallorca; (a) 2♂ 3km N Valdemossa, mixed forest, under stones among rocks, JW leg. in VIII, holotypus R7/AR/CJW, paratypus MNHNP; 2♀ paratypes, near Valdemossa, JW leg. in VI, 1♀ R8/AR/CJW, 1♀ MNHNP.

Remark: Both males have been collected at the same locality at the same day, and the structures of their bulbi show no differences.

Diagnosis: Tibiae I–II ventrally with 4–6 pairs of bristles, metatarsi ventrally with 3 (rarely 2) pairs. ♂: Chelicerae: Figs. 42–44, pedipalpus (figs. 45–46): Embolus wide, with a dorsal-distal hook. ♀: Epigyne/vulva (figs. 45c–e) with a large helm-shaped structure and a pair of lateral depressions near the receptacula seminis.

Description (♂):
Measurements (in mm): See the tab. Leg I of the holotype: Femur 4.0, patella 1.85, tibia 4.4, metatarsus 3.85, tarsus 1.55. Longest ventral bristle of the anterior tibia: 0.5 in the holotype, 0.53 in the paratype.

Measurements (usually the length) of body and pedipalpal parts of the holotype and the paratype of *Liocranum variabilis* n. sp. (♂):

specimen	body	prosoma	chelicerae		pedipalpus		
		length/width	basal*)/fang	tibia I/IV	tibia	cymbium	median ap.
holotype	5.6	2.5/2.4	2.7/1.8	4.4/3.5	1.8	1.0	0.21
paratype	4.9	2.15/1.85	1.15/0.8	3.1/2.9	0.95	0.85	0.20
relation hol./par.	1.14	1.16/1.3	2.35/2.25	1.42/1.21	1.9	1.18	1.05

---

*) free visible part of the basal article, see fig. 42.

Discussion of the variability (see figs. 42–45, and the photos): The prosomal length of the holotype is only 1.16 times of the paratype, but the length of chelicerae, anterior legs and pedipalpal articles are surprisingly more or almost twice as long; they vary more than double compared with the variability of body and prosomal length. Because of the low differences in body and prosomal length these differences are probably not caused by an “allometric growth”. – Most conspicuous are the greatly elongated and more slender chelicerae (basal articles and fangs, too) of the holotype (fig. 44): The basal cheliceral articles are 5.4 times longer than wide at the base in the holotype but only 2.9 times in the paratype; the labium is almost twice as long. – Pedipalpus: The more distal the position of the articles/structures the less are the differences: Tibia 1.9, cymbium 1.18, median apophysis 1.05. The lowest differences exist in the structures of the bulbus, both are almost identical in size, the emboli show no difference.

These may be no new findings. EBERHARD et al. (1998: 416) noted: “At least in arthropods, the size of other, nongenitalic body characters appear to be more variable than in those of genitalia...”.

Colour: Prosoma and legs yellow brown, opisthosoma ventrally light grey, dorsally medium to light grey, with dark w-shaped markings in the distal half.

Prosoma (figs. 42–44, photo) 1.04–1.16 times longer than wide, thoracal fissure long, eyes fairly small, the medians smaller than the laterals, posterior row slightly recurved, posterior median eyes separated from each other by 1.6 of their diameter. Clypeus very short, basal cheliceral articles long to very long, diverging; condylus well developed, anterior margin with 3 teeth which are widely spaced, the distal tooth is the largest, posterior margin with 2 teeth, fangs long, labium free, as long as wide to 1.9 times longer than wide (holotype), gnathocoxae 3.3 times longer than wide in the middle, laterally inclined in the middle. Sternum only short elongated betwen the posterior coxae, praecoxal triangles II–IV and intercoxal triangles I/II are present. – Legs (photo) long and slender (more slender in the males), order IV/I/II/III, I and IV almost equal in length, III relatively long, feathery hairs present, bristles thin and fairly short, absent on patellae, femora 2 dorsally, distally 1 or a pair, tibiae I–II ventrally 4–6 pairs, metatarsi I–II ventrally 3 (rarely 2) pairs, bristles thinner and only shortly overlapping in the males; claw tufts absent, divided scopulae on tibiae, metatarsi and tarsi I–II well developed in the females but quite indistinct in the males. Tarsi with long trichobothria in at least two rows, pseudosegmentations absent. – Opisthosoma (photo) 1.5 times longer than wide, covered with short hairs; a single pair of widely spaced epiandrous gland spigots; anterior spinnerets fairly short, almost contiguous, conical. Colulus reduced to a larger flat and hairy field, compare fig. 45b. – Pedipalpus (figs. 45–47) with long articles (see above), tibia with a long and slender retrolateral apophysis, cymbium proventrally with a bristle in the distal half, median apophysis long and slender, tegular apophysis wide, embolus wide and directed retrolaterally.

♀:

Measurements (in mm): Body length 8.0–8.6, prosoma: Length 2.8–3.0, width 2.3–2.4, length of tibia I 2.5–2.9, length of tibia IV 2.7–3.3, length of the basal cheliceral articles 1.5–1.7, length of the fangs 0.75–0.9.

Colour and teeth of the cheliceral furrow as in the male.

The basal cheliceral articles and the fangs are much shorter than in the males, the basal cheliceral articles are not diverging, the legs are more stout and the leg scopulae are stronger developed. A flat (not "fleshly") and weakly sclerotized hairy "colulus" (fig. 45b) is well observable in one of the females. The epigyne has a large helm-shaped structure and a pair of distinct depressions near the receptacula seminis which are divided (figs. 45c–e), and may be the introductory openings.

Relationships: In *L. majus* SIMON 1878 and *L. segmentatus* SIMON 1878 (see below) the helm-shaped structure of the epigyne is smaller and the paired epigynal depressions are quite indistinct, see SIMON (1932: Fig. 1435).

Distribution: Spain, Mallorca.

Liocranum majus **SIMON 1878, with notes on related species and questionable synonyms**

The prosomal length of 3♀ from Spain (MNHNP no. 2099) is 2.8–4.3 mm, the epigyne has a distinctly smaller helm-shaped structure than *L. variabilis*.
I do not find remarkable differences between *L. majus* and *L. segmentatus* SIMON 1878 (1♀ MNHNP no. 2097); the prosomal length of this female is 2.7mm. Both species may well be synonym. – A female from France (Banyuls, coll. SIMON, MNHN 4108) has a very similar epigyne but a smaller helm-shaped epigynal structure than *L. majus* and is similar to females from Crete (CJW). Males are needed to check the questionable synonymy of these taxa.

Remark: 3♀ from Spain (Sierra Nevada, JANETSCHEK leg., coll. SIMON, MNHNP, J. DENIS det. *Liocranum majus*) possess a quite different epigyne and are surely not conspecific with *majus* but may be members of an undescribed species.

Remark on German names of the Zoridae: I propose the name “Feldspinnen” for the Zoridae, and “Gefleckte Feldspinnen” for the Zorinae.

REFERENCES

See also the paper no. 5 in this volume.

AGNARSSON, I. (2004): Morphological phylogeny of cobweb spiders and their relatives (Araneae, Araneoidea, Theridiidae).-- Zool. J. Linnean Soc., 141: 447–626.

ARCHER, A. F. (1950): A study of theridiid and mimetid spiders with descriptions of new genera and species. -- Mus. paper Alabama Mus. nat. Hist., 30: 1–40.

ARNEDO, M. A. et al. (2004): From a comb to a tree: phylogenetic relationships of the comb-footed spiders (Araneae, Theridiidae) inferred from nuclear and mitochondrial genes.-- Molecular Phyletics and Evolution, 31: 225–245.

ARNOLD, V. (1998): Vergessene Einschlüsse – Blütenstaub in Baltischem Bernstein. -- Mitt. Geol.-Paläont. Inst. Univ. Hamburg, 81: 269–282.

BAERT, L. (1984): Mysmenidae and Hadrotarsidae from the Neotropical Guarani Zoogeographical Province (Paraguay and South Brasil) (Araneae). -- Rev. suisse Zool., 91 (3): 603–616.

BARRION, A. T. & LITSINGER, J. A. (1995): Riceland Spiders of South and Southeastern Asis. 716 pp.

BAUM, S. (1974): Zum “Cribellaten-Problem”: Die Genitalstrukturen der Oecobiinae und Urocteinae (Arach.: Aran.: Oecobiidae). -- Abh. Verh. naturwiss. Ver. Hamburg (NF), 16: 101–153.

BEATTY, J. A. (1970): The Spider Genus *Ariadna* in the Americas (Araneae, Dysderidae). -- Bull. Mus. Comp. Zoo., 139 (8): 433–517.

BECHLY, G. (2000): Mainstream Cladistics versus Hennigian Phylogenetic Systematics. -- Stuttgarter Beitr. Naturk., Ser. A, Nr. 613: 1–11.

-- (2005): Book review: J. Wunderlich: Fossil spiders in amber and copal. -- Naturwiss. Rundschau, 58 (10): 1.

BENJAMIN, S. P. & ZSCHOKKE, S. (2003): Webs of theridiid spiders: construction, structure and evolution. -- Biol. J. Linn. Soc., 78: 293–305.

BERLAND, L. ((1939): Description de quelques aragnees fossiles. -- Rev. franc. d’entom., 6 (1): 1–9.

BLICK, T. et al. (2006) : *Theridion palmgreni* MARUSIK & TSELLARIUS 1986 : first record for Poland, new data from Finland, Russia and Estonia – with a review of distribution and ecology (Araneae, Therididae). -- Fragmenta Faunistica, 49 (2) : 115–126.

BOSSELAERS, J. & JOCQUE, R. (2002): Studies in Corinnidae: cladistic analysis of 38 corinnid and liocranid genera, and transfer of Phrurolithinae. -- Zoologica Scripta, 31 (3): 241–270.

BRIGNOLI, P. M. (1968): Notizie sui Theridiidae della Calabria. -- Mem. Mus. Vivico di Storia Naturale, Verona, 16: 261–270.

CARICO, J. E. (1978): Predatory Behavior in *Euryopis funebris* (HENTZ) (Araneae: Theridiidae) and the Evolutionary Significance of Web Reduction. -- Symp. zoo. Soc. London, 42: 51–58.

CODDINGTON, J. A. (1986): The Genera of the Spider Family Theridiosomatidae. -- Smithsonian contrib. Zool., 422: 1–96.

DALMAS, M. (1916): Revision du genre *Orchestina* suivie de la description de nouvelles especies du genre *Oonops* et d'une etude sur les Dictynidae du genre *Scotolathys*. -- Ann. Soc. Ent. France, 85: 203–258.

DAVILA, D. S. (2003): Higher-level relationships of the spider family Ctenidae (Araneae: Ctenoidea). -- Bull. Amer. Mus. Nat. Hist., 274: 1–86.

DEELEMAN-REINHOLD, C. L. (2001): Forest Spiders of South East Asia. 591 pp.

DI FRANCO, F. (1988): *Cybaeodes marinae*, nuova species di Gnaphosidae (Arachnida, Araneae) d'Italia. -- Animalia, 15: 25–36.

DUNLOP, J. (2005): Book review: Fossil Spiders in Amber and Copal. -- Newsl. Br. arachnol. Soc., 104: 10–11.

-- (2006): Review of J. WUNDERLICH (2004): Fossil Spiders in Amber and Copal. -- Beitr. Araneol., 3 A, B: 1-1865.

EBERHARD, W. G. et al. (1998): One size fits all? Relationships between the size and degree of variation in genitalia and other body parts in twenty species of insects and spiders. -- Evolution, 52 (2): 415–431.

EXLINE, H. & LEVI, H. W. (1962): American spiders of the genus *Argyrodes* (Araneae Theridiidae). -- Bull. Mus. Comp. Zoology, 127 (2): 1-73-204 + 15 plates.

FITZGERALD, B. M. & SIRVID, P. J. (2003): The genus *Trigonobothrys* in New Zealand and a redescription of *Achaearanea blata* (Theridiidae: Araneae). – Tuhinga, 14: 25-3.

-- & -- (2004): Notes on the genus *Phycosoma* Cambridge, 1879, senior synonym of *Trigonobothrys* Simon 1889 (Theridiidae: Araneae) . – Tuhinga, 15: 7–12.

FOELIX, R. (1996): Biology of Spiders. 330 pp.

FORSTER, R. & FORSTER, L. (1999): Spiders of New Zealand and their Worldwide Kin. 270pp. University of Otago Press.

FORSTER, R. R. & PLATNICK, N. I. (1985): A review of the austral spider family Orsolobidae (Arachnida, Araneae) with notes on the superfamily Dysderoidea. -- Bull. Amer. Mus. Nat. Hist., 181 (1): 1–229.

GRIMM, U. (1986): Die Clubionidae Mitteleuropas: Corinninae und Liocraninae (Arachnida, Araneae). -- Abh. Naturwiss. Verein Hamburg (NF), 27: 1–91.

GRISWOLD, C. E. (1990): A revision and phylogenetic analysis of the spider subfamily Phyxelidinae (Araneae, Amaurobiidae). – Bull. Amer. Mus. Nat. Hist., 196: 1–206.

HAWKESWOOD, T. J. (2003): Spiders of Australia. 264pp.

HOFFEINS, H. W. (2001): On the preparation and conservation of amber inclusions in artificial resin. -- Polish J. entom., 70: 215–219.

HOLM, A. (1962): The Spider Fauna of the East African Mountains. -- Zool. Bidr. Uppsala, 35: 19–204, 6pl.

JOCQUE, R. & DIPPENAAR-SCHOEMAN, A. S. (2006): Spider Families of the World. 336pp. – Second edition 2007.

KASTON, B. J. (1938): Family names in the order Araneae. -- The American Midland Naturalist, 19 (3): 638–646.

KNOFLACH, B. (1993): *Theridion conigerum* Simon – redicovered in Austria (Araneida: Therididae). -- Bull. Br. arachnol. Soc., 9 (6): 205–208.

-- (1994): Zur Genitalmorphologie und Biologie der *Crustulina*-Arten Europas (Arachnida: Araneae, Theridiidae). -- Mitt. Schweiz. entom. Ges., 67: 327–346.

-- (1995): Two remarkable afromontane Theridiidae: *Proboscidula milleri* n. sp. and *Robertus calidus* n. sp. (Arachnida, Araneae). -- Rev. Suisse Zool., 102 (4): 979–988.

-- (1996): *Steatoda incomposita* (DENIS) from Southern Europe, a close relative of Steatoda albomaculata (DEGEER) (Araneae: Theridiidae). -- Bull. Br. arachnol. Soc., 10 (4): 141–145.

-- (1996): Three new species of *Carniella* from Thailand (Araneae, Theridiidae). -- Rev. suisse Zool., 103 (3): 567–579.

-- (1996): Die Arten der *Steatoda phalerata*-Gruppe in Europa (Arachnida: Araneae: Theridiidae). -- Mitt. Schweiz. entom. Ges., 69: 377–404.

-- (1999): The comb-foted spider genera *Neottiura* and *Coleosoma* in Europe (Araneae, Theridiidae). -- Mitt. Schweiz. Entom. Ges., 72: 341–371.

KNOFLACH, B. & PFALLER, K. (2004: 111–160): Kugelspinnen – eine Einführung (Araneae, Theridiidae). -- In Biologiezentrum/Oberösterreichisches Landesmuseum (ed.): Diversität und Biologie von Webspinnen, Skorpionen und anderen Spinnentieren. -- Denisia, 12: 1–586.

KNOFLACH, B. & VAN HARTEN, A. (2000): Palpal loss, single palp copulation and obligatory mate consumption in *Tidarren cuneolatum* (Tullgren, 1910) (Araneae, Theridiidae). -- J. Nat. Hist., 34: 1639–1659.

KOCH, C. L. & BERENDT, G. C. (1854): Die im Bernstein befindlichen Crustaceen, Myriapoden, Arachniden und Apteren der Vorwelt. In: BERENDT, G. C., Die im Bernstein befindlichen Organischen Reste der Vorwelt, 1 (2): 1–124.

KRAUS, O. (2005): Book review. Wunderlich, J. (2004): Fossil spiders in amber and copal. -- Verh. naturwiss. Ver. Hamburg (NF), 41: 376–377.

LEVI, H. W. (1957): The spider genera *Crustulina* and *Steatoda* in North America, Central America and the West Indies (Araneae, Theridiidae). -- Bull. Mus. Comp. Zool. 117 (3): 367–424 + 156 figs.

-- (1962): The spider genera *Steatoda* and *Enoplognatha* in America (Araneae, Theridiidae). -- Psyche, 69 (1): 11–36.

-- (1963): The spider genera *Cerocida, Hetschkia, Wirada* and *Craspedisia*. -- Psyche, Camb., 70: 170–179.

-- (1964): American spiders of the genus *Phoroncidia* (Araneae: Theridiidae). – Bull. Mus. Comp. Zol., 131 (3): 65–86.

-- (1973): Taxonomic-nomenclatural notes on misplaced theridiid spiders (Araneae: Theridiidae), with observations on *Anelosimus*. -- Trans. Amer. Micros. Soc., 91 (4): 533–538.

-- (1981) : The male of *Echinotheridion* (Araneae : Theridiidae). – Psyche, 87 (3-4) : 177–179.

-- (2005): The spider genera *Heterognatha, Testudinaria* and *Ursa* in South America (Araneae: Araneoidea). -- Bull. Br. arachnol. Soc., 13 (6): 185–198.

LEVI, H. W. & LEVI, L. R. (1962): The genera of the spider family Theridiidae. -- Bull. Mus. Comp. Zool., 127 (1): 1–99.

LEVY, G. (1998): Araneae: Therididae. In Fauna Palaestina. Arachnida III: 1–230.

LEVY, G. & AMITAI, P. (1982): The Cobweb Spider Genus *Steatoda* (Araneae, Therididae) of Israel and Sinai. -- Zool. Scripta, 11 (1): 13–30).

LOTZ, L. N. (1994): Revision of the genus *Latrodectus* (Araneae: Theridiidae) in Africa. -- Navors. Nat. Mus. Bloemfontein, 10 (1): 1–60.

MARUSIK, Y. M. & CELLARIUS, A. Y. (1986): New species of spiders of the genus *Theridion* (Aranei, Therididae) from Karelia. – Zool. Zh., 65 (11): 1736–1738.

MARUSIK, Y. M. & PENNEY, D. (2005): A survey of Baltic amber Theridiidae (Araneae) inclusions, with descriptions of six new species. -- Arthropoda Selecta (Special Issues No. 1, 2004: 201–218).

MILLER, J. A. (2007): Repeated evolution of male sacrifice behavior in spiders correlated with genital mutilation. -- Evolution, 61 (6): 1301–1315.

MURPHY, F. & MURPHY, J. (2000): Introduction to the spiders of South East Asia. 624pp + 32 plates. Malaysian Nature Society, Kuala Lumpur.

OKUMA, C. (1994): Spiders of the Genera *Episinus* and *Moneta* from Japan and Taiwan, with Descriptions of Two New Species of *Episinus* (Araneae: Theridiidae). -- Acta arachnol., 43 (1): 5–25.

PAQUIN, P. & DUPERE, N. (2003): Guide d'identification des Aragnees (Araneae) du Quebec. – Fabreries, suppl. 11: 1–251.

PENNEY, D. (2000): Miocene spiders in Dominican amber (Oonopidae, Mysmenidae). -- Palaeontology, 43 (2): 343–357.

-- (2002): Spiders in Upper Cretaceous amber from New Jersey (Arthropoda: Araneae). -- Palaeontology, 45 (4): 709–724.

-- (2004): New spiders in upper Cretaceous amber from New Jersey in the American Museum of Natural History (Arthropoda: Araneae). -- Palaeontology, 47 (2): 367–375, 1pl.

-- (2005): The fossil spider family Lagonomegopidae in Cretaceous amber with descriptions of a new genus and species from Myanmar. -- J. Arachnology, 33: 439–444.

-- (2006): Fossil oonopid spiders in Cretaceous ambers from Canada and Myanmar. -- Palaeontology, 49 (1): 228–235.

-- (2007): A new fossil oonopid spider in lowermost Eocene amber from the Paris Bassin, with comments on the fossil spider assemblage. -- African Invertebrates, 48: 71–75.

-- (2007): The oldest fossil pholcid and selenopid spiders, in lowermost Eocene amber from the Paris Basin, France. -- J. Arachnol., 34: 592–598.

PENNEY, D. et al. (2003): Resistance of spiders to Cretaceous-Tertiary Extinction events. -- Evolution, 57 (11): 2599–2607.

PENNEY, D. & LANGAN, A. M. (2006): Comparing amber fossil assemblages across the Cenozoic. -- Biol. Letters, 2: 266–270.

PENNEY, D. et al. (2007: First fossil Micropholcommatidae (Araneae), imaged in Eocene Paris amber using X-Ray Computed Tomography. -- Zootaxa, 1623: 47–53.

PETRUNKEVITCH, A. (1942): A study of Amber Spiders. -- Trans. Connect. Acad. Arts Sci., 34: 119–464.

-- (1946): Fossil spiders in the collection of the American Museum of Natural History. -- Amer. Mus. Novit., 1328: 1–36.

-- (1950): Baltic Amber Spiders in the Museum of Comparative Zoology. -- Bull. Mus. Comp. Zool., 103: 257–337.

-- (1958): Amber Spiders in European collections. -- Trans. Connect. Acad. Arts Sci., 41: 97–400.

PLATNICK, N. I. (1998): Advances in Spider Taxonomy 1992-1995. 976pp. – (2007) Internet. ed.

PLATNICK, N. I. & DI FRANCO, F. (1992): On The Relationships of the Spider Genus *Cybaeodes* (Araneae, Dionycha). -- Amer. Mus. Novit., 3053: 1–9.

PLATNICK, N. I. & SHADAB, M. U. (1993): A review of the Pirate spiders (Araneae, Mimetidae) of Chile. -- Am. Mus. Novit.m 3074: 1–30.

POINAR, G. (Jr.) (2005): Book Review. Review of Fossil Spiders in Amber and Copal by Joerg Wunderlich. -- J. Arachnol., 33: 878–879.

SAARISTO, M. I. (1978): Spiders (Arachnida, Araneae) from Seychelles Islands, with notes on taxonomy. -- Ann. Zool., Fennici, 15: 99–126.

-- (2001): Dwarf hunting spiders or Oonopidae (Arachnida, Araneae) of the Seychelles. -- Insect Syst. Evol., 32: 307–358.

-- (2006): Theridiid or cobweb spiders of the granitic Seychelles islands (Aaraneae, Theridiidae). -- Pheisuma, 14: 40–89.

SAARISTO, M. I. & MARUSIK, Y. M. (2004): *Ferchestina*, a new genus of oonopid spiders from Russian Far East (Aranei: Oonopidae). -- Arthropoda Selecta, 13 (1–2): 51–54.

SAUER, F, & WUNDERLICH, J. (1995): Die schönsten Spinnen Europas. 300 pp.

SAUPE, E. E. & SELDEN, P. A. (2007): First fossil Mecysmaucheniidae (Arthropoda: Chelicerata: Araneae) from Lower Cretaceous (Upper Albian) amber of Charente-Maritime, France.

SZINETAR, C., HORVATH, R. & EICHARD, J. (2004): *Chrysso nordica* (Theridiidae, Araneae), found in Eastern Hungary is a new spider species for Central Europe. – In European Arachnology 2002 (20th European Colloquium of Arachnology), ed. bySAMU & SZINETAR: 303–307.

SONG DAXIANG & ZHU MINGSHENG (1997): Thomisidae, Philodromidae. In Fauna Sinica, Arachnida: Araneae. 259 pp.

TANIKAWA, A. (1991): Two newly recorded spiders, *Theridion rufipes* LUCAS, 1846, and *Coleosoma floridanum* BANKS, 1900 (Araneae: Theridiidae), from Japan. -- Atypus, 98/99: 1–7.

THALER, K. & M.-T. NOFLATSCHER (1990): Neue und bemerkenswerte Spinnenfunde in Südtirol (Arachnida: Aranei). -- Veröff. Mus. Ferdinandeum Innsbr., 69: 169–190.

UBICK, D. & PLATNICK, N. I. (1991): On *Hesperocranum*, A New Spider Genus from Western North America (Araneae, Liocranidae). -- Am. Mus. Novit., 3019: 1–12.

UBICK, D. et al. (eds.) (2005): Spiders of North America. An identification manuel. -- American Arachnological Society. 377pp.

ULRICH, H. (2003): How recent are the Empidoidea of Baltic amber? -- Studia dipterologica, 10 (1): 321–327.

VANUYTVEN, H. (1991): A rediscription of *Phoroncidia paradoxa* (LUCAS, 1846) (Araneae: Theridiidae). -- Phegea, 19 (3): 103–105.

WIEHLE, H. (1934): Zur Morphologie und Biologie einer paläarktischen *Lithyphantes*-Art (*L. gerhardti* n. sp.). -- Zool. Anz., 106 (3-4): 71–83.

-- (1937): Theridiidae oder Haubennetzspinnen (Kugelspinnen). -- Tierwelt Deutschlands, 33: 119–222.

-- (1960): Micryphantidae – Zwergspinnen. -- Tierwelt Deutschlands, 47: 1–620.

WUNDERLICH, J. (1978): Zu Taxonomie und Synonymie der Taxa Hadrotarsidae, *Lucarachne* BRYANT 1940 und *Flegia* C. L. KOCH & BERENDT 1854, (Arachnida: Araneida: Theridiidae). -- Zool. Beitr. (N. F.), 24 (1): 25–31.

-- (1981): Fossile Zwerg-Sechsaugenspinnen (Oonopidae) der Gattung *Orchestina* SIMON 1882 im Bernstein, mit Anmerkungen zur Sexual-Biologie (Arachnida: Araneae). -- Mitt. Geol.-Paläontol. Inst. Univ. Hamburg, 51: 88–113.

-- (1986): Spinnenfauna gestern und heute. Fossile Spinnen und ihre heute lebenden Verwandten. 283pp; Publishing House Joerg Wunderlich, 69493 Hirschberg, Germany.

-- (1988): Die fossilen Spinnen im Dominikanischen Bernstein. -- Beitr. Araneol., 2: 1–378.

-- (2000): Ant mimicry by spiders and spider-mite interactions preserved in Baltic amber (Arachnida: Acari, Araneae). -- European Arachnology 2000 (S. Toft & N. Scharff eds).: 35–358. (Proc. 19th European Coll. Arachnol.).

-- (2004): Fossil Spiders in Amber and Copal. -- Beitr. Araneol., 3 (A, B). 1908pp; Publishing House Joerg Wunderlich, 69493 Hirschberg, Germany.

YIN, CHANG-MIN et al. (2003): A new species of the spider genus *Craspedisia* from the Gaoligong Mountains, Yunnan, China (Araneae, Theridiidae). -- Bull. Br. arachnol. Soc., 12 (8): 383–384.

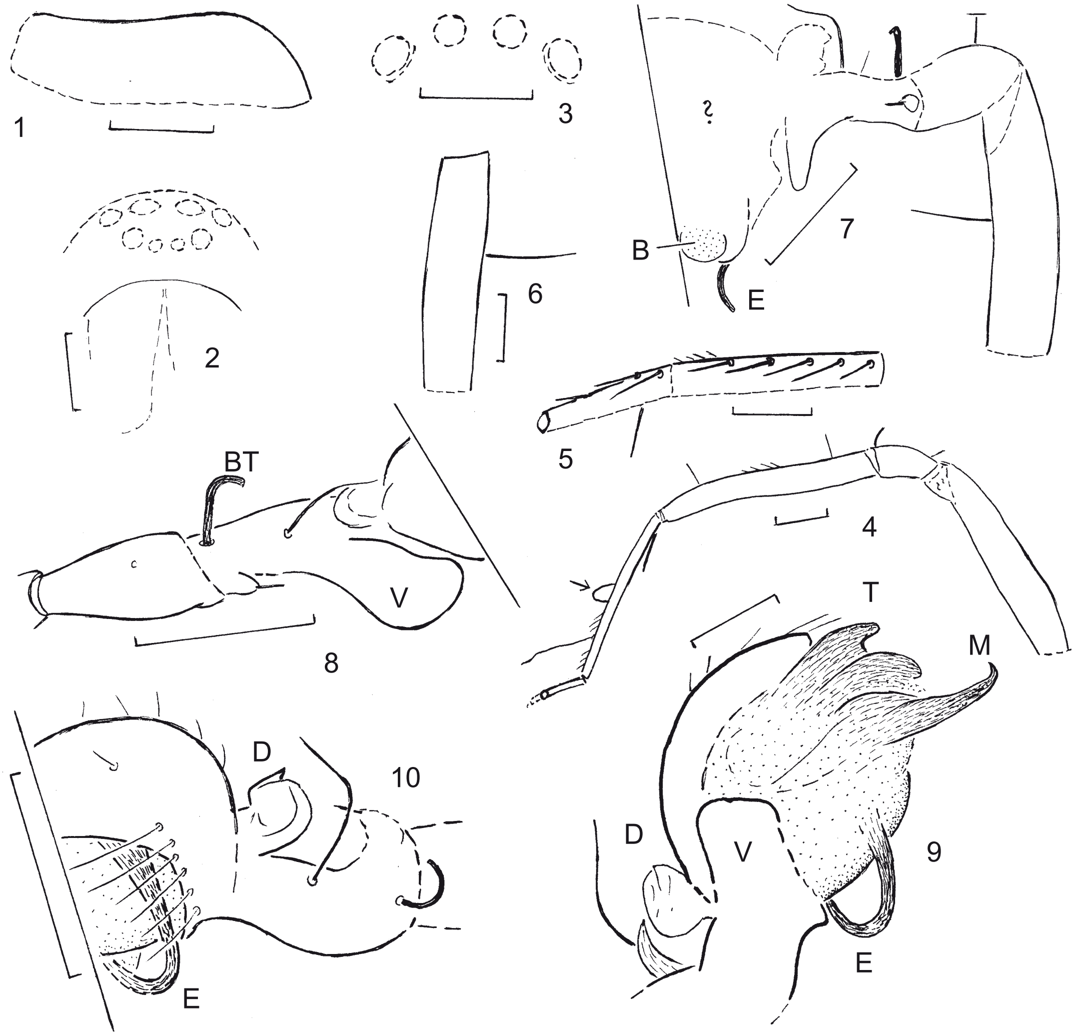
YOSHIDA, H. (1985): Three New Species of the Spider Genera *Phoroncidia* and *Pholcomma* (Araneae, Theridiidae) from Japan. -- Proc. Jap. Soc. syst. Zool., 31: 7–13.

-- (2001): A revision of the Japanese genera and species of the subfamily Theridiinae (Araneae: Theridiidae). -- Acta Arachnol., 50 (2): 157–181.

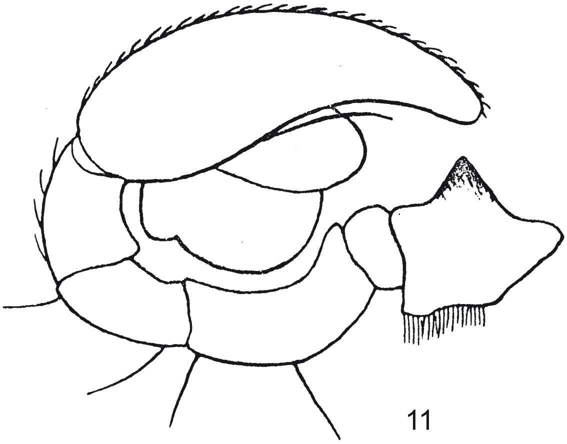
-- (2002): A revision of the Japanese genera and species of the subfamily Hadrotarsinae (Araneae: Theridiidae). -- Acta Arachnol., 51 (1): 7–18.

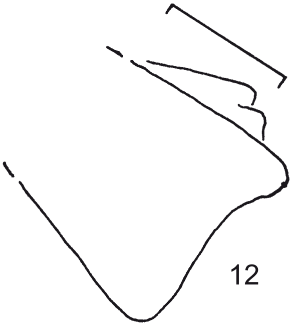
-- (2003): The Spider Family Theridiidae (Arachnida: Araneae) from Japan. -- Arachnological Society of Japan. 224pp.

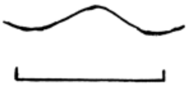
ZHU MINGSHENG (1998): Therididae. In Fauna Sinica: Arachnida: Araneae. 437pp.

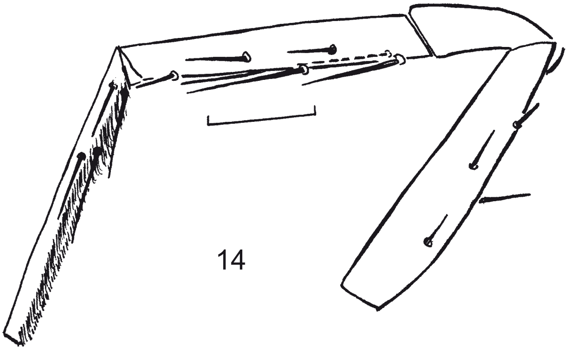


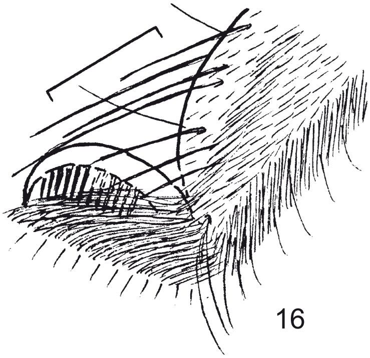
Figs. 1–10: ***Eohalinobius scutatus*** **n. gen. n. sp.**, ♂; 1) outline of the prosoma, lateral aspect; eyes not drawn; 2) anterior aspect of the prosoma. Parts are hidden by a white emulsion; 3) dorsal aspect of the posterior eye row; 4) retrolateral aspect of the l. leg I. The tip of the tarsus is cut off, the basal metatarsal trichobothrium is strongly bent (arrow), only few hairs are drawn; 5) r. tibia and metatarsus I (its tip is cut off), oblique proventral-dostal aspect. The ventral side is covered with a thick white emulsion; therefore are most of the retroventral bristles hidden (a single long metatarsal bristle is an exception); 6) dorsal aspect of the l. pedipalpal femur; 7) retrolateral and slightly apical aspect of the basal part of the l. pedipalpus. Distal parts are hidden by a white emulsion; the patella appears shortened in perspective; 8) retrodorsal aspect of the r. pedipalpal patella and tibia; 9) oblique retroventral-basal aspect of the r. pedipalpus; 10) prolateral (slightly apical) aspect of the r. pedipalpus; B = bubble, BT = basal tibial bristle, D = dorsal tibial apophysis, E = embolus, M = median apophysis, T = terminal apophysis V = retroventral tibial apophysis; scale bars = 0.2 mm in figs. 6) 9), 0.4 mm in fig. 4), 0.5 mm in the remaining figs.;

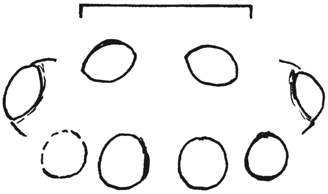

11


12


15


14

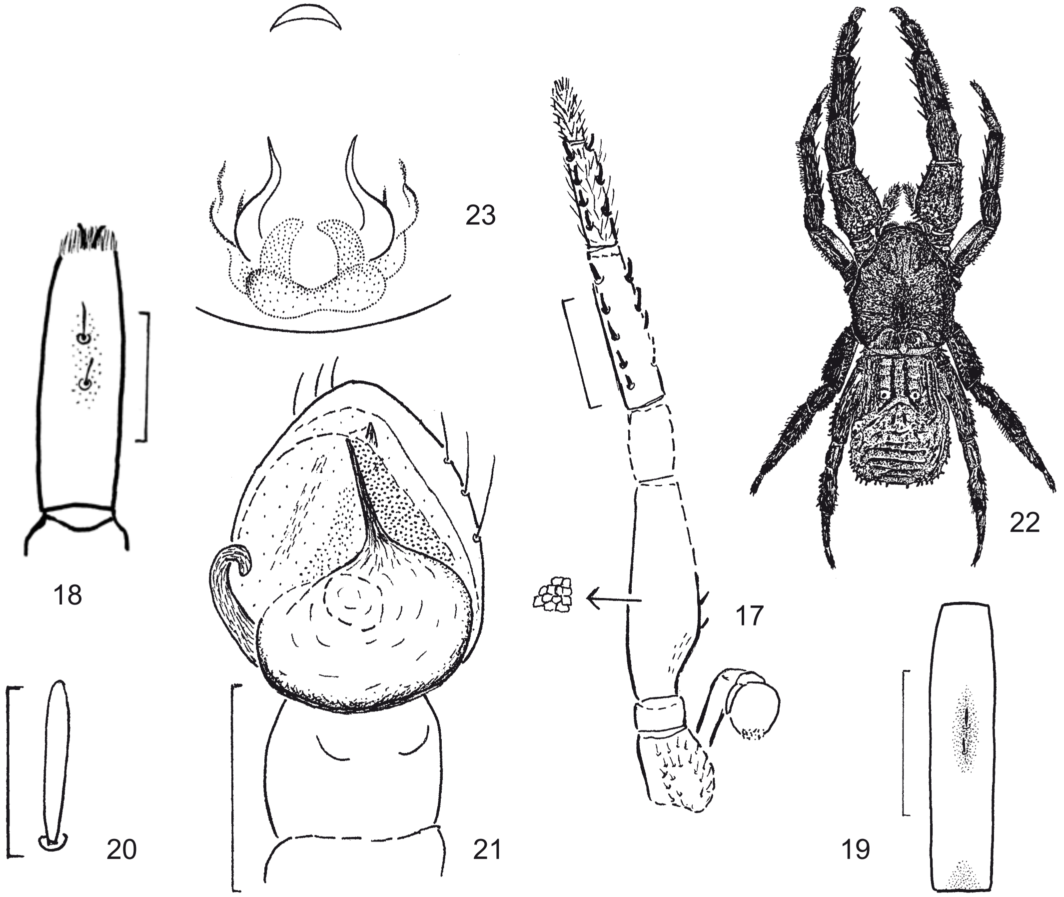

16


13

Figs. 11-12: <u>*Ablator niger*</u> (PETRUNKEVITCH 1942), ♂ holotypus; 11) prolateral aspect of the l. pedipalpus; taken from PETRUNKEVITCH (1942: Fig. 156); 12) ventral aspect of the l. gnathocoxa; the medial part is hidden. Note the retrolateral outgrowths; scale bar 0.2 mm in fig. 12);

figs. 13-15: <u>Sparassidae indet., sp. 1</u>, juv. ♂, CJW, ex coll. W. LUDWIG; 13) anterior-dorsal aspect of the eyes; 14) prolateral spect of the r. leg I (tarsus not drawn); 15) dorsal aspect of the trilobate membrane of the r. metatarsus I; scale bars (in mm): 1.0 in fig. 13), 2.0 in fig. 14), 0.2 in fig. 15);

fig. 16) <u>Sparassidae indet., sp. 2</u>, juv., F1883/BB/AR/CJW, prolateral aspect of the distal part of the r. tarsus II; scale bar = 0.2 mm;



figs. 17-23: Fossil and extant spiders of the family Borboropactidae:

figs. 17-21: *Succiniraptor radiatus* (KOCH & BERENDT 1854) in Baltic amber; figs. 17, 19: ♂ F1654/CJW, figs. 18, 29-21: holotypus ♂ of *Succiniraptor paradoxus* WUNDERLICH 2004; 17) ventral aspect of the r. anterior leg and the r. pedipalpus. The scaly cuticula is enlarged (arrow). Only few hairs are drawn. Note the very small pedipalpus and the two stout anterior femoral spines; 18) dorsal and slightly basal aspect of the l. anterior tarsus; 19) dorsal-basal aspect of the l. anterior metatarsus. Note the two thick (probably feathery or plumose) trichobothria which are situated in a low furrow; 20) thickened hair of the retrolateral side of an anterior tarsus; 21) ventral aspect of the r. pedipalpus; scale bars (in mm) = 1.0 in fig. 17), 0.5 in fig. 19), 0.2 in figs. 18) and 21), 0.02 in fig. 20;

22) *Borboropactus* sp. indet. (♀), extant, Malaysia, dorsal aspect of the body. Body length ca. 10 mm. – Taken from MURPHY & MURPHY (2000: 431, fig. 5);

23) *Borboropactus hainanus* SONG 1993, ♀, extant, China, epigyne. – Taken from SONG & ZHU (1997: 22, fig. 8 C);

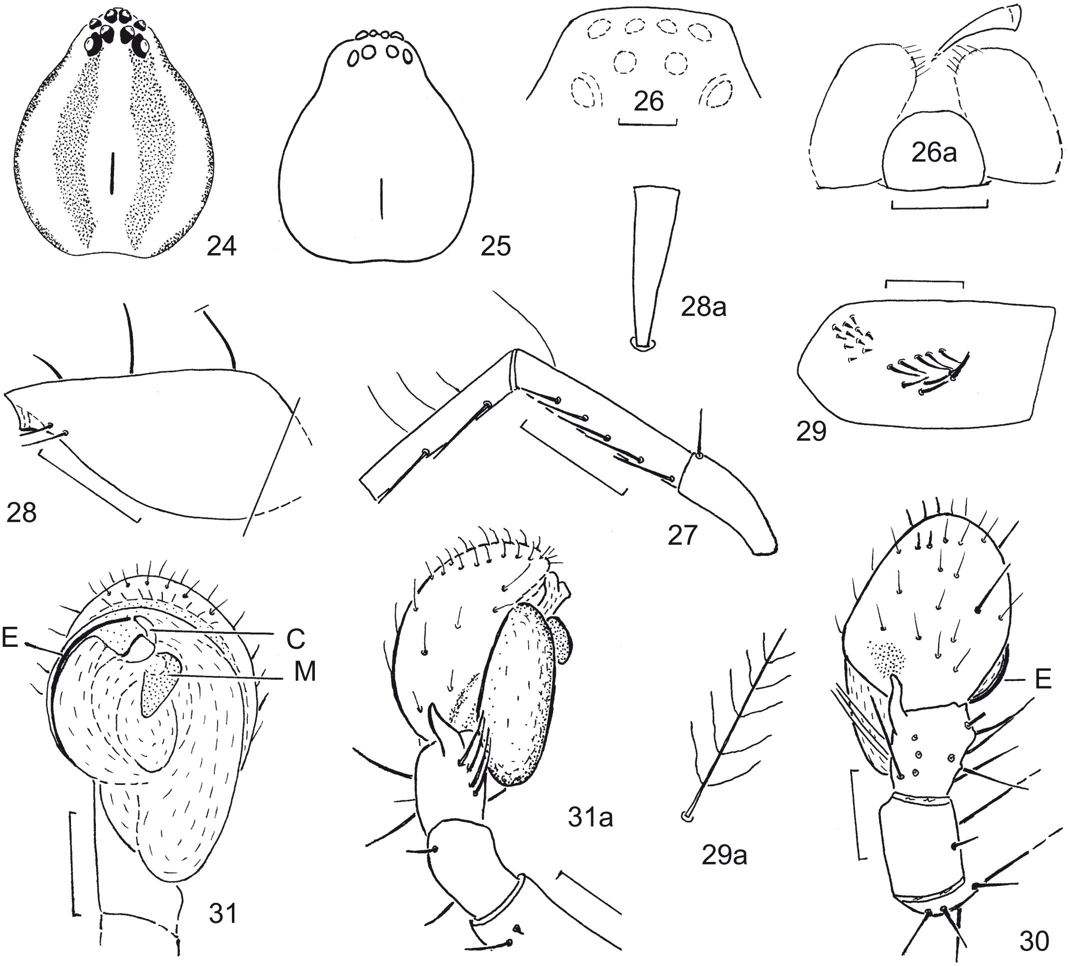
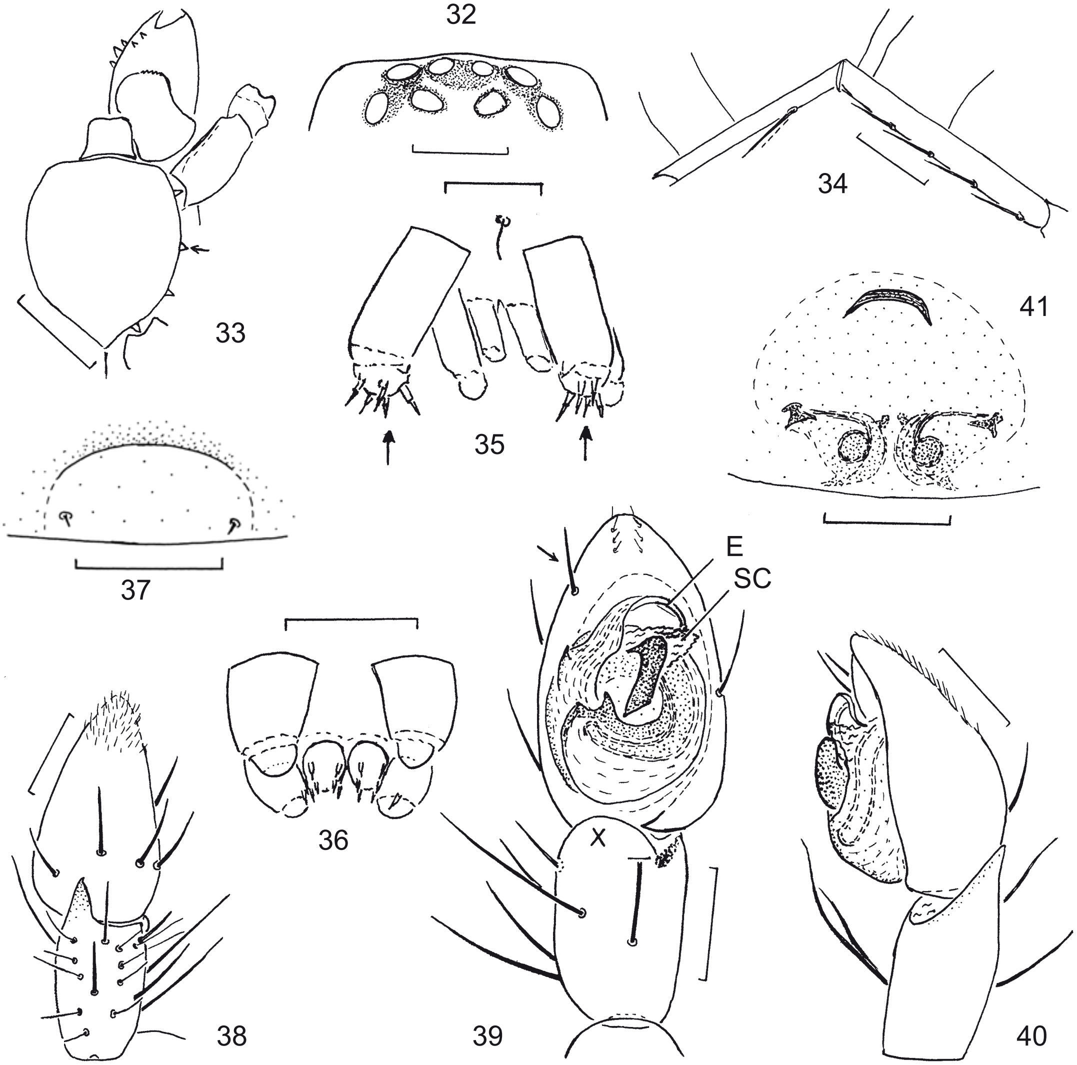


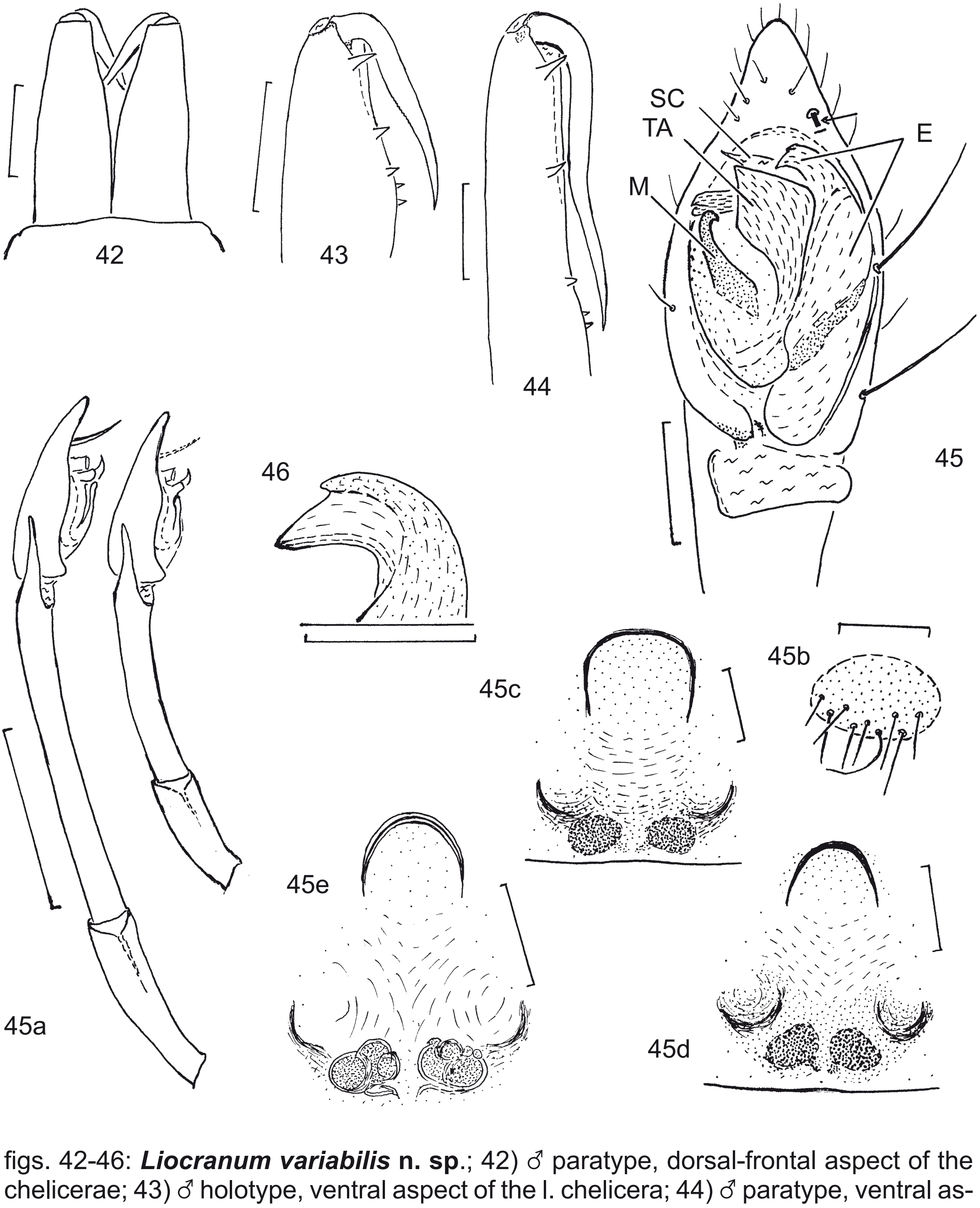
fig. 24) Zora sp. (extant), dorsal aspect of the prosoma. Taken from UBICK et al. (eds.) (2005: Fig. 69.3);

fig. 25) Apostenus fuscus WESTRING 1851 (extent), dorsal aspect of the prosoma. Taken from GRIMM (1986: Fig. 3);

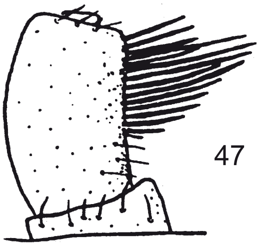
figs. 26-31a: ***Zorapostenus raveni* n. gen. n. sp**. in Baltic amber, ♂; 26-31) holotype, 31a) paratype; 26) dorsal aspect of the eyes which are partly covered by small bubbles; 26a) ventral aspect of labium, gnathocoxae and left fang; 27) prolateral aspect of the r. patella, tibia and metatarsus II; 28) retrolateral and slightly dorsal aspect of the l. femur IV which basal part is hidden; 28a) spatulate hair of the claw tufts; 29) ventral aspect of the l. coxa IV. Note the two groups of stridulatory bristles/spines: Short ones near the sternum (left) and long distal ones (right). Hairs are not drawn; 29a) feathery leg hair; 30-31) dorsal and ventral aspects of the l. pedipalpus; 31a) retrolateral aspect of the r. pedipalpus (only few hairs and bristles are drawn); C = conductor, E = embolus, M = median apophysis; scale bars (in mm) = 0.5 in figs. 27-28), 0.1 in fig. 28a), no scale bar in fig. 29a), 0.2 in the remaining figs.



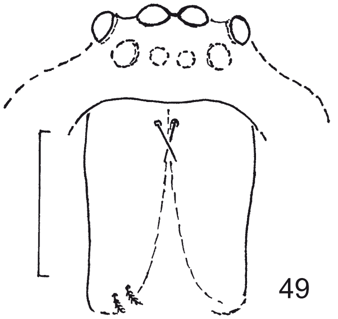
figs. 32-41: ***Cybaeodes mallorcensis* n. sp.**, ♂; 32) ♀, dorsal aspect of the eyes; 33) ♀, ventral aspect of sternum, labium, l. gnathocoxa and l. chelicera as well as the l. anterior coxa and trochanter. The arrow points to a praecoxal triangle of the sternum; 34) ♂, retrolateral aspect of the l. tibia and metatarsus I. Only the retroventral bristles and five of the longest trichobothria are drawn; 35) ♂, ventral aspect of the spinnerets. The base of the anterior spinnerets is somewhat expanded, these spinnerets are in an unnatural position. Note the presence of enlarged piriform gland spigots on the anterior spinnerets (arrows) in contrast to the female (fig. 36); 36) ♀, ventral-posterior aspect of the spinnerets. Hairs are not drawn. Only 3 of 4 pairs of enlarged gland spigots of the median spinnerets are drawn; 37) ♂, genital area. Note the single pair of epiandrous gland spigots; 38) ♂, dorsal aspect of the l. pedipalpus. Note the large number of tibial trichobothria; 39-40) ♂, ventral and retrolateral aspect of the l. pedipalpus; 41) ♀, epigyne; E = embolus, SC = scinny conductor, X = proapical outgrowth of the tibia; scale bars = 0.5mm in figs. 32-34), 0.1 in fig. 37), 0.2 in the remaining figs.;



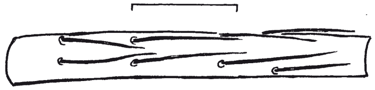
figs. 42-46: ***Liocranum variabilis* n. sp**.; 42) ♂ paratype, dorsal-frontal aspect of the chelicerae; 43) ♂ holotype, ventral aspect of the l. chelicera; 44) ♂ paratype, ventral aspect of the l. chelicera; 45) ♂ paratype, ventral aspect of the r. pedipalpus; 45a) retrolateral aspect of the r. ♂-pedipalpus of the holotype (left) and paratype; 45b) ♀ (paratype MNHNP), hairy and flat area of the "colulus"; 45c-d) ♀ paratypes MNHNP and CJW, epigyne; 45e) ♀ (CJW), dorsal aspect of the vulva; 46) ♂ paratype, proventral aspect of the distal part of the r. embolus; M = median apophysis, SC = scinny conductor, TA = tegular apophysis; scale bars = 1.0mm in fig. 45a), 0.5 in figs. 43-44), 0.1 in figs. 45b) and 46), 0.2 in the remaining figs.;

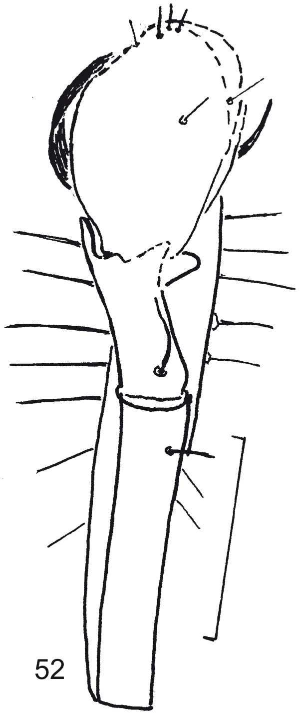

47

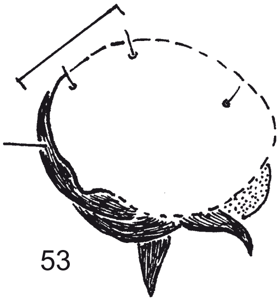

48

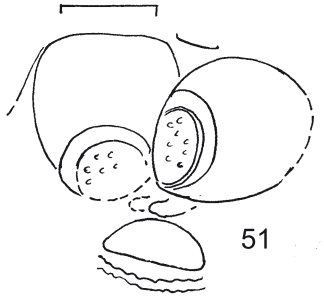

49

50




52


53


51

54

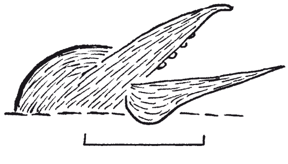


fig. 47) ***Zora* sp.**, ♂, lateral aspect of an anterior spinneret;

fig. 48) ***Scotina* sp.**, dorsal aspect of the posterior eye row;

figs. 49-54: ***Succinomus duomammillae* n. gen. n. sp.** in Baltic amber, ♂; 49) anterior aspect of the prosoma; 50) ventral aspect of the l. tibia I; 51) ventral aspect of spinnerets and anal tubercle; hairs are not drawn; 52) dorsal aspect of the r. pedipalpus but ventral aspect of the femur (below); 53) basal aspect of cymbium and bulbus of the r. pedipalpus; parts are hidden by articles of the pedipalpus; 54) retroletarel aspect of the tegular apophyses (median apophysis and questionable conductor) of the l. pedipalpus; C = cymbium, E = embolus; scale bars = 0.5 in figs. 50) and 52), 0.1 in fig. 51), 0.2 in the remaining figs.

BEITR. ARANEOL., 5 (2008)

THE DOMINANCE OF ANCIENT SPIDER FAMILIES OF THE ARANEAE: HAPLOGYNAE IN THE CRETACEOUS, AND THE LATE DIVERSIFICATION OF ADVANCED ECRIBELLATE SPIDERS OF THE ENTELEGYNAE AFTER THE CRETACEOUS-TERTIARY BOUNDARY EXTINCTION EVENTS, WITH DESCRIPTIONS OF NEW FAMILIES

PROBABLE EFFECTS OF THE CRETACEOUS-TERTIARY BOUNDARY EVENTS ON THE EVOLUTION AND DIVERSIFICATION OF HIGHER SPIDERS (INFRAORDER ARANEOMORPHA), THE LATE (EARLY TERTIARY) DIVERSIFICATION OF HIGHER ENTELEGYNE SPIDERS IN THE AGE OF ANTS AND ANGIOSPERMS, CO-EVOLUTION WITH ANTS, A KEY TO THE SPIDER FAMILIES IN CRETACEOUS AMBERS, FIRST DESCRIPTIONS OF SIX EXTINCT CRETACEOUS SPIDER FAMILIES, SPIDER'S PREY AND CAPTURE WEBS, THE GEOLOGICALLY OLDEST INDIRECT PROOF OF ARANEOPHAGY, AND OF REPRODUCTORY BEHAVIOUR IN CRETACEOUS SPIDERS

JOERG WUNDERLICH, 69493 Hirschberg, Germany.

ABSTRACT: See also the subheading of this paper which regards mainly fossil Cretaceous spiders (Araneae), predominantly of the infraorder Araneomorpha. – It is supposed that during the relatively short span of time of about 20 or 30 million years – 50 to 70 or 80 million years ago – about 90% of the **EXTANT** araneomorph spider families diversified (and some probably even originated), probably mainly around or during the Palaeocene of the Palaeogene. This mainly Palaeocene "Explosion of spiders evolution/diversification" may have taken only about 1/16 or 1/20 of the ca. 400 m. y. of the entire spiders' evolution. Most families of araneomorph spiders may be younger than 70 or 100 m. y.; this is a span of only 1/4 or 1/6 of the entire spider's evolution. If this – totally surprising! – finding is correct, the overwhelming number of araneomorph spider families are quite young in a geological sense. Derived haplogyne families displaced the ancient families of the Haplogynae, and numerous advanced entelegyne families of the Araneoidea and of the RTA-clade were added to the few ancient families of orb-weaving Araneoidea s. l.. – A taxonomical revision of the Cretaceous taxa of the infraorder Araneomorpha is presented (see the summary): At least 17 families of spiders are reported from Lower and Middle Cretaceous ambers of the Northern Hemisphere; at least 8 families – about 50% – are extinct, 6 families from the Cretaceous are described for the first time, see the appendix; most families are members of the Hyplogynae and are still known from the Burmese amber only. – Connecting ("missing") links (taxa) are reported and discussed from Cretaceous spiders. – It is supposed that (mainly about 50 to 70 million years ago) a COMBINATION OF EVENTS – which may have been linked – caused an enormous change in the araneomorph spider faunas: (a) climatic changes including the K-T events, (b) the diversification of non-flying insects (mainly the high number of workers of social living ants which provided a huge biomass as the prey for spiders), (c) losses of the cribellum in certain spider taxa, which were linked to the origin of sticky droplets of the capture webs, and (d) changes from the orb web to various kinds of irregular capture webs as well as (e) numerous losses of the capture web.

SUMMARY: The composition of the Cretaceous, Early Tertiary (Eocene) and extant areneomorph spider FAUNAS show conspicuous differences: **(1)** HAPLOGYNE FAMILIES are strongly dominating in Cretaceous ambers which may be called the age of the Haplogynae; **(2)** GAP (a): there is no hint of an early diversification of members of the RTA-clade which is very diverse today, e. g. Corinnidae, Salticidae, Thomisidae, and of modifications/losses of the capture web; only cribellate taxa of this clade have been found up to now: A single family (questionable Dictynidae) in the Lower or Mid Cretaceous ambers of the Northern Hemisphere. An "explosive" diversification of entelegyne spiders (the Entelegynae) happened most probably not before the end of the Cretaceous; they firstly were frequent in the Early Tertiary (Eocene), e. g. in the Baltic amber forest. Several erroneous determinations of Cretaceous spiders – which were published during the last decade mainly by PENNEY – are corrected: Proofs of (e.g.) the families Corinnidae, Linyphiidae, Pisauridae, Salticidae, Sparassidae, Tetragnathidae, Theridiidae and Thomisidae have to eleminate from the list of the known Cretaceous spider faunas; most "ghost lines" in previous cladograms which refer to these taxa are regarded as incorrect; **(3)** GAP (b): There is also no proof or hint of a diversification of higher taxa of the non orb-weaving spiders of the very diverse superfamily Araneoidea

(e. g. Linyphiidae, Synotaxidae, Theridiidae); only (ancient) orb-weaving taxa of this superfamily are known from the Cretaceous. The orb web has turned out as a very old structure in a geological sense but its losses are apparently "young" and not reported from the Cretaceous. The families of the Araneoidea s. l. are 3 times more frequent in the Eocene (the ecribellate araneoid families are even 5 times more frequent) than in Cretaceous ambers; **(4)** EXTINCTIONS: Not a single spider genus is surely known from the Cretaceous which survived up to now or only to the Eocene Baltic amber forest; *Ariadna* AUDOUIN (Segestriidae) may be an exception. About 50% of the Cretaceous spider families are extinct; **(5)** the GEOGRAPHICAL DISTRIBUTION of some families – e. g. Archaeidae – in the Cretaceous is totally different from their distribution today. The relict family Segestriidae and the Oonopidae: Orchestininae may be old Pangaean taxa, the Lagonomegopidae was a "pan-cretaceous" family; **(6)** the LOSSES OF THE CRIBELLUM are connected to the diversification of spiders, especially to the evolution of the ecribellate Araneoidea; **(7)** the CO-EVOLUTION OF SPIDERS AND ANTS is discussed; it seem to have existed in several perspectives; **(8)** BEHAVIOUR, PREY and WEBS: Cheliceral stridulatory files in Cretaceous spiders of the superfamily Archaeoidea and "clasping spurs" in males of the superfamily Dysderoidea s. l. indicate the geologically oldest proofs of special kinds of spiders' courtship behaviour. By far the main prey of spiders in Burmese amber was Diptera. Structures of the chelicerae and the first legs in Cretaceous spiders of the superfamily Archaeoidea indicate the oldest proof of spider-eating spiders. The shape of the prosoma and the position of the eyes led to conclusions on the basic pattern of the capture web in extinct Uloboridae. The geologically oldest draglines (of Uloboridae), threads of capture webs and sticky droplets as well, and furthermore a nursery web (see *Pholcochyrocer* n. gen.) are reported from Cretaceous spiders. Camouflage: See the paragraph below on the family Uloboridae; **(9)** The BODY SIZE of the Cretaceous spiders in amber is – on average or even absolutely – less than the size of their Eocene or extant relatives. – **(10)** A LIST OF AND AN IDENTIFICATION KEY to the araneomorph spider families of the superfamilies Araneoidea s. l. (= "Orbiculariae"), Archaeoidea (= Palpimanoidea), Dysderoidea and Oecobioidea (Oecobiidae) as well of the RTA-clade (questionable Dictynidae) in Cretaceous ambers is given. – **(11)** The following TAXA IN CRETACEOUS AMBERS are described for the first time; various other – named or unnamed – taxa of various kinds of amber are shortly described, revised or listed:

(**A**) from **MYANMAR** (= **BURMA**, Birma), the Burmite: (1) Dysderoidea: (I) ?Segestriidae indet.; (II) Oonopidae: (a) Gamasomorphinae: *Eogamasomorpha* **n. gen**. with *E. nubila* **n. sp**., and (b) Orchestininae (**n. fam**.) (described in the paper no.2 in this volume); (III) Plumorsolidae **n. fam**. (see below: Lebanese amber): P. indet.; (IV) Eopsilodercidae **n. fam**.: (a) Eopsilodercini **n. trib** with *Eopsiloderces* **n. gen**. and *E. loxosceloides* **n. sp**., and (b) Furcembolusini **n. trib**. with *Furcembolus* **n. gen**. and *F. andersoni* **n. sp**.; (V) Praeterleptonetidae **n. fam**.: (a) Praeterleptonetini **n. trib**. (from Pisauridae, **n. relat**.): *Praeterleptoneta* **n. gen**. with *P. spinipes* **n. sp**., (b) Palaeohygropodini **n. trib**.: *Palaeohygropoda myanmarensis* PENNEY 2004 (**n. relat**.) and (c) Pholcochyrocerini **n. trib**.: *Pholcochyrocer* **n. gen**. with *P. guttulaeque* **n. sp**.; (2) Archaeoidea (= Palpimanoidea): (I) Archaeidae s. l.: (a) Archaeinae: *Burmesarchaea*. **n. gen.** with *B.* (sub *Afrarchaea*) *grimaldii* (PENNEY 2003) (**n. comb**.); (b) Lacunaucheniinae **n. subfam**.: *Lacunauchenius* **n. gen**. with *L. speciosus* **n. sp**., *Eomysmauchenius* **n. gen**. with *E. septentrionalis* **n. sp**., *Filiauchenius* **n. gen**. with *F. paucidentatus* **n.**

sp.; (II) Lagonomegopidae: *Burlagonomegops* with *B. eskovi* PENNEY 2005; (III) Micropalpimanidae **n. fam**.: *Micropalpimanus* **n. gen**. with *M. poinari* **n. sp**.; (IV) Questionable Huttoniidae; (3) Doubtful superfamily: Burmascutidae **n. fam**.: *Burmascutum* **n. gen**. with *B. aenigma* **n. sp**., (4) Oecobioidea: Oecobiidae: Mizaliinae: *Zamilia* **n. gen**. with *Z. antecessor* **n. sp**.; (5) Araneoidea s. l: Uloboridae: *Burmuloborus* **n. gen**. with *B. parvus* **n. sp**., *Palaeomiagrammopes* **n. gen**. with *P. vesica* **n. sp**. and *Paramiagrammopes* **n. gen**. with *P. cretaceus* **n. sp**.; (6) RTA-clade: Questionable Dictynidae: *Burmadictyna* **n. gen**. with *B. pecten* **n. sp**.;

(B) from **LEBANESE amber** are described: Dysderoidea: Plumorsolidae **n. fam**.: *Plumorsolus* **n. gen**. with *P. gondwanensis* **n. sp**. and Segestriidae: Lebansegestriinae **n. subfam**. with *Lebansegestria* **n. gen**. and *L. azari* **n. sp**.;

(C) from **JORDANIAN amber**: (1) Dysderoidea: Segestriidae: ?*Ariadna amissiocoli* **n. sp**.; (2) doubtful superfamily: Salticoididae **n. fam**.: *Salticoididus* **n. gen**. with *S. kaddumiorum* **n. sp**.; (3) questionable Oecobioidea indet.; (4) Araneoidea: ?Protheridiidae WUNDERLICH 2004: Zarqaraneini **n. trib**.: *Zarqaraneus* **n. gen**. with *Z. hudae* **n. sp**.. – Extant taxon: The subfamily Psilodercinae DEELEMAN-REINHOLD 1995 (Ochyroceratidae) is eleveted to family rank (**n. stat**.). – Suprageneric extinct and extant taxa: See the list in the appendix of this volume.

Keywords: Alava, amber, angiosperms, ants, Araneae, Araneidae, Araneoidea, Araneomorpha, araneophagy, Archaeidae, Archaeoidea, Baltic amber, Birma, Burma, body size, Burma, Burmascutidae, Burmite, camouflage, Canada, capture web, clasping spine, clasping spur, co-evolution, connecting link, C-Pg boundary event, courtship behaviour, Cretaceous faunas, cribellum loss, Deinopidae, Dictynidae, diversification, dragline, Eocene European amber forests, Eopsilodercidae, erroneous determinations, evolution, extinction, Formicidae, fossils, France, Gamasomorphinae, Gondwanaland, historical biogeography, Jordan, K-T boundary event, Kurnub sandsone formation, Lacunaucheniinae, Laurasia, Lebanese amber, Lebanoecobiinae, Lebanon, Lebansegestriinae, Linyphiidae, Loxoscelidae, Micropalpimanidae, Lebanon, Microsegestriinae, missing link, Mizaliinae, Myanmar, Mygalomorpha, new taxa, New Jersey, Ochyroceratidae, Oecobiidae, Oonopidae, Orbiculariae, orb web, Orchestininae, palaeobiogeography, palaeofaunistic, Palpimanidae, Palpimanoidea, Pangaea, phylogeny, Pisauridae, Plumorsolidae, Praeterleptonetidae, preservation of amber, prey of spiders, Protheridiidae, Psilodercidae, relict taxa, Salticidae, Salticoididae, Selenopidae, Sicariidae, Spain, spiders, stridulation, Theridiidae, Uloboridae, USA, webs, Zarqa river, Zodariidae, Zygiellidae.

CONTENTS

Acknowledgements: From GEORGE POINAR (Jr.) I kindly got the loan of his private collection, 50 fossil spiders in mid Cretaceous Burmese (Myanmar) amber, stored in the OSU. From the NHML (Palaeontol. dept., ANDREW ROSS) I kindly got the loan of a dozen spiders in mid Cretaceous Burmese (Myanmar) amber. From the MNHNP, lab. d'entomology (DANY AZAR) I kindly got some spiders in Lower Cretaceous Lebanese amber. HANI KADDUMI (Jordan, Amman) showed me more than a dozen fossil spiders in Lower Cretaceous amber from Jordan from the Kurnub Sandstone formation of the Zarqa river canyon which were collected by him and his wife, and which are kept in his private collection of the ERMNH; he entrust me three spiders in Lower Cretaceous Jordan amber. From the collector SCOTT ANDERSON (USA) I got some very interesting spiders in Burmese amber, from RON BUCKLEY, an US-american dealer of amber inclusions, I bought 50 spiders in mid Cretaceous Burmese (Myanmar) amber. – If not otherwise mentioned the fossils are kept in the collection of J. WUNDERLICH (CJW) in the Laboratory of Arachnology in 69493 Hirschberg, Germany (up to July 2004 it was located in Straubenhardt, Germany). Furthermore I thank very much WOLFGANG WEITSCHAT (GPIUH) who was involved with the loan of fossil spiders and gave hints to amber collectors. ALEX BEIGEL also gave important hints to dealers of Cretaceous spiders. Furthermore I thank for the loan of material, help with literature as well as discussions and corrections of parts of the manuscipts THEO BLICK, CARSTEN BRAUCKMANN, JASON DUNLOP, HEINRICH GRABENHORST, JONAS DAMZEN, FRIEDHELM EICHMANN, DANILO HARMS, CHRISTEL & HANS WERNER HOFFEINS, BERNHARD HUBER, PETER JÄGER, FRIEDRICH KERNEGGER, OTTO KRAUS, MANFRED KUTSCHER, WALTER LUDWIG, ZHU MINGSHENG, EVGENY PERKOVSKY, NORMAN PLATNICK, SIGITAS PODENAS, RUTHILD SCHÖNEICH, NORBERT VAVRA, and HAJIME YOSHIDA.

Material: The material which has been investigated is/will be stored in the following institutions:

CJW = private collection of J. WUNDERLICH, Laboratory of Arachnology in 69493 Hirschberg, Germany. – Note: Most parts of this material will probably be given to the Senckenberg-Museum in Frankfurt a. M. and to the Staatliches Museum für Naturkunde in D-02806 Görlitz in the future; the exact storage will be published,
ERMNH = Eternal River Museum of Natural History in Jordan (Amman) (still in construction) (H. F. KADDUMI),
MNHNP = Musem National d'histoire Naturelle Paris (D. AZAR),
NHMLP = Natural History Museum London, dept. of Palaeontology, England (A. ROSS),
GPIUH = Geological-Palaeontological Institute, University Hamburg, Germany (W. WEITSCHAT),
OSU = Oregon State University, Corvallis, USA (G. POINAR jr.),
SMF = Senckenberg-Museum, Frankfurt a. M., Germany (P. JÄGER).

Note: Fossil spiders in Cretaceous amber from Spain (Alava; V. ORTUNO) and from North America (D. A. GRIMALDI) as loans were not available to me, and will probably studied by PAUL SELDEN.

INTRODUCTION

Spiders (Araneae) is a diverse order of arthropods which has a worldwide distribution; 40 000 extant species of more than 100 families are described today (more than 100 000 species are expected). Fossils: Far less than one thousand species have been described; only one to two thousand spider specimens in Cretaceous ambers have been studied up to now more or less closely; they may be compared with the number of more than 100 000 specimens of spiders which have been observed or studied in Eocene European – mainly Baltic – ambers.

In this paper I focus on members of the infraorder Araneomorpha*, especially on the more basal haplogyne superfamilies Dysderoidea s. l. (incl. Scytodidae, Pholcidae and related families) and Archaeoidea (= Palpimanoidea), but also on members of the superfamilies Oecobioidea and Araneoidea s. l., as well as few members of the cribellate Dictynoidea of the advanced RTA-clade.

---

*Araneomorpha (including e. g. Orb Web Spiders and Jumping Spiders) – in contrast to the much older archaic (“primitive”) Mesothelae and Mygalomorpha (e. g. “Tarantulas” and “Bird Spiders”) – is by far the most diverse infraorder of spiders today.

During the last few years numerous taxa of araneomorph spider families – including several families of the RTA-clade – were mentioned or described from ambers of the Cretaceous Period (see the paragraph on erroneous determinations below!); they are known from different deposits of the Northern Hemisphere only and are most often preserved in amber from North America (Canada, USA), the Mediterranean (Jordan, Lebanon, Syria, N-Spain), France, Siberia and Myanmar (= Burma), see the papers of MCALPINE & MARTIN, PENNEY, SELDEN as well as the book of WUNDERLICH (2004) and below. In this paper I describe new species mainly from Burmese amber, few from Jordanian and Lebanese amber, taxa in other kinds of amber are mentioned.

The investigation of fossil spiders of the Cretaceous Period is still at its very beginning; only some hundred fossil specimens – including about three dozen well preserved adult males – are known to me personally from this period, but it is already obvious that fossil spiders from the Cretaceous are of very special interest: So araneophagy (by members of the Archaeoidea), dwarfism (within the Archaeoidea and Dysderoidea, see the genera *Burmarachne* and *Praeterleptoneta*), and peculiar courtship behaviour (stridulation in members of the superfamily Archaeoidea, clasping in the superfamily Dysderoidea) have already been well established in the mid and early Cretaceous. (Most probably such structures have been much earlier evolved in mygalomorph spiders).Conspicuous morphological structures may confirm such and also other peculiar behavour. Draglines are reported for the first time from Cretaceous spiders – as the geologically oldest proof – in the family Uloboridae (*Paramiagrammopes*). The geologically oldest spiders nursery is reported from a piece of Burmese amber which also contains the male holotype of *Pholcochyrocer guttulaeque* n. sp. (see this species of the Praeterleptonetidae), the geologically oldest threads of capture webs – which even bear remains of sticky droplets – are reported from spiders in Early Cretaceous Jordanian amber, see e. g. the superfamily Araneoidea, the extinct new family Salticoididae, and Diptera as prey of spiders in Burmese amber as well. The knowledge of the structures of capture webs in Cretaceous spiders is still poor, although there are indications to the existence of orb webs, see below (the family Uloboridae). See also KADDUMI (2007: 4, photo 43).

Close investigation of Cretaceous spiders – and a comparison with the extant and the Eocene (mainly Baltic amber) spider faunas – may provide conclusions on evolution, palaeobiogeography and behaviour of araneomorph spiders, e. g. ideas on effects of the Cretaceous-Tertiary boundary extinction events as well as proofs of connecting (“missing”) links, and – hopefully in the future – conclusions on the relationships of the extinct families Burmascutidae, Plumorsolidae and Salticoididae as well as of the extant families Dictynidae (doubtful fossil taxa) and Salticidae. The diversification of certain superfamilies and families as well as their rareness or absence in Cretaceous ambers – examples are Archaeoidea, Dysderoidea, Araneoidea, Corinnidae, Linyphiidae, Salticidae, Theridiidae and Zodariidae as well as the extinct families – may provide hints to the era and geographical region of their diversification or even of their origin. Huttoniidae is restricted today to New Zealand but – based on not surely determined juvenile – members of this family have recently been reported from the Cretaceous of North America, see PENNEY & SELDEN (2006).

The age of the ambers: Most of the known Cretaceous arthropod-bearing ambers which were studied are 80–140 million years old. The amber from Burma (Myanmar) – Burmite – is usually dated as Lower or mid-Cretaceous, see e. g. ZHERIKHIN & ROSS (2000), POINAR & SZADZIEWSKI (2007). Its age is regarded as about 90 (80 to >110?) million years; that is two or three times the age of Baltic amber and about five times the age of most kinds of Dominican ambers. The age of the Jordanian and Lebanese ambers from the Kurnub Sandstone Formation is usually dated as Lower Cretaceous, 120–130 million years (about three times the age of the Baltic amber), see e. g. BANDEL et al. (1997); but according to KADDUMI (2005, 2007) the oldest Jordanian amber may be even up to 140 million years old, quite near to the Jurassic border, and being probably the oldest known arthropod-bearing amber. Of greatest interest regarding the spiders' evolution would be the discovery of larger amber deposits which are only 60–80 million years old.

Preservation of the inclusions: The inclusions in Burmese, Jordanian and Lebanese ambers – similar to most inclusions of other kinds of Cretaceous ambers – are most often more or less deformed and darkened by natural pressure and heating, and the pieces of amber are frequently quite breakable. The spiders' eyes frequently bear bubbles/emulsions. Parts of – more often – the upper side of the body – including the eyes – are cut off at a layer within the Cretaceous amber quite more frequently than in Baltic amber, e. g. in the holotypes of *Eopsiloderces loxosceloides* n. gen. n. sp. and *Zarqaraneus hudae* n. gen. n. sp., see the photos and the figs. below. The typical white emulsion of most animal inclusion in Baltic amber is absent or only weakly developed on Cretaceous arthropod inclusions. The surface of Cretaceous pieces is generally thought to be quite stable in time, but I found tiny fissures on the surface of some pieces of Burmese amber, e. g. on a piece which is stored in the NHMLP – In. no. 19132 – which includes several holotypes. This piece may have been collected and poolished about 80 years ago. The fissures hinder already the recognition of some inclusions; they most probably will grow in the future, and will demage the inclusions if the pieces of amber will not be preserved, e.g. in artificial resin.

Producer of the amber and environment: The producent of the Jordanian and the Lebanese amber is said to be *Araucaria*, of the Burmite probably *Araucaria*, too or species of *Metasequoia* or related members of the Coniferae. Stellate hairs and leafs indicate the existence of angiosperms within the Cretaceous amber forest. Insects and their frequent and various excrements indicate a diverse fauna of insects in these amber forests; ants are extremely rare and even (still) unknown from the old Jordanian and Lebanese ambers. `Simple` stellate hairs in Burmite and other Cretaceous ambers are much rarer than in Baltic amber but plant hairs which consists of several parts/branches or brushes are not rare.

Climate: The climate of the Burmese amber forest is said to be humid-warm; the reports of typical tropical spider families like Deinopidae indicate tropical regions (too). The climate of the Jordanian and the Lebanese amber forests may have been quite similar.

Camouflage in the Uloboridae: OPELL & WARE (1987: 99) discussed the “predator avoidance hypothesis” regarding the cryptic behaviour in *Miagrammopes*, whose slender and long-legged members may resemble thorns or broken twigs as they monitor their webs in a stretched position. The similar shape of body and anterior legs indicate a similar behavior in the Eocene genus *Eomiagrammopes,* and in the Cretaceous genus *Palaeomiagrammopes*, see the photos 106–109 in the book of WUNDERLICH (2004) and the photos (e.g. 107) of *Palaeomiagrammopes* in this volume. Note that the legs possess usually an unnatural position in fossil spiders. In some fossil Uloboridae in the amber – see the photos – the pair of first legs are apparently rised in a defensive position. – Camouflage (mimesis) by the “stout” members of *Hyptiotes*: See the paper no. 6 in this volume.

Dwarfism and female gigantism: Dwarf spiders are frequent in Cretaceous ambers (see the descriptions of the families below); members of certain species are smaller than all known extant relatives of their families: Extinct Cretaceous spiders of the Segestriidae are the tiniest known members of this family and its relatives (even smaller than their relatives in Eocene Baltic amber), the Cretaceous Micropalpimanidae are the tiniest known members of the superfamily Archaeoidea, the Cretaceous spiders of the Uloboridae are the tiniest known members of this family and of the cribellate (deinopid) branch of the Araneoidea s. l. (“Orbiculariae”) as well, the Cretaceous spiders of the – questionable – Deinopidae (*Palaeomicromenneus*) are the tiniest known members of the Deinopidae. – Does dwarfisms really exist in Cretaceous spiders or were spiders of those taxa small/tiny at the beginning of their evolution? The geologically oldest mammals were also very small animals...
There is no indication of female gigantism in Cretaceous (or Eocene) araneoid spiders which is known from extant spiders like Araneidae and Deinopidae. But we have to take into consideration that large spiders in amber are very rare, and females in amber are still much rarer than males.

Courtship behaviour of spiders in Burmese amber: (a) Males of at least two families of the superfamily Archaeoidea (= Palpimanoidea) – Archaeidae: Lacunaucheniinae (fig. 49) and Micropalpimanidae n. fam. (*Micropalpimanus poinari* n. sp., fig. 76) – possess lateral cheliceral files which form a stridulatory organ in combination with structures of a basal pedipalpal article. Similar stridulatory organs are known from numerous extant as well as Eocene spider taxa, and apparently it – or its tendency – is an apomorphic character of the superfamily Archaeoidea s. l., see WUNDERLICH (2004). Such organs are used in the courtship behaviour; the existence of these structures in the Cretaceous provide indirectly the geological oldest proof of this kind of courtship behaviour in spiders. (b) Praeterleptonetidae n. fam.: Males of *Palaeohygropoda myanmarensis* PENNEY 2004 (fig. 36) possess a “clasping spur” of their pedipalpal patella which probably was used for fixing the female during or before the copulation. (c) A cheliceral “clasping spur” exists in males of *Eopsiloderces loxosceloides* n. sp. (fig. 15) (Eopsilodercidae).

Capture webs and threads (see also below: “prey”): Members of numerous spider families in Cretaceous ambers were apparently weavers of capture webs. Questionable cribellate threads are preserved with certain members of the family Uloboridae in Burmese amber. The existence of a calamistrum and a cribellum of *Burmadictyna pecten* (figs. 139–140) indicate the existence of a cribellate capture web. Remains of

certain capture webs – which even may bear sticky droplets (fig. 25, photos 52f) – have been found with members of all superfamilies in question, and in several families, like Araneidae, Eopsilodercidae, Praeterleptonetidae (fig. 25), Protheridiidae, Salticoididae, and Uloboridae, see below. Threads are preserved e. g. in Jordanian amber of the CJW nos. F2002, 2003 and 2004 and in Burmese amber, OSU no. B-A-1-21 of the G. POINAR coll. (incl. remains of sticky droplets, photos), questionable threads in Jordanian amber F1999 and F 2000. Deinopidae is a tropical family; their striking specialized prey capturere behaviour (with the help of a strongly modified orb web) existed probably – according the shape of the body and the position of the eyes – already in the mid-Cretaceous (but the posterior median eyes of these spiders were smaller).
No taxon of the superfamily Araneoidea is known from the Cretaceous Period up to now which indicates the existence of an irregular capture web or a loss of the capture web; apparently the orb web changed to an irregular web or got lost within members of this superfamily only late, probably not before the Upper Cretaceous about 80 million years ago or the Palaeocene. Losses of a capture web within the RTA-clade – in or within e. g. the families Corinnidae, Salticidae, Thomisidae or Zodariidae – happened probably also first in the Late Cretaceous or the earliest Tertiary.
Cribellate spiders are known from the Cretaceous but cribellate silk has not been reported from this period up to now; see Dictynidae and Uloboridae below. (Cribellate threads in Eocene spiders: See WUNDERLICH (2004: 62–63, photos 533–534 p. 537).

Prey: Diptera were apparently by far the most frequent prey of Cretaceous spiders (which built capture webs) at least in Burmese in amber; I saw several Diptera in collections of dealers which are spun in in spiders silk or are hanging on threads (see the photo), Coleoptera and Hymenoptera are much rarer. – Remains of Diptera are preserved near the male holotype and a female of *Burmorchestina pulcher* n. sp., and near a questionable Dictynidae may have been the prey of these spiders. A member of the Diptera: Nematocera (body length 1.3mm), captured in a spiders web, is preserved in Burmese amber, F2012/BU/AR/CJW. The midge has most probably been succed out by a spider, the margins of its incomplete antennae bear hyphae. The threads around the midge bear probably few tiny droplets (photo). Another midge (Psychodidae?), coll. SCOTT ANDERSON (USA), is well and completely preserved in a light orange piece of amber. It is hanging on a spiders thread which bears remains of two droplets. The deformed abdomen of the midge may indicate that it has been the prey of a spider which may have been a member of the superfamily Araneoidea, see the photo 58. – KADDUMI (2007: 268) reports on a small wasp "which was found in Jordanian amber wrapped in a spider's web.".
Archaeidae, Micropalpimanidae, Oonopidae, and Plumorsolidae were free hunters.
Morphological specializations in members of the family Archaeidae as well as of special hairs on the anterior legs of certain members of the palpimanoid branch (superfamily Archaeoidea), e.g. of the families Archaeidae, Micropalpimanidae and certain Lagonomegopidae, indicate spider feeding (araneophagy) of these spiders, similar to their extant or Eocene relatives, see below and WUNDERLICH (2004: 567, photo 626).
Members of these families are the geologically oldest reports of spider eaters. Members of the Archaeidae used most probably a "sit-and wait-position" upside-down.
The most frequent spiders' prey which has been preserved in Eocene Baltic amber was ants, contrarily to Cretaceous spiders, see WUNDERLICH (2004: 91); ants are still not reported from the old – Early Cretaceous – Jordanian and Lebanese ambers.

LIST OF AND REMARKS ON THE SPIDER FAMILIES AND SUBFAMILIES IN CRETACEOUS AMBERS, with remarks on erroneous identifications:

About 17 families in Cretaceous ambers are reported in this paper; at least 8 families (50%!) (and several subfamilies of extant families) are extinct (they are marked below with an asterix.

I focus on members of the infraorder Araneomorpha, the superfamilies Dysderoidea, Archaeoidea s. l. (= Palpimanoidea), less on the Oecobioidea (Oecobiidae only, but see Burmarachnidae and a probably undescribed family), Araneoidea s. l. (= “Orbiculariae”; two cribellate and about three ecribellate families) as well as of the RTA-clade (only questionable members of the family Dictynidae are known). Remains of the Mygalomorpha in Cretaceous ambers are mainly preserved as exuvia or legs; they are only shortly described and photographed but not closely studied in this paper.

Araneomorph spiders includes two main groups:

(1) The “Haplogynae”: The more “ancient” and haplogyne superfamilies (a) the Dysderoidea s. l. and (b) the Archaeoidea s. l. (= Palpimanoidea), which both were diverse in Cretaceous ambers, and which frequently have only six eyes (figs. 7, 19), most often thickened articles of the ♂-pedipalpus, a short cymbium, a simple bulbus (figs. 6, 18, 21), and a non-sclerotized genital area of the female, as well as

(2) the "Entelegynae”: The more advanced entelegyne spiders which usually possess eight eyes, more complicated genital organs including an sclerotized genital plate (epigyne) in the female sex, and usually a large cymbium which covers largely the bulbus. This branch includes most extant spider taxa, the superfamilies (c) Oecobioidea (Hersiliidae, Oecobiidae), (d) two families of doubtful superfamilies: Burmascutidae and Salticoididae, (e) Araneoidea s. l. (= Orbiculariae”) (e. g. Orb Weavers, Araneidae, Deinopidae and Uloboridae), as well as (f) the RTA-clade (e. g. Dictynidae, Jumping Spiders (Salticidae) and Wolf Spiders (Lycosidae); Lycosidae and Salticidae are unknown from Cretaceous ambers, the proof of the Dictynidae is doubtful).

(a) Dysderoidea s. l. (5 families): Segestriidae (Ariadninae, *Lebansegestriinae, *Microsegestriinae, questionable subfamily), Oonopidae (Gamasomorphinae, Orchestininae: see the paper no. 2 in this volume), *Eopsilodercidae n. fam. (2 tribus), *Plumorsolidae n. fam., and *Praeterleptonetidae n. fam. (3 tribus). – (Remark: Dysderidae, Filistatidae, Leptonetidae Ochyroceratidae, and Pholcidae – the absence of this family is a surprising gap in the Cretaceous spider faunas – are probably present in Cretaceous ambers, too, but they still have not been found, see below);

(b) Archaeoidea (= Palpimanoidea) (4 or 5 families): Archaeidae s. l. (Archaeinae, *Lacunaucheniinae n. subfam.), questionable Huttoniidae, Lagonomegopidae, and *Micropalpimanidae. – Remarks: (1) The extinct Jurassic Jurarchaeinae (a subfamily of the Archaeidae) and the extinct Tertiary family Spatiatoridae (Baltic amber) could also well exist in Cretaceous ambers in my opinion. (2) ESKOV (1987) tentatively assigned *Baltarchaea conica* (KOCH & BERENDT 1854) (= *Archaea conica*) to the subfamily Mecysmaucheniinae, but Mecysmaucheniidae sensu PENNEY (2003, tab. 1) has to delete from the list of Eocene spiders: The report is based on *Baltarchaea* ESKOV which is – e. g. according to its femoral humps and their three pairs of spinnerets – actually a member of the Archaeinae, see WUNDERLICH (2004). (3) Mecysmaucheniidae sensu SAUPE & SELDEN with *Palaeomysmauchenius archingeayensis* SAUPE & SELDEN (in prep.) is – according to its at least two pairs of spinnerets – probably not a member of the Mecysmaucheniinae but it may be a member of the Lacunaucheniinae n. subfam., see below Archaeidae s. l.: Lacunaucheniinae.

(c) Oecobioidea (at least a single family): Oecobiidae (*Lebanoecobiinae, *Mizaliinae and questionable Oecobiinae) as well as a questionable family of the Oecobioidea;

(d) Doubtful superfamilies: Two ancient families: *Burmascutidae n. fam. and *Salticoididae n. fam..

(e) Araneoidea s. l. (= “Orbiculariae”): About 4–6 families: The cribellate deinopid branch: Deinopidae? and Uloboridae, and the ecribellate araneoid branch): Araneidae, *Protheridiidae?, Zygiellidae (subfamily of the Araneidae?), probably *Salticoididae, and a questionable taxon indet. of the “spineless femur clade”. All described spiders were probably taxa of orb-weaving families (!) (the extinct Protheridiidae, too?).

Notes: (1) Proof of Linyphiidae (erroneous determination): See below: Questionable Zygiellidae. (2) In Cretaceous ambers I expect members of certain extinct araneoid families like Baltsuccinidae, see WUNDERLICH (2004) which are – rarely – reported from Baltic amber; at least members of the families Anapidae s. l. and Theridiosomatidae could be present, too. (3) The oldest possible/questionable taxa of the superfamily Araneoidea were described by SELDEN et al. (1999) from sediments of the Triassic (225 million years old), but according to the insufficient preservation the determinations of these taxa are quite unsure – even incorrect in my opinion –, and they may be members of another superfamily, probably of the Dysderoidea s. l. Conclusions which are drawn on such badly preserved specimens are curageous but some of them seem not well founded to me.

(f) Members of the RTA-clade s. l. (probably a single family only; an adult male is still unknown): Dictynidae (questionable): Two juveniles sensu PENNEY (2002) in amber from New Jersey (USA) may be members of an undescribed genus. Based on a female the new genus *Burmadictyna* is described below as a questionable taxon of the Dictynidae.

Remark on the families Pisauridae and Selenopidae: An adult male of *Palaeohygropoda myanmarensis* PENNEY 2004 has been described in Burmese amber; but it actually has turned out as a member of the superfamily Dysderoidea s. l., a member of the new family Praeterleptonetidae (see below, Palaeohygropodini).– Allegedly Eocene Selenopidae sensu PENNEY (2007): See below, the paragraph “Remarks on erroneous determinations” (?= Dysderoidea).

Remarks on erroneous determinations and conclusions on relationships:

The determinations of fossils which are based on juveniles may easily cause errors: In contrast to my earlier opinion I now regard the determination of a member of the Thomisoidea in Cretaceous amber from Taimyr (and some others) as erroneous, too, see ESKOV & WUNDERLICH (1995). These spiders were not determined to species or genus level. Spiders in Cretaceous ambers – which are not well preserved – missled me to date back the genus *Orchestina* SIMON (Oonopidae) to the Cretaceous Period, see WUNDERLICH (2004: 690), and the paper on Orchestininae in this volume p. 60ff. I estimate that more than 80% of the earlier determined Cretaceous spider taxa are incorrectly determined on genus or family or even on superfamily level. One of the rare correct determinations of Cretaceous spiders is *Mesozygiella* PENNEY & ORTUNO 2006 as a taxon related to the extant genus *Zygiella*. The relationships of the new families Burmascutidae, Plumorsolidae and Salticoididae are unsure.
Strange conclusions on fossil spiders are known e. g. from certain (early) geologists who did/do not or only scarcely cooperate with araneologists. A long time ago a faked myrmecomorph spider was mistaken even for a "crossing" (!) of a spider and an ant by HOLL (1828), see WUNDERLICH (2004: 34). – I investigated some fossil spiders in Burmese amber from the NHMLP which were determined by ESKOV, see the list which was given by RASNITSYN & ROSS (2000: 22), e. g. (a) In no. 20197: Sparassidae (sub "Eusparassidae") and Corinnidae (sub "Myrmeciidae"); these juvenile spiders are surely not members of these families, and the larger one may be a member of the new family Plumorsolidae. (b) In no. 20193, according to ESKOV juvenile spiders of the "Theridiidae" and "Myrmeciidae" are also taxa of different families: A comb of tarsus IV is absent in one specimen, the second specimen has a "segestriid" eye position and is a member of the superfamily Dysderoidea. – A female spider was described as a member of the family Linyphiidae from Cretaceous Lebanese amber by PENNEY & SELDEN (2002), but according to its characters – see WUNDERLICH (2004: 1299) – this taxon is certainly not a member of the Linyphiidae, but probably of the Protheridiidae, see below. The proof of the "Linyphiidae" indet. sensu PENNEY (2002) in Cretaceous amber from New Jersey seems unlikely to me: The paracymbium which is strongly standing out is untypical for Linyphiidae, there is no indication to the existence of a free/movable paracymbium, and the chaetotaxy is similar in various families. Certain spiders in Burmese amber were erroneously determined as Salticidae, see PENNEY (2004: 241); and Salticidae in ?Eocene French amber sensu NERAUDEAU et al (2002) were also misidentifications, see PENNEY (2007: 74). According to the taxonomic characters of the Cretaceous juvenile or adult spiders which are published as members of the genera *Segestria* LATREILLE 1804 (Segestriidae) and *Orchestina* SIMON 1882; see PENNEY (2002): There is no sure proof of these genera from the Cretaceous. – The new genus *Burmesarchaea* (Archaeidae) has erroneously been regarded as a member of an extant genus (*Afrarchaea*) by PENNEY (2003), see below. Pisauridae sensu PENNY (2004) is not a taxon of the Pisauridae (and even not of the superfamily Lycosoidea or the RTA-clade) but of a quite different branch and superfamily, the Dysderoidea s.l. (the new family Praeterleptonetidae), see below. The report of the family Huttoniidae in Cretaceous ambers of North America was only

based on juveniles – see PENNEY (2006) –, and has to regard as doubtful. The proof of Cretaceous members of the families Deinopidae and Dictynidae has also to confirm, see below.

The allegedly "report" (a foundation of this "determination" was not given!) of a Cretaceous member of the family Zodariidae in French amber, see PERRICHOT et al. (2008: 89), seems – in respect to numerous erroneous reports of Cretaceous spiders – quite doubtful to me. A loan of material was impossible.

The allegedly Eocene report of a spider of the Selenopidae in French amber – according to PENNEY (2007) it "clearly belongs in *Selenops*" – was based on an "extremely juvenile" (1.81 mm long) specimen only, but in respect to the proportions of prosoma, legs and opisthosoma, the spider may be subadult or even adult. In contrast to the Selenopidae the tarsal claws are DISTINCTLY toothed in the spider in question, leg bristles are seemingly absent, the shape of the allegedly trichobothria of the tarsi and metatarsi is more hair-like (due to the photos in the original description tarsal trichobothria are absent in my opinion), there is no hint of a laterigrade leg position, the allegedly anterior lateral eyes may be nothing else than artefacts; and only six eyes exist probably. In respect to the combination of these characters I regard the specimen in question more likely being a member of the superfamily Dysderoidea than a member of the family Selenopidae or even of the RTA-clade; some characters are quite similar to the extinct family Eopsilodercidae n. fam., see below. In my opinion there is no proof of the family Selenopidae in Eocene European ambers up to now.

From such miss-identifications or quite unsure determinations some dubious or erroneous conclusions on spiders' evolution and palaeobiogeography may result – for example "ghost lines" which seemingly date back the Theridiidae and other families to the Lower Cretaceous, see PENNEY (2002, 2004, 2008). An enigmatic and very dubious taxon of the Pararchaeidae – see PENNEY et al. (2003: 2603) – SEEMINGLY "dates back per ghost lines" quite a number of families even to the Jurassic Period. (Pararchaeidae has erroneously been regarded as a member of the Archaeoidea instead of the Araneoidea, see WUNDERLICH (2004: 1257)).

I don't know a single member of Linyphiidae, Theridiidae or "pararchaeid" spiders from the Cretaceous up to now which is determined with certainty. Such highly speculative conclusions can probably be avoided if specialists of certain taxa would asked before publishing a paper; reviewing papers means asking too much of certain reviewers which sometimes are hand in glove with the authors or editors. – Speculations may be useful if they are well founded and clearly marked but in my opinion one has to be quite careful when drawing conclusions in respect to "ghost lines" (with the help of pretended or imaginary sister groups) which may turn out simply as "lines of phantasy". (Archosauriea and Saurischia are dated back to the Trias but no one would seriously date back the "related" Aves to that period by a "ghost line"! See WUNDERLICH (2004: 270)). The "evolutionary time table" of araneomorph spiders has completely to revise. – The situation in Triassic and Jurassic araneomorph spiders – which are not enclosed in amber and which usually are badly preserved – is still bader: Their determination even on family level is usually quite unsure but frequently no question mark is added with their publication.

PALAEOBIOGEOGRAPHY of selected families and subfamilies:

The disjunct distribution of certain fossil and extant spiders – e. g. of the families (and their subfamilies) Archaeidae, Cyatholipidae, Huttoniidae, Mimetidae, Plectreuridae, Segestriidae and Synotaxidae – supports the theory of "ousted relicts" over the "mobilistic biogeography", see WUNDERLICH (1995, 2004) (*). In my opinion the biogeography of these families demonstrates additional evidence that the global catastrophes of the K-T boundary events had strong effects on almost all parts of the Northern Hemisphere and relict some spider families to a restricted range, e. g. the Huttoniidae to New Zealand and the Plectreuridae to only certain parts of Central and North America in contrast to their fossil relatives. (Plectreuridae survived to the Eocene in Europe).
According to my recent knowledge only 4 of about 30 extant haplogyne spider families SURVIVED from the early/mid Cretaceous up to now: Archaeidae and probably Huttoniidae of the Archaeoidea, Oonopidae and Segestriidae of the Dysderoidea. Why survived just these families? Archaeidae are specialized spider-eaters, Huttoniidae (spider eaters, too?) survived in a restricted and isolated area (New Zealand), Orchestininae of the Oonopidae possesses a particular – jumping – behaviour which is quite rare or even unique within the Dysderoidea, Segestriidae are specialized hidden tube-dwellers. Archaeidae, Orchestininae and Segestriidae were very "successful" diverse taxa during the mesozoic periods.
Members of two extinct suprageneric taxa – of subfamilies – survived from the Cretaceous only up to the Tertiary (Eocene Baltic amber): The Mizaliinae of the Oecobiidae (known from Burmese amber), and probably the Zarqaraneini questionable members of the Protheridiidae are known from Jordanian amber (if their determination is correct). See also the Eopsilodercidae below.
We have to keep in our mind that the fossil record of spiders (and other fossils) is fundamentally quite incomplete, and most extinct taxa probably died out much later than the most recent fossil has been found ("Signor-Lipps effect"); and they also may have existed for millions of years before the first fossil record.
Members of the Oonopidae: Orchestininae have today a cosmopolitical distribution and are known in Cretaceous ambers from North America, Spain and – quite frequent – from Myanmar (Burma), but there is (still?) no proof in Gondwanan Jordanian and Lebanese amber. Did this subfamily originate in Laurasia and invaded the Southern Hemisphere only in the Early Tertiary?
The relict family Segestriidae (**) was much more diverse in the Cretaceous than today: At least four subfamilies did exist. Extinct Cretaceous taxa/subfamilies are known in New Jersey amber (questionable subfamily) of the previous Laurasia, and in Lebanese amber from the NE margin of the previous Gondwanaland: Lebansegestriinae and Microsegestriinae. A member of the extant cosmopolitical subfamily Ariadninae is furthermore reported from Jordanien amber of the previous Gondwanaland, see below. So Segestriidae may be one of the oldest surviving araneomorph families which origin may go back already to the Triassic or – according to their Cretaceous distribution – even to the palaeozoic (Permian) era of the old continent Pangaea. This suggestion corresponds with the basal branching of this family in the cladogram which was given by the present author (2004: 644–645). – See also the families Archaeidae, Lago-

nomegopidae, Oecobiidae, Oonopidae, as well as the superfamilies Araneoidea s. l., Archaeoidea (= Palpimanoidea), “Dictynoidea”, Dysderoidea s. l. and Oecobioidea.
In the following the distribution of two old spider families is shown, which is of particular interest (figs.1–2): Archaeidae: Archaeinae and the extinct Lagonomegopidae (both Archaeoidea s. l.).

(*) Here we have the case of a “disjunct distribution of authors” from (a) the New World – which mainly accept(ed) “mobilistic biogeography” (as well as in the existence of numerous “Gondwanaland taxa”) – and (b) Old World’s (eurasiatic) authors which mainly prefer the theory of “ousted relicts”, which is well founded; see the papers of e. g. ESKOV (1987, 1992), PENNEY (2006), SAUPE & SELDEN (in prep.), WUNDERLICH (1995, 2004: 243, 1156) as well as the proofs of certain fossils of the Eocene mine/lagerstaette (grube) Messel near Darmstadt in Germany which show some remarkable relationships to taxa of the Southern Hemisphere, e. g. of a mammal of the order Edentata, see SCHAAL & ZIEGLER (1988: 211–215).

(**) extant known are only the subfamilies Ariadninae and Segestriinae as well as the probably related genus *Gippsicola* HOGG 1900 from New Zealand.

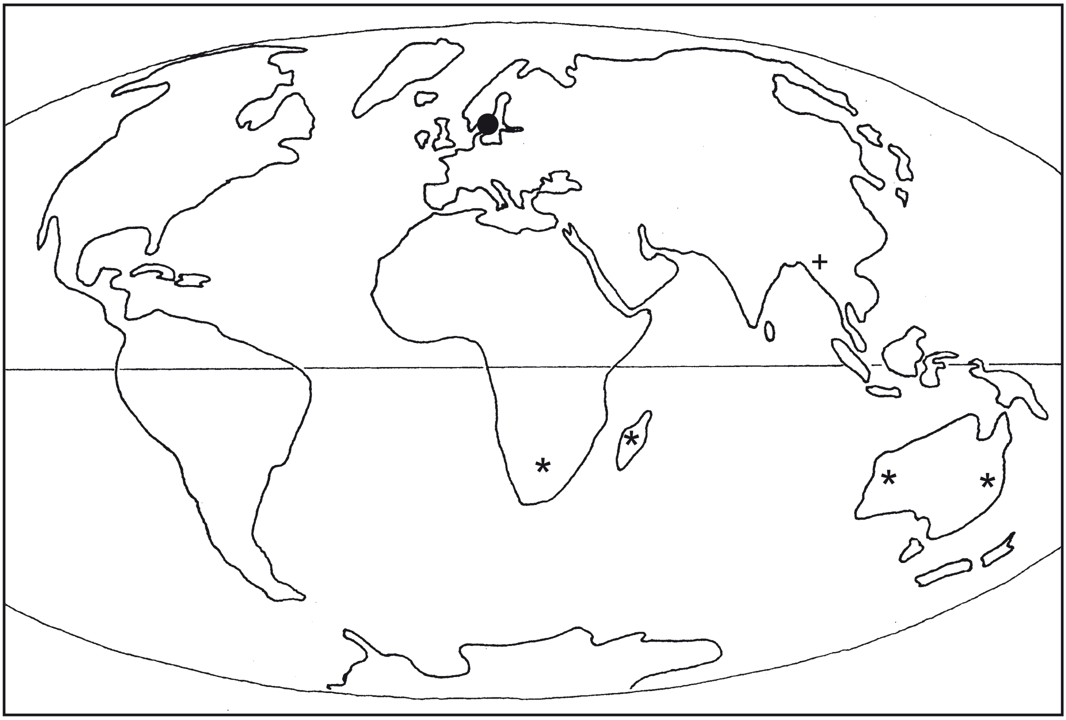


Fig. 1) Distribution of the Archaeidae: Subfamily Archaeinae which is one of the rare extant subfamilies which are known from Eocene Baltic amber and from Cretaceous ambers as well, and additionally from both hemispheres. Fossil taxa are simply known from the Northern Hemisphere: Eocene (black circle, Baltic amber forest) and Cretaceous (+, Burma), extant members are known from the Southern Hemisphere only: South Africa, Madagascar and Australia. (Note: Large amber deposits from the Cretaceous Period of the Southern Hemisphere are still unknown).

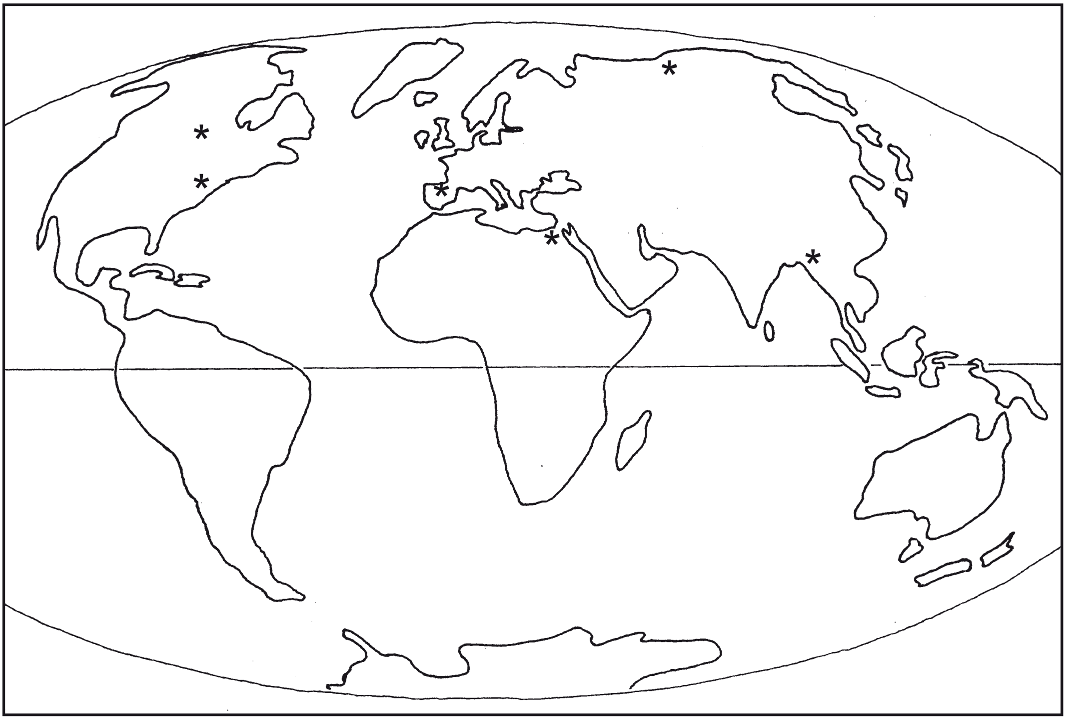


Fig. 2) Distribution of the family Lagonomegopidae (*) which is an extinct familiy of the Cretaceous Period and has proofs in a wide range of the Northern Hemisphere: North America, Siberia, Burma, and the Near East (Jordan).

BIODIVERSITY, PHYLOGENY, EVOLUTION, AND EXTINCTIONS; EFFECTS OF THE K-T BOUNDARY EVENTS

The Cretaceous spider faunas

The CRETACEOUS FAUNAS OF ARANEOMORPH SPIDERS IN AMBER are mainly – probably about 90% – composed of the following higher taxa of spiders (Eocene spiders: See WUNDERLICH (2004)):
a) the "ancient" haplogyne superfamilies DYSDEROIDEA s. l. and ARCHAEOIDEA s. l. (= PALPIMANOIDEA) (a Cretaceous proof of the Dysderidae is still wanting!),
b) the "derived" entelegyne superfamily ARANEOIDEA s. l. (= Orbiculariae) (Araneidae, Deinopidae, Protheridiidae, Uloboridae, Zygiellidae (?= Araneidae) are examples of the Cretaceous).
Members of the superfamily OECOBIOIDEA (Oecobiidae) and of the most advanced members of the RTA-clade s. l. (questionable Dictynidae) are less frequent; see also the families Burmascutidae and Salticoididae which relationships are unsure.

Exists really the proof of a distinct change in the composition of the spider faunas on suprageneric level during the time span ("gap") of about 20 or 30 million years which lies between (a) the Cretaceous amber forests – about 70–80 million years ago – and (b) the Eocene European amber forests about 40–50 million years ago? Here I provide some results based on my present-day knowledge on fossil spiders in amber, spiders which mainly were dwellers of higher strata of the vegetation:

There are enormous differences between the Cretaceous and the Early Tertiary (Eocene) spider faunas (*), the faunas before and after the K-T boundary events. These differences are much greater than the differences between the Early Tertiary and the extant spider faunas; see below and above, e. g. the family Segestriidae. During the period ~70–50 million years ago the entelegyne spiders displaced the haplogyne spiders at least in higher strata of the vegetation and at least in certain parts of the Northern Hemisphere (Europe). Members of the more "ancient" superfamilies Archaeoidea and Dysderoidea are haplogyne spiders, frequently six-eyed and longer-living. Families and genera of these more "ancient" superfamilies dominate in Cretaceous ambers (**); I know (see below) about 11 of the "ancient" haplogyne families – but only about 5–6 families of the more advanced entelegyne superfamily Araneoidea s. l. (Araneidae, Deinopidae, questionable Protheridiidae, Uloboridae, Zygiellidae (?= Araneidae), fam. indet.) (***), as well as a single family of the Oecobioidea (Oecobiidae), and a single family of the RTA-clade (questionable Dictynidae) (all together about 7 families). From the Early Tertiary (Eocene) ambers 11 families are reported from the

„Haplogynae“ (Archaeoidea and Dysderoidea) but 38 families of the „Entelegynae“ (16 of the Araneoidea s. l., 2 of the Oecobioidea, and 20 of the RTA-clade). See also below (“gaps of the amber faunas”).

(*) Unfortunately we still do not know an important amber deposit of the Paleocene bearing inclusions which I consider of greatest interest regarding the evolution of entelegyne spiders, although this geological period took only ten million years: As the first period after the K-T boundary events the Paleocene connects the Cretaceous and Eocene which both had so different faunas of araneomorph spiders. Probably the amber-bearing strata under the River Oise Quaternary deposits in France – determined as lowest Eocene – possess a late Palaeocene (or even a Cretaceous?) age, see PENNEY (2007); Salticidae – typical for Tertiary ambers – are absent, but Lagonomegopidae – typical for the Lower and Mid Cretaceous – are also missing. The last ten million years of the Cretaceous may also be of great interest, and important deposits are wanted.

(**) The cribellate entelegyne Deinopidae and Uloboridae may be regarded as relatively ancient spider families within the advanced superfamily Araneoidea s. l. (= “Orbiculariae”).

(***) The number of Cretaceous specimens of the “ancient” families may be high, too: PENNEY (2006: 443) found 7 specimens (almost 7%) of the archaeoid family Huttoniidae (in my opinion the determination is not sure) within 107 specimens of spiders in two kinds of Cretaceous Canadian ambers. The rare extant species of this family are resticted to New Zealand. I found a quite similar percentage of Oonopidae: Orchestininae in Burmese amber.

	“Haplogynae”	“Entelegynae”	ratio
(a) In Cretaceous ambers:			
families	~11	~5 –6 (*)	2 : 1
extinct families	6 (= 60%) (!)	0?	6 : 0
genera (all are extinct)	>12 (?)	>5 (?)	2.4 : 1
(b) In Eocene European ambers:			
families	~11	~38 (!) (**)	1 : 3.5
extinct families	1 (<10%)	4 (>10%)	1 : 4
genera (90% are extinct)	~20	~200	1 : 10
(c) genera today worldwide:	~350	~4000	1 : 11.4

(*) this number regards the superfamily Araneoidea s. l. only.

(**) 16 families of the Araneoidea s. l.

Tab. 1a: Faunal differences in the extinct and extant families and genera of araneomorph spiders which are known in 2008.

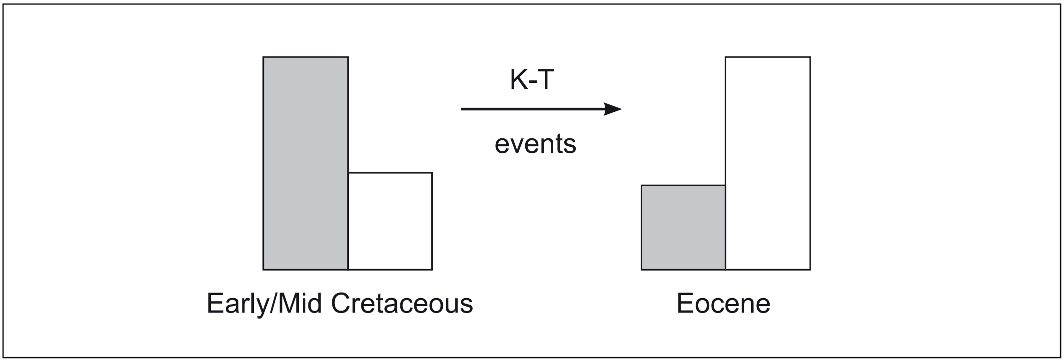
Groups of araneomorph families	in Cretaceous ambers	in Eocene ambers
(a) "ancient" members of the Dysderoidea & Archaeoidea (= "Haplogynae")	~ 65%	~ 25%
extinct families	~ 50% (!)	<1%
(b) "derived" members: Araneoidea s. l. of the "Entelegynae" (*)	~ 35%	~ 50%
extinct families	<1% (!)	>10%
(c) percentage of cribellate genera within the Araneoidea s. l. (= "Orbiculariae")	~50% (!)	~7%

(*) Further entelegyne families of the Cretaceous are Oecobiidae and questionable Dictynidae.

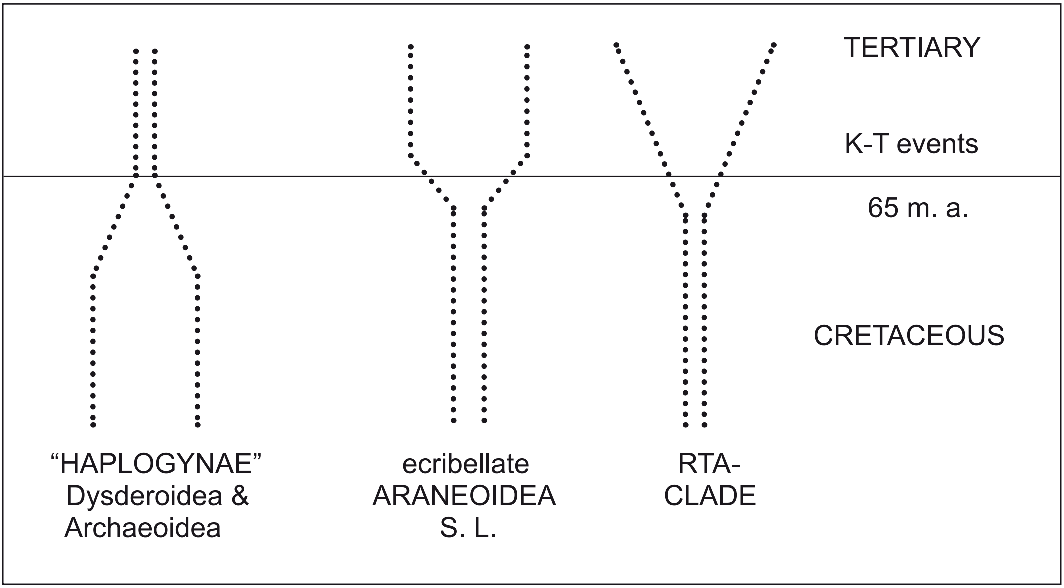
Tab. 1b: Percentage of spider families of two groups of araneomorph spiders ("Haplogynae" and Araneoidea of the "Entelegynae") which are kown from Cretaceous and Eocene amber faunas (a, b), and percentage of cribellate families within the superfamily Araneoidea s. l. (= "Orbiculariae") (c).

kind of amber; area and age	families	genera	species
Dominican amber, ~22 m.a.	0	27%	100%
Baltic amber, ~40–50 m. a.	~10%	90%	100%
Cretaceous ambers, ~80–140 m.a.	~50%	100%?	100%

Tab. 2: Extinct taxa of araneomorph spiders (Araneae: Infraorder Araneomorpha) on three taxonomical levels, and of three areas and eras



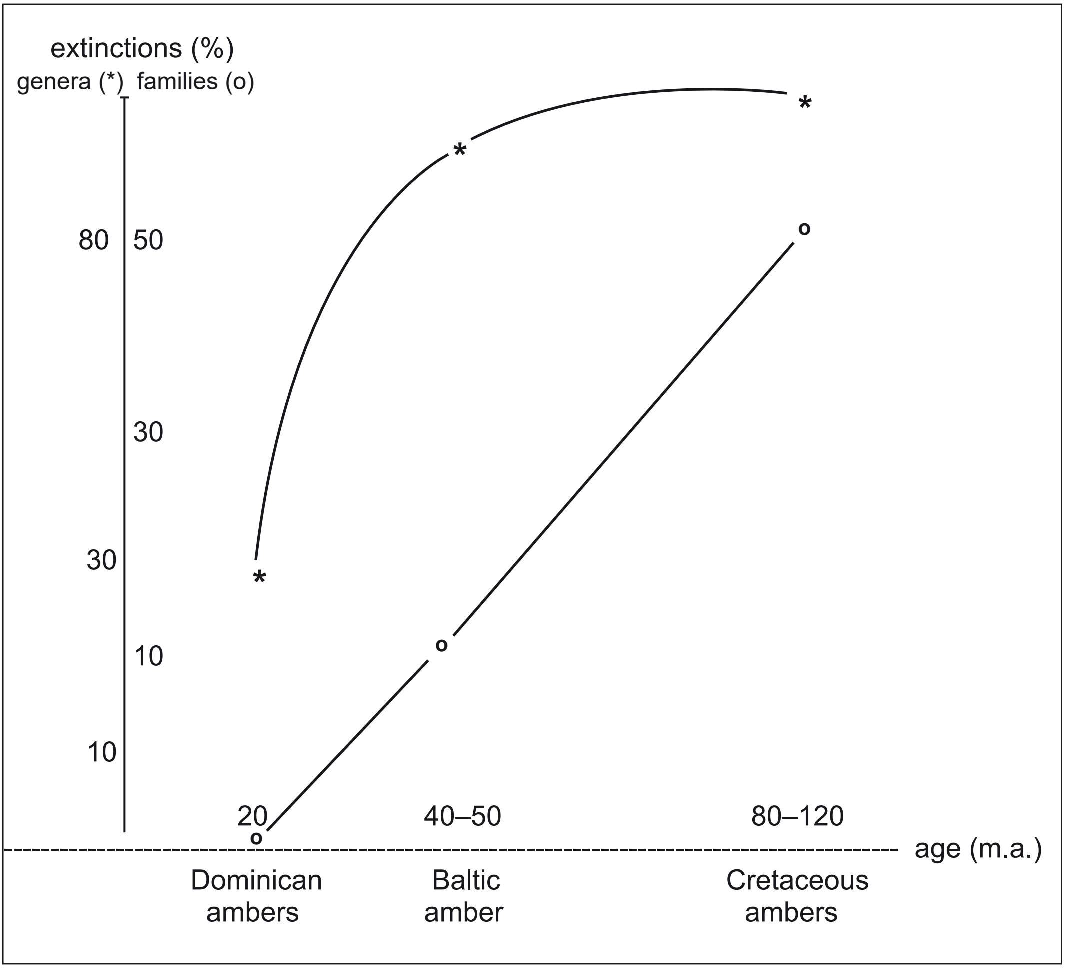
Tab. 3: Relative diversity of "haplogyne" spiderfamilies (the left bars) and derived "entelegyne" spiders which are preserved in Cretaceous ambers (at the left) and Eocene ambers.



Tab. 4: A rough and provisorical graphic: Diversity of three main groups of araneomorph spiders on genus and species level before and after the Cretaceous-Tertiary boundary events which apparently had dramatic consequences.

Note: Numerous groups of flowering plants – e. g. Gramineae and orchids – and animals – e. g. ants, papilionoids, placental mammals and singing birds – diversified also elatively late, like the ecribellate Araneoidea (s. str.) did.

The KNOWN number of "ancient" haplogyne spider families of the Lower/Upper Cretaceous and of the Early Tertiary – about 11 each – is almost identical, but the number of families of the Araneoidea s. l. increased from at least 5 to 16 by about 300% (!) from the Cretaceous to the Early Tertiary (Eocene). It is striking that most families of the Araneoidea s. l. – whose members are frequent or not rare in Early Tertiary ambers – are unknown from the Cretaceous so far, e. g. Anapidae s. l., Cyatholipidae, Linyphiidae, Mimetidae, Nesticidae, Synotaxidae and Theridiidae. All these families are *ECRIBELLATE* members of the superfamily Araneoidea s. str., and – with the exception of the Anapidae – they are not orb-weavers but build irregular capture webs; Mimetidae lost the capture web.



Tab. 5: Extinct araneomorph spider genera and families during the last 120 million years.

Comparing the cribellate (Deinopidae and Uloboridae) genera with the ecribellate genera (remaining families) of the superfamily Araneoidea s. l. (= “Orbiculariae”) (see tab. 1 above) we find A STRONGLY INCREASING PERCENTAGE OF ECRIBELLATE GENERA from the mid Cretaceous to the Early Terciary:

Within the Cretaceous . . . . ~ 50% (!),
in the Early Tertiary (Eocene) Baltic amber . . . . ~ 93%,
today in Central Europe. 99%,
today in Central Europe excl. Linyphiidae . . . . 96%.

The increasing percentage of the ecribellate genera is most pronounced between the Cretaceous and the Early Tertiary, but the difference is only low between Baltic amber and today in Central Europe.

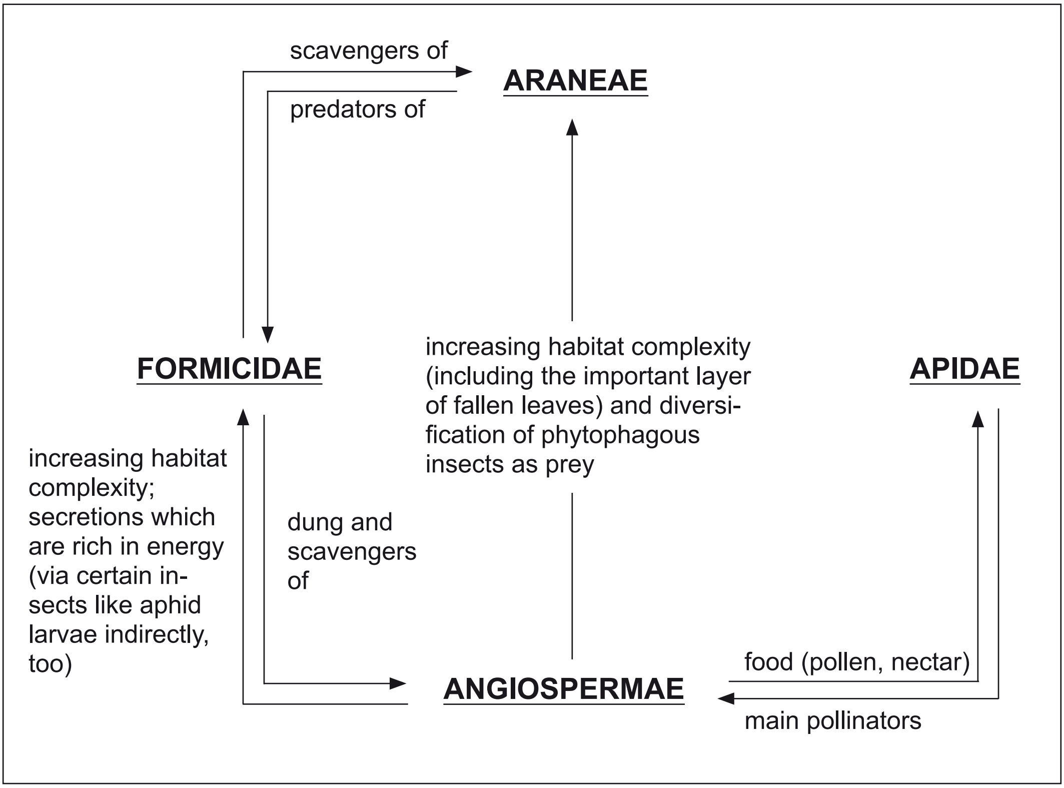
The oldest kown ecribellate Araneoidea s. l. may be Jurassic members of the families Araneidae/Zygiellidae (?= Juraraneidae ESKOV). Relatives – really ecribellate? – are probably also known from the Cretaceous deposit of Santana (Brasil) (person. observ., CJW, unpublished, see the photos 113–115). According to SELDEN (2007; talk at the 17th Internat. Congr. of Arachnology in Brazil) members of the Uloboridae – a family of the cribellate branch of the Araneoidea s. l. – are most frequent in JURASSIC SEDIMENTS of the Inner Mongolia (China).

Numerous families of the RTA-clade – like Corinnidae, Salticidae (*), Trochanteriidae and Zodariidae – have to add to the list of those spider families which were frequent already in Early Tertiary European amber forests but are not reported from the Cretaceous.
Adult males of only two families – Salticidae and Theridiidae – taken apart cover already one quarter of the whole spider fauna in the Eocene Baltic amber (similar to the extant fauna), but both families are unknown in all Cretaceous ambers (!). – So there exist two peculiar “gaps” in the Cretaceous spider faunas compared with the Eocene and the extant faunas worldwide which regard (a) the RTA-clade and (b) the non orb-weaving families of the superfamily Araneoidea.
See below and above: e. g. the remark on “ghost-lines” of these and other families.
Changes in the faunas of the archaic mygalomorph spiders may have happened quite different – more limited – compared to changes in araneomorph spiders but we know much less about fossil mygalomorphs which are preserved in ambers because of their larger size and their habitats more on/within the ground which protect them usually from being captured in fossil resins.

(*) Salticidae is also unknown from the (really?) Eocene (or Palaeocene) fauna of the Paris Basin, see PENNEY (2007: 74) (not a single record exists among >230 specimens!).

Note on the biology of Cretaceous spiders: According to PENNEY et al. (2003: 2604) "Spiders may also have undergone a diversification during this time, from a predominantly ground-dwelling mode of life to fill the new arboreal niche and take advantage of the richly evolving insect communities." According to my results in earliest Cretaceous spiders this surely does not concern haplogyne taxa which were already diverse in the Lower Cretaceous, and were dwellers of higher strata of the vegetation probably MORE PRONOUNCED than today; but why are entelegyne spiders – e. g. members of the RTA-clade – so relatively rare in the Cretaceous ambers, and most of their families absent?

Spiders evolution and co-evolution



Tab. 6: Relationships of spiders (Araneae) within the global biosysteme which probably evolved/diversified around the K-T boundary. Included are – besides the spiders – the Angiospermae as primary producers of energy, and two selected important taxa of arthropods, of (eu)social insects: Ants and bees. The arrows indicate the relationships within these co-evolutionary groups, of mutualisms and antagonisms.

Which structures and behaviours did the advanced taxa of araneomorph spiders – members of the Araneoidea s. l. and of the RTA-clade – evolve in contrast to members of the more ancient and haplogyne Dysdeoidea and Archaeoidea? These may be:

(a) a structural character of their genital organs: the entelegyne level (convergently evolved in certain Haplogynae),
(b) a more rapid sequence of generations, once a year (or even twice), e. g. in Linyphiidae, several Lycosidae, Salticidae and Theridiidae,
(c) a more intensive pattern of brood-care behaviour (convergently evolved in several successful taxa of the Dysderoidea s. l. like Pholcidae, see below), and
(d) a wide range of interrelationships and adaptations to – as well as co-evolution with – certain social insects, the very diverse ants (Formicidae) – see tab. 6 above, ESKOV & WUNDERLICH (1995:103), and WUNDERLICH (2004: 186–200) –, which were and are very important to spiders, because of the huge biomass of ants which is by far the largest of all arthropod families, about 10% of the biomass of all terrestrial arthropods (more than the biomass of all man) (to my estimation it may be more than 10% in the Eocene Baltic amber). About 5% of arthropod specimens in Baltic amber are ants, the quota in spiders is the same, and is 3.5% in Cretaceous amber from Jordan, according to KADDUMI (2007: 256). The enormous amount of "biological energy" of the ants in the Eocene (*) could not be "ignored" by predators like spiders (comparable with snakes which could not "ignore" the large biomass of rodents). Thus members of the entelegyne araneomorph spiders, of the superfamily Araneoidea s. l. and of the RTA-clade (as well as of the Oecobioidea which are not dealt with here in detail) evolved special "strategies" – as "key characters" of their diversification – in attacking and defending ants apparently latest in the Early Tertiary:

(1) A unique attacking and bite behaviour in respect to ants in Zodariidae as well as in numerous members of other families like the Theridiidae (e. g. the Hadrotarsinae), Gnaphosidae, Salticidae (mainly in basal branches), Thomisidae, Trochanteriidae;
(2) prey wrapping behaviour (convergently evolved in the successfull haplogyne family Pholcidae, and in the Oecobioidea);
(3) the – in the geological sense – old and two-dimensional orb web of (e. g.) the families Araneidae and Uloboridae is very useful for capturing flying insects, but it is not proper for capturing specimens of worker ants. Orb web weavers were diverse in the early and mid Cretaceous which is shown by the present study – in which ants were extremely rare (*). The evolution – e. g. by members of the family Theridiidae: Episinae and Theridiinae – of specialized irregular three-dimensional capture webs like tangled webs which contain sticky droplets, and which are proper for capturing worker ants, happened probably late, and a sure proof of irregular capture webs producing spiders in Cretaceous araneoid spiders is still wanting. Such spiders of the superfamily Araneoidea which produced irregular capture webs diversified apparently only in the beginning of the "age of ants", in the (Early) Tertiary in which their orb web changed to an irregular three-dimensional capture web. In the Eocene Baltic amber forest we find – in the geological sense – "suddenly" numerous taxa of ants as well as numerous taxa of three-dimensional capture web building spiders of (e. g.) the families Cyatholipidae, Linyphiidae, Synotaxidae and Theridiidae *AT THE SAME PERIOD*.
(4) *ARANEOIDEA s. l. (= "ORBICULARIAE")*: Several authors discuss the superiority of the viscid threads over cribellate threads, the viscid (orb) web (**) over the cribellate

web; they discuss the "cribellum loss in connection to the increase in diversity among araneoid spiders", see KAWAMOTO & JAPYASSU (2007), talk at the 17th International Congress of Arachnology in Brazil. *RESULTS OF MY PRESENT STUDY CONFIRM STRONGLY THIS IDEA*: Within the Cretaceous I found about 50% ecribellate genera but 93% in the Eocene Baltic amber spiders (see the tab. above below tab. 5); the number of cribellate genera decreased from 50% to 7%, that is only 1/7 (!) (***). It is remarkable that a sure proof of Cretaceous genera of the Araneoidea which built irregular webs is still wanting (!). So the ecribellate spiders – at least the irregular web builders of the Araneoidea – diversified apparently (not only late but also) quite enormouos after the Cretaceous in contrast to the haplogyne spiders, and at the same time as the members of the RTA-clade *AND ANTS AS WELL*.

(5) concerning special defending and hiding behaviour against powerful ants: Hiding and moulting sacs evolved in numerous families of the RTA-clade as well as hidden/camouflaged egg sacs, watching and carrying of egg sacs like the behaviour in Lycosidae and Pisauridae (convergently evolved in certain taxa of certain more advanced Dysderoidea s. l. within the scytodoid branch (like Pholcidae), see WUNDERLICH (2004: 186ff). Carrying of egg sacs by spiders in the Cretaceous is unknown but not unlikely in my opinion in members of the superfamily Dysderoidea s. l. – Certain advanced spiders evolved a unique "healing system" of injured legs, see WUNDERLICH (2004: 154–158), and the papers nos. 3 and 11 in this volume. – Camouflage: Ant mimicry evolved in several families as Batesian mimicry, see above and WUNDERLICH (2004: 189ff). – In numerous spider taxa (e. g. Corinnidae, certain Theridiidae and Salticidae) evolved – in contrast to most haplogyne spiders – a more or less armoured body. – Furthermore synoecy in ants nests evolved in several families of spiders.

What about preying on ants by the more ancient members of the Dysderoidea and Archaeoidea? Archaeoidea do not feed on ants, most of these spiders are specialized as spider eaters, et least some fed apparently on spiders in the Cretaceous, see below. Dysderoidea feed apparently only rarely on ants (although some Segestriidae apparently feed on ants). The derived members of the Araneoidea and of the RTA-clade – as well as of the Oecobioidea – are probably more proper praeadapted in ant-capturing than members of the Haplogynae, see above.

(*) The diversification of ants – causing a high number of wingless worker specimens – did not yet happen in the Lower Cretaceous. Not a single ant has been reported from Jordanian or Lebanese amber up to now. "Undisputed true ants of the family Formicidae appear only during the mid Cretaceous (90–95 mye)." (KADDUMI (2007: 251).

(**) (1) In most extant taxa of the ecribellate Araneoidea exist an irregular web (an orb web is much rarer), but the cribellate taxa of the Uloboridae and Deinopidae build orb webs only (they may be strongly modified). – (2) Apparently the – dry! -cribellate threads are superior over sticky threads in dry areas of tropical regions.

(***) Today exists in Europe only 1% of cribellate genera of the Araneoidea s. l. (= "Orbiculariae") (4% if the genera of the Linyphiidae are excluded, which prefer a moderate clima in contrast to most cribellate Araneoidea s. l. (Uloboridae)).

Gaps of the amber faunas: In respect to the gaps of the Cretaceous spider faunas (compared with the extant faunas): Araneoidea (e. g. Linyphiidae and Theridiidae), RTA-clade (e. g. Lycosidae and Salticidae): See WUNDERLICH (2004) and above, mainly tab. 1a. The gaps of the Cretaceous spider faunas are enormeous and concern

mainly the “Entelegynae”: In the dominating “Haplogynae” exists the proof of about 11 families but only 5–6 (= 50%) of the Araneoidea s. l. (rsp. ~9 if all families of the Entelegynae are included). In the Eocene we have the same number of haplogyne families as in the Cretaceous but the number of araneoid families is 1 ½ times (16 : 11) the number of haplogyne families, and the sum of all entelegyne families is even 3 ½ times (38 : 11) (!).
Most striking is the rarity, sure proofs or even absence of families of the RTA-clade in the Cretaceous; Salticidae is an example: According to ESKOV & WUNDERLICH (1995: 100) “only a Cenozoic age of this largest spider family can be assumed.” – Orchestininae are not – probably only still not – reported from the gondwanan Jordanian and Lebanese ambers; the reason of this absence may simply be our poor knowledge of the spider fauna which is preserved in this kinds of ambers. Or did this subfamily originate within the old northern land mass of Laurasia and invaded the Southern Hemishere only in the Tertiary?

The absence of the following entelegyne spider families and subfamilies (subf.) in the Cretaceous is striking; they are frequent today in higher strata of the vegetation and are known from the Eocene as well (with the exception of the Lycosidae):

	Cretaceous ambers	Eocene European ambers	Miocene Dominican ambers
Lycosidae (TRA-clade)	--	--	-- (?)
Salticidae (RTA-clade)	--	ancient subf. only	advanced subf.
Linyphiidae (Araneoidea)	--	ancient subf. only	advanced subf.
Theridiidae (Araneoidea)	--	almost all subfamilies	

Species of only these four families cover about one third of all extant spiders, and – except the Lycosidae which were absent in the Eocene – represent the majority of the Eocene spider fauna in amber; adult males of Salticidae + Theridiidae taken apart already cover not less than one quarter of the Eocene fauna (!). But not a single sure proof of these taxa exists in Cretaceous amber faunas worldwide (!).

Notes on the advanced and diverse haplogyne family Pholcidae (superfamily Dysderoidea s. l.), and short remark on two other families: Pholcidae is surprisingly not (yet) with certainty reported from the Cretaceous; see PENNEY (2007). This family has a particular combination of features including characters which are similar to certain diverse and advanced entelegyne families like Araneidae, Linyphiidae and/or Theridiidae: Prey-wrapping behaviour, sticky droplets of the capture threads, existence of a comb of tarsus IV similar to Theridiidae, a vibrating capture web when disturbed like numerous Araneidae (as a result the spiders are hard to recognize in their web), and a well developed brood-care behaviour (carrying the egg sac; a behaviour which is frequent in the Dysderoidea s.l.). The COMBINED existence of these characters is probably the reason for the pronounced diversification of pholcid taxa during the Tertiary, see WUNDERLICH (1988): Taxa in Dominican amber.

Other – in the geological sense probably relatively old spider families – which are known from the Eocene but still not from the Cretaceous – may have existed already at that period but a proof is wanting; they evolved certain characters which may have been important for their surviving: A special prey capture behaviour (the Scytodidae), and a strong poison (the Loxoscelidae).

On the evolution of higher spider taxa; palaeophyletic investigations

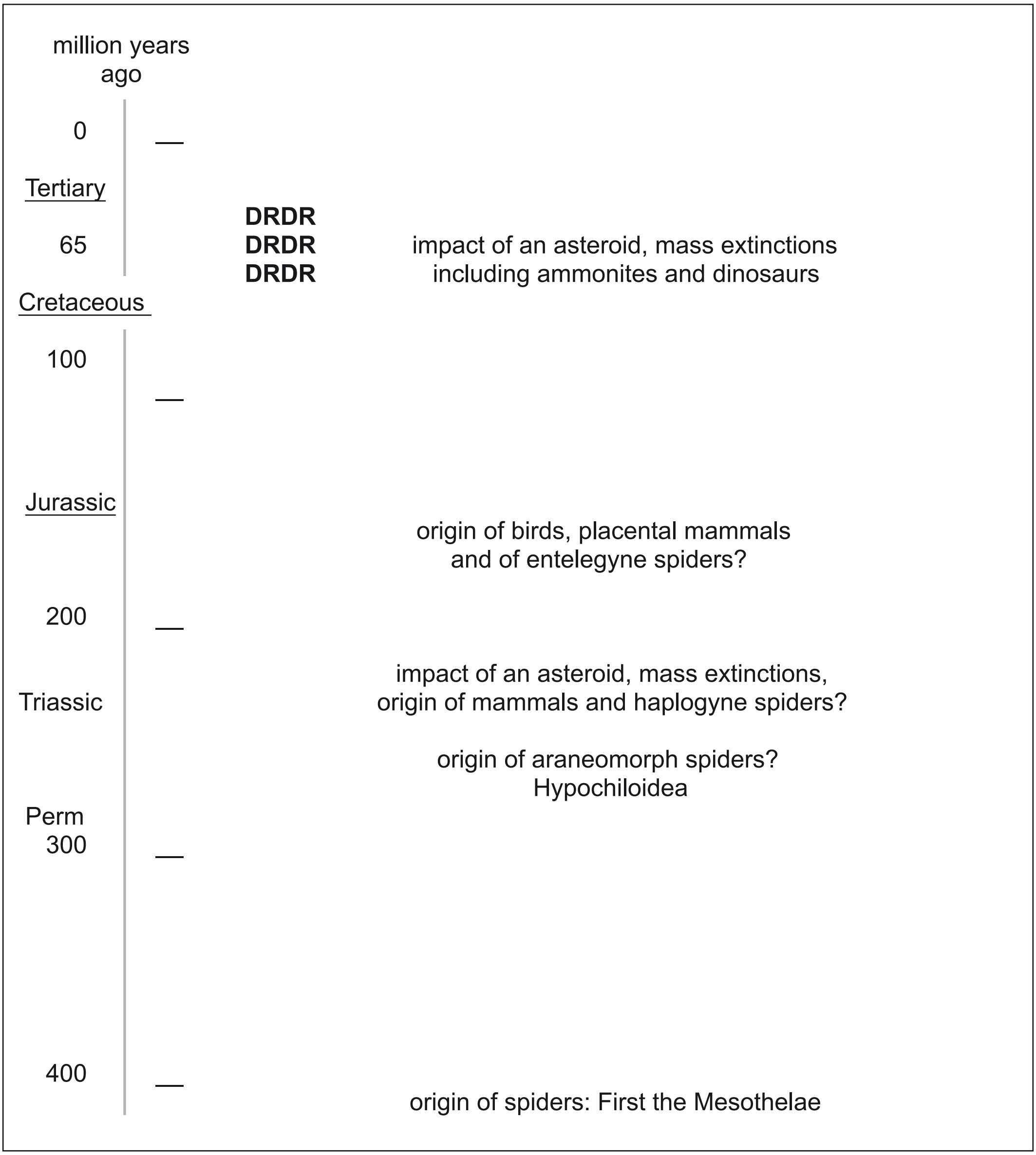
We still know hardly anything about the era of the origin of most higher spider taxa but we have some information about the ages of their diversifications. On the one hand particular questions remain unanswered: Why did radiations and diversifications of certain arthropod orders happen in such different eras? On the other hand we know of events in the Palaeocene (after the K-T boundary) – in which apparently numerous *SIMULTANEOUS* diversifications (and probably radiations as well) happened of such different, non-related, and quite derived groups like certain higher spider taxa (Araneoidea, RTA-clade), social living ants (of the single family Formicidae), certain mammals (the Plazentalia), certain birds (e.g. the Passeriformes), and certain flowering plants like Gramineae and orchids. Are there common causes for the diversifications of such different groups of animals and plants?

The impact of an asteroid at the K-T border may well have been the *FIRST IMPULSE FOR FURTHER EVENTS*, it was followed by numerous extinctions and an enormous loss of biodiversity – see STORCH et al. (2001: 90, 161) –, which provided radiations and diversifications of a high number of taxa. The co-evolution of flowering plants, taxa of winged insects as well as their interrelations (see below) were surely further important reasons for diversifications in that era within and after the Palaeocene. The evolution of social life and casts in ants, the homoiothermy in birds (archosaurs) and higher mammals, the origin of a well developed placenta in the Plazentalia, and of feathered wings in birds – are examples of advanced functions and structures. – What about advances regarding the complete huge group of entelegyne spiders? Their probable advances are discussed above and below; they are not so evident as in birds and placental mammals.

The ancient – and in former times very diverse group – of haplogyne spiders ("Haplogynae") of the infraorder Araneomorpha seems to be comparable in some evolutionary respect to the ancient marsupials of the mammals, which overwhelming portion is extinct but which are still diverse in the Australian Region today ("Haplogynae" is not restricted to a particular area today); and the derived as well as – after the Cretaceous – far more diverse and strongly dominating "Entelegynae" is comparable to the placental mammals.

Generally spoken: "Successful" suprageneric groups of plants and animals – arthropods and vertebrates as well – evolved particular advancements especially IN THEIR REPRODUCTION, IN THEIR GENITAL AND MATING SYSTEMS, AND – ANIMALS – IN THEIR BEHAVIOUR (E. G. IN THEIR BROODCARE); SOCIALITY (limited in spiders), AND CO-EVOLUTION PLAYED APPARENTLY AN IMPORTANT ROLE, TOO.

It is highly interesting to compare the evolution of higher taxa of the advanced spiders with the higher homoiotherm vetrebrates. Apparently mass extinctions – see ETTER (1994) – stimulated largely the evolution of quite different groups of animals:



A supposed "geological time table" of the evolution of higher spider taxa, with selected groups of vertebrates for a comparison. **DRDR** = the era of the "exploding diversification (and radiation of lower taxa)" of the ADVANCED spider taxa of the Araneoidea and the RTA-clade (including almost 90% of the extant araneomorph families).

The origin of entelegyne spiders may have happened almost simultaneously with the most advanced vertebrates, birds and placental mammals, and the haplogyne spiders originated probably almost simultaneously with the first mammals. Note the instants of the impacts of asteroids and of the mass extinctions. Remark: Only the last third of the spiders' evolution is documented by fossils in amber; the reports of their taxa are quite incomplete. See SELDEN et al. (1999: 412).

"Connecting structures" and "connecting taxa" ("missing links"):

In palaeontological studies it is of special interest to search for structures of animals which allow conclusions on their phylogeny or behaviour; see WUNDERLICH (2004) for Eocene spiders. The age of the Cretaceous taxa may be about three times the age of the Eocene spiders in Baltic amber. Mainly the adult Cretaceous spiders (although only relatively few are known) led to peculiar conclusions and reports of "missing links" (more correctly: "connecting taxa" which possess "connecting structures"). In the following survey I focus mainly on patterns of fossil members of the family Uloboridae (f):

(a) Leptonetidae, Ochyroceratidae and Psilodercidae (all are six-eyed): Their probable relative of the Cretaceous – the Praeterleptonetidae n. fam. – had 8 eyes and numerous leg bristles (figs. 23–24) in contrast to their extant relatives.

(b) Burmascutidae n. fam.: This extinct Cretaceous family offer a unique mixture of characters, see the description of the family below.

(c) Archaeidae: Lacunaucheniinae n. subfam.: In the Cretacous genus *Palaeomysmauchenius* SAUPE & SELDEN 2008 (Cretaceous amber from France, probably a member of the Lacunaucheniinae) at least the anterior and the posterior spinnerets are present; in the Lacunaucheniinae (Burmese amber) all the three pairs of spinnerets are not reduced. Posterior and median spinnerets are strongly reduced/absent (and replaced by spigots) in their extant relatives, of the subfamily Mecysmaucheniinae.

(d) Micropalpimanidae n. fam.: The discussion on several plesiomorphic characters: See the family below.

(e) Deinopidae (unsure determination): Size and position of the eyes in the extinct Lebanese genus *Palaeomicromenneus* PENNEY 2003 are not as specialized as in extant or Tertiary (Eocene) taxa; their posterior median eyes are smaller (fig. 114).

(f) Uloboridae (figs. A-E as well as 118 and 123, photos 105–110). In the Cretaceous members I found several "unusual" and most probably plesiomorphic characters of this old and quite remarkable family, see below: The description of the uloborid taxa. – The shape of the prosoma and the position of the eyes are quite variable within this family, and some extinct taxa are of particutar interest in this respect:

The extant and Miocene tropical genus *Miagrammopes* O. PICKARD-CAMBRIDGE 1869 shows the most pronounced REDUCTION of the eyes within this family besides *Tangaroa*: All eyes of the anterior row are lost (fig. A below). (In the extant genus *Tangaroa* LEHTINEN 1967 the anterior lateral eyes are lost). In members of the same genus – see WUNDERLICH (2004: Photos 110–112) – exist a quite long prosoma, long anterior legs as well large tuberculate posterior lateral eyes in a marginal position (fig.A). So their anterior optical view is lost, but prey detection at the capture threads exists with the help of their long anterior legs.

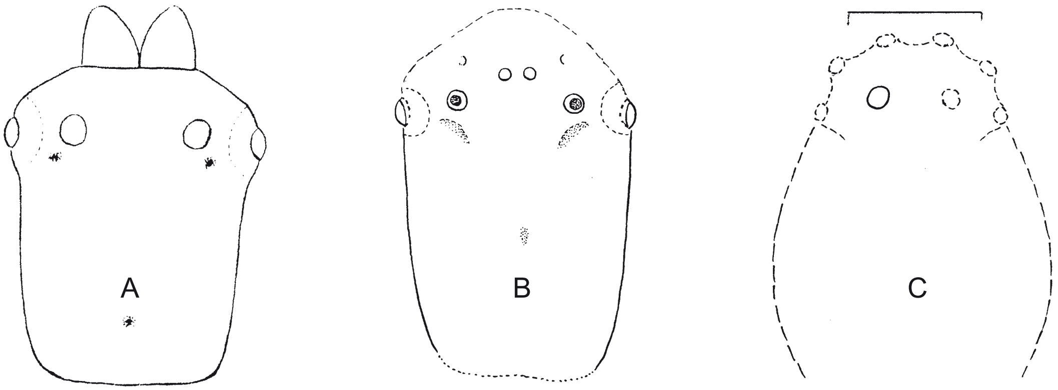
"Missing (connecting) links or taxa": A long and slender body and long anterior legs exist in the EOCENE genus *Eomiagrammopes* WUNDERLICH 2004 and in the CRETACEOUS genus *Palaeomiagrammopes* n. gen. as well, but their eyes are different: In *Palaeomiagrammopes* exists two rows of 8 eyes which are not reduced (fig. C) but the eyes of the anterior row are strongly reduced in *Eomiagrammopes* (fig. B) (the lenses of the anterior lateral eyes may even be absent). The conditions in *Eomiagrammopes* can be regarded as the model of a "missing link" between the plesiomorphic conditions in *Palaeomiagrammopes* and in the derived conditions in the – extant as well as Miocene (Dominican amber, see WUNDERLICH (1988)) – genus *Miagrammopes*. Or is *Eomiagrammopes* probably even a "true" "missing link"? Unfortunately we got only tiny "windows to the past" – how many other uloborid genera did exist during the Jurassic (SELDEN in prep.), the Cretaceous and the Eocene periods? – See also below: the family Uloboridae.

CAPTURE WEBS: Can the shape of the body and the position of the eyes led to conclusions about the basic pattern of the capture webs of fossil species of the family Uloboridae? Spiders of *Miagrammopes* usually construct horizontal orb capture webs (they may be irregular and/or strongly reduced; certain members are called "single-line-weavers"). OPELL & WARE (1987) demostrated connections (e. g.) between the reduction of the capture web, size, position and view of the eyes, the shape of the body and the length of the anterior legs in species of this family: "Uloborids that spin reduced webs are characterized by reduction or loss of the four anterior eyes ... necessary for them to effectively monitor and manipulate their reduced webs.".....”Thus, ocular changes act in consort to maintain relatively complete visual surveillance in the face of eye loss ... necessary for the operation of reduced webs.".

The widely spaced posterior median eyes, the position of the large posterior lateral eyes at the prosomal margin and their position on low tubercles, the reduced/absent eyes of the anterior row (fig. B), as well as – probably less important – the slender body and the long anterior legs in *Eomiagrammopes* are very similar to the conditions in *Miagrammopes* (fig. A), and indicate the – hypothetical – existence of a strongly reduced capture web in this extinct Eocene genus. In *Miagrammopes* (fig. E) exists no view in the anterior direction, apparently it is superfluous; in *Eomiagrammopes* the view in the anterior direction is strongly resticted and quite similar to *Miagrammopes*. The existence of 8 eyes in a plesiomorphic position of *Palaeomiagrammopes* (fig. C; compare the corresponding view in fig. D) which are not reduced, and which allow a well view in the anterior direction (similar to the Cretaceous *Paramiagrammopes* n. gen.), as well as remains of numerous spiders' threads – which are preserved near the spiders (see below) – indicate the existence of a not or not strongly reduced (orb) web in these extinct Cretaceous genera.

In summary: The derived reduced type of the capture web of the extant genus *Miagramopes* has been completed latest in the Miocene (proof of this genus in Dominican amber); its evolution started probably during the Eocene (taxa in Baltic amber). The Eocene genus *Eomiagrammopes* may be a "link" to the plesiomorphic conditions in the Cretaceous genera *Palaeomiagrammopes* and *Paramiagrammopes*.

Remarks: (1) The lenses of the anterior lateral eyes are reduced in certain members of the extant genus *Hyptiotes* WALCKENAER 1837; (2) A reduction of the size of eye lenses in geological time is also known in extant members of the genus *Mastigusa* MENGE 1854 of the family Dictynidae – which live in ants' nests – in contrast to extinct Eocene congenerics which have large eyes and which most probably did not live in ants nests, see WUNDERLICH (2004).

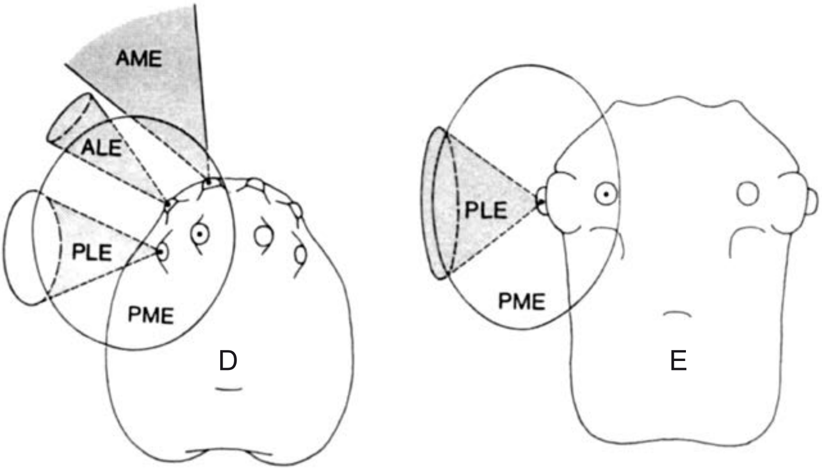


Figs. A-C: Prosoma, as well as number and **position of the eyes** in three – one extant and two extinct – genera of the family Uloboridae which probably are related. A "row of reduction" in a span of time of about 100 million years. The Eocene genus *Eomiagrammopes* (fig. B) may be a model of a "morphological link" between *Palaeomiagrammopes* (fig. C) and the most advanced genus *Miagrammopes* (fig. A):

A) *Miagrammopes* O. PICKARD-CAMBRIDGE 1869 in Miocene Dominican amber (about 20 million years old) and extant as well: Complete loss of the lenses of the eyes of the anterior row. This eye loss has nothing to do with cave dwelling but with prey capturing.

B) *Eomiagrammopes* WUNDERLICH 2004 in Eocene Baltic amber (about 40–50 million years old): Eight eyes; lenses of the eyes of the anterior row are strongly reduced, lenses of the anterior lateral eyes may even be absent.

C) *Palaeomiagrammopes* n. gen. in Cretaceous Burmese amber (probably more than 80–100? million years old): Eight eyes in two rows, eyes not reduced. This is the basic number and position of the eyes in related genera and probably in the whole family. In all known Cretaceous uloborid spiders the eyes are still not reduced in size or number.



Figs. D-E: Dorsal views of the VISUAL FIELDS of two extant uloborid species, *Waitkera waitkerensis* (CHAMBERLIN 1946) (D) and *Miagrammopes animotus* CHICKERING 1968 (E). The openings of visual cones that are directed upward and downward are represented as ellipses. A dashed line denotes the ventral rim of an ellipse, and the width of its opening is directly proportional to its dorsal or ventral orientation. Since the PME are directed dorsally, their visual fields are shown as circles. AME = anterior median eye, ALE = anterior lateral eye, PME = posterior median eye, PLE = posterior lateral eye. – Taken from OPELL & WARE (1987: Fig. 4).

CONCLUSIONS AND DISCUSSION

Taxonomical – genital and non-genital morphological – characters of the Cretaceous spider taxa, indications of their behaviour as well as the composition of the Cretaceous spider faunas, the proofs and the “negative records” (that means the *PROBABLE* absence, the seemingly or actual gaps), faunal changes, and comparisons with Tertiary and extant faunas lead me to the following conclusions (some surprising conclusions are taken into account with hesitation and may be regarded as provisorical):

(1) The strange spider faunas in Cretaceous ambers show that the evolution of the suprageneric taxa – even of the more ancient haplogyne spiders – has by far not been completed at that time (compared with the taxa of today), see the high number of extinct families and the absence of extant families during the Cretaceous. The *FIRST BRANCHINGS OF FAMILIES AND SUBFAMILIES OF CERTAIN “ANCIENT” SU-*

PERFAMILIES like Dysderoidea s. l. and Archaeoidea s. l. may go back at least to the Jurassic and/or Triassic, see PENNEY et al. (2003), SELDEN et al. (1999) and the "Supposed geological time table" above. Certain dysderoid families (e. g. the Pholcidae) diversified probably only or mainly in the Tertiary, see p. 553.

(2) The diversifations/radiations of the advanced and very diverse superfamily Araneoidea s. str. (especially of its ecribellate branch), and of the very diverse RTA-clade *HAPPANED MOST PROBABLY AFTER THE CRETACEOUS*, probably quite *RAPIDLY* in a short post-Cretaceous period of only about 20 (–30?) million years *) between the K-T boundary events and the origin of the Baltic amber forest. Their diversification happened (a) very pronounced in (the latest Cretaceous? or) the Early Tertiary (Palaeocene and probably Eocene), and (b) less distinctly a second time during and after the Oligocene cooling (e. g. of the advanced Linyphiidae: Erigoninae, the Lycosidae, and the advanced subfamilies of the Salticidae as well as probably of few subfamilies of the Theridiidae (Argyrodinae and Theridiinae);

(3) the Cretaceous-Tertiary boundary events had apparently – at least indirectly – an enormous influence on the diversification of the advanced taxa of the Araneoidea and of the RTA-clade: Apparently *AN "EXPLODING DIVERSIFICATION"* of most families of both groups took place in the Early Tertiary (and probably already in the latest Cretaceous from which well-preserved spider fossils are still needed) – similar to most groups of advanced mammals (Placentalia) like bats and rodentia, birds like Passeriformes (which represents more than half of the extant species of birds) (*), furthermore numerous insects like ants (Formicidae), Papilionoidea, and certain Diptera like Mycetophilidae as well as plants like cacti, palms (both appeared first in the Paleocene), numerous angiosperms like Gramineae and orchids (and numerous other groups of animals and plants). See the fig. above.

(*) The most advanced birds, the "Passeriformes", as well as the most advanced mammals, the Placentalia, evolved an intensive brood-care behaviour besides the constant temperature of their body, and they displaced most of their ancient kin. Flowering plants (Angiospermae) evolved special reproductive/genital structures, e. g. coloured flowers and seed vessels, as well as nectar glands which all together provided a co-evolution with several groups of insects like ants, butterflies and bees, see the papers of ENGEL (2001), GRIMALDI & ENGEL (2002), GROSSMANN & JUNGHEIM (2007), MOREAU et al. (2006), PAULUS (1978), POINAR & DANFORTH (2006), ZWÖLFER (1978), and above. Angiosperms became more and more diverse, and displaced several groups of their ancient kin, the Cycadophytina/Gymnospermae. This displacement in the largest groups of plants is analogous to the displacement in the largest groups of spiders, and it happened mainly during the same era around the K-T boundary events. (The main diversification of the Angiospermae took place apparently much later than supposed previously, see e. g. ZWÖLFER (1978: Fig. 2)). While bees were very important partners of angiosperm co-evolution, *ANTS* – the diverse social Formicidae – influenced apparently the diversification of angiosperms *AND SPIDERS* as well – see the antagonistic behaviour, the construction of specialized capture webs by spiders, myrmecomorphy and synoecy in ants nests, see WUNDERLICH (1995, 2004). – The global change of ecosystems worked probably with the help of relatively few co-evolutioning main partners as an initial of numerous diversifications, see tab. above and the paragraph "On the evolution ...".

(4) The reasons for the "late" diversification – and their (in the geological sense) "sudden" appearence (*) – of this particular branches of spiders – the ecribellate branch of the superfamily Araneoidea and the taxa of the RTA-clade – in the Eocene are still unknown (**). Reasons may be the diversification of certain groups of flowering plants as well as of certain insects – mainly ants – during the same period, the Early Tertiary, which causes certain co-evolutions; see the fig. below, the paper no. 3 on the family Theridiidae in this volume, as well as *ADAPTATIONS TO ANTS* in certain families of spiders like Corinnidae, Theridiidae and Zodariidae which were described by WUNDERLICH (2004), furthermore the diversification of winged insects, changes of the climate (warmer and more humid), and of biotopes, but also the evolution within the higher groups of araneomorph spiders, probably mainly losses of the cribellum.

(*) Interestingly some authors suppose that the "Early Cambrian explosion" – the origin of the "Ediacara faunas" of higher groups of animals almost 600 million years ago – took about the same relatively – in a geological sense – short time only. Are both diversifications comparable with respect to their time span?
(**) Spider fossils in Palaeocene ambers are still almost unknown (!); see PENNEY (2007).

(5) the Cretaceous-Tertiary boundary events had conspicuous effects on the extinction of higher taxa of the araneomorph spiders:
EIGHT EXTINCT CRETACEOUS SPIDER FAMILIES – Burmarachnidae n. fam., Burmascutidae n. fam., Lagonomegopidae ESKOV & WUNDERLICH 1995, Micropalpimanidae n. fam., Eopsilodercidae n. fam., Plumorsolidae n. fam., Praeterleptonetidae n. fam., and Salticoididae n. fam. – (= about one third of the known Cretaceous araneomorph spider families, and about two third of the reported at least 11 haplogyne Cretaceous spider families) are already known, although the knowledge of Cretaceous spider faunas is still poor. These families are members of the more ancient haplogyne spider superfamilies Archaeoidea and Dysderoidea. For a comparison: Only about 10% of insect's families of the Cretaceous Taimyr ambers are regarded as extinct, see ESKOV & WUNDERLICH (1995: 100). (Lacunaucheniinae n. subfam. of the Archaeidae, as well as Lebansegestriinae n. subfam., and Microsegestriinae WUNDERLICH 2004 of the Segestriidae are further higher extinct Cretaceous taxa of haplogyne spiders).

Remark: According to PENNEY et al. (2003: 2602) "... it is unlikely that we will discover many, if any, more strictly fossil spider families in the Cretaceous." (!).

The extinction of several families and subfamilies of haplogyne spiders during the Early Tertiary was apparently indirectly influenced by the K-T events, caused by the competition and displacing by the diversifying advanced entelegyne families like the Theridiidae as well as advanced subfamilies of Linyphiidae, Salticidae and Synotaxidae. Such (sub)families – and three tribus –, which became apparently extinct during the Early Teriary – are the following (as supposed already previously by WUNDERLICH (2004): Araneidae: Miraraneinae, Baltsuccinidae, Ephalmatoridae, Oecobiidae: Mizaliinae, Protheridiidae, Spatiatoridae, Trochanteriidae: Sosybiini as well as Zoropsidae s. l.: Eomatachiini and Eoprychiini. The Mizaliinae of the Oecobiidae and probably the Zarqaraneini of the Protheridiidae: Praetheridiini are the only extinct taxa in question – and the only suprageneric spider taxa known up to now – which survived from the Cretaceous (the Burmese amber forest) up to the Eocene Baltic amber forest, and became extinct during the Tertiary.

Extinction of genera: No Cretaceous spider genus survived or is known from the Eocene European amber forests, see figs. 1 and 5 above; the questionable proof of *Ariadna* AUDOUIN (Segestriidae) may be the only exception, see below. – For a comparison: Almost 90% of the Eocene spider genera are extinct. So the overwhelming part of the extant spider fauna on genus level is relatively young in the geological sense, younger than the Eocene.

(6) The taxonomical pattern of most spider taxa in Cretaceous ambers is a mixture of plesiomorphic and apomorphic characters. The number of Cretaceous “morphologically connecting taxa” is distinctly higher than of such taxa in Eocene spiders, see above.

(7) The number of tiny spiders of the Cretaceous ambers – see the Deionopidae, Micropalpimanidae and the Uloboridae – is higher than the number of tiny Eocene or extant spiders in the families which were studied. The reasons are unknown.

(8) Behaviour: In the Early Cretaceous spiders existed already araneophagy, a well developed courtship behaviour, orb webs, threads of capture webs which bears sticky droplets, and the use of a dragline. A proof of changes of the orb web to irregular capture webs (and losses of the cribellum) are wanting in Cretaceous amber spiders.

(9) The main prey of the Cretaceous amber spiders which were studied was Diptera. The proof of an ant as the prey of a Cretaceous spider is wanting.

DESCRIPTIONS OF CRETACEOUS SPIDER TAXA IN BURMESE, JORDANIAN AND LEBANESE AMBERS, with remarks on fossil spiders in other kinds of Cretaceous ambers as well as few lagerstaetten, and on certain extant higher taxa

In this chapter I describe araneomorph spiders of the Cretaceous period which are preserved mainly in Burmese (Myanmar), Jordanian and Lebanese ambers; remarks on few taxa of the Mygalomorpha (indet.) are added. See also the paper on fossil and extant members of the family Oonopidae: Orchestininae in this volume, paper no. 2.

Composition of the Cretaceous spider faunas of the Middle East and Burma: The spider faunas of the Cretaceous amber forests are far away from being well-known. Among numerous other arthropods more than two dozen families of spiders were reported from Burmese amber – see PENNEY (2003), RASNITSYN & ROSS (2000) –, but the proof of some families is quite unsure, and wrong determinations – mainly based on juveniles – caused serious confusion, see the remarks above and the list. – Most pieces of Burmese and Lebanese ambers are distinctly smaller than the everage of Baltic amber pieces, frequently broken off from larger pieces, and most Burmese and Lebanese fossil spiders are small or even tiny. The still unknown larger spiders of the Cretaceous amber forests – e.g. members of the infraorder Mygalomorpha – may offer a quite different composition of these extinct faunas than known today.
Members of the families Araneidae/Zygiellidae, questionable Dictynidae, Lagonomegopidae, Oonopidae: Orchestininae (the genus *Burmorchestina*), and Uloboridae are not rare in Burmese amber; the extinct Lagonomegopidae is a “pan-cretaceous” family. Orchestininae is still not reported from the “gondwanan” Jordanian and Lebanese amber forests, see below; is this a subfamily of Laurasean origin?
Advanced families like Corinnidae Linyphiidae, Lycosidae, Pisauridae, Salticidae, Sparassidae, Tetragnathidae, Theridiidae and Thomisidae are not surely reported and most probably absent in Cretaceous ambers (erroneous reports exist, see above).

Extinctions: 6 or 7 extinct spider families are reported from Burmese amber: Burmarachnidae, Burmascutidae, Eopsilodercidae, Lagonomegopidae, Micropalpimanidae Praeterleptonetidae and probably Plumorsolidae. Two further extinct families – Protheridiidae (questionable) and Salticoididae – are known from the Jordanian amber. A single extinct spider family is known from Lebanese amber: The Plumorsolidae. Questionable members of the extinct family Protheridiidae (Zarqaraneini in Jordanian amber and a female in Lebanese amber), and of the extinct subfamily Mizaliinae (Oecobiidae) (in Burmese amber) survived most probably from the Cretaceous until the Early Tertiary (Eocene) European amber forests. Not a single genus of spiders of these kinds of ambers is certainly known to have survived up to now or even to the Eocene Baltic amber forest; *Ariadna* may be an exception. See also above, the events at the K-T boundary.

Key to the families of spiders which are known up to now in Cretaceous ambers:

Remarks: (1) Six-eyed spiders are frequent in Cretaceous ambers (Dysderoidea); they exist in Oonopidae (nos. 1, 3), Plumorsolidae (no. 5), Segestriidae (no. 9), Eopsilodercidae (no. 9) and – at least some – Lagonomegopidae (no. 4). – (2) Cribellate spiders are Deinopidae (no. 6), questionable Dictynidae (no. 12), Uloboridae (no. 11) and certain Oecobiidae (no. 10). – (3) A large opisthosomal scutum exists in the Burmascutidae (no. 3) and in the Oonopidae: Gamasomorphinae (no. 3). – (4) Leg bristles are absent in Archaeidae s. l., probably in male Burmascutidae, some Eopsilodercidae and Cretaceous Oonopidae; only very few or indistinct/thin leg bristles or bristle-shaped hairs exist in some Eopsilodercidae, Lagonomegopidae, Micropalpimanidae (no. 8) (fig. 79), and questionable Huttoniidae (absent on legs I–II in the Huttoniidae, no. 8). – (5) An unpaired tarsal claw is absent only (!) in the Oonopidae (nos. 1, 3) and in the Plumorsolidae (no. 5). – (6) Proof by juveniles only: Plumorsolidae, questionable Huttoniidae, questionable Eopsilodercidae indet. (no. 9), and probably in the Lagonomegopidae and questionable Dictynidae. Mygalomorpha (questionable Dipluridae, see below) is not included in this key. – (7) Extinct families are Burmascutidae n. fam., Eopsilodercidae n. fam., Lagonomegopidae, Micropalpimanidae n. fam., Plumorsolidae n. fam., Protheridiidae, Praeterleptonetidae n. fam., Salticoididae n. fam. as well as the subfamilies Archaeidae: Lacunaucheniinae n. subfam., Oecobiidae: Lebanoecobiinae and Mizaliinae, Segestriidae: Lebansegestriinae and Microsegestriinae. – (8) Extinct Eocene families like Baltsuccinidae and Spatiatoridae – see WUNDERLICH (2004) – may be recognized in Cretaceous ambers in the future; questionable members of the Protheridiidae: Praetheridiinae have just been found in Jordanian amber.

1 Posterior femora strongly thickened (fig. 14), distinctly thicker than femora I–III, 6 eyes in a position similar to the Segestriidae (fig. 7), thoracal part distinctly higher than the cephalic part. Unpaired tarsal claw and distinct leg bristles absent, tiny spiders, body length of adults ~1–1.5 mm. Various ambers. See the chapter on the subfamily Orchestininae within the paper no. 2 in this volume . . . . . . Oonopidae: Orchestininae

- Posterior femora not distinctly thicker than the remaining femora. 6 or 8 eyes, thoracal part usually not higher than the cephalic part (see no. 8), usually larger spiders but see nos. 3, 8, 11 2

2(1) Basal cheliceral articles very long and diverging, anteriorly bearing “peg teeth” (thick bristles), and with a large gap to the gnathocoxae (foramen) (figs. 49, 57). Legs bristle-less. Archaeinae and Lacunaucheniinae (probably including *Palaeomysmauchenius*). Various Cretaceous ambers. . . . . .Archaeidae s. l.

- Shape of the basal cheliceral articles normal, large in the questionable Dictynidae, no. 12, chelicerae not strongly diverging, foramen absent. “Peg teeth” (present in the Huttoniidae and Lagonomegopidae, nos. 4, 8) and leg bristles absent or present . . . 3

3(2) Opisthosoma with a large dorsal scutum, as wide as long, and distinctly elongated beyond the spinnerets (fig. 106). 8 eyes in a wide field (fig. 93), no (♂) or only few thin leg bristles, body length 1.1–1.3 mm (♀). Burmese amber . . . . Burmascutidae n. fam.

- Opisthosoma with a large dorsal scutum, long oval, not elongated (fig. 10). 6 eyes, no conspicuous leg bristles, body length ca. 1 mm. ♀ unknown, ♂-pedipalpus figs. 12–13. Burmese amber . . . . Oonopidae: Gamasomorphinae

- Opisthosoma dorsally soft, not elongated. 6 or 8 eyes, larger spiders 4

4(3) Very large eyes exist in a lateral position which are directed almost sideward; 4 or 6 eyes (figs. 69–73). Leg bristles absent or hair-shaped (rarely a single femoral bristle exists, fig. 66). Ecribellate. Adult male unknown. Extinct, various Cretaceous ambers. . . . . Lagonomegopidae

- Eye position quite different, no conspicuously large eyes in this position; 6 or 8 eyes. Distinct leg bristles present or absent. Cribellate or ecribellate. 5

5(4) Conspicuous claw tufts of thickened/spatulate hairs (fig. 44) and numerous feathery leg hairs (fig. 43) existing. Leg bristles present, 6 eyes in a “segestriid” position (fig. 40). Juvenile (?). Lebanese amber and probably Burmese amber . . . Plumorsolidae n. fam.

- Claw tufts absent; feathery hairs exist in the Salticoididae (no. 15). Leg bristles and eye position similar or different. 6

6(5) Embolus long, describing about three loops/circles. Leg bristles present. Habitus as in fig. 114. Calamistrum and cribellum present (similar to figs. 139–140). Lebanese amber and probably Burmese amber . . . . Deinopidae

- Embolus shorter, not describing several loops. Leg bristles as well as cribellum and calamistrum present or absent 7

7(6) Prolateral spatulate hairs exist on tibiae, metatarsi and tarsi of legs I–II (fig. 79) . . 8

- Prolateral spatulate leg hairs absent. 9

8(7) Cephalic region distinctly raised (fig. 74). Body length only about 1.5–1.7 mm. ♀ unknown. Extinct. Burmese amber . . . . Micropalpimanidae n. fam.

- Prolateral spatulate leg hairs exist on metatarsi and tarsi I–II. Cephalic region not raised. Juvenile. Canadian amber. . . . . questionable Huttoniidae

- Spatulate leg hairs absent. Shape of the prosoma variable. Various ambers. 9

9(8) Six eyes similar to fig. 7. Legs bristle-less, very long and slender, femur I longer than the prosoma (see the photos). Bulbus attached at the end of the cymbium (figs. 18, 22). Extinct, Burmese amber . . . . Eopsilodercidae n. fam.

- Six eyes (fig. 7). Legs stout or fairly stout. Tibiae and metatarsi I–II bear strong, long and paired ventral bristles (only a single pair in *Lebansegestria* n. gen.) which are – in their usual position – lying close to their articles; legs III are directed foreward as legs I and II in their natural position, see photo 62 and WUNDERLICH (2004: Photos p. 344). Bulbus simple, conductor usually absent (fig. 6) (present in *Microsegestria*). Various ambers. . . . . Segestriidae

- Eight eyes (e. g. fig. 23). Legs variable in length, with numerous bristles. No pair-ed strong ventral tibial and metatarsal I–II bristles which lie close to their article, legs III are directed backward or sideward (Palaeohygropodini) in their natural position . . . 10

10(9) Anal tubercle large, with a fringe of hairs (fig. 87); tarsi III–IV with ventral bristles (fig. 91). Cribellate: taxon indet. sensu PENNEY (2002) (sub *Oecobius*) – or ecribellate: *Zamilia* n. gen. in Burmese amber. Various ambers . . . . Oecobiidae

- Anal tubercle unknown, tarsi with ventral bristles, probably ecribellate. ♂-pedipalpus: Fig. 92. Jordanian amber, F2006/CJW . . . . ?Oecobioidea: Fam. indet.

- Anal tubercle of normal size, without a fringe of hairs; posterior tarsi without ventral bristle(s) or with ventral bristles (Dictynidae, Uloboridae, nos. 11–12, fig. 120, 138). Cribellate (Dictynidae, Uloboridae) or ecribellate 11

11(10) Femora with trichobothria (figs. 125–126), with the supposed exception of *Burmuloborus* n. gen.. Lateral eyes widely spaced (figs. 115, 123). Cribellum present (similar to fig. 140), calamistrum present (fig. 116, 129), metatarsus IV dorsally depressed/concave (fig. 116) (*Paramiagrammopes* – fig. 120 – is an exception). (The anterior spinnerets are basally widely spaced and strongly converging in cribellate spiders). Three genera in Burmese amber. . . . . Uloboridae (*)

- Femoral trichobothria absent. Lateral eyes not widely spaced (e. g. fig. 136). Cribellate (questionable Dictynidae, see no. 12) or ecribellate. Metatarsus IV probably dorsally not depressed, but see the deformed metatarsus in fig. 139 12

12(11) Calamistrum and cribellum present (figs. 139–140), metatarsi with several trichobothria which may be short and hard to recognize, legs stout or fairly stout. Adult males unknown. Various ambers. . . . . questionable Dictynidae

- Calamistrum/cribellum absent, the metatarsi bear a single trichobothrium only 13

13(12) Metatarsi bristle-less; ♂: Cymbium with a horn-shaped structure (figs. 132–135) or with strong spines (figs. 28–30). 14

- The metatarsi bear bristles; ♂: Cymbium without a "horn" or spines 15

14(13) The tibiae bear a pair of inconspicuous dorsal-apical bristles (fig. 24). ♂-pedipalpus: Figs. 26–31, 36–37, 39, a true paracymbium is absent. Extinct, Burmese amber . . . . Praeterleptonetidae n. fam.

- The tibiae bear a pair of strong dorsal-apical bristles (fig. 130). Teeth of the paired tarsal claws are absent. ♂: Cymbium with an almost erect paracymbial "horn" (figs. 133–134). Extinct, Jordanian amber . . . . (?) Protheridiidae: Zarqaraneini

- Juvenile. Clypeus long and vertical. Questionable member of the “bristle-less femur clade”. Burmese amber, OSU no. B-A-1-10. See also a female in Lebanese amber, “questionable Araneoidea” coll. AZAR no. 491, which has long, slender and blunt teeth of the posterior cheliceral margin (fig. 128) and no teeth on the paired tarsal claws . . . . (?) Araneoidea: Fam. indet.

15(13) Anterior median eyes quite large (fig. 108), the legs bear feathery hairs (figs. 109, 113), ♂-pedipalpus (fig. 111) without a retrobasal paracymbium. Jordanian amber. . . . . Salticoididae n. fam.

- Anterior median eyes not quite large, legs without feathery hairs, clypeus very short. ♂-pedipalpus complicated (fig. 127b–c), retrobasal paracymbium present (it may be small). Various ambers 16

16(15) Eye field usually wide, and the anterior median eyes distinctly less separated from each other than from the lateral eyes; ♂-pedipalpus: Frequently exists a pair of patellar bristles, paracymbium integrade, bulbus more or less twisted with the ventral side retrolateral side . . . . Araneidae

- Eye field more narrow and lateral eyes more close to the median eyes (the anterior median eyes are wider spaced); ♂-pedipalpus: Patella with a single bristle, paracymbium a more or less free sclerite, bulbus not twisted. (Subfamily of the Araneidae?) . . . . Zygiellidae

---

(*) See also the enigmatic *Macryphantes cowdeni* SELDEN 1990 (sub Tetragnathidae below) from a Lower Cretaceous deposit (Lagerstaette) in N-Spain which probably possesses a paracymbium, and which may be a member of the family Uloboridae or of an undescribed family. According to SELDEN are plumose hairs and ventral bristles of tarsus IV absent in *Macryphantes* in contrast to most Uloboridae.

THE FOSSIL TAXA in systematic order (see the list above, the contents)

INFRAORDER MYGALOMORPHA

Members of this infraorder – especially adult specimens – are quite rare in fossil resins. Exuviae are occasionally found in Eocene Baltic amber, and at least two of the few known pieces of Mygalomorpha in Cretaceous Burmese amber are apparently remains of exuviae; their determination to the family level is not sure; they may be members of the family Dipluridae. In Baltic amber Dipluridae and Ctenizidae are known. A questionable part of a mygalomorph leg is preserved with the holotype of *Paramiagrammopes cretaceus* n. gen. n. sp.. KADDUMI (2007: 269) reports on several more than 10 mm long legs of spiders in Jordanian amber; they may well be legs of large mygalomorph spiders which escaped from the fossil resin by loosing their legs.

Mygalomorpha indet. 1 (figs. 3–4, photo 61)

Material: Remains of an exuvia in mid Cretaceous Burmese amber from Myanmar, OSU no. B-A-1-6.

Remains of the chelicerae (length of the basal article ca. 1.6mm), the pedipalpi (length of the femur 2mm), and several leg articles are preserved, see the photo; the dorsal part of the prosoma (peltidium) is lost. A cheliceral rastellum is absent, the anterior margin of the cheliceral furrow bears about half a dozen of teeth (fig. 3), the pedipalpal claw bears 4 teeth (fig. 4). The body length of the spider may probably have been almost 1 1/2 cm. Remains of several insects – e. g. spiny leg articles and a long antenna of a questionable member of the Blattaria – are preserved near the spider. I do not want to exclude that the spider is a member of the family Dipluridae which is known e. g. from the Cretaceous Santana formation in Brasil and from Eocene Baltic amber, see WUNDERLICH (2004).

Mygamolorpha indet. 2

Material: Part of a leg – probably of an exuvia – in mid Cretaceous Burmese amber from Myanmar at the margin of a large piece which also includes the holotype of *Palaeohygropoda myanmarensis* PENNEY 2004, NHMLP, In. no. 19132.

The distal part of a stout leg is well preserved. Measurements (in mm): Tarsus ca. 0.5, metatarsus ca. 0.85, incomplete distal part of the tibia 1.2. Strong bristles are apparently absent, the articles bear thick ventral scopulae, a well developed claw tuft exists which is undevided. Based on these characters I suppose that the leg most likely has been part of a mygalomorph spider, probably of a member of the family Dipluridae.

Mygalomorpha indet. 3

Material: Remains of few parts of spiders legs in a piece of mid Cretaceous Burmese amber from Myanmar, NHMLP, In. no. 19104-6.

Remains of legs of a mygalomorph spider – apparently partly decomposited – are preserved, a tarsus is 3 mm long, bears 1 dozen of strong ventral spines and 3 large tarsal claws with long teeth; furthermore exist some metatarsal bristles (especially apically) and some thin tibial bristles.

INFRAORDER ARANEOMORPHA

(1) SUPERFAMILY DYSDEROIDEA s. l. sensu WUNDERLICH (2004) (incl. Filistatidae and Scytodoidea s. str. auct.)

Members of this superfamily are most frequent in Cretaceous ambers in contrast to Eocene ambers (except members of the family Segestriidae). Within the collections of the MNHNP, the NHML, the OSU and CJW numerous juveniles indet. are kept (only few specimens are studied more closely); adults are rare. Juveniles can be mistaken for members of the Araneoidea.

(I) Family SEGESTRIIDAE

The family is known from the Lower Cretaceous to today, see WUNDERLICH (2004) and this volume. Most Cretaceous spiders are conspicuously smaller than Tertiary or extant spiders.
The diverse suprageneric taxa of the family Segestriidae in the Cretaceous period – members of two or even three extinct subfamilies are known in contrast to only two extant and Tertiary subfamilies (Ariadninae and Segestriinae) – indicate clearly that Segestriidae is a relict family. Members of probably two subfamilies in gondwanan Lebanese and Jordanian ambers as well as Laurasian taxa may indicate an early origin of the geologically very old – pangaean? – family Segestriidae; Lebansegestriinae and Microsegestriinae may well be “Gondwanan taxa”. – There is a conspicuous rupture between (a) the diverse and “strange” Cretaceous taxa which are extinct (the questionable genus *Ariadna* may be the single exception), and (b) the remaining genera *Ariadna* and *Segestria* from the Eocene (Baltic amber, see WUNDERLICH (2004)) which both survived up to now as well as the extinct genus *Vetsegestria* WUNDERLICH 2004 which is only known from the Eocene. – Note: *Ariadna* may be a “living fossil”, but true *Ariadna* may well be different from the Cretaceous taxon besides (genital)morphological similarities.

Remark: I regard the familiar relationships of the extant genus *Gippsicola* HOGG 1900 from the Australian Regian as quite unsure, see WUNDERLICH (2004: 657).

PENNEY (2004) described *Palaeosegestria lutzzii* (n. gen. n. sp.) (fig. 7) from Cretaceous amber of New Jersey, N-America. The genus is characterized by the basal cheliceral articles which bear a basal brush of hairs and the fangs which are placed on prologations of the chelicerae (fig. 7A). According to the position of the large median eyes the genus may be a member of the Ariadninae WUNDERLICH 2004 or of an undescribed subfamily; the position of the cymbial insertion of the bulbus has not been described, the cheliceral dentition is hidden and the shape of the fang is not clearly figured.
The monotypic Microsegestriinae WUNDERLICH with *Microsegestria poinari* WUNDERLICH & MILKI 2004: 1869ff has been described from Lebanese amber; its bulbus bears a conductor besides the embolus (an exception within the Segestriidae). Below I describe a second segestriid species which is preserved in Lebanese amber and which subfamiliar relationships are unsure as well as a questionable member of the genus *Ariadna* AUDOUIN 1826 in Jordanian amber.

Key to the extant and extinct genera and subfamilies of the family Segestriidae (♂):

1 Conductor present, see WUNDERLICH (2004: 1873: Fig. 4) 2

- Conductor absent (figs. 6, 9) 3

2(1) Bulbus with complicated sclerites. Extant, New Zealand . . . . *Gippsicola*

- Bulbus with embolus and conductor only, clypeus widely projecting, cymbium very short, see WUNDERLICH (2004: 1873, figs. 1–4). Lebanese amber. *Microsegestria* . . . . Microsegestriinae

3(1) The basal cheliceral articles bear anteriorly numerous strong basal bristles (fig. 7A). Extinct, USA, New Jersey amber . . . . *Palaeosegestria*

- Strong cheliceral bristles absent 4

4(2) Tibiae and metatarsi I–II bear only a single pair of ventral bristles besides apicals, bulbus very long and slender (figs. 8–9). *Lebansegestria.* Lebanese amber . . . . Lebansegestriinae

- Tibiae and metatarsi I–II bear at least two pairs of ventral bristles besides apicals (fig. 5), bulbus much shorter (fig. 6). Extant and extinct; see WUNDERLICH (2004: 656–669) 5

5(4) Position of the median eyes between the anterior lateral eyes, fangs long and more slender, cymbium long and basally wide, bulbus pear-shaped, inserted in the basal part of the cymbium. Extant (*Segestria*) and Eocene ambers *Segestria* and *Vetsegestria* . . . . Segestriinae

- Median eyes in a more posterior position, fangs stout, cymbium short and blunt, bulbus almost globular, inserted in the middle of the cymbium (fig. 6). Extant, Tertiary ambers (*Ariadna*) and probably Cretaceous ambers (*Ariadna*?) (*) . . . . . . Ariadninae

---

(*) See below (?*A. amissiocoli*). *Segestria* ? sp. indet. sensu PENNEY (2002) in amber from New Jersey may – according to its eye position – be a member of *Ariadna*.

ARIADNINAE WUNDERLICH 2004

?*Ariadna amissiocoli* n. sp. (figs. 5-6)

Material: Holotypus ♂ in Lower Cretaceous Jordanian amber from the Zarqa river canyon, ex coll. H. KADDUMI (ERMNH), F2007/JB/AR/CJW.

Preservation and syninclusions: The spider is incompletely preserved: The dorsal surface of the prosoma, the opisthosoma and several leg articles are broken off and missing, most of the right legs and some articles of the left legs as well both pedipalpi are preserved. The prosoma is naturally filled with a dark brown substance, the opisthosoma is bent ventrally in a strong angle. – Some thin threads of spiders silk and numerous particles of detritus are also preserved in the small piece of amber.

Diagnosis (♂; ♀ unknown): Tibia I bears two pairs of ventral bristles plus apical ones, metatarsus I bears three pairs of ventral bristles plus apicals (fig. 5); the eye position is unknown. The pedipalpus (fig. 6) bears a long embolus which is strongly bent dorsally.

Description (♂):
Measurements (in mm): Body length about 1.8, width ca. 1.6, tibia I 1.6.
Most parts of the body are missing or hidden.
Colour: Remains of the internal parts of the prosoma dark brown, legs medium brown.
– Legs of medium length; bristles (fig. 5) exist at least ventrally on tibiae and metatarsi, metatarsus III bears an apical preening comb of bristles which is well developed, a short trichobothrium exists apparently in the basal half of the metatarsi, the unpaired tarsal claw is well developed, the large paired tarsal claws bear long teeth. – Pedipalpus (fig. 6) with stout articles, cymbium quite short, position of the alveolus in the middle or slightly distally, bulbus almost globular, embolus long and strongly bent dorsally.

Relationships: According to the position of the alveolus and the shape of cymbium and bulbus I regard *amissiocoli* as a member of the subfamily Ariadninae; it could well be a member of the genus *Ariadna* AUDOUIN 1826; unfortunately the eyes and the chelicerae are not preserved. – See also below: Questionable Segestriidae indet in Burmese amber.
If correctly determined *Ariadna* would be the only known genus of araneomorph spiders which survived from the Cretaceous up to now, but see the remark above.

Distribution: Lower Jordanian amber forest.

LEBANSEGESTRIINAE n. subfam.

Diagnosis (♂; ♀ unknown): Tibiae and metatarsi I–II bear only a single pair of ventral bristles besides apical ones; pedipalpus (figs. 8–9): Bulbus very long and slender, position of the alveolus probably in the middle of the cymbium, embolus long, sickle-shaped and widened.

Further characters: Body length only 1.7 mm, clypeus vertical, fangs probably stout, tibia I unmodified, pedipalpal tibia thick.

Type genus (by monotypy): *Lebansegestria* n. gen.

Relationships: The position of eyes and legs – III is directed foreward like I and II – are typical of characters of the family Segestriidae. The shape of the bulbus is quite unusual. In *Lebansegestria* exists fewer bristles on tibiae and metatarsi I–II than in most other taxa of the Segestriidae.

Distribution: Lower Cretaceous Lebanese amber forest.

***Lebansegestria* n. gen.**

Diagnosis, relationships and distribution: See the new subfamily.

Type species (by monotypy): *Lebansegestria azari* n. sp.

***Lebansegestria azari* n. gen. n. sp.** (figs. 8–9, photo 62)

Derivatio nominis: This species is dedicated to DANY AZAR, MNHNP and Beirut, who collected and recognized important arthropod inclusions from the Cretaceous, including this holotype.

Material: Holotypus ♂ in Lower Cretaceous amber, from Central Lebanon, Hammana-Mdeyriy outcrop; MNHNP (Laboratoire d' Entomology).

Preservation and syninclusions: Artificial resin encloses the piece of amber with the spider which is fairly deformed by natural pressure and heating; some leg articles are flattened, prosoma and opisthosoma are depressed laterally, two fissures within the amber are running through some leg articles and the opisthosoma longitudinally, the left leg II and the right legs I and IV are lost beyond the coxa apparently by autotomy. A longer hair-shaped (plant?) structure is situated below the spider, a dark brown area lies left above the spider, some particles of detritus are present, too.

Diagnosis (♂; ♀ unknown): See above. The spider's prosoma is distinctly longer than wide.

Description (♂):
Measurements (in mm): Body length 1.7, prosomal length 0.9; leg I: Femur 0.9, patella 0.3, tibia 0.85, metatarsus 0.68, tarsus 0.32, tibia III 0.65, tibia IV ca. 0.7.
Colour mainly light grey. Prosoma (it is deformed) distinctly longer than wide, not strongly smaller anteriorly; 6 eyes similar to *Plumorsolus gondwanensis* n. sp., fovea indistinct, position of the clypeus vertical. Mouth parts strongly deformed, chelicerae fairly large, lateral files absent or not recognizable, teeth of the forrows margins and shape of the labium unknown, fangs probably stout. – Legs only fairly long and slender, III is directed foreward; bristles: Femora dorsally 1/1/1, prodistally usually a single additional one (2 on I), patellae none, tibiae I–II a single ventral pair in the basal half and a ventral-apical pair, metatarsi I–II with a ventral pair in the basal half and few hair-shaped apical bristles, tibia IV bears several ventral and lateral bristles. Tarsal trichobothia absent, position of the metatarsal trichobothria IV in 0.85, scopulae and claw tufts absent, unpaired tarsal claw well developed, paired claws with long teeth in a single row. I did not recognize the tarsal organ between the hairs of the holotype. – Opisthosoma oval, fairly densily covered with short hairs, position of the tracheal spiracles unknown, anal tubercle well developed, 6 pairs of short spinnerets. – Pedipalpus (figs. 8–9; tibia and bulbus are fairly deformed): Femur and patella slender, tibia very thick, cymbium of medium length, position of the alveolus probably in its middle, bulbus very long and slender, embolus long and sickle-shaped, thickened distally.

Relationships: See above.

Distribution: Lower Cretaceous Lebanese amber forest.

?**Segestriidae indet**.

Material: 1 juv. in Burmese amber, NHMLP In. no. 20193.

The spider is 2.8 mm long, the eyes possess a “segestriid” position with the three groups wider spaced than in all other Segestriidae which are known to me. The tarsi are relatively short, the patellae are relatively long, the chelicerae are protruding, the legs III are more directed backward (!) (but the leg position of amber inclusions may be unnatural), an unpaired tarsal claw exists apparently, the leg bristles are short, the opisthosoma bears short hairs. According mainly to the position of the eyes I do not want to exclude with certainty that this spider may be a member of the family Segestriidae. – See also above: ?*Ariadna amissiocoli* n. sp..

Distribution: Mid Cretaceous Burmese amber forest.

(II) Family OONOPIDAE

The family "Dwarf six-eyed Spiders" – including members of the subfamilies Gamasomorphinae and Orchestininae n. subfam. – is known from the Cretaceous to today. Its tiny members are known from almost all Cretaceous and Tertiary ambers, see PENNEY (2006, 2007), WUNDERLICH (2004: 690), and are most often published under the genus name *Orchestina* SIMON (s. l.). In my opinion the diverse genus *Orchestina* has to split up, see the description of the subfamily Orchestininae, as well as the new genera *Burmorchestina* and *Canadaorchestina* in Burmese rsp. Canadian Cretaceous ambers in this volume. The taxa of the Orchestininae in Cretaceous ambers as well as in Tertiary ambers and extant are not congeneric due to my investigations; at least two extinct Cretaceous genera face to several subgenera of the extant genus *Orchestina* and the monotypic extant genus *Ferchestina*. – Remark: I do not want to exclude that a member of the "Oonopidae indet." sensu PENNEY (2002: 212) may be a taxon of the new family Psilodercidae, see below.
In Burmese amber I found members of two oonopid subfamilies (photos 65–70); (1) the Orchestininae is most frequent (the spiders have distinctly thickened femora of their posterior jumping legs, fig. 14), and a high thoracal part, (2) the Gamasomorphinae is reported by a single male only (these spiders possess an armoured opisthosoma, fig. 10).

(IIa) Subfamily GAMASOMORPHINAE

The first fossil member of this subfamily was described as *Gamasomorpha incerta* WUNDERLICH 1988 – transferred to *Stenoonops* SIMON by PENNEY 2000: 348 – in Miocene Dominican amber. In the following the first gamasomorphine member is described from the Cretaceous.

Eogamasomorpha n. gen.

Diagnosis (♂; ♀ unknown): Prosoma low (fig. 10), its cuticula almost smooth (not rugose), 6 small eyes with 4 eyes in the anterior row, legs without bristles, opisthosomal scuta as in fig. 10; pedipalpus (figs. 12–13) with slender articles, bulbus not fused to the cymbium, inserted in the distal half of the cymbium, conductor absent.

Type species (by monotypy): *Eogamasomorpha nubila* n. sp.

Relationships: A closely related genus is unknown to me. In *Gamasomorpha* KARSCH 1881 the prosomal cuticula is rugose, the eyes are large and their position is different, bulbus and cymbium are fused together, and a conductor exists.

Distribution: Mid Cretaceous Burmese amber forest.

Eogamasomorpha nubila n. gen. n. sp. (figs. 10–13, photo 65)

Material: Holotypus ♂ in mid Cretaceous Burmese amber from Myanmar, OSU no. B-A-1-1, G. POINAR jr. coll.

Preservation and syninclusions: The spider is well preserved, darkened, prosoma and pedipalpal articles are deformed, the ventral side of the opisthosoma is covered with a thin emulsion. – Thin spider's threads are preserved directly below the opisthosoma and in various parts of the piece of amber. A tiny deformed beetle, stellate hairs, and particles of detritus and insects excrements are also preserved in different layers of the piece.

Diagnosis (♂; ♀ unknown): See above; opisthosomal scuta as in fig. 10; embolus long (figs. 12–13).

Description (♂):
Measurements (in mm): Body length 0.9, prosomal length ~0.4; leg I: Femur ~0.28, patella ~0.12, tibia ~0.23, metatarsus 0.16, tarsus 0.2, tibia III ~0.19, tibia IV 0.3.
Colour: Body dark brown (darkened), legs medium brown.
Prosoma (photo, fig. 10) (it is deformed, parts are hidden) low, longer than wide; 6 small/tiny strongly deformed eyes, 4 in the anterior row, the posterior pair is widely spaced. Basal cheliceral articles of medium size, bearing longer anterior hairs. – Legs (photo, fig. 11) only fairly long, tarsi relatively long, order IV/I/II/III, bristle-less, covered with long and conspicuous hairs. Trichobothria: Tibiae with 2 long ones, metatarsi with a single one near its end. Unpaired tarsal claw absent, paired claws with few long teeth. – Opisthosoma (photo, fig. 10) long oval, covered with short hairs, dorsally completely covered with a scutum, laterally with few scutate longitudinally furrows, ventrally

apparently scutate, too (partly covered with an emulsion), anterior spinnerets fairly long. – Pedipalpus (figs. 11–13): See above, the embolus is bent dorsally.

Relationships: See above.

Distribution: Mid Cretaceous Burmese amber forest.

(IIb) Subfamily ORCHESTININAE including *Burmorchestina* (n. gen.) and *Canadaorchestina* (n. gen.). Descriptions: See the paper no. 2 on this subfamily of the Oonopidae in this volume. The tiny members of *Burmorchestina pulcher* (n. sp.) are frequent in Burmese amber (see the photos 66–70), and are easily recognizable by their thickened posterior femora as in fig. 14 in contrast to all other Burmese amber spiders.

(III) Family EOPSILODERCIDAE n. fam.

Diagnosis (♂; ♀ unknown): Cheliceral lamina most probably absent, the anterior margin of the cheliceral furrow bears two tiny teeth, six eyes in a "segestriid" position (so in *Furcembolus*, but not quite sure in the holotype of the type taxon), clypeus not or only fairly protruding, legs without distinct bristles, ♂-pedipalpus (figs. 18, 21–22): Tibia large, cymbium bristle-less, bulbus simple, originating at the tip of the cymbium.

Further characters: Prosoma longer than wide, a cheliceral “clasping bristle” (fig. 15) exists in the type genus, teeth of the paired tarsal claws absent or strongly reduced in the type species of the type genus (but different in indet. sp. 2 and 3!), legs extremely long and slender and onychium well developed in the type taxon, existence of lungs unknown (lung covers may be present in *Eopsiloderces*), colulus large in the type taxon, position of the epigastral furrow and the tracheal spiracle are unknown.

Type tribus: Eopsilodercini. Further tribus: Furcembolusini n. trib. (questionable).

Relationships: In the Ochyroceratidae and Psilodercidae – which I regard as strongly related – the prosoma is about as long as wide, the clypeus is usually distinctly protruding, and the cymbium bears usually bristles or spines, (the cymbial attachment of the bulbus is variable). – The similar attachment and shape of the bulbus (not the strong pedipalpal tibial bristles) in the extant (SE-asian) species *Psiloderces howarthi*

DEELEMAN-REINHOLD 1995 should have been evolved convergently. – Certain extant New World Pholcidae – e. g. *Cibchea mayna* HUBER 2000 and *Pisaboa mapiri* HUBER 2000 – possess different retroapical spines of the ♂-chelicerae which evolved doubtless convergently to *Eopsiloderces*. – In members of the family Loxoscelidae an unpaired tarsal claw is absent and cheliceral stridulatory files exist. – Juvenile (quite questionable!) fossil Eopsilodercidae in amber (see below) are difficult to determine and can easily be mistaken for Pholcidae in first view, in which a comb of tarsus IV exists, clypeus and eye position are different.

Distribution: Mid Cretaceous Burmese amber forest. See also above: *Selenops* sp. sensu PENNEY 2007 in allegedly Eocene amber from France, the “Remarks on erroneous determinations”.

(IIIa) EOPSILODERCINI n. trib.

Diagnosis (♂): Chelicerae (fig. 15) with a strong retroapical "clasping bristle"; pedipalpus (fig. 18): Embolus long and only slightly bent, an embolic apophysis is absent.

Type genus (by monotypy): *Eopsiloderces* n. gen.

Relationships: See Furcembolusini n. trib..

Distribution: Mid Cretaceous Burmese amber forest.

Eopsiloderces n. gen.

The gender of the name is masculine.

Type species (by monotypy): *Eopsiloderces loxosceloides* n. sp.

Diagnosis, relationships and distribution: See the Eopsilodercini. The legs are very long and slender (photo).

***Eopsiloderces loxosceloides* n. gen. n. sp.** (figs. 15–18, photo 71)

Material: Holotypus ♂ in mid Cretaceous Burmese amber from Myanmar, F1914/BU/AR/CJW.

Preservation and syninclusions: The spider is fairly well preserved in a yellow-orange piece of amber, two large fissures are running through the piece and through most legs; a dorsal part of the opisthosoma, the right side of the prosoma including most eyes, the right legs I–III and the basal articles of the right pedipalpus are cut off at a layer within the amber. Larger "bubbles" are preserved each within the pro- and the opisthosoma. – Left in front of the spider a tiny loose pincer, 0.22 mm long – probably of a pseudoscorpion – is preserved. One Acari (0.5 mm long) is preserved at the margin of the piece of amber, few thin remains of spider threads, insect's excrements and plants (stellate hair shaped) are also present.

Diagnosis (♂; ♀ unknown): Pedipalpus (fig. 18) with a large tibia and a long bulbus/embolus.

Description (♂):
Measurements (in mm): Body length 1.8, prosomal length 0.85; leg I: Femur 1.6, patella 0.28, tibia 1.45, metatarsus 1.35, tarsus 0.5, tibia III 1.1, leg IV: Femur 1.5, patella 0.28, tibia 1.4, metatarsus + tarsus 1.9; pedipalpal tibia: Length 0.35, hight 0.15.
Colour: Body grey, legs medium brown.
Prosoma (fig. 15) incompletely preserved, dorsally distinctly convex, most probably longer than wide, with long dorsal hairs; eyes (most eyes are cut off) most probably in a "segestriid" position, a lateral elevation bears apparently two small eyes. Fovea unknown, clypeus only fairly protruding. Chelicerae partly cut off, fairly large, probably not fused together, lateral files absent, laterally with a single strong and straight spine which may be a clasping spine, the spines of both sides possess an almost parallel position, teeth of the furrows absent or small, fangs long and slender. – Legs (photo, figs. 16–17) very long and slender, prograde, I about as long as II and IV, III shorter, hairs long, distinct bristles absent but questionable remains of thin and almost hair-shaped lateral bristles exist on femora and tibia I–II. All metatarsi bear a long trichobothrium, its position on III in 0.68. Comb of tarsus IV absent, onychium well developed, tarsi indistinctly pseudoarticulate, paired claws large, teeth tiny or probably even absent, unpaired claw long, slender and bent in a right angle. – The deformed opisthosoma is 1.7 times longer than high, the hairs are fairly long. Anterior spinnerets stout, colulus apparently large. – Pedipalpus (fig. 18): Femur slender, patella small, dorsally convex, without bristles, bulbus long, bottle-shaped, originating apically at the cymbium, embolus long and fairly bent.

Relationships: See above.

Distribution: Mid Cretaceous Burmese amber forest.

?Eopsilodercidae indet. sp. 1 (photo 74)

Material: 1 ?ad. ♀ in mid Cretaceous amber from Burma (Myanmar), OSU no. B-A-1-12, G. POINAR jr. coll.

Preservation and syninclusions: The deformed spider is situated flat – most probably flattened – within two narrow layers of the amber; the “laterigrade” position of the legs may well be caused by this flattening. The spiders legs are complete, the dorsal part of the prosoma is cut off within the fossil resin, the right pair of the eyes is preserved. – Remains of three questionable Nematoda: Rhabditida are preserved in front of the spider, two Diptera: Nematocera and remains of other insects are preserved mainly below and behind the spider in different layers.

Description (?ad. ♀):
Measurements (in mm): Body length 2.0, prosoma: Length ~ 0.7, width ~ 0.65; leg I: Femur 1.2, patella 0.16, tibia 1.2, metatarsus ~ 1.05, tarsus ~ 0.4, tibia II 1.1, tibia III ~ 0.65, tibia IV ~ 1.0.
Colour light grey brown.
Prosoma deformed and incomplete, almost as wide as long, dorsally covered with few longer hairs; probably 6 eyes in three pairs, laterally is apparently a pair preserved. Clypeus only fairly long and not strongly protruding, basal cheliceral articles stout, most probably not fused basally, lamina apparently existing, lateral stridulatory files absent, shape of the fangs unknown. – Legs extremely long and thin (photo 74), without bristles, hairs long and thin, trichobothria unknown, ventral comb of tarsus IV absent, tarsi with 3 long and thin claws which may be smooth. The coxae IV are widely separated by the sternum. – Opisthosoma strongly deformed, ca. 1.7 times longer than wide, scarcely covered with hairs.

Relationships: According to the position of the eyes and the absence of a ventral comb of tarsus IV the spider is not a member of the Pholcidae but probably of the Eopsilodercidae which also possesses long and bristle-less legs and probably a similar position of the eyes. In the remaining members of the Eopsilodercidae which are known to me are the legs not extremely long and thin. In similar members of the family Loxoscelidae an unpaired tarsal claw is absent and lateral cheliceral files exist.

Distribution: Mid Cretaceous Burmese amber forest.

?Eopsilodercidae indet. sp. 2 (photo 72)

Material: 1 juv. ♀ in mid Cretaceous Burmese amber from Myanmar, F1915/BU/AR/CJW.

Preservation: The spider is completely and very well preserved in a clear and light yellow piece of amber, and is not deformed.

Description (juv. ♀):
Measurements (in mm): Body length 1.05, prosomal length 0.5, opisthosoma: Length 0.65, height 0.35; leg I: Femur 0.65, patella 0.18, tibia 0.53, metatarsus 0.47, tarsus 0.4, tibia II 0.45, tibia III 0.35, tibia IV 0.45.
Colour light brown.
Prosoma longer than wide, 6 eyes in a "segestriid position", clypeus long and fairly protruding, basal cheliceral articles fairly large, apparently not fused together, stridulatory files absent, gnathocoxae strongly converging above the labium which is about as wide as long. Pedipalpus long, tarsal claw present. Legs (photo 72) long and bristle-less, hairs fairly long, trichobothria unknown, paired tarsal claws with long teeth, unpaired claws thin and bent in a right angle, onychium present. Opisthosoma oval, covered dorsally with fairly long hairs, lung covers probably existing, three pairs of spinnerets, the anteriors stout, colulus tiny.

Relationships: The long and bristle-less legs as well as the number and the position of the eyes are similar to the family Eopsilodercidae but the teeth of the paired tarsal claws are large in the present specimen and lungs may be present.

Distribution: Mid Cretaceous Burmese amber forest.

?Eopsilodercidae indet. sp. 3 (photo 73)

Material: 1 juv. ♀ in mid Cretaceous Burmese amber from Myanmar, NHMLP no. 20152.

Preservation: Most parts of the spiders are deformed or cut off (photo 73), some legs and parts of the right side of the prosoma are preserved, both anterior legs are lost beyond the coxa, the eyes are partly hidden and deformed.

Description:
Measurements (in mm): Body length probably ca. 1.7, prosomal length 1.0, length of the basal cheliceral article ca. 0.35, pedipalpal tarsus 0.36; leg II: Femur 1.4, patella 0.27, tibia 1.65, metatarsus ca. 1.3, tarsus ca. 0.32, femur III 0.9.
Prosoma incomplete, apparently not domed, 8 or 6 eyes (deformed); clypeus probably fairly short and not protruding, chelicerae slender and fairly short, a basal fusion is not observable. Legs long and very slender (photo) but III distinctly shorter, bristle-less, tarsi straight, probably without peudosegments and not flexible, paired claws with long teeth, unpaired claw unknown, trichobothria unknown. Pedipalpus with long articles, tarsal claw absent. The opisthosoma is cut off.

Relationships: According to the bristle-less legs like in the holotype of of *Eopsilodercés loxosceloides* this juvenile female may be a member of the Eopsilodercidae.

Distribution: Mid Cretaceous Burmese amber forest.

(IIIb) FURCEMBOLUSINI n. trib.

Diagnosis (♂; ♀ unknown): Prosoma with distinct wrinkles (fig. 20); pedipalpus (figs. 21– 22): Embolus long and with a long apophysis.

Note: Chelicerae, tarsal claws and opisthosoma are unknown.

Type genus (by monotypy): *Furcembolus* n. gen.

The **relationships** are unsure (the tarsal claws are unknown), the taxon is probably not a member of the Eopsilodercidae. The legs are long and bristle-less as in the Eopsilodercini, and the bulbus is attached to the tip of the cymbium, too, but the prosoma is not rugose in *Eopsiloderces*, and an embolic apophysis is absent. – A similar embolic apophysis exists in *Pholcochyrocer* n. gen. (Praeterleptonetidae) in which numerous leg bristles exist, the cymbium bears an outgrowth, and the bulbus is larger.

Distribution: Mid Cretaceous Burmese amber forest.

***Furcembolus* n. gen.**

Diagnosis, relationships and **distribution**: See above.

Type species (by monotypy: *Furcembolus andersoni* n. sp.

***Furcembolus andersoni* n. gen. n. sp.** (figs. 20–22, photos 75–76)

Derivatio nominis: With pleasure I name this species after SCOTT ANDERSON (USA) from which I got the holotype.

Material: Holotypus ♂ in mid Cretaceous amber from Myanmar (Burma), F2011/BU/AR/CJW.

Preservation and syninclusions: The spider is partly well but incompletely preserved apparently at the beginning of a composing process, the chelicerae and the opisthosoma are missing within the amber, the distal parts of all legs are cut off, the right pedipalpus is lying loose in front of the spiders body (see the photo). The spider is darkened and parts are deformed. Numerous particles of detritus and stellate hairs as well as the distal part of a leg of an Opiliones indet. (ca. 5 mm long, lying near the margin of the piece of amber) are preserved in the same piece. GIRIBET & DUNLOP (2005) published recently on a harvestman in Burmese amber.

Diagnosis (♂; ♀ unknown): See above (Furcembolusini); the embolus bears a long apophysis which is longer than the embolus and stronger bent, fig. 21–22.

Description (♂):
Measurements (in mm): Body length probably about 3.0, prosomal length 1.5; femora: I 2.4, II 1.9, III 1.15, IV ~1.8, tibia II 1.5, tibia III 1.0, metatarsus III 1.1, femur of the pedipalpus 0.7.
Colour mainly dark brown.
Prosoma (fig. 20) (most parts of the dorsal aspect are hidden) with indistinct hairs, a distinct furrow between the cephalic and the troracal part; especially the thoracal part and the sternum bear distinct wrinkles. Six eyes in a wide "segestriid" position (similar to figs. 7A, 19) with four eyes in the anterior row. Clypeus long and vertical, chelicerae lost, gnathocoxae very long and slender, only slightly converging, labium longer than wide, coxae IV spaced by about their diameter. – Legs very long, slender and hairy, bristle-less, I the longest, III distintly the shortest, tarsal claws lost, trichobothria unknown. – Opisthosoma lost. – Pedipalpus (figs. 21–22): Femur long, slender and almost straight, patella short, tibia long and thick, bulbus small, attached at the tip of the short cymbium, embolus "furcate" (with a long apophysis); with some hesitation I regard the slightly shorter ventral branch as the embolus which is not pointed in contrast to the dorsal apophysis which is stronger bent.

Relationships: See above.

Distribution: Mid Cretaceous Burmese amber forest.

Selected characters of 6 related families of the superfamily Dysderoidea – the branch of “capture web dwellers” –, with remarks on the families Loxoscelidae, Tetrablemmidae and Telemidae:

(See WUNDERLICH (2004: 737–738))

character	Praeter-leptonetidae	Leptonetidae	Pholcidae	Psilodercidae	Eopsilodercidae *(1)*	Ochyroceratidae *(2)*
number of eyes	8	6	8 or 6 in triads (rarely 2)	6 (in a “segestriid position”)	6	6
onychium	-- (?)	--	+	+	+	+
femoral/tibial and/or metatarsal bristles	+	+/-	-*(3)*	-	-	-*(3)*
sticky droplets of the capture web	+?	--	+ (!)	- ?	- ?	- ?
special characters	--	patella-tibia autotomy, tibial glands *(4)*	procursus, ventral comb of tarsus IV, reduced colulus *(5)*	frequ. several pairs of receptacula seminis	terminal cymbial attachment of the bulbus	no lungs, labium incised, frequently very wide genital fold *(6)*
extinct/ extant; distribution	extinct Burma	almost cosmopolitical, excl. Africa	cosmopolitical	SE-Asia	extinct Burma	pantropical

---

(1) In similar members of the family Loxoscelidae (they are not listed here) an unpaired tarsal claw is absent in contrast to all other families which are listed here –, the chelicerae bear retrolateral stridulatory files, and the leg position is mediograde or even laterigrade.

(2) Ochyroceratinae and Theotiminae. – In numerous male Theotiminae exist modified chelicerae which may bear lateral teeth similar to numerous Pholcidae.

(3) Leg bristles/spines are extremely rare in the Pholcidae, e. g. exist ventral (!) femoral I-II spines in ?*Cryssocnemis velteni* WUNDERLICH 2004; in some species of *Speocera* (Ochyrocetidae) the posterior tibiae and/or metatarsi bear bristles. The anterior median eyes are the smallest or are even absent in the Pholcidae.

(4) Most often typical eye position and with a cymbial constriction, see WUNDERLICH (2004: 718, 720, figs. 13c, r). Tibial glands exist as in Telemidae which are not listed here (see *(6)*). Several – up to 7 – promarginal cheliceral teeth similar to Ochyroceratidae (up to >7 teeth). Archoleptonetinae with a cribellum according to GRISWOLD et al. (in prep.).

(5) No teeth on the margins of the cheliceral furrows (as in some Psilodercidae), fangs usually stout, the basal cheliceral articles may be partly fused. Lateral cheliceral stridulatory files exists frequently in contrast to the Psilodercidae. (A similar comb of ventral hairs of tarsus IV exists in numerous taxa of the families Theridiidae, Nesticidae, and in the Nicodamidae: The ecribellate Nicodaminae).

(6) Position of the tracheal spiracle half-way between epigastral fold and spinnerets. Typical “segestriid” eye position (similar in Psilodercidae and Telemidae). Lungs are also absent in the Telemidae in which a zig-zag abdominal sclerite above the pedicel exists and a single dorsal bristle on their tibiae.

Remarks: (1) In the cladogram to Tetrablemmidae, Pholcidae + Ochyroceratidae – see WUNDERLICH (2004: 645) – "loss of leg bristles" has to eliminate after the discovery of the Praeterleptonetidae, and "tendency to the existence of anterior cheliceral and clypeal outgrowths" has to add. Remarkably tendencies to the presence of peculiar anterior clypeal and of cheliceral outgrowths/teeth in the male sex exist solely in the branch of dysderoid "capture web dwellers": Tetrablemmidae (e. g. *Brignoliella*), Pholcidae, Eopsilodercidae, Psilodercidae and Ochyroceratidae, see WUNDERLICH (2004: 645). – (2) The convergences in certain taxa of the Ochyroceratidae/Psilodercidae and Pholcidae are quite remarkable and may support the thesis that both are sister groups: (a) The colouration as well as the shape of legs and opisthosoma may be similar (compare e. g. *Leclercera* and *Pholcus*), (b) the tendency to a reduced number of six eyes, (c) a long and ventrally protruding clypeus, (d) outgrowths of the clypeus in the male sex (e. g. *Psiloderces penaerorum*, *Hedypsilus culicinus, Merizocera* sp. and numerous Pholcidae), (e) modified chelicerae with outgrowths in the male sex (e. g. *Speocera* sp. and numerous Pholcidae), (f) tarsal and metatarsal pseudosegmentation in long-legged species (e. g. *Althepus mulcatus*, *Speocera vilhenai* as well as numerous Pholcidae).

(IV) Family PSILODERCIDAE DEELEMAN-REINHOLD 1995 (n. stat.) (extant)

Fossil reports of this family are absent.
According to several important characters I already previously suggested that the Psilodercinae DEELEMAN-REINHOLD 1995 has to split off from the Ochyroceratidae FAGE 1912, see WUNDERLICH (2004: 732). The discovery of taxa in Cretaceous Burmese amber is an impulse for the actual splitting.

Diagnosis: Six eyes in a "segestriid position" (fig. 19), leg bristles absent; frequently with several pairs of receptacula seminis, cymbium with strong apical bristles.

Further characters: Ecribellate, haplogyne, lungs and unpaired tarsal claws present, prosoma about as long as wide, clypeus distinctly protruding, cheliceral stridulatory files absent, legs prograde, colulus large.

Remark: The diverse type genus *Psiloderces* FAGE 1892 has to split up in my opinion.

Relationships: See the tab. above; Ochyroceratidae, Pholcidae, and especially Eopsilodercidae which may be most related. Lungs are existing in contrast to the related Ochyroceratidae.

Distribution: SE-Asia (extant).

(V) Family PRAETERLEPTONETIDAE n. fam.

Diagnosis (♂; ♀ unknown): 8 eyes in two rows (fig. 23), the ventral tibial bristles may be paired, onychium absent or tiny. Order of legs I/II/IV/III. Cheliceral teeth exist at least in *Palaeohygropoda*. ♂-pedipalpus (figs. 27–31, 36–37, 39): with SLENDER ARTICLES, CYMBIUM LARGE, with paracymbial spoon/spine(s). Sticky droplets of the capture web are probably existing. – Unknown are: The position of the tracheal spiracle, the existence of a colulus, tibial glands, and cheliceral stridulatory files as well as the kind of autotomy.
Further character: Unpaired tarsal claw present, paired tarsal claws with long teeth in *Palaeohygropoda* and *Pholcyrocer*; the existence of such teeth is unknown in the type genus *Praeterleptoneta*.

Type genus: *Praeterleptoneta* n. gen. Further genera: *Palaeohygropoda* PENNEY 2004 and *Pholcochyrocer* n. gen.

Tribus: Praeterleptonetini, Palaeohygropodini and Pholcochyrocerini (its relationships are unsure).

Relationships: Praeterleptonetidae offer a mixture of characters of related families: 8 eyes as in various Pholcidae (eye position, chaetotaxy and tarsus IV are different), femoral, tibial and metatarsal bristles as well as a reduced/absent onychium like in certain Leptonetidae, a cymbial spoon – as well as apical cymbium bristles in *Praeterleptoneta* and *Palaeohygropoda* – like in certain Leptonetidae, Ochyroceratidae and Psilodercidae; see also the probable existence of sticky droplets of the capture web like in the Pholcidae. I do not want to exclude that this is not a monophyletic family; better preserved specimens are needed for further studies. – The existence of 8 eyes and of numerous leg bristles are surely basic characters of the superfamily Dysderoidea; unpaired leg bristles which stand out from their article (*Praeterleptoneta*) is a pattern of the “branch of egg-carrying females”, see WUNDERLICH (2004: 644–645). According to the presence of anterior median eyes Praeterleptonetidae is apparently a member of the “branch of capture web dwellers”. In respect to the reduced onychium the family Leptonetidae may be most related, according to the single spigot of the median spinnerets at least in *Praeterleptoneta* (fig. 26) the family Ochyroceratidae may be related; in the extant members of both families exist only 6 eyes; in the Ochyroceratidae are lungs furthermore absent (lungs exist probably in the Praeterleptonetidae), in the Leptonetidae exists a patella-tibia autotomy (the kind of autotomy is unknown in the Praeterleptonetidae). – The cymbium is similar in some species of (e. g.) *Althepus* THORELL 1898 of the Psilodercidae, see DEELEMAN-REINHOLD (1995: Figs. 145, 149, 152). – In respect to certain basal patterns – the (high) number of 8 eyes, the presence of several leg bristles (on the femora, too, fig. 38) as well as the high geological age – Praeterleptonetinae may well be the sister group to all the families in question, see the tab. above, but sure conclusions can only be drawn if the existence/absence of lungs (lung covers), teeth of the cheliceral furrow, the shape of the labium, the position of the tracheal stigma, the size of the colulus, and the kind of the autotomy – or at least some of these characters – of the fossil spiders in question are known. Within all of these families several convergences evolved like the loss of the anterior median eyes and of leg bristles as well as the evolution of slender articles of the male pedipalpus (thickened articles are regarded as a plesiomorphic character), as well as a modified cymbium and modified male chelicerae.

Distribution: Mid Cretaceous Burmese amber forest.

Key to the tribus of the family Praeterleptonetidae:

1 Legs very long and slender, tarsi and metatarsi flexible and pseudoarticulate (photo 82), III not much shorter than the remaining legs, numerous bristles (fig. 34), patella of the ♂-pedipalpus (figs. 36–37) with a strong outstanding spur . . . . Palaeohygropodini

- Legs not very long, fewer bristles, pseudoarticulations absent, III distinctly shorter than the remaining legs, male pedipalpal patella without a spur 2

2(1) ♂-pedipalpus (figs. 27–31): Cymbium with a prolateral spur close to the article, bulbus with an undevided sclerite . . . . Praeterleptonetini

- ♂-pedipalpus (fig. 39): Cymbium with a prolateral spur which stand widely out, bulbus with a divided sclerite (in my opinion embolus and embolic apophysis) . . . .
. . . . Pholcochyrocerini

(Va) PRAETERLEPTONETINI n. trib.

Diagnosis (♂; ♀ unknown): Metatarsal bristles probably absent (or very thin) (figs. 24, 32), median spinnerets with a single large spigot (fig. 26); pedipalpus (figs. 27–31): Position of the attachment of the bulbus probably in the middle part of the cymbium, embolus of medium size, directed foreward.

Type genus (by monotypy): *Praeterleptoneta* n. gen.

Relationships: In the Pholcochyrocerini exists distinct metatarsal bristles, the cymbial spoon is standing out widely, and the embolus bears a large apophysis. In the Palaeohygropodini the legs are very long, tarsi and metatarsi I–II are pseudoarticulate, the number of leg bristles is higher, a patellar spur of the pedipalpus exists.

Distribution: Mid Cretaceous Burmese amber forest.

***Praeterleptoneta* n. gen**.

Diagnosis, relationships and distribution: See the Praeterleptonetini. Further characters: See the family diagnosis. Threads of the capture web bears probably sticky droplets.

Type species (by monotypy): *Praeterleptoneta spinipes* n. sp.

***Praeterleptoneta spinipes* gen. n. sp**. (figs. 23–31, photos 77–78)

Material: Holotypus ♂ in mid Cretaceous Burmese amber from Myanmar, F1836/BU/AR/CJW.

Preservation and syninclusions: As known from other inclusions in Burmite the holotype and the syninclusions are distinctly deformed by – apparently – natural heating and pressure of the small (6.5 mm long) piece of amber, parts of the spider and the syninclusions are strongly darkened. A bubble is (e. g.) preserved dorsally-basally on the right femur I of the spider, the mouth parts are hidden, several leg articles are laterally strongly depressed, the eyes are unnaturally protruding. Several thin threads as part of a capture web – in respect to their position apparently built by the holotype – are preserved in various parts of the piece of amber, e. g. at the tip of the right tarsus I (fig. 25), on the spiders body and legs, and on the body of the fly in the same layer as the spider. Remains of probably sticky droplets: Fig. 25. – Other syninclusions: A fly (Diptera: Brachycera), body length 1.5 mm, is preserved 2 mm behind/above the spider, the part of a long and slender leg of an insect and two small Collembola: Symphypleona. At least the spider has been a prey – and has probably been sucket out –; threads are running from the spider to the fly which probably has been spun in. I did not recognize threads on the Collembola. Stellate hairs are absent, pollen grains were not recognized by me.

Diagnosis (♂; ♀ unknown): See above.

Description (♂):
Measurements (in mm): Body length 1.0, prosomal length 0.5, opisthosoma: Length 0.65, hight 0.37; leg I: Femur 0.67, patella 0.22, tibia 0.45, metatarsus 0.52, tarsus 0.25, tibia II ca. 0.3, tibia III ca. 0.2, tibia IV < 0.3.
Colour grey brown, inner parts of some leg articles dark brown, see above (heating).
Prosoma (fig. 23; it is distinctly deformed) with long dorsal hairs, not rugose, fovea, chelicerae (their basal articles may be protruding and possess probably an anterior outgrowth), and mouth parts are hidden; 8 large eyes in two rows, posterior row almost straight, posterior median eyes separated by about their diameter, lateral eyes contiguous; the sternum separates the coxae IV by their diameter. – Legs (figs. 24–25) fairly long and slender, hairy, order I/II/IV/III; the long hairs are finely granulate. Bristles long, 2 dorsally on the femora at least on I and IV, 2 on the patellae (the basal one is thin), tibiae 2 dorsally and 4 short ones near the end, at least I bears additionally a long prolateral one. Metatarsal bristles are probably absent although on some metatarsi a thin and erect questionable bristle – or hair, trichobothrium? – is preserved in the basal third. Tibia I bears at least 3 long trichobothria, position of the metatarsal II trichobothrium in 0.25. No ventral comb of tarsus IV. Paired tarsal claws long, teeth unknown, unpaired claw tiny and strongly bent. Onychium absent, autotomy unknown. – Opisthosoma oval, soft, dorsally covered with long hairs which are finelly granulate. Anterior spinnerets long and slender (probably deformed by heating and pressure); the median spinnerets (fig. 26) bear apparently a single large spigot only. I cannot recognize colulus, lung covers and the tracheal spiracle; the colulus may be small. – Pedipalpus (figs. 27–31; some parts of the bulbus are hidden) with slender articles, cymbium with a long retrolateral spine and a long apical bristle, embolus long and directed forward, a conductor is present.

Capture web and prey: See above, “Preservation and syninclusions”.

Relationships: See above.

Distribution: Mid Cretaceous Burmese amber forest.

(Vb) PALAEOHYGROPODINI n. trib.

Diagnosis (♂; ♀ unknown): Legs very long, III almost as long as the others, tarsi and metatarsi flexible and pseudoarticulate (photos), numerous leg bristles, tibiae I–II with paired ventral bristles close to their articles (fig. 34), clypeus long and protruding ventrally (fig. 33). ♂-pedipalpus (figs. 36–37): Patella with a strong and bent prolateral bristle (clasping spur), tibia very long, without apophysis, cymbium with dorsal spines.

Further characters: Ecribellate, 8 eyes, unpaired tarsal claw present, posterior row recurved (fig. 33), bristles present on femora, patellae, tibiae and metatarsi, paired claws long and with long teeth, tarsal trichobothria absent, all metatarsi bear a single trichobothrium in a distal position, paired tarsal claws with long teeth, trochanteral notchs and respiratory organs unknown, bulbus very large and prodruding basally.

Type genus (by monotypy): *Palaeohygropoda* PENNEY 2004.

Relationships: According to PENNEY (2004) *Palaeohygropoda* is a member of the family Pisauridae (Lycosoidea) within the RTA-clade but I regard it as the member of quite another superfamily and branch. Based on the absence of tarsal trichobothria, the existence of a single metatarsal trichobothrium only, the absence of leg scopulae and a retrolateral tibial apophysis of the ♂-pedipalpus as well as the simple and very large bulbus the genus *Palaeohygropoda* is surely not a member of the Pisauridae and even not of the RTA-clade; the eye position is different from the position of the Lycosidae – in which a pedipalpal tibial apophysis is absent, too – and of most Pisauridae. According to the combination of characters, the shape of the opisthosoma, the spiny ♂-pedipalpus, the absence of a retrobasal paracymbium – in contrast to most Araneoidea in which furthermore the shape of the rosette-like spinnerets is quite different, and the anterior spinnerets are stout – I regard *Palaeohygropoda* as a taxon of the Dysderoidea s. l. (the scytodoid branch), and regarding to the slender articles of the ♂-pedipalpus as a taxon of the Praeterleptonetidae. – In the Praeterleptonetini and the Pholcochyrocerini chaetotaxy and pedipalpal structures are different, the legs are shorter, the number of their leg bristles is lower, tarsi and metatarsi are not pseudoarticulate; see the key above.

Remark on the “cladogram” which was given by PENNEY (2004: 143, fig. 3): Contrarily to this “cladogram” there is no proof of a member of the superfamily Lycosoidea in Cretaceous ambers; most “ghost lines” which run down to the Cretaceous are unfounded and incorrect (in my opinion they should better called “lines of phantasy”). The same is true for several “lines” of the “evolutionary trees” which were published by PENNY (2002: text fig. 7), PENNEY & SELDON (2002: Fig. 4), and D. D. PENNEY (2008: 18, 138). See the remarks on erroneous determinations above on which such so-called “back dating” is based on incorrect determinations.

Distribution: Mid Cretaceous Burmese amber forest.

Palaeohygropoda PENNEY 2004 (**n. relat**.): Diagnosis, relationships and distribution: See above (the new tribe). Type species (by monotypy):

Palaeohygropoda myanmarensis PENNEY 2004 (figs. 33–37, photos 80–83)

2004 *Palaeohygropoda myanmarensis* PENNEY, J. Syst. Palaeontol., 2 (2): 141–145, figs. 1–2, pl. 4, figs. 1–5.

Material: Holotypus ♂ in mid Cretaceous Burmese amber from Myanmar, NHMLP, In. no. 19132.

Preservation and syninclusions. Remark: Tiny fissures exist on the surface of the piece of amber, most probably as the result of aging after poolishing ca. 80 years ago. – The spider is almost completely preserved, only the tip ot the left anterior spinneret is cut off. Parts of the spider – e. g. of the legs, the eye lenses and of the pedipalpi – are distinctly deformed by natural heating and pressure. Some spider's threads without droplets are preserved near the spider; numerous remains of arthropods like an Acari as well as insects excrements and numerous stellate hairs are present in the same piece of amber.

Revised description (♂; ♀ unknown). Note: The main errors of the original description – regarding measurements, trichobothriotaxy, leg scopula, spinnerets, and the pedipalpal structures – are corrected herewith; the pedipalpus was not figured in detail).
Measurements (in mm): Body length ca. 4 mm (according to PENNEY "approximately 5 mm"), leg I: Femur 3.8, patella 1.1, tibia 4.2 (according to PENNEY 4.5), metatarsus 3.85, tarsus 1.75; total 14.7; tibia II 4.1, tibia III r/l 3.7/3.9, tibia IV 3.9 (according PENNEY 3.5).
Prosoma (fig. 33) high and wide, caput fairly separated from the thorax by a depression, thorax high. 8 eyes which lenses are partly deformed, subaequal in size, posterior row fairly recurved, clypeus long, protruding medially-ventrally. Basal cheliceral articles (they are deformed) free, fairly long, anterior margin of the furrow with at least two smaller teeth, fangs long. The gnathocoxae are long and not converging, the labium is strongly deformed. – Legs very long, order I/II/IV/III (according to PENNEY I/II/III/IV), III almost as long as the remaining legs, prograde, feathery hairs absent. Bristles numerous, on femora, patellae, tibiae and metatarsi of all legs, tibia I bears 3 pairs of ventral bristles which not overlap (fig. 34). All metatarsi bear a fringe of apical bristles. Trichobothria: According to PENNEY are "Numerous trichobothria present on tibiae, metatarsi and tarsi of all leg..."; contrarily in my opinion most of these are not trichobothria but nothing else than "normal" long hairs: On the tarsi I found not a single trichobothrium, on all metatarsi only a single one near the end of the articles, 0.1–0.15 mm away from their tips. Claw tufts and scopulae absent (according to PENNEY "Metatarsi and tarsi with relatively long, fine scopular hairs,..."), but the hairs of these leg articles build surely no scopulae (as usually in the Pisauridae), the hairs are thin

and may build "pseudoscopulae"). Onychium small. The paired tarsal claws are well developed and bear long teeth. Autotomy unknown. – Opisthosoma twice as long as high, not widened posteriorly as in numerous Pisauridae, anterior spinnerets long (fig. 35), slender, close together and apparently two-segmented, median spinnerets hidden, posterior spinnerets short (according to PENNEY is "only one spinneret visible"), most parts of the respiratory organs hidden, lung covers may exist. – ♂-pedipalpus (figs. 36–37) (parts of the bulbi are hidden): Articles slender, patella with a bent strong prolateral bristle (apparently a "clasping spur"), tibia very long, CLEARLY WITHOUT AN APOPHYSIS (according to PENNEY a retrolateral apophysis is "prosumably present", but what is the meaning of "prosumable" if there is none?), cymbium slender, bearing three strong dorsal bristles, bulbus (subtegulum, tegulum) large, sclerites including the questionable embolus in a more distal position, insufficiently recognizable. The stronger and flattened apical-dorsal margin of the tibia may fit in a retrobasal-dorsal depression of the cymbium (probably as a "locking system").

Note: According to the shape of the tarsal claws and the existens of spiders' threads near the spider I suppose that this species was capture web building.

Relationships: In the questionable member of the Praeteleptonetidae (below) the leg III is distinctly shorter than the remaining legs.

Distribution: Mid Cretaceous Burmese amber forest.

?**Praeterleptonetidae: ?Palaeohygropodini indet.** (fig. 32, photo 79)

Material: ♀-exuvia with few thin spider's threads nearby in mid Cretaceous Burmese amber from Myanmar, NMHLP, In. no. 20152.

Preservation: The exuvia is situated at the margin in the middle of the convex side of a larger piece of amber. The peltidium and the left leg IV are missing, the remains of the opisthosoma are strongly deformed, the right tarsus IV may be a regeneration.

Description (♀-exuvia, fig. 32):
Tibia I about 2.4 mm long. Pedipalpus long, slender and spiny, tarsal claw probably present. Legs long and slender, order I/II/IV/III, III distinctly the shortest, metatarsi slightly longer than tibiae, almost twice as long as the tarsi, with longer hairs and numerous long bristles which stand more or less out from their articles, on femora (several), patellae, tibiae and metatarsi: Patellae 2 dorsally and a lateral pair, tibiae I–II 2 dorsally, 2 prolaterally, 2 retrolaterally and 3 pairs ventrally, metatarsi I–II at least a dozen incl. 2 ventral pairs and 4 apicals. Calamistrum absent, unpaired tarsal claw large, tarsal trichobothria apparently absent, metatarsi probably with a single trichobothrium. The opisthosoma is covered with short hairs, the spinnerets are hidden.

Relationships: According to the existence of an unpaired tarsal claw and the absence of tarsal trichobothria the spider may be a member of the superfamilies Dysderoidea, regarding to its numerous leg bristles I do not want to exclude that it may be a member of the Praeterleptonetidae: Palaeohygropodini, see *Palaeohygropoda myanmarensis* above.

Distribution: Mid Cretaceous Burmese amber forest.

(Vc) PHOLCOCHYROCERINI n. trib.

Diagnosis (♂; ♀ unknown): Metatarsal bristles present, a large cymbial spoon exists which stands widely out (fig. 39), embolus with a large apophysis. The probably conspecific capture web bears sticky droplets, see below.

Type genus (by monotypy): *Pholcochyrocer* n. gen.

The **relationships** are unsure; Praeterleptonetini n. trib. is probably most related, see above and the key. – A similar embolic apophysis exists – it evolved convergently – in *Furcembolus* n. gen. (Eopsilodercidae, see above) in which the legs are bristle-less and a cymbial apophysis exists.

Distribution: Mid Cretaceous Burmese amber forest.

Pholcochyrocer n. gen.

The gender of the name is neuter.

Diagnosis (♂; ♀ unknown): See the Pholcochyrocerini. Further characters: See the family. The cymbium is probably large.

Type species (by monotypy): *Pholcochyrocer guttulaequae* n. sp.

Relationships: See above.

Distribution: Mid Cretaceous Burmese amber forest.

Pholcochyrocer guttulaeque n. gen. n. sp. (figs. 38–39, photo 84)

Material: Holotypus ♂ in Cretaceous Burmese amber from Myanmar, F1913/BU/AR/CJW.

Preservation and syninclusions: The spider is almost completely preserved in a partly redbrown piece of amber which has some fissures inside and contains numerous tiny (red)brown droplets which most probably are caused by heating and pressure and hinder observing the inclusions. Body and legs are strongly darkened by heating and pressure, parts of the left legs I – and mainly – II are missing within the amber. The piece of amber is 4.2 cm long and seems to be broken off from a larger piece. – Syninclusions are numerous: Most remarkably is a nursery (the geological oldest which is known in spiders): More than 20 spiderlings, body length ca. 1.1 mm, which most often are deformed and apparently originate from a single egg sac, are preserved around the holotype. Their stouter legs and longer leg bristles indicate that they most probably are not related to *Pholcochyrocer*, and I do not want to exclude their relationships to the family Araneidae although in some spiderlings the metatarsus IV is bent similar to an article which bears a calamistrum similar to certain cribellates, but deformations may be the reason for the curved metatarsi. – Most of these spiderlings are preserved in the same layer of the amber and near to spiders' threads which partly bear droplets. Threads with and without droplets – their origin is unknown – are situated near the spiderlings, and one thread bearing droplets is preserved in the same layer as the holotype of *Pholcochyrocer*. I regard some loose wool-shaped threads – which are preserved near the margin of the piece of amber – as remains of the cover of the egg sac of the spiderlings, see the photo 84. – Another tiny spider – see the photo – is preserved near the margin of the piece of amber. It is not related to the numerous spiderlings; its prosomal length is 0.6 mm, its prosoma is strongly raised, see the description below (?Dictynidae indet.). – Numerous particles of detritus, remains of plants and fungi, questionable stellate hairs and questionable bacteria are preserved in the same piece of amber.

Diagnosis (♂; ♀ unknown): Bulbus with a large furcate apophysis (fig. 39).

Description (♂):
Measurements (in mm): Body length ca. 3.3 mm, prosoma: Length ca. 1.9, width 1.4; tibia I ca. 1.8, metatarsus II ca. 1.2, tarsus I ca. 0.7.
Colour dark brown (the spider is darkened by heating and pressure).
Prosoma about 1.35 times longer than wide, apparently low, structure of the epicuticula, hairs and fovea not recognizable, 8 eyes in two rows on a fairly protruding deformed area are difficult to recognize; clypeus apparently not protruding, mouth parts hidden. – Legs long and slender, order I/II/IVIII, I and II distinctly longer than III and IV, III not much shorter than IV, hairs fairly indistinct. Questionable remains of muscles are preserved mainly within the right femora III and IV. Bristles long and slender: Femora (fig. 38) dorsally 1/1, the basal one about as long as the femoral diameter, patellae with a distinct dorsal-distal bristle, tibiae dorsally 1/1 (length of the basal one on IV 1.6 tibial diameters), III additionally with a long ventral bristle, IV with a long proventral-distal bristle; metatarsus I bears at least 3 apical bristles and a single ventral one in the

basal half. Additional bristle exist most probably but are hidden; tarsal bristles are absent. Trichobothria unknown, the paired and unpaired tarsal claws are well developed, bearing long teeth, onychium absent. – Opisthosoma: Most parts are destroyed, the posterior part completely, probably by decomposition. – Pedipalpus (fig. 39) with slender articles, femur distinctly bent, patella and tibia badly observable, tibia with a long dorsal bristle, shape of the cymbium not surely recognizable (hairs are not observable) probably large, probably protruding and pointed apically, apparently without an apical bristle; bulbus large, with a large furcate apophysis which stands widely out (the embolus is most probably a part of it), an apical apophysis may exist furthermore.

Relationships: See above.

Distribution: Mid Cretaceous Burmese amber forest.

(VI) Family PLUMORSOLIDAE n. fam.

Diagnosis (juv.?): Six eyes in a "segestriid" position (fig. 40), unpaired tasal claw absent, dense claw tufts of thickened hairs (fig. 44) and numerous feathery hairs on the legs (fig. 43) are present, too.

Further characters: Ecribellate, legs rather long and slender, bearing thin bristles (fig. 42), chelicerae free, lamina and stridulatory files absent, teeth of both furrows present (fig. 41), leg autotomy between coxa and trochanter.

Type genus (by monotypy): *Plumorsolus* n. gen.

Relationships: According to the "segestriid" eye position and the absence of tarsal trichobothria I regard this taxon with only little doubt as a member of the superfamily Dysderoidea s. l.. According to the eye position, the absence of an unpaired tarsal claw and the hairs of the claw tufts the family Orsolobidae may be most related but in the Orsolobidae an exposed mound of the tarsal organ and biserically dentate paired tarsal claws exist. – The existence of feathery leg hairs is a remarkable character of this family which discriminates it from most (or even all?) remaining dysderoid families. (Feathery hairs occur e. g. in certain Oecobiidae and cribellate Araneoidea s. l.: Deinopidae and certain Uloboridae; see also the family Salticoididae below).

Ecology and behaviour: According to the presence of a well developed claw tuft the spiders of this taxon built no capture web but were free living hunters.

Distribution: Lower Cretaceous Lebanese amber forest, and probably mid Cretaceous Burmese amber forest.

***Plumorsolus* n. gen.**

The gender of the name is masculine.

Diagnosis (♂; ♀ unknown): See above.

Type species (by monotypy): *Plumorsolus gondwanensis* n. sp.

Relationships: See above.

Distribution: Lower Cretaceous Lebanese amber forest.

***Plumorsolus gondwanensis* n. gen. n. sp.** (figs. 40–45, photo 85)

Material: 2 probably juvenile female specimens in Lower Cretaceous Lebanese amber from Central Lebanon, Hammada-Mdeyriy outcrop, coll. D. AZAR nos. 490 (holotype) and 724A (paratype), MNHNP (Lab. d'Entomology).

Remark: The deformed paratype is probably not conspecific with the holotype; in the paratype the (deformed) prosoma may be more slender and the bristles on the anterior tibiae are lying closer to their articles.

Preservation and syninclusions: The holotype is well and almost completely preserved in a thin piece of yellow amber which has been embedded in artificial resin; only the tip of the right tarsus I is cut off, the opisthosoma is somewhat deformed. Parts of body and legs are partly darkened apparently by natural heating and pressure. A fissure runs through the piece of amber, the prosoma and some leg articles. – The paratype is also preserved in a clear yellow piece of amber which has been embedded in a bloc of artificial resin. Two fissures run cross through the opisthosoma of the spider. Its body is strongly deformed, a white emulsion covers parts of the opisthosoma, the legs are incomplete, most articles are separated from the body or cut off, the left leg IV is completely preserved, lying below the body. Darkened parts are preserved within the opisthosoma and some leg articles. Tiny remains of an insect are preserved left behind the spider, a large bubble is preserved within the prosoma. Numerous loose feathery hairs, few bristles and threads of silk are preserved around the spider's body.

Diagnosis (juv.?): See above.

Description:
Measurements (holotype/paratype in mm): Body length 1.9/2.5, prosomal length 1.0/1.2; leg I (holotype): Femur 1.0, patella 0.3, tibia 0.85, metatarsus 0.7, tarsus, 0.4,

tibia II 0.83/1.15, tibia III 0.34, tibia IV 0.75; tarsus of the pedipalpus 0.13.
Colour: Holotype grey, paratype yellowish.
Prosoma (figs. 40–41) distinctly longer than wide, not rugose, with numerous shorter dorsal hairs (holotype). Six large eyes in a "segestriid" position, the medians almost touching (paratype) (the eyes are partly hidden and deformed in the holotype), fovea unknown, clypeus in a vertical position. Basal cheliceral articles of medium size, not fused, without stridulatory files; the anterior and posterior margin of the cheliceral furrow bear 2 wide teeth each; fangs of medium size (paratype), gnathocoxae in an almost parallel position (paratype), labium hidden, sternum distinctly longer than wide. – Pedipalpal articles of medium size, tarsal claw slender and fairly long. – Legs (figs. 42–44) slender and fairly long, prograde, III directed backward, covered with numerous feathery hairs and with undivided thin hairs. Bristles thin and long, existing on femora, patellae, tibiae and metatarsi: Femora 1/1/1 and frequently with a retrodistal one at least on III and IV, patellae dorsally 1/1 (very thin), tibia I ventrally with few (a pair or a single one in the basal half and a probasal one) which stick out from the article in the holotype but not in the paratype; metatarsus I bears 1–2 bristles in a ventral-basal position and apical-ventrals. Trichobothria are absent on the tarsi, at least metatarsi I–III bear a trichobothrium, their position on II is in 0.8 (holotype). Unpaired tarsal claws absent, paired claws with at least 8 long teeth in a single row; dense claw tufts exist which hairs are thick but not distinctly spatulate. Onychium short, tarsal organ indistinct. – Opisthosoma cylindrical, hairs short, spinnerets fairly short (fig. 45), respiratory system and colulus are hidden.

Relationships: See the short notes on a ?Plumorsolidae indet. below as well as the note above, in "Remarks on erroneous determinations".

Distribution: Lower Cretaceous amber forest.

?**Plumorsolidae indet**.

Material: Juv. or adult ♀ in mid Cretaceous Burmese amber, NHMLP In. no. 20197.

The small spider posesses long and slender legs which bear feathery hairs and well developed claw tufts. I do not want to exclude that it is a member of the family Plumorsolidae.

Distribution: Mid Cretaceous Burmese amber forest.

Dysderoidea s.l. indet. 1 (Praeterleptonetidae??) (photo 63)

Material: 1/2 ?ad. ♀ in mid Cretaceous Burmese amber from Myanmar, OSU no. B-A-1-14, G. POINAR jr. coll.

Preservation and syninclusions: Only most parts of the prosoma are preserved (partly deformed, bubbles on the eye lenses), the posterior part is cut off as well as both pedipalpi, legs II, the left leg I, and the distal parts of the left legs III and IV. – Also preserved – in different layers – are long threads of spiders silk which partly bear droplets and stellate hairs, a female of *Burmorchestina* n. gen., 2 1/2 Diptera: Nematocera, particles of detritus and small insects' excrement.

Description (1/2 ?ad. ♀):
Measurements (in mm): Prosomal length ca. 0.55; leg I: Femur 1.1, patella 0.23, tibia ca. 1.2, metatarsus 1.1, tarsus 0.4.
Six eyes in a wide field of a "segestriid position", supposingly ecribellate. Prosoma long and slender, low; clypeus very short and not protruding. Chelicerae fairly large, stridulatory files most probably absent, fangs long; gnathocoxae (deformed!) long and pointed. Legs long and slender, paired tarsal claws short, unpaired tarsal "claw" (really a claw?) short as well, straight and strongly sclerotized, onychium absent, numerous leg bristles of medium size on femora, tibiae (unpaired and fairly close to their articles) and metatarsi. Trichobothria: Absent on the femora and tarsi, a single metatarsal trichobothrium exists in the position of 0.95. Pedipalpus long and slender, tarsal claw present.

The **relationships** are unsure. According to the long legs, the chaetotaxy and the six eyes I regard the spider as a member of the scytodoid (pholcoid) branch of the Dysderoidea. Praeterleptonetidae possesses a similar chaetotaxy and an onychium is absent, too, but eight eyes exist and a long and bent unpaired tarsal claw. The spider may be the member of an undescribed family.

Distribution: Mid Cretaceous Burmese amber forest.

?**Dysderoidea s.l. indet**. 2 (photo 64)

Material: 1 ?juv. ♀ in mid Cretaceous Burmese amber from Myanmar, OSU no. B-A-1-9, G. POINAR jr. coll.

Preservation and syninclusions: The spider is preserved in a yellow piece of amber, the legs are stretched sideward in an unnatural position (photo), the right anterior leg I is missing beyond the coxa probably by autotomy, most dorsal parts of the prosoma are cut off within the amber, a bubble is preserved inside the opisthosoma which is deformed. – Some thin spiders' threads are preserved above the spider in another layer of the fossil resin, a dragline originates at the tip of the anterior spinnerets.

Description (?juv. ♀):
Measurements (in mm): Body length 2.0, prosomal length 1.0; leg I: Femur 1.2, patella 0.32, tibia 1.15, metatarsus ~1.1, tarsus ~0.43, femur II 0.85, femur III 0.65, femur IV 0.9.
Colour: Legs and prosoma light grey, opisthosoma dark grey.
Prosoma (it is incompletely preserved) longer than wide, not rugose, eye field wide (only remains of the left lateral eye lenses are preserved near the margin of the prosoma. Basal cheliceral articles of medium size, lamina absent, the posterior margin of the furrow bears at least two teeth, fangs of medium size. Pedipalpus of medium size, tarsal claw present. Legs only fairly long, order I/II/IV/III, III distinctly the shortest, hairs not distinct, few bristles which are thin and hair-shaped. Trichobothria absent on tarsi, a single one near the end of the metatarsi. Calamistrum absent, three tarsal claws, paired claws well developed. Opisthosoma oval, covered with numerous hairs of medium length, soft, genital area hidden, lung covers not recognizable; 3 pairs of spinnerets, the anteriors fairly slender, two-jointed.

Relationships: According to the chaetotaxy, trichobothriotaxy and the existence of an unpaired tarsal claw the spider is a member of the infraorder Araneomorpha. In contrast to most members of the RTA-clade tarsal trichobothria are absent and only a single metatarsal trichobothrium exist. In the Araneoidea the anterior spinnerets are stout. According to the wide eye field and the absence of “peg teeth” I do not want to exclude that the spider may be a member of the Dysderoidea s.l.

Distribution: Mid Cretaceous Burmese amber forest.

(2) SUPERFAMILY ARCHAEOIDEA (= Palpimanoidea sensu FORSTER & PLATNICK (1984), = Eresoidea sensu WUNDERLICH (2004))

Previously I included Archaeidae, Palpimanidae and related families in the superfamily Eresoidea in a wide sense, see WUNDERLICH (2004: 747ff), but – because of the still doubtful relationships and the entelegyne character of the Eresidae – I question my former opinion: Eresidae MAY BE the member of a branch of its own or is probably more related to the Oecobioidea, although I still do not exclude definitively close relationships of the Eresidae to the superfamily Archaeoidea (and Eresoidea may be the correct name for this superfamily in this case).

In the members of the Archaeoidea – see WUNDERLICH (2004: 759ff) – leg bristles are absent (Archaeidae s. l.) or strongly reduced, a tendency to the reduction of the median and the posterior spinnerets exists.

At least 3 of the ca. 7 described families of the Archaeoidea are extinct (the relationships of the Burmascutidae are quite unsure (Oecobioidea?), see below).

There exist two main branches within the Archaeoidea s. l., see WUNDERLICH (2004: 761):

(a) The "archaeoid branch" which includes only the Archaeidae s. l. with the following subfamilies (which may be regarded as families of their own): Archaeinae (fossil and extant), Jurarchaeinae (extinct), Lacunaucheniinae (extinct), and Mecysmaucheniinae (probably only extant). Adult spiders of the Jurarchaeidae, females of the Lacunaucheniinae and probably fossils of the Mecysmaucheniinae are unknown. The spiders have a cheliceral foramen (fig. 57) as well as very long (except *Baltarchaea*), slender and always bristle-less legs, as well as:

(b) the remaining extinct and extant taxa, the "palpimanoid branch", which members have stout or only fairly long legs which usually possess distinct prolateral spatulate hairs on the legs I (–II) (fig. 79) (absent or thin in the Lagonomegopidae), rarely (few) leg bristles (see Huttoniidae, Lagonomegopidae and Micropalpimanidae), and which frequently possess enlarged anterior femora, long patellae as well as short tarsi (in the extant families). A cheliceral foramen is absent. This branch contains about the same number of extinct families as extant families, see below.

Revised diagnosis of the superfamily Archaeoidea (s. str.): (a) Presence of cheliceral "peg teeth" (figs. 46, 51, 58, 65) (1); (b) frequenly a raised cephalic part (2) and a wide eye field (figs. 50, 58, 69, 71); (c) Presence of modified prolateral hairs of articles of leg I and usually leg II (figs. 68, 79) as well (3); (d) absence of distinct tibial bristles (4); (e) basicly existence of retrolateral cheliceral stridulatory files (figs. 49, 73, 76) (5); (f) loss of the capture web; (g) they are usually spider eaters. – Further relevant characters: Ecribellate and haplogyne (if Eresidae is excluded). Unpaired tarsal claw basicly present but reduced in some taxa, lost in the Stenochilidae and Palpimanidae: Otiothopinae, metatarsal III (IV) preening hairs usually present. Body – at least the prosoma – usually heavily armoured and rugose, and with a sclerotized ring around the spinnerets (fig. 47), tendency to reduced median and posterior spinnerets (in the extant taxa); see also below: The palpimanoid branch. – Remarks:

---

(1) "Peg teeth" are slender, usually blunt and not flattened modified bristles which are surrounded by a basal "ring" in contrast to normal cheliceral teeth which are more or less flattened, usually pointed, and lacking a basal "ring". Such teeth are lost in the family Stenochilidae in which other cheliceral teeth are absent, too. ("Peg teeth" evolved convergently e. g. in certain Mimetidae s. l. (superfamily Araneoidea), in certain Thomisidae, and probably in certain Theridiidae of SE-Asia, person. obs.).

(2) An only low/not raised cephalic part exists in Huttoniidae, Lagonomegopidae, and Stenochilidae.

(3) Their structure is basicly almost spatulate (figs. 79–80) but thin and pointed hairs exist in certain Lagonomegopidae (fig. 68); such hairs may be reduced or even absent (in certain Archaeidae and most Lagonomegopidae).

(4) distinct dorsal femoral, tibial and metatarsal bristles are basicly absent; rarely exist hair-shaped bristles (figs. 79, 81, Micropalpimanidae) or distinct femoral bristles (certain Lagonomegopidae, fig. 66); in the Huttoniidae exist distinct bristles on legs III–IV.

(5) Such files are absent in the Lagonomegopidae.

Remarks on losses/reversals of relevant characters:

- "Peg teeth" are lost in the Stenochilidae,
- retrolateral stridulatory files are lost in the Lagonomegopidae,
- an only low/not raised cephalic part exists in the Huttoniidae, the Lagonomegopidae, and the Stenochilidae,
- modified prolateral hairs of leg I–II are lost in certain Archaeidae and Lagonomegopidae; they are strongly reduced or even lost on leg II of the Palpimanidae, see above (3),
- a narrow eye field exists in the Huttoniidae and certain Stenochilidae,
- distinct leg bristles exist – probably as a reversal – in the Huttoniidae (legs III–IV), certain Lagonomegopidae, and hair-shaped bristles or bristle-shaped hairs exist in the Micropalpimanidae.

Remarks on ecology and behaviour. Morphological structures may indicate particular ecological and behavioural characters:

(1) According to LEHTINEN (1982: 116) "The apomorphic anterior legs of both Stenochilidae and Palpimanidae are undoubtedly adaptations to digging habitats." The modified thin or spatulate hairs in these families – as well as in the Micropalpimanidae – are soft and in my opinion therefore not adapted to a digging behaviour; more likely they are in connection with the capturing behaviour of those spiders which are araneophaguous. Members within the superfamily Archaeoidea – e. g. Archaeidae (extants and Tertiary fossils), Palpimanidae (extants) and probably Spatiatoridae (Tertiary fossils) are known to feed on spiders. Tiny (juvenile?) members of the genus *Burmorchestina* (Oonopidae: Orchestininae) – see the paper no. 2 on this subfamily in this volume – may have been the prey of a member of the tiny Micropalpimanidae in which spatulate prolateral hairs of the anterior legs (figs. 76–77) exist similar to extant relatives which build no capture web. The Cretaceous male of the family Micropalpimanidae should represent the geological oldest proof of an araneophag spider. The special shape of the chelicerae of the Cretaceous Archaeidae (figs. 51, 58, 69) indicate the same kind of prey as in extant and Eocene spiders; see WUNDERLICH (2004: 772).

(2) In most extant and fossil members of the superfamily Archaeoidea exist retrolateral stridulatory cheliceral files (Lagonomegopidae is an exception). Stridulating is used during the courtship behaviour in numerous families of spiders, it may be the most

common kind of courtship behaviour in spiders, and such files are usually present in both sexes, see WUNDERLICH (2004: 163). The proof of stridulatory files in about 90 million years old males of the Archaeidae: Lacunaucheniinae (fig. 49) and Micropalpimanidae (figs. 74, 76, 84) indicate the existence of particular courtship behaviour in Cretaceous spiders which are the geological oldest proofs of such a behaviour. The stridulatory organ of the Micropalpimanidae is apparently of a quite particular kind which I do not know from any other taxon.

A. The ARCHAEOID BRANCH

(I) Family ARCHAEIDAE s. l.

The family is known from the Jurassic to today. It is one of the geologically oldest known araneomorph families and – in various respects – one of the most fascinating ones, see WUNDERLICH (2004: 771–774).
The conspicuous members of the family Archaeidae s. l. – I include the Lacunaucheniinae n. subfam. and the Mecysmaucheniinae which are frequently regarded as a family of its own – possesses usually powerful long and diverging chelicerae (they are short/stout in the genus *Baltarchaea* in Baltic amber) which bear rows of long "peg teeth"; a prosomal gap (foramen) exists between chelicerae and gnathocoxae (figs. 49, 57), the legs are long, slender and bristle-less (short legs exist in *Baltarchaea*); see WUNDERLICH (2004: 768ff). Archaeidae construct no capture web and were spider-eaters already in the Eocene, see WUNDERLICH (2004: 769, photo 626) (*Archaea* sp. indet. with a spider as its prey) and the report by FORSTER & PLATNICK (1984: 32) (*Mecysmauchenius segmentatus* feeding on a spider as well as – in captivity – on Lepidoptera and Diptera).

In the Archaeidae s. l. I include about four higher taxa which may be regarded as subfamilies or even as families:

(a) The extinct Jurassic Jurarchaeinae which relationships are unsure (see below),

(b) the extinct Lacunaucheniinae in Cretaceous Burmese amber (3 extinct genera, but even 4 genera if *Palaeomysmauchenius* SAUPE & SELDEN (in prep.) is included),

(c) the Archaeinae (2 genera extant and subfossil as well), in Eocene European ambers (5 extinct genera), and in Burmese amber (still only a single extinct genus, *Burmesarchaea* n. gen.), and

(d) the Mecysmaucheniinae (several genera, extant only) (*). This subfamily was considered as a family of its own by FORSTER & PLATNICK but not by ESKOV and WUNDERLICH (1995) and WUNDERLICH (2004).

(*) *Baltarchaea* ESKOV is a member of the Archaeinae, see above.

Fossil taxa are known from the Northern Hemisphere only, extant and subfossil taxa are restricted to the Southern Hemisphere. As demonstrated by their fossils the family Archaeidae is surely not a "Gondwanan" one.

Jurarchaeinae ESKOV 1987 – the single specimen of this taxon, a female or juvenile spider (fig. 46), is not preserved in amber but in a lake sediment (of Kazakhstan) – has originally been regarded as a subfamily of the Archaeidae, and erroneously as related to *Pararchaea* and *Holarchaea*; but these genera were considered as members of another superfamily, the Araneoidea – family Mimetidae s. l. – by WUNDERLICH (2004). – In the Jurarchaeinae only a restricted number of characters is preserved; e. g. nothing is known about the eyes and the existence of anterior cheliceral bristles or stridulatory files; there are probably three pairs of spinnerets which may be well developed, the legs bear numerous adpressed hairs, a ring around the spinnerets is absent. According to the powerful basal cheliceral articles (fig. 46) and the existence of cheliceral "peg teeth", as well as – apparently – the existence of a foramen the Jurarchaeinae may be a taxon of the Archaeidae although the relatively large ♀-pedipalpus and the presence of a – really existing? – epigynal plate are unusual characters at least of the subfamily Archaeinae (a large ♀-pedipalpus exists in the subfamily Mecysmaucheniinae in contrast to the Archaeinae). "Peg teeth" is not a strict character of the Archaeidae but a synapomorphic character of the hole superfamily Archaeoidea.

Taxa in Cretaceous Burmese amber: The first member of this family in Burmese amber – and the first one of the Cretaceous Period – was recently described as *Afrarchaea grimaldii* by PENNEY (2003) (figs. 47–48). It is a member of the subfamily Archaeinae but not of *Afrarchaea*; *grimaldii* is the generotype of the new genus *Burmesarchaea*. In the present paper I add three new genera of a second subfamily in Burmese amber, the newly described Lacunaucheniinae.

The high percentage of newly or recently described archaeid taxa from the Cretaceous – 4 species of 4 genera among 5 specimens only – may provide a much higher number of unknown/undescribed Cretaceous taxa of this relict spider family; and the newly described subfamily Lacunaucheninae was probably quite diverse during the Cretaceous, more diverse than the Archaeinae, the only archaeid subfamily which is known from the Eocene European ambers.

Key to the subfamilies, genera and species of the Archaeidae in Burmese amber:

1 Hair-bearing thoracal and opisthosomal pustules in rows, and sclerotized ring around spinnerets present (fig. 47); anterior-basal cheliceral bristle present (see WUNDERLICH (2004: 806, fig. 46); ♂-pedipalpus: Fig. 48. ♀ unknown. – Subfamily Archaeinae (*). . . . . *Burmesarchaea grimaldii*

- Hair-bearing prosomal pustules indistinct and arranged not in rows, sclerotized ring around spinnerets absent (fig. 49); anterior-basal cheliceral bristle absent (fig. 49). – Subfamily Lacunaucheninae 2

2(1) Leg III not distinctly the shortest, femur > prosoma, ♀-pedipalpus (fig. 62) much longer than the prosoma, only few cheliceral "peg teeth" (fig. 63). ♂ unknown . . . . *Filiauchenius paucidentatus*

- Leg III distinctly the shortest, femur < prosoma, ♀-pedipalpus shorter, chelicerae with numerous "peg teeth" (figs. 51, 58). 3

3(2) Prosoma obliquely protruding to the chelicerae, and gradually raising posteriorly (fig. 57, photo). ♂ unknown . . . . *Eomysmauchenius septentrionalis*

- Prosoma anteriorly vertically raising, posteriorly overhanging (fig. 49, photo). ♂-pedipalpus (figs. 54–56) with a long and slender cymbium and bulbus. ♀ unknown . . . . *Lacunauchenius speciosus*

(*) A dorsal femoral hump – which is characteristic for the members of this subfamily, see WUNDERLICH (2004: 805: Fig. 42) – is unknown in *Burmesarchaea*; it has not been reported in the original description of this taxon, but it may exist like in all other taxa of the Archaeinae.

(Va) Subfamily ARCHAEINAE

The subfamily is known from the Cretaceous to today.
There are at least six extinct genera of this relict subfamily (five are known from Baltic amber, one from Burmese amber), but only two genera are known from today, see below. All extant taxa are known from the Southern Hemisphere, all extinct taxa from the Northern Hemisphere. Archaeinae had apparently a cosmopolitical distribution in the Mesozoic Period and probably in the Jurassic and in the Eocene, too, and became extinct later – during the “oligocene cooling”? – in the Northern Hemisphere. See the map above.

***Burmesarchaea* n. gen.**

Diagnosis (♂; ♀ unknown): Body (fig. 47): Frontal-basal cheliceral bristle present, dorsal opisthosomal scutum probably indistinct; ♂-pedipalpus (fig. 48): Bulbus with a bent tegular apophysis, embolus long and coiled, according to PENNEY with a long and spoon-shaped basal outgrowth.

Further characters: Cephalic part distinctly raised, prosomal setose pustules and large sclerotized ring around spinnerets present, foramen well developed, cheliceral stridulatory files unknown, probably only a single row of cheliceral peg teeth, existence of femoral humps unknown (absent? It was not reported by PENNEY(2003)), leg bristles absent; a stridulatory tooth of a pedipalpal article was not reported by PENNEY (2003). – Remark: I did not yet get the opportunity to study the holotype for adding important characters which were not described by PENNEY (2003).

Relationships: *Afrarchaea* FORSTER & PLATNICK was regarded as a junior synonym of *Eriauchenius* O. PICKARD-CAMBRIDGE 1881 by WUNDERLICH (2004: 791). In the extant genus *Eriauchenius* the cephalic part is overhanging posteriorly, a stridulatory tooth is present on a pedipalpal article, the embolus is short, femoral humps are present. – In *Archaea* KOCH & BERENDT 1854 – and other extinct genera in Baltic amber – exist a well developed dorsal opisthosomal scutum and a frontal-basal cheliceral bristle is absent in contrast to *Burmesarchaea* (and the extant taxa).

Type species: *Afrarchaea grimaldii* PENNEY 2003 in Burmese amber, the only known species of the genus; *Burmesarchaea grimaldii* (PENNEY 2003) (**n. comb**.): *Afrarchaea grimaldii*: PENNEY (2003), Arachnology, 31: 122–130, figs. 1-5; WUNDERLICH (2004), Beitr. Araneol., 3A: 795, figs. 57–58.

Distribution: Mid Cretaceous Burmese amber forest (Burmite from Myanmar).

(Vb) Subfamily LACUNAUCHENIINAE n. subfam.

Diagnosis (based on taxa in Burmese amber) (*): Three pairs of spinnerets, anterior-basal cheliceral bristles absent (fig. 49), opisthosoma (fig. 49) not armoured and no ring around the spinnerets, ♂♀ pedipalpus (figs. 54–56, 60, 62), long to very long (e. g. the cymbium), ♀-pedipalpus not reduced in length, bulbus slender and not standing out from the bulbus.

(*) The monotypic genus *Palaeomysmauchenius* SAUPE & SELDEN 2008? (in prep.) will be described from the Lower Cretaceous of France, based on a single adult male. In this taxon the posterior spinnerets exist in contrast to the Mecysmaucheniinae and the median spinnerets are absent according to SAUPE & SELDEN (but they may be hidden!), a sclerotized ring around the spinnerets is present as in the Archaeinae, and the cymbium is not distinctly elongated. According to the combination of these characters this genus may be a member of the Lacunaucheniinae – likely in my opinion – or of the Mecysmaucheniinae or of an undescribed subfamily.

<u>Further characters</u>: Prosomal cuticula fine rugose (no rows of pustules, fig. 49), 8 eyes, cheliceral stridulatory files present, no femoral humps (but see femur III of *Lacunauchenius speciosus*, fig. 52), their three pairs of spinnerets are well developed (fig. 53) (see the remaks on *Palaeomysmauchenius* above), prolateral spatulate hairs of legs I–II unknown, probably absent.

Type genus: *Lacunauchenius* n. gen., in which the adult male is konwn. Further genera: *Eomysmauchenius* n. gen., *Filiauchenius* n. gen., and probably *Palaeomysmauchenius* SAUPE & SELDEN 2008? (in prep., see above).

Relationships: A hump on all femora (but see femur III of *Lacunauchenius*, fig. 52), pustules in rows and a sclerotized ring around the spinnerets are all absent, and the ♀-pedipalpus is long (unknown in *Lacunauchenius*) in contrast to the Archaeinae. According to the structure of the prosomal and opisthosomal cuticula, the absence of femoral humps and a ring around the spinnerets as well as the relatively long ♀-pedipalpus the Mecysmaucheniinae may be more related to the Lacunaucheniinae; in the Mecysmaucheniinae – which are not reported from the Cretaceous – the posterior and median spinnerets are strongly reduced and retrolateral denticles of articles of the ♂-pedipalpus exist, see the tab. in the book of WUNDERLICH (2004): 769–770) (*). In the Jurarchaeinae (♂ unknown) the legs bear numerous adpressed hairs, the ♀-pedipalpus is more stout, and an epigynal plate exists probably. – According to the plesiomorphic kind of not reduced posterior and median spinnerets as well as the absence of apomorphic characters which are known from the Archaeinae and the Mecysmaucheniinae the Lacunaucheniinae is the most archaic subfamily of the Archaeidae besides the Jurassic Jurarchaeinae.

(*) In this tab. one may add the character "size of the ♀-pedipalpus": Very weak and distinctly shorter than femur III in the Archaeinae, as long as or longer than femur III in the Mecysmaucheniinae, and longer than femur III in the Lacunaucheniinae.

Distribution: Mid Cretaceous Burmese amber forest, and probably Lower Cretaceous amber forest of France (*Palaeomysmauchenius* SAUPE & SELDEN (in prep.), see above).

Lacunauchenius n. gen.

Diagnosis (♂; ♀ unknown): Prosoma (fig. 49) anteriorly vertically raising, posteriorly overhanging. Pedipalpus (figs. 54–56) with a large and slender cymbium, bulbus not prominent, cheliceral "peg teeth" long, arranged in a wide row (fig. 51).

Further characters: Prosomal cuticula with tiny cuspules which are nor arranged in rows, legs fairly short, I not much longer than II. Femur III bears a dorsal “organ” (fig. 52), cymbium retrolaterally with long hairs (figs. 54–55).

Type species (by monotypy): *Lacunauchenius speciosus* n. sp.

Relationships: In the related genera the shape of the prosoma is different, see the key above.

Distribution: Mid Cretaceous Burmese amber forest.

***Lacunauchenius speciosus* n. gen. n. sp.** (figs. 49–56, photos 86–87)

Material: Holotypus ♂ in mid Cretaceous Burmese amber from Myanmar, F1923/BB/AR/CJW.

Preservation and syninclusions: The holotype is excellently but incompletely preserved in a relatively clear yellow-orange piece of amber. The large number of 10 layers of the amber within 4mms height indicate quick flows of the thinly liquid resin. The spider’s body is depressed laterally, median parts of the right legs II–IV and the tip of the left tarsus IV are cut off, two gas bubbles are preserved on the left side of the opisthosoma. Right in front of the spider larger organic structures are preserved which may be remains of a decomposed leaf.

Diagnosis: See above.

Description (♂):
Measurements (in mm): Body length 1.9, prosoma: Length 0.4, hight 0.37; leg I: Femur ~0.85, patella ~0.27, tibia 0.62, metatarsus ~0.5, tarsus 0.34, femur II ~0.75, tibia IV ~0.55; length of a basal cheliceral article 0.9; pedipalpus: Femur 0.3, patella 0.17, tibia 0.24, cymbium 0.33.
Colour: Prosoma and legs medium to light brown, opisthosoma yellow brown.
Prosoma (photo 87, figs. 49–51; it is depressed laterally) almost as high as long, overhanging posteriorly, finely rugose, covered with thin hairs which are not arranged in

rows, 8 eyes in a wide field, anterior mdians large, the remainings small, foramen large, basal cheliceral articles powerful, lateral stridulatory files indistinct, in a distal position, numerous very long "peg teeth" in at least two rows (or a field?), fangs of medium size; most parts of the long labium and gnathocoxae are covered with an emulsion. – Legs (photo 86) only fairly long, bristles absent, hairs thin and fairly short, spatulate hairs of I–II unknown (hidden?), III distinctly the shortest, the remainings almost equal in length, I slightly the longest, most tarsi are distinctly shorter than the metatarsi but tarsus and metatarsus III are almost equal in length. Femoral humps absent on I, II and IV, femur III (distinctly depressed laterally!) bears a circular dorsal structure (fig. 52) (probably a sensory organ) which has a diameter of 0.02 mm, looks membraneous, and which I do not regard as an artefact. The tarsal claws are large, the trichobothria are unknown. – Opisthosoma (figs. 49–50, 53; it is depressed laterally) long oval, covered with thin hairs of medium length, lung covers not recognizable. Three pairs of spinnerets which are well developed and not surrounded by a sclerotized ring. – Pedipalpus (figs. 54–56) with slender articles, the tibia bears a dorsal-distal hump, cymbium long, slender and modified, elongated basally, here with long retrolateral hairs and a questionable probasal stridulatory pick (arrow in fig. 55); tegulum long, with an apophysis which stands widely out and a needle-shaped embolus.

Relationships: See above.

Distribution: Mid Cretaceous Burmese amber forest.

***Eomysmauchenius* n. gen.**

Diagnosis (juv. ♀): Prosoma very high, obliquely protruding to the chelicerae, and gradually raising posteriorly (fig. 57), cheliceral peg teeth in an irregular position (figs. 58–59), cheliceral stridulatory files probably absent.

Type species: *Eomysmauchenius septentrionalis* n. sp. (the only known species of the genus).

Relationships: According to the combination of characters – three pairs of spinnerets which are well developed, the long pedipalpus as well as the absence of setose pustules of the prosoma and of femoral humps – *Eomysmauchenius* is a member of the subfamily Lacunaucheniinae. See the key above. In *Filiauchenius* the ♀-pedipalpus is much longer.

Distribution: Mid Cretaceous Burmese amber forest.

***Eomysmauchenius septentrionalis* n. gen. n. sp.** (figs. 57–60, photos 88–89)

Material: Holotypus ?ad. ♀ in mid Burmese amber, F1837/BU/AR/CJW. – Remark: I do not want to exclude that this small spider may be inadult.

Preservation and syninclusions: The spider is fairly well preserved in a small piece of amber which most probably was heated in a natural way as other pieces of Burmite; prosoma – especially chelicerae – and legs are deformed, some leg articles are cut off, e. g. the left patella I and adjacent parts, the left metatarsus and tarsus II and the right patella IV are also cut off. A fissure runs cross through the prosoma and the piece of amber. The spider was kept in paraffin; after half an hour parts of the spider became translucent and "bubbles" appeared within the chelicerae and some leg articles. – Small bubbles are preserved near the spider. A short part of a thin spider's thread in front of the left femur III may be part of a dragline.

Diagnosis (?ad. ♀; ♂ unknown): See the diagnosis of the genus.

Description (?ad. ♀) :
Measurements (in mm): Body length 1.15, prosomal length 0.6, length of the basal cheliceral articles ca. 0.42, opisthosoma: Length 0.52, hight 0.37, leg I: Femur 1.0, patella 0.16, tibia ca. 0.58, metatarsus 0.7, tarsus 0.4, femur III ca. 0.52, pedipalpus: Femur >0.18, tibia ca. 0.18, tarsus 0.28.
Colour light yelowish brown, anterior median eyes redbrown.
Prosoma (figs. 57–59; it is partly deformed): Cuticula finely scaled, setose pustules absent, dorsally distinctly raised and with few longer hairs, profile slightly convex, fovea apparently absent, foramen large. 8 eyes in a wide field, anterior medians largest, separated by ca. 1 1/2 diameters, posterior eyes small, their row recurved. Clypeus fairly short, basal cheliceral articles slender and very long, distally distinctly diverging, frontal-basal bristle absent, with long peg teeth in an irregular position of more than one row, fangs fairly long, retrolateral stridulatory files not visible or absent, gnathocoxae and labium apparently long, sternum convex. Pedipalpus (fig. 60) long and slender, distinctly longer than femur III (see above). – Legs long and slender, bristle-less, covered with longer hairs, I longest and III shortest, femora without dorsal hump, metatarsal trichobothria difficult to recognize, their position probably in ca. 0.42. – Petiolus short. – Opisthosoma (fig. 57) oval, lateral furrows low, covering hairs short, dorsal scutum absent, spinnerets deformed, anteriors longest, posterior spinnerets most probably existing, ring around spinnerets absent, genital area deformed, markings absent.

Relationships and distribution: See above.

***Filiauchenius* n. gen.**

Diagnosis (♀; ♂ unknown): Leg III long (not distinctly the shortest; patella + tibia + metatarsus of the pedipalpus longer than the prosoma, fig. 62), only few cheliceral "peg teeth" (figs. 63–64), pedipalpus very thin and much longer than the prosoma.

Type species (by monotypy): *Filiauchenius paucidentatus* n. sp.

Relationships: See the key above. In *Eomysmauchenius* the ♀-pedipalpus is distinctly shorter.

Distribution: Mid Cretaceous Burmese amber forest.

***Filiauchenius paucidentatus* n. gen. n. sp.** (figs. 61–64)

Material: Holotypus ♀ (probably adult) in Cretaceous Burmese amber from Myanmar, F1924/BU/AR/CJW.

Preservation and syninclusions: The spider is fairly deformed and incompletely preserved in a corner of a small piece of amber which contains numerous tiny brown bubbles. Most leg articles are cut off through their femora, only the right leg III and the right pedipalpus (except its patella) are complete, the opisthosoma is fairly deformed. – A thin thread of spiders silk is running through the piece of amber behind/below the spider; sticky droplets are absent. A Diptera – body length 1 mm – is preserved right of the spider.

Diagnosis: See above.

Description (♀):
Measurements (in mm): Body length 2.4, prosoma: Length ~1.4, width ~0.8; leg III: Femur 1.8, patella 0.3, tibia ~1.4, metatarsus ~1.4, tarsus ~0.6; length of the basal cheliceral article 0.5; pedipalpus: Length of patella + tibia + tarsus = 1.7.
Colour: Body medium to dark brown (the darkened prosoma), legs medium brown.
Prosoma (figs. 61, 63–64; it is partly hidden and deformed) 1.75 times longer than wide, slender (especially the cephalic part); rows of pustules are absent. Probably 8 eyes (the area of the posterior medians is not recognizable), anterior medians distinctly the largest, directed sideward, clypeus short, basal cheliceral articles powerful, directed backward in a position which I regard as unnatural, anterior bristles absent, lateral stridulatory files absent or not observable, only few "peg teeth", the – deformed – sternum separates the coxae IV by more than their diameter. – Pedipalpus (fig. 62) very long and very thin; patella + tibia + tarsus longer than the prosoma, claw hidden or absent. – Legs – most articles are lost – very long and slender femur, III longer than

the prosoma (and longer than in related genera), bristle-less, femoral humps absent; trichobothria and tarsal claws are unknown. – Opisthosoma (fig. 61) oval, hairs short, sclerotized ring around the spinnerets absent, spinnerets well developed, apparently three pairs. The genital area is hidden.

Relationships: See above.

Distribution: Mid Cretaceous Burmese amber forest.

B. The Palpimanoid branch

At least 3 of the 4 families of the palpimanoid branch are monogeneric. The branch contains probably more extinct (3 or 4) than extant families (3):

Extant are Huttoniidae (the only family of this branch which has – by a quite unsure determination – probably been found already in the Cretaceous period, in Canadian amber), Palpimanidae and Stenochilidae (= Palpimanidae: Stenochilinae sensu WUNDERLICH 2004, but it has more likely to regard as a family of its own);
extinct are Lagonomegopidae ESKOV & WUNDERLICH 1995 and Micropalpimanidae n. fam. – which are preserved in Cretaceous ambers –, as well as Spatiatoridae which is known from Eocene Baltic amber. (See also Burmascutidae below which relationships are quite unsure).

Three families of this relict branch are reported with this paper from Cretaceous ambers (see the the key of Cretaceous families, the diagnosis of the Archaeoidea above and the tab. below): Lagonomegopidae has been widely distributed in the Northern Hemisphere. Micropalpimanidae is known from a single male in Cretaceous Burmese amber only; the dwarf members of this family are the tiniest members of the palpimanoid branch which are known up today, the body length in the male sex is only 1.5 mm; contrarily the body length of extant relatives is usually more than 3 mm. – The shape of the modified prolateral hairs of legs I–II – if preserved – are quite different in the extinct families from their extant relatives; most often they are almost spatulate (actually rounded apically), rarely thin and pointed or absent; see the tab. below.

Selected relevant characters of the families of the palpimanoid branch of the superfamily Archaeoidea which are known as fossils, and the questionable Burmascutidae:
(The extant families Palpimanidae and Stenochilidae: See WUNDERLICH (2004).

Character	Spatiatoridae	Lagonomegopidae	questionable Huttoniidae	Burmascutidae	Micropalpimanidae
Modified hairs of legs I–II	spatulate	absent or pointed	spatulate	absent	spatulate (fig. 79)
cheliceral stridulatory files	+	--	+	+	+
very long and pointed labium	+	+	+	-- (*) (fig. 95)	+? (fig. 77)
strongly enlarged femur I	--	--	--	+	+ (fig. 78)
distribution	Tertiary: Eocene European forests	Cretaceous:Jordan, Burma, Siberia, Spain, N-America	Cretaceous: Canada	Cretaceous: Burmese amber forest	

(*) Labium wider than long, different from extant members of the Palpimanidae in which the labium is usually triangular and deeply notched apically. The large unpaired tarsal claw (fig. 98) and the large and spiny anal tubercle (fig. 97) may indicate relationships of the Burmascutidae to the Oecobioidea.

The extinct Cretaceous families of the palpimanoid branch show certain plesiomorphic characters within this branch (in contrast to the extant families Palpimanidae and Stenochilidae): The median spinnerets are not reduced, the patellae are not strongly elongated, and the tarsi and/or metatarsi are not strongly shortened as in the Palpimanidae. Few thin – almost hair-shaped – leg bristles (figs. 76, 78) exist in the Micropalpimanidae (a plesiomorphic character or a reversal?). The labium is very long and usually pointed in most Cretaceous members of the palpimanoid branch (fig. 74) – an apomorphic character of this branch? – but it is triangular in the extant Palpimanidae, and wide in the Cretaceous Burmascutidae (fig. 95) – as reversals?
Palpimanidae and Stenochilidae are the most advanced families in some respect; in Palpimanidae spatulate hairs of leg II are lost, members of the Stenochilidae have a quite unusual shape of the prosoma, cheliceral “peg teeth” are lost, and its copulatory organs are highly specialized in both sexes, see LEHTINEN (1982). Palpimanidae and the also advanced Stenochilidae are the only families of the palpimanoid branch in which at least the median spinnerets are strongly reduced (or even absent in the male sex), the unpaired tarsal claws are reduced or even absent as well, and which are not reported from fossils (I regard the fossil proof of the Huttoniidae as being quite unsure because the fossils are known only as juveniles).
Two or three of six or seven families of the palpimanoid branch (Lagonomegopidae, Micropalpimanidae and probably the Burmascutidae which relationships are quite unsure) are only known from the Cretaceous and became extinct probably during this period; their extinction happened in my opinion probably in connection with the K–T

boundary event. A further family: The Spatiatoridae (known from the Eocene Baltic amber forest), became extinct during the Tertiary. Only Huttoniidae, Palpimanoidae and Stenochilidae are extant families of the palpimanoid branch of the family Archaeoidea. It becomes more and more clear that the taxa of the Archaeoidea were far more diverse in the Cretaceous than today. The dwarfism of members of the Cretaceous families Burmarachnidae and Micropalpimanidae may indicate (too) a long phylogenetic history of the whole superfamily Archaeoidea.

(I) Family LAGONOMEGOPIDAE ESKOV & WUNDERLICH 1995

The strangeness of the Cretaceous spider fauna was first hinted at with the discovery of the extinct and until then unknown spider family Lagonomegopidae thirteen years ago. It was first described from Siberian amber and had to our recent knowledge the widest known – almost pantropical – distribution during the Cretaceous: Burma, Jordan, Lebanon, North America, Siberia and Europe (Spain). Its extinction happened latest at the end of the Cretaceous. The first specimen which may be adult, a female, is described below; an adult male is still unknown.

Most characteristic of this family are the unique position and shape of the eyes with widely spaced and powerful posterior median eyes in a marginal (!) position (figs. 69–73, photos 91–92), see WUNDERLICH (2004: 765). Particular spatulate prolateral hairs of the legs I–II – which are characteristic for most Archaeoidea (fig. 79) – are absent; hairs of legs in this position are either completely absent or they are thin and pointed as in specimens of *Grandoculus* in Canadian amber (fig. 68), see PENNEY (2004).

Revised diagnosis of the family Lagonomegopidae: 6 (*Lagonomegops* and *Zarqagonomegops* (figs. 69–73)) or 4 eyes (the remaining genera), posterior median eyes very large (powerful), widely spaced to the prosomal margin and directed anteriorly-laterally, clypeus with a pair of bulging structures (low humps) (fig. 73), lateral cheliceral stridulatory files absent, prolateral spatulate hairs of legs I–II absent (but thin and pointed hairs may be present, in *Grandoculus* PENNEY 2004, fig. 68); leg bristles usually absent but a single dorsal-distal femoral bristle may exist (fig. 66) and few more thin bristle (or hairs?) (fig. 67) may exist; see the tab. below.

Remarks: (1) PENNEY (2004, 2006) reports several metatarsal and tarsal trichobothria in *Burlagonomegops* (repeated by KADDUMI), but I did not find trichobothria on the tarsi and only a single one on the metatarsi in Burmese specimens which most probably are congeneric (see below). Thus there may be a doubt regarding the existence of tarsal trichobothria and more than a single metatarsal one in the Lagonomegopidae, which would be unique within the whole superfamily Archaeoidea (= Palpimanoidea), and which I regard more likely as long “normal” (non-trichobothrial) hairs. – (2) PENNEY (2004) reports “feathery” (!) hairs on legs of *Grandoculus* (no figure was given, and I did not found such hairs) but such feathery hairs may actually have been mistaken by this author for hairs of the “plumose” type. – (3) The only lagonomegopid taxon in which the tarsus I is distinctly longer than the metatarsus I is to my knowledge *Lagonomegops sukatchevae* from Siberia; in the remaining taxa the tarsi are about as long as the metatarsi; compare legs I and IV of *Burlagonomegops* ?*eskovi* F1918/CJW below. The ratio of tarsus/metatarsus varies apparently in different legs and in different stages of the ontogeny. – (4) According to the number of eyes, the differences in the ratio of tarsal and metatarsal length and the existence of a femoral bristle I regard “*Lagonomegops*” *americanus* not as congeneric with *sukatchevae* but probably with *Grandoculus* or – more likely – as a species of an undescribed/unnamed genus. The absence of prolateral hairs on legs I–II in *americanus* may be caused by the young stage and minuteness of the juvenile type material of this species. – (5) The median spinnerets may be strongly reduced, see below (F1918/CJW).

Relationships: See the tab. above.

Distribution: Cretaceous: N-American, Burmese, European (N-Spain), Jordanian, and Siberian amber forests; see the tab. below and the map above.

Differences in the described genera (*) of the Lagonomegopidae:

character	*Lagonomegops sukatchaevae*	“*Lagonomegops*” *americanus*	*Burlagonomegops alavensis,eskovi*	*Grandoculus chemahavinensis*
number of the eyes	6 (figs. 69– 71)	4	4	4 (fig. 68)
femoral bristles	--	on femur I only?	on femora I–IV (fig. 70) (**)	--
prolateral hairs of tibia I-II	--	--	--	+ (fig. 68)
distribution	Siberia (Taimyr)	USA (New Jersey)	Burma N-Spain	Canada

---

(*) The genus *Zarqagonomegops* KADDUMI 2007 in Jordanian amber is not included, see below; its characters in this table are identical with *Lagonomegops*.

Remark: The species of *Burlagonomegops* are probably not congeneric in my opinion.
(**) not in the youngest spiderlings.

Zarqagonomegops wunderlichi KADDUMI 2007 (figs. 72–73)

The monotypic genus *Zarqagonomegops* was recently described by KADDUMI (2007: 57–63, figs. 52A–B). The description is based only on a single juvenile spider from Jordanian amber which is incompletely preserved; its body length is about 1.8 mm. Six eyes are existing (figs. 72–73) as – most probably – in *Lagonomegops sukatchaevae* ESKOV & WUNDERLICH 1995, which may be strongly related or even congeneric. A significant difference of both taxa is unknown to me, see the tab. above. The seemingly total absence of leg trichobothria may be caused by the preservation by heating and pressing of the holotype. More material which is better preserved is needed for a revision of this taxon.

Burlagonomegops ?*eskovi* PENNEY 2005 (figs. 65–77, photos 90–93)

Material: A dozen specimens in mid Cretaceous Burmese amber from Myanmar: 2 juv., F1918/BU/AR/CJW and F2017/BU/AR/CJW (ex coll. SCOTT ANDERSON, USA); 1 ?ad. ♀, OSU no. B-A-1-2, G. POINAR coll.; 1 juv. OSU no. B-A-1-20, G. POINAR coll.; 8 juv. in a single piece of amber, private coll. SCOTT ANDERSON.

Spiders of *Burlagonomegops* PENNEY 2005 are not rare in Burmese amber and at least the juveniles may well have been dwellers of the bark of resin-producing *Araukaria* sp.. It is striking that almost all specimens are juvenile, only a single female is known which may be adult, see below (OSU no. B-A-1-2), and never an adult male. The conspecifity of the specimens is unsure.

F1918/CJW is completely and well preserved (photo 92), the prosoma is dorsally strongly depressed. Measurements (in mm): Body length 1.4, prosomal length 0.6, leg I: Femur > 0.5, patella 0.22, tibia 0.36, metatarsus 0.3, tarsus 0.3; leg IV: Femur 0.52, patella 0.2, tibia 0.35, metatarsus 0.25, tarsus 0.3. Tarsal trichobothria are absent; thee pairs of spinnerets, the medians are strongly reduced, the remainings are well developed, a colulus is apparently absent.

F2017/CJW: The spider is excellently and well preserved in a small yellow-orange piece of amber (see the photos 90, 93), ist body length is 1.2 mm. Six eyes, the very large and widely spaced posterior median eyes are well preserved, the anterior median eyes are absent. A pair of humps exists between and in front of the posterior median eyes, the clypeus is short, the basal cheliceral articles are weak, the labium is long, triangular and pointed, the strongly converging gnathocoxae are long and touching medially-apically. The tarsi are about as long as the metatarsi but longer on leg III. The patellae and tibiae bear a very weak bristle (or hair?) basally-dorsally (fig. 67). Specialized hairs of the anterior legs are absent. Tarsal trichobothria are absent. Three pairs of spinnerets, the anteriors are stout. A colulus is not recognizable and may be absent.

OSU no. B-A-1-2 (figs. 65–66): Remains of a female which is probably adult; it is decomposed and incomplete (see the photo 91); only remains of the prosoma, leg articles and the strongly deformed opisthosoma are preserved, the right half of the prosoma is cut off within the fossil resin, the loose right chelicera is lying behind the prosoma.
Measurements (in mm): Prosomal length 1.35 (the body length of the spider may have been about 3.5), length of femur II 1.0, size of a posterior eye 0.33 x 0.27, diameter of an anterior eye 0.1, length of a basal cheliceral article 0.7.
The prosoma is high, the clypeus bulging, the four eyes are mainly directed sidewards, the posterior eyes are powerful, the anterior cheliceral furrow bears 5 long “peg teeth”, the femora bear a dorsal-distal bristle, tarsal trichobothria are absent, a badly preserved tarsus I may be not longer than metatarsus I.

OSU no. B-A-1-20 is an incompletely and badly preserved juvenile spider, its prosoma is about 0.7 mm long. Some questionable threads of spiders silk are preserved in the same piece of amber.

8 juv. of the coll. S. ANDERSON: In a bloc of 10 x 9 x 7.3 mm remains of 8 juvenile members of ?*Burlagonomegops* are preserved which are deformed and some are incomplete; they all may originate from a single egg sac. Their prosomal length is 0.9 mm. A row of long cheliceral “peg teeth” and the large posterior median eyes are recognizable. Long leg hairs exist on the femora (2 distally), patellae (1 basally), and tibiae (1 basally). A long trichobothrium exists on all metatarsi in about the middle of the article. – Syninclusions are some spiders’ threads without droplets, stellate hairs, a small Diptera and particles of insects’ excrement.

(II) Family MICROPALPIMANIDAE n. fam. (figs. 74–84, photos 94–96)

Diagnosis (♂; ♀ unknown): Existence of a special stridulatory organ (files to files) between the chelicerae und the pepalpal femur (figs. 76, 84), labium and gnathocoxae very long (fig. 74), legs with questionable thin bristles (fig. 79, 81–82), legs I and II bear distinct spatulate prolateral hairs (figs. 79–80), metatarsi and tarsi not shortened, posterior eye row procurved (fig. 75).

Further characters: Body length only 1.5 mm, cephalic part strongly raised (fig. 74), prosomal cuticula finely rugose (fig. 79), legs with three pairs of tarsal claws which are well developed, metatarsal III preening hairs present (fig. 82), patellae not strongly elongated, three pairs of well developed spinnerets; a sclerotized ring around the spinnerets is probably existing.

Type genus (by monotypy): *Micropalpimanus* n. gen.

Ralationships: According to the spatulate prolateral hairs of legs I and II, the reduced (thin or even absent) leg bristles, the cheliceral stridulatory files and "peg teeth", as well as the raised cephalic part the family Micropalpimanidae has to regard as a member of the superfamily Archaeoidea (= Palpimanoidea). The absense of a cheliceral foramen indicates a membership of the "palpimanoid branch". In the Palpimanidae – which seems most related – the median and posterior pairs of spinnerets are strongly reduced or even absent in the male sex, the paired claws of the tarsi I–II are short, leg bristles as well as spatulate prolateral hairs on leg II are absent, the tarsi are shorter than the long patellae, labium and gnathocoxae are shorter, a different type of stridulatory organs exists. – Burmascutidae: See below. – Plesiomorphic characters of the Micropalpimanidae within the palpimanoid branch are the position of the eyes in two wide rows of four, well developed posterior spinnerets, large claws of tarsi I and II, the relatively short patellae which are not strongly elongated, the tarsi and metatarsi which are not shortened, and the probable existence of thin leg bristles (or hairs?).

Distribution: Mid Cretaceous Burmese amber forest.

***Micropalpimanus* n. gen.**

Diagnosis and relationships: See the family Micropalpimatidae.

Type species (by monotypy): *Micropalpimanus poinari* n. sp.

Distribution: Mid Cretaceous Burmese amber forest.

***Micropalpimanus poinari* n. gen. n. sp.** (figs. 74–84, photos 94–96)

Material: Holotypus ♂ in mid Cretaceous Burmese amber from Myanmar, OSU no. B-A-1-3, G. POINAR jr. coll.

Preservation and syninclusions: The spider is completely and excellently preserved in a yellow piece of amber; a prominent white "emulsion" (Bacteria?) covers parts of its right side ventrally.

Diagnosis (♂; ♀ unknown): Pedipalpus (figs. 83–84): Tibia with ventral humps, conductor in a more distal position.

Description (♂):
Measurements (in mm): Body length 1.5, prosoma: Length ca. 0.65, width >0.55; leg I: Femur ca. 0.44 (width 0.2 in ventral aspect), patella 0.27, tibia 0.37, metatarsus 0.3, tarsus ca. 0.25, tibia II 0.37, tibia III 0.35, tibia IV 0.5, diameter of an anterior median eye 0.06.
Prosoma (figs. 74–77) strongly raised, thoracal part abruptly lower, cuticula almost smooth, hairs indistinct, fovea probably absent; eye field wide, anterior eyes largest, posterior row strongly procurved, posterior eyes small and widely spaced. Basal cheliceral articles large, bulging anteriorly in the middle, laterally with distinct stridulatory files. Posterior margin of the cheliceral furrow with at least 2 "peg teeth", fangs fairly long. Labium not fused to the sternum, longer than wide (parts of its tip are hidden), gnathocoxae very long, converging and pointed; a serrula is not recognizable. Sternum wide, coxae IV separated by their diameter. – Legs (figs. 78–82) fairly slender, order IV/I=II/III, patellae shorter than metatarsi, femur I strongly enlarged, distinct bristles absent but few thin – almost hair-shaped – bristles (or strong hairs?) exist on femora, patellae and tibiae. Prolateral spatulate hairs exist on leg I (tibia, metatarsus and tarsus) and II (distal part of the tibia, the metatarsus and in the basal half of the tarsus). Trichobothria absent on the tarsi, a single long one exists in the distal half of all metatarsi. Tibiae, metatarsi and tarsi bear long dorsal hairs which are similar to trichobothria. Metatarsus III bears apically-ventrally some preening bristles. Three well developed tarsal claws which may be smooth. – Opisthosoma oval, slightly longer than wide, hairy; sigillae probably absent. Epigaster sclerotized, lung covers present, tracheal spiracle hidden. Three pairs of spinnerets which may be surrounded by a sclerotized ring, the anteriors – and apparently the remaining ones – are well developed. – Pedipalpus (figs. 83–84): Femur enlarged, prolaterally with stridulatory files, patella short, tibia about as long as wide, ventrally with two humps, cymbium large, bulbus prominent, with a large conductor in a distal position, embolus unknown (hidden).

Relationships: See above.

Distribution: Mid Cretaceous Burmese amber forest.

Micropalpimanus ?poinari n. gen. n. sp.

Material: 1♂ in mid Cretaceous Burmese amber, F2020/BU/AR/CJW.

Body, legs and pedipalpi of the spider are strongly deformed and lengthened by natural heating and pressing, parts of the right legs I and II and of the right pedipalpus are broken off with a part of amber. Measurements (in mm): Body length less than 1.9, leg IV: Femur ~0.45, patella 0.25, tibia 0.53, metatarsus 0.5, tarsus ~0.28, leg I long and slender, not enlarged, leg IV is the longest, tarsi and metatarsi are slender, the metatarsi are not shortened, the patellae are not distinctly elongated. Spatulate hairs exist prolaterally at least on metatarsi I–II. I did not find leg bristles (probably they are rubbed off). The epigaster is sclerotized, a sclerotized ring around the spinnerets or the epigaster is apparently absent. Three pairs of – deformed – spinnerets, the anterior long and slender (apparently expanded), colulus apparently large. – This badly preserved male could well be conspecific with *M. poinari* n. sp..

Distribution: Mid Cretaceous Burmese amber forest.

(III) Questionable HUTTONIIDAE (N-American amber)

PENNEY & SELDEN (2006) reported on spiders in Cretaceous amber from Canada. In this kind of fossil resin allegedly Huttoniidae represents 6–7% of the spider faunas. Extant spiders of this family are only known from New Zealand. Bristles are absent on legs I–II, metatarsus IV bears a ventral-apical "preening comb" (a group of strong bristles).
The report of this family is based on juvenile spiders only, and therefore the determination is quite unsure in my opinion; an adult male and well preserved structures of its pedipalpus are needed for a sure determination.

The following taxa are members of various "advanced" superfamilies of the Entelegynae.

(3) SUPERFAMILY OECOBIOIDEA

Only two families are combined to the superfamily Oecobioidea, see WUNDERLICH (2004: 809–848):
(a) Hersiliidae (Eocene to extant; a report from the Cretaceous is still absent), and
(b) Oecobiidae (Cretaceous to extant) which are known from several extinct and extant subfamilies.

See also the enigmatic family Burmascutidae n. fam. below.
Oecobioidea are cribellate or ecribellate spiders, they possesses usually eight eyes (rarely six) on a wide prosoma (fig. 85), a long clypeus which is protruding medially, a mediograde leg position, ventral tarsal bristles/spines, a large anal tubercle with a fringe of hairs, widely spaced anterior spinnerets and long posterior spinnerets (fig. 87).

Family OECOBIIDAE

The family is known from the Cretaceous to today.
The fringe of conspicuous hairs of the large anal tubercle (fig. 87) is the most important and usefull diagnostic character of this family (compare fig. 97). The prosoma (fig. 85) is about as wide as long; a protruding clypeal "nose" – similar to the related Hersiliidae – exists usually but is apparently absent in *Zamilia* n. gen.. Their body has usually a position near to the ground, the leg position is almost star-like and mediograde, and they are almost equal in length: III is relatively long and IV is frequently not shorter or even longer than I. The tarsi (!) – at least IV – bear longer ventral bristles (fig. 91) similar to (e. g.) Hersiliidae and some Dictynidae and Uloboridae. – Cretaceous fossils:

(3a) Questionable OECOBIINAE indet. in amber from New Jersey

A single specimen, a questionable adult female in Cretaceous amber from New Jersey, has been described, see PENNEY (2002: 714–716, t. 2, fig. 2; fig. 4), sub *Oecobius*? sp. indet. A long calamistrum is reported by PENNEY as it is typical in Oecobiini sensu WUNDERLICH (2004) but a cribellum has not been recognized because its area is hidden; the shape of the opisthosoma and the leg bristles are not typical for the Oecobiini. Further material – mainly an adult male – is needed to confirm the relationships of this species which well may be the member of an undescribed genus. Lebanoecobiinae WUNDERLICH 2004, see below, is also cribellate and may be related.

(3b) LEBANOECOBIINAE WUNDERLICH 2004

A single taxon in Lower Cretaceous Lebanese amber is known, *Lebanoecobius schleei* WUNDERLICH 2004, see WUNDERLICH (2004: 828–829, figs. 26–31), and Oecobioidea fam. indet. below. It is cribellate; see (3a).

(3c) MIZALIINAE: A fossil spider in Burmese amber

Mizaliinae has been reported from Eocene Baltic amber only: See WUNDERLICH (2004: 830–837, figs. 10–15a); *Zamilia* n. gen is the first report of this subfamily in Burmite. Apical cymbial bristles, a calamistrum – in both sexes – and most probably a funtioning cribellum are absent in this subfamily, and the cymbium is wide. – Remark: The structure “C” in fig. 11 – WUNDERLICH (2004: 845) – means a non-functional cribellum or probably a very large/wide colulus. The kind of this structure – it is much larger than a “usual” colulus – is difficult to interprete more closely, and its function is unknown. Because of the absence of a calamistrum its function as a cribellum appears unlikely.

The subfamily Mizaliinae is the only known extinct subfamiliar and suprageneric taxon which is known from the Cretaceous AND the Tertiary besides the questionable Protheridiidae. But it is well-known that the fossil record is fundamentally quite incomplete, and most of the extinct taxa may have died out much later than the most recent fossil has been found (the “Signor-Lipps effect”) or is surprisingly still existing (see *Latimeria*).

***Zamilia* n. gen**.

The gender of the name is feminine.

Diagnosis (♂; ♀ unknown): Posterior eye row most probably distinctly procurved (fig. 85), a protruding clypeal "nose" is most probably absent (the prosoma is not well preserved); pedipalpus (figs. 88–89): Bulbus with two blunt apophyses which stand out; embolus and leg autotomy are unknown.
Further characters: Calamistrum and cymbial bristles absent, cymbium wide.

Type species (by monotypy): *Zamilia antecessor* n. sp.

Relationships: According to its characters – mainly the wide and bristle-less cymbium and the absence of a calamistrum, but also due to the spiny legs – I regard *Zamilia* with some doubt as a member of the Mizaliinae THORELL. In the Eocene genus *Mizalia* KOCH & BERENDT 1854 – the only known further genus of this subfamily – a calamistrum and bristles of the wide cymbium are absent, and a large colulus exists, too, but a distinct clypeal "nose" exists, the posterior eye row is almost straight, and blunt bulbus apophyses which stand out like in *Zamilia* are absent.

Distribution: Mid Cretaceous Burmese amber forest.

***Zamilia antecessor* n. gen. n. sp.** (figs. 85–89, photos 97–98)

Material: Holotypus ♂ in mid-Cretaceous Burmese amber from Myanmar, F1919/BU/AR/CJW.

Preservation and syninclusions: The spider is completely preserved, partly deformed and strongly darkened by natural pressing and heating in former times, some femora are flattened. – Several particles of excrement – most probably of insects – and detritus, some stellate hairs and numerous tiny bubbles are preserved in the same piece of amber.

Diagnosis (♂; ♀ unknown): Bulbus (it is deformed) with two blunt apophyses which stand clearly out (figs. 88–89).

Description (♂):
Measurements (in mm): Body length 2.5, prosoma: Length and width 1.0; leg I: Femur ~ 0.9, patella 0.38, tibia 0.75, metatarsus 0.6, tarsus 0.45, tibia II ~ 0.75, tibia III ~ 0.75, leg IV: Tibia 0.8, metatarsus 1.0, tarsus 0.55.
Colour mainly dark brown, some – mainly basal – femoral parts yellow.
Prosoma (photo, fig. 85; it is darkened and slightly deformed) as wide as long; apparently 8 eyes, posterior row probably strongly procurved, but the position of the posterior median eyes is quite unsure. Clypeal "nose" apparently absent, basal cheliceral articles small, ventral parts hidden or deformed. – Legs (photos, fig. 86) only fairly long, IV longest, III not much shorter, tibia I > metatarsus I but tibia IV < metatarsus IV. Bristles long and numerous on femora, patellae, tibiae, metatarsi and tarsus IV: Femur I ca. 8, patellae dorsally 1/1 as well as laterals, tibia IV 8, metatarsus IV 6 + an apical ring of 4, tarsus IV 3–4 ventrally. Calamistrum absent. Trichobothria unknown. 3 large tarsal claws, the paired bear long teeth. – Opisthosoma (photo, fig. 87) oval, fairly flattened, covered with hairs of medium length. Posterior spinnerets long, anal tubercle large, bearing a fringe of thin hairs. Colulus difficult to recognize (the area is strongly darkened), probably wide. – Pedipalpus (figs. 88–89) with stout/thick articles, patella and tibia with a long bristle, cymbium wide and bristle-less, bulbus with two apophyses which stand clearly out.

Relationships: See above.

Distribution: Mid Cretaceous Burmese amber forest.

?**Oecobioidea fam. indet**. (figs. 90–92)

Material: Remains of a ♂ in Lower Cretaceous Jordanian amber from the Zarqa river canyon, ex coll. ERMNH-ZRA no. 296, F2006/JB/AR/CJW.

Preservation and syninclusions: The spider is not well and only incompletely preserved at the margin of a small piece of amber; most parts of the prosoma are hidden or missing, the opisthosoma is cut off, the left legs and the right leg I are preserved. – Numerous particles of detritus and some thin threads of spiders' silk are preserved close to the spider, the longest thread is about 3 1/2 mm long. At least one of the threads bears some questionable tiny oval pollen grains which are ~0.015 mm long.

Diagnosis (♂; ♀ unknown): Legs spiny (fig. 90), feathery hairs present, all tarsi with short ventral bristles (fig. 91), bulbus (fig. 92) wide and flat.

Further characters: Three tarsal claws, eyes as well as cribellum and calamistrum unknown (most dorsal parts of metatarsus IV are hidden).

Description (♂):
Measurements (in mm): Body length probably ca. 2 1/2, femur I ~2.6, metatarsus I ~1.6, pedipalpal femur 0.62.
Legs (figs. 90–91) long and spiny, IV probably the longest, III distinctly the shortest, feathery hairs present, metatarsi undivided and without basal trichobothria like in the Hersiliidae, bristles numerous and well developed, existing on femora, patellae, tibiae (tibia I bears at least 14 bristles), metatarsi (dorsally and ventrally) and ventrally on tarsi (especially on IV), tarsal trichobothria absent, unpaired tarsal claws well developed, paired claws short and only slightly bent. – Pedipalpus (fig. 92): Femur long and slender, patella short, tibia fairly long, cymbium wide, without apical bristles, bulbus flat, its structures are difficult to recognize (they are partly hidden by emulsions), a large subtegulum may exist, the questionable embolus runs probably distally inside the conductor which has an apical position.

The **relationships** are doubtful. According to the existence of numerous ventral tarsal bristles and feathery leg hairs the spider may well be a member of the Oecobioidea or related to the family Dictynidae. I do not want to exclude relationships to the Lebanoecobiinae WUNDERLICH 2004 in Lower Cretaceous Lebanese amber. In contrast to the Uloboridae are femoral trichobothria absent.

Distribution: Lower Cretaceous Jordanian amber forest.

(4) DOUBTFUL SUPERFAMILIES

(4a) Family BURMASCUTIDAE n. fam.

Diagnosis: Spinnerets in an anterior position (figs. 97, 106), opisthosoma strongly armoured (photo, fig. 106), 8 eyes in two wide rows (figs. 93, 101), no (♂) or few thin leg bristles including a bristle on femur I (fig. 104), the tarsal claws are probably tooth-less (fig. 105); the large anal tubercle bears strong basal bristles (fig. 97), the epigyne is a sclerotized plate (fig. 106), the bulbus bears one or two apophyses and a long conductor in a position close to the cymbium (figs. 99–100), the embolus is hidden.

Further characters: Ecribellate, unpaired tarsal claw present, tarsal trichobothria absent, metatarsi with a single trichobothrium, prosomal cuticula fine rugose (fig. 93), labium dsitinctly wider than long (figs. 95, 102), legs stout especially in the male (photos, fig. 104), claw of the ♀-pedipalpus long and tooth-less, lungs probably reduced (small covers: Fig. 106), three pairs of well developed spinnerets (figs. 97, 106), embolus unknown (probably hidden within the long conductor), dwarf spiders, body length 1.1–1.3 mm.

Type genus (by monotypy): *Burmascutum* n. gen.

The **relationships** of the Burmascutidae are enigmatic, even on the suprafamiliar level; regarding to its unique combination of characters it seems not unlikely to me that it may be the member of a twig of its own, branching between the superfamilies Oecobioidea and Araneoidea, see below. – The existence of a sclerotized epigyne and the structures of the ♂-pedipalpus are different from the Dysderoidea s. l., and the Archaeoidea, too, in which "peg teeth", and most often a raised part of the cephalic part as well as – usually – spatulate hairs of the anterior legs exist. The position of the eyes – two wide rows which build no groups – is furthermore different in most Dysderoidea. Shape and size of the spinnerets are different from those of the Oecobioidea, Araneoidea and the Dictynoidea. The anterior spinnerets are not widely spaced like in the Oecobioidea (and most Dictynidae), the posterior spinnerets are not elongated, a fringe (!) of hairs of the anal tubercle and ventral bristles of the posterior tarsi are absent in contrast to members of the Oecobioidea. According to the genital organs – so far as observable – *Burmascutum* may be entelegyne. – A retrobasal paracymbium and a scapus of the epigyne are absent in contrast to most Araneoidea, and the position of the spinnerets is not rosette-shaped like in the ecribellate branch of this superfamily. A retrobasal paracymbium is absent in the Theridiidae of the Araneoidea like in the Burmascutidae, tooth-less tarsal claws and an intern paracymbium exist in certain rsp. in numerous members of this family, but the anterior spinnerets are short in the Theridiidae, femoral bristles are absent, and a ventral comb of tarsus IV as well as a prosomal-opisthosom-

al stridulatory organ exist in numerous taxa of this family. In the extinct Protheridiidae WUNDERLICH 2004 (superfamily Araneoidea) exists a retrobasal paracymbium. – A tibial apophysis of the ♂-pedipalpus is absent in *Burmascutum* in contrast to members of the RTA-clade, and the trichobothriotaxy is also different in this branch in which usually several tarsal and metatarsal trichobothria exist. The structures of the bulbus are simpler than in most members of the Araneoidea and of the RTA-clade.
Putting all characters, relationships, and supposed convergences together I do not want to exclude that Burmascutidae may be the member of a branch which is related to the Oecobioidea and to the Araneoidea as well, probably the sister group to both superfamilies. Main derived/apomorphic characters of this branch are the anterior position of the spinnerets (similar to certain Araneoidea), and the existence of a large prolateral conductor in a parallel position to the cymbium (similar e. g. to certain Agelenidae and Dictynidae of the RTA-clade). Reduced leg bristles and lungs, an armoured opisthosoma and stout legs are frequent in dwarf spiders of numerous families besides the Burmascutidae.

Distribution: Mid Cretaceous Burmese amber forest.

Burmascutum n. gen.

Diagnosis and relationships: See the family Burmascutidae. The (deformed!) prosoma is wide and bears few short spines; its cuticula is fine rugose. Genital-organs figs. 99–100, 106.

Type species (by monotypy): *Burmarachne aenigma* n. sp.

Distribution: Mid Cretaceous Burmese amber forest.

***Burmascutum aenigma* n. gen. n. sp.** (figs. 93–106, photos 99–103)

Material: Holotypus ♂ in mid Cretaceous Burmese amber from Myanmar and a separated piece of amber, OSU no. B-A-1-7. Paratypus ♀ in the same kind of amber, OSU no. B-A-1-10, G. POINAR coll.

Remark: The female possesses thin leg bristles in contrast to the male and its legs are more slender; therefore I regard its conspecifity with the male as not quite sure. According to the position of the eyes, the shape of the body, the structure of the prosomal cuticula, the armoured opisthosoma, and the anterior position of the spinnerets I am not in doubt about the congenerity of holotype and paratype. Both pieces of amber come from the same collection (OSU), are very small, and I do not want to exclude that they have been separated from a common piece of amber.

Preservation and syninclusions: Holotype: The spider is almost completely preserved and strongly deformed, body and legs are depressed dorsoventrally on a layer in the amber, distal parts of the left pedipalpus including the bulbus are cut off. On the left side of the spider a large gas bubble is preserved, right behind and below the spider a larger particle of questionable detritus is situated. – Paratype:The spider is completely preserved in a clear yellow-orange piece of amber; body and legs are partly strongly deformed, most leg articles are flattened laterally, the opisthosoma is depressed dorsally were a concavity exists. A thin thread of spiders silk runs foreward from the anterior part of the prosoma.

Diagnosis: Body length only 1.1 (♂) – 1.3 mm (♀); ♂-pedipalpus (figs. 99–100) with a large and sickle-shaped conductor (which is probably not in its natural position). ♀: Epigyne with a triangular plate which is strongly sclerotized (fig. 106).

Description:

Measurements (in mm): ♂: Body length1.1, prosoma: Length ca. 0.35, width probably about 0.38; leg I: Femur ca. 0.3 (width of the flattened article 0.13), patella ca. 0.15, tibia ca. 0.24, metatarsus ca. 0.24, tarsus ca. 0.18; diameter of an anterior median eye 0.05. ♀: Body length 1.3, prosoma: Length 0.55, width >0.4; opisthosoma: Length and width 0.8; leg I: Femur 0.65, patella 0.23, tibia 0.5, metatarsus 0.4, tarsus 0.23, femur IV 0.6; pedipalpal claw ca. 0.05.

Colour: ♂: Prosoma and legs medium brown, opisthosoma light brown; ♀: Body yellow brown, legs medium to dark brown.

Prosoma (figs. 93–94, 101–102) (strongly deformed, compressed and folded in both specimens) about as wide as long, fine rugose, strongly sclerotized, dorsally bearing short spines at least in the male; 8 eyes in a wide field of two rows which are almost in a parallel position, partly deformed and covered with emulsions; posterior row straight to slightly recurved, anterior median eyes largest, fovea unknown, clypeus of medium length, its margin with strong bristles. Basal cheliceral articles fairly large, not fused at base, distinctly deformed, lateral – widely spaced – folds (♂) are apparently artefacts, no stridulatory files, fangs long, several tiny teeth – no "peg teeth" – exist on the anterior and posterior margin of the cheliceral furrow which are fairly thick; labium wider than long, not fused to the sternum, gnathocoxae stout and strongly converging above the labium in the male but strongly deformed, long and not converging in the female; the sternum separates the coxae IV by their diameter. A prosomal-opisthosomal stridulatory organ is most probably absent. – ♀-pedipalpus (fig. 103) fairly long and slender, with some longer bristle-shaped hairs, and a long and apparently tooth-less claw which is as long as the diameter of the pedipalpal tarsus. – Legs (photos, figs. 98, 104–105) sexual-dimorph, stout in the male, more slender in the female, bristles probably absent in the male but two thin dorsal bristles exist in the female on patellae and tibiae, and a single prolateral bristle in the distal half on femur I; spatulate and feathery hairs absent, stronger pointed hairs are present in the male (rubbed off in the female?), femur I artificially thickened and flattened laterally in the male; order I/II/IV/III in the female; I, II and IV almost equal in length, IV seemingly (stronger deformed!) the longest in the male; III distinctly the shortest. Scopulae and "preening hairs/bristles" of metatarsi III and IV absent. Trichobothria difficult to observe, most probably absent on the tarsi, I recognized a long trichobothrium on the right metatarsus II in a position of ca. 0.4 of the male, and a single one in the distal half of the tibiae in the female. Three tarsal claws (fig. 98) which are well developed and probably toothless, the unpaired one is large and bent in a right angle; ventral comb of tarsus IV, claw tufts and onychium absent (deformed tips of some tarsi are similar to an onychium). – Opisthosoma (photos, figs. 94, 106) about as wide as long, fairly flattened but artificially depressed dorsoventrally in both specimens (stronger in the male), furrowed laterally, completely strongly sclerotized, dorsally with three pairs of small sigillae and with pointed hairs (several hairs are covered with an emulsion and seemingly thickened in the male), standing on small sclerotized sockets. There exists a conique structure at the genital area of the male (fig. 96). Lung covers small and distinct (the lungs are probably reduced), tracheal spiracle hidden. Three pairs of spinnerets which are well developed, flattened by deformation in the male (especially the medians); the anterior spinnerets are two-segmented, separated by about their basal diameter, not converging (bearing a larger median structure as an artefact in the male). A sclerotized ring around the spinnerets is absent. The large, blunt, and – in the male strongly deformed – anal tubercle bears basally a row of strong bristles which are more difficult to recognize in the female. – ♂-pedipalpus (figs. 99–100) with the femur enlarged (partly artificially flattened), no prolateral stridulatory pick, tibia almost as wide as long, the retrolateral side is deformed and partly hidden; I do not want to exclude the existence of a short blunt retrodistal tibial apophysis; cymbium large and with long hairs, distally-ventrally with a more sclerotized and sickle-shaped structure (I in fig. 99) similar to the internal paracymbium of certain Theridiidae; bulbus (its structures are darkened and difficult to recognize) with a blunt “median” apophysis, a short and strongly bent apophysis (?), and a long sickle-shaped conductor in a position parallel to the cymbium (probably not its natural position); embolus unknown, probably hidden within the conductor. – The epigyne (fig. 106) is a strongly sclerotized triangular plate.

Relationships: See above.

Ecology, behaviour: According to the absence of leg scopulae and claw tufts as well as long tarsal claws, short legs III, and the presence of silk (droplets are not preserved) with the female the spiders were probably dwellers of capture webs.

Distribution: Mid Cretaceous Burmese amber forest.

(4b) Family SALTICOIDIDAE n. fam.

Diagnosis (♂; ♀ unknown): Anterior median eyes very large and directed anteriorly, 8 eyes in two rows (figs. 107–108). Feathery leg hairs present (figs. 109, 113). ♂-Pedipalpus (fig. 111): patella with a dorsal-apical outgrowth, tibial apophysis and paracymbium absent, cymbium large, embolus probably describing few circular loops, conductor unknown, “median” apophysis large and standing out from the bulbus. The spiders were most probably dwellers of capture webs.

Further characters: Cribellum/calamistrum apparently absent, the legs bear numerous bristles (fig. 107, 110, 112), ventral tarsal bristles are most probably absent, unpaired tarsal claws are apparently present (Salticoididae indet.).

Type genus (by monotypy): *Salticoididus* n. gen. See below: Salticoididae indet.

The **relationships** are doubtful, even on the suprafamiliar level; morphological relationships exist to certain members of the Araneoidea and the Oecobioidea as well. According to the large cymbium and the complicated structures of the bulbus this taxon is most probably entelegyne. The position of the eyes is similar in certain Araneoidea but due to the absence of a paracymbium I suppose that it may be not a member of the superfamily Araneoidea s. str. (the ecribellate branch). Probably a paracymbium has “not yet” evolved in *Salticoididus,* or it has been lost? – In contrast to most members of the RTA-clade a tibial apophysis of the ♂-pedipalpus is absent. Position and shape of the anterior median eyes as well as the shape of the prosoma (less distinct) are a bit similar to members of the family Salticidae which possesses 3 or 4 rows of eyes. The existence of strong leg bristles and feathery hairs as well as the absence of a tibial apophysis are similar in members of the superfamily Oecobioidea in which shape and position of eyes and clypeus are different, the eye field is usually (!) more narrow. The anal tubercle of the two fossil specimens is unknown, and can therefore not compared with the typical large anal tubercle of the Oecobioidea; the existence of ventral tarsal bristles in the holotype is also unknown. Feathery leg hairs are also present in the family Plumorsolidae in which only six eyes exist, see above. I do not want to exclude that Salticoididae is the member of a branch which is related to the Araneoidea and – probably stronger – to the Oecobioidea as well. – An apical outgrowth of the pedipalpal patella exists also in *Zarqaraneus* n. gen. (Araneoidea: Protheridiidae) which is known in Cretaceous Jordanian amber, too, and in which feathery hairs as well as metatarsal bristles are absent, the anterior median eyes are not enlarged, and a – large and erect – paracymbium exists.

Distribution: Lower Cretaceous Jordanian amber forest.

Salticoididus n. gen.

The gender of the name is masculine.

Diagnosis and distribution: See above; **relationships**: See above and Salticoididae indet. below.

Type species (by monotypy): *Salticoididus kaddumiorum* n. sp.

***Salticoididus kaddumiorum* n. gen. n. sp.** (figs. 107–113, photo 104)

Fam. indet.: KADDUMI (2007: 55, figs. 50A–B).

Derivatio nominis: This species is dedicated to my Jordanian friend HANI FAIG KADDUMI and his family in Amman. H. K. and his wife collected and discovered highly interesting Cretaceous spiders – and other arthropods – among numerous inclusion-bearing pieces of Cretaceous amber, and H. K. kindly made the spiders available for a scientific study. See the book published by KADDUMI (2007).

Material: Holotypus ♂ and a part of a capture web in Lower Cretaceous Jordanien amber from the Kurnub Sandstone Formation of the Zarqa river basin; ERMNH ZRA no. 108.

Preservation and syninclusions: The spider is not well and only partly preserved in a small and flat piece of amber, the ventral sides of body and legs are missing, they are broken off within the amber, the dorsal part of the thorax and the opisthosoma are hidden by fissures and emulsions, the opisthosoma is bent ventrally in a strong angle, the dorsal parts of the femora – except some apical parts – and some patellae are preserved, the internal parts of pro- and opisthosoma and the ventral parts of both pedipalpi are also missing. – Five thin spider’s threads are preserved nearby the spider at its right side, four of these are running above the spider in a parallel position to the right femur II, a single thread is running to the opisthosoma; droplets are absent. Numerous particles of detritus are preserved below and sindeward of the spider as well as on the threads.

Diagnosis (♂; ♀ unknown): See above.

Description (♂):
Measurements (in mm): Body length ~2.6, prosomal length ~1.7, femur I ~1.6, width 0.28, diameter of an anterior median eye ~0.13.
Colour: Prosoma and legs dark brown, opisthosoma light brown.
Prosoma (most parts are hidden): 8 eyes in two rows (figs. 107–108), the anterior medians distinctly the largest and directed foreward, the anterior laterals are obliquely di-

rected anteriorly-laterally, the posterior laterals are the smallest, lateral eyes contiguous, the posterior row is slightly recurved. The position of the clypeus is apparently vertical like the sides of the caput. – The legs are strongly sclerotized, the femora bear some – incomplete? – thin feathery hairs (fig. 109; see fig. 113) as well as strong bristles, femur I bears at least 4 prolateral bristles (figs. 107, 110). According to the remains of a capture web – which may have been spun by this male – an unpaired tarsal claw has most probably been existed in this specimen. – The opisthosoma bears short hairs, a dorsal sctum is most probably absent, the posterior part with the spinnerets is lost. – Pedipalpus (fig. 110) with stout but not thickened spiny articles, patella with a dorsal-apical apophysis/outgrowth which is directed anteriorly, tibial apophysis most probably absent (or hidden?), cymbium large and hairy, paracymbium apparently absent, subtegulum and tegulum large, median apophysis large and standing out from the bulbus, embolus hidden, probably in a circular position and describing loops, existence of a conductor unknown.

Relationships: See the questionable Salticoididae indet. below.

Distribution: Lower Cretaceous Jordanian amber forest.

(?) **Salticoididae indet**. (figs. 112–113)

Material: Remains of large legs of a probably juvenile – or adult female? – spider, and a part of a capture web are preserved in Lower Cretaceous Jordanian amber from the Kurnub Sandstone Formation of the Zarqa river basin; ERMNH ZRA no. 295.

Preservation: Only remains of large legs and a part of a capture web – about 10 thin threads without droplets and partly in parallel lines – are preserved.

Description (juv.?):
The diameter of a patella is 0.4 mm. The legs are strongly sclerotized, dark brown, and bear numerous bristles and feathery hairs (figs. 112–113) which are only ~0.7 mm long. An unpaired tasal claw exists, tarsal trichobothria are most probably absent, a single metatarsal trichobothrium may be present, paired ventral tibial bristles and ventral scopulae are absent (the leg articles are partly hidden and hard to observe), the ventral bristles of the anterior tibiae are standing fairly wide out. The spinnerets and the anal tubercle are unknown/not preserved.

Relationships: According to the feathery hairs of the strongly sclerotized spiny legs as well of the presence of remains of a capture web this specimen may well be a member of the family Salticoididae. In *Salticoididus kaddumiorum* n. sp. the legs are smaller/thinner, their thin feathery hairs are almost twice in length and seemingly more simple or “incomplete”.

Distribution: Lower Cretaceous Jordanien amber forest.

(5) SUPERFAMILY ARANEOIDEA s. l. (= “ORBICULARIAE”)

Araneoidea sensu WUNDERLICH (2004: 1127)

About 1/3 of all extant araneomorph taxa are members of this largest superfamily of spiders.

There are two „branches“ of this taxon: (a) The cribellate branch (= Deinopoidea s. str.), the fossil and extant families Deinopidae and Uloboridae (an extinct family has not yet been described), and (b) the ecribellate branch which include the numerous remaining – extant and extinct – families. See WUNDERLICH (2004: 1112ff), and the family Salticoididae just above.

Remark: Both branches are regarded as separate superfamilies by most recent authors, but since the single origin of the orb web became clearer and clearer both branches should be regarded as members of the single superfamily Araneoidea, and the name “Orbiculariae” is superfluous, see WUNDERLICH (2004: 1127).

Note: Juveniles of this superfamily can be mistaken for members of the Dysderoidea and juvenile Dysderoidea/pholcidoids can be mistaken for members of the Araneoidea.

The cribellate branch (= Deinopoidea s. str.):

(5a) Family DEINOPIDAE (questionable)

?Cretaceous to today. – Eocene spiders of this cribellate family in Baltic amber: See WUNDERLICH (2004). – PENNEY (2003) described the first fossil taxon in Cretaceous – Lebanese – amber, *Palaeomicromenneus lebanensis* (n. gen. n. sp.) (fig. 114). Its embolus has three loops, the conductor is protruding outwards further than in extant genera. Size and position of the eyes – especially the not enlarged posterior median eyes – as well as the long femoral hairs? of the holotype (which are similar to trichobothria) remember on the pattern of the family Uloboridae. According to PENNEY it is a member of the family Deinopidae, but in my opinion this determination is not well founded.

I studied two juveniles in Burmese amber, F1838/BUR/AR/CJW (photo 111) and F1886/BUR/AR/CJW which may be members of the Deinopidae, but their posterior median eyes are small and their eye position is similar to the Uloboridae. Both spiders are about 1 mm long; their body is deformed, their calamistrum is recognizable, femoral trichobothria are apparently absent; but are they really absent on femur IV? (See fig. 114!). According to the size and the position of the eyes (small posterior median eyes, posterior eye row procurved – fig. 3 in the original description, although the posterior eye row is said to be "distinctly recurved" (!) –, and the relatively small legs II, as well as the possible existence of trichobothria on femur IV, I do not want to exclude the possibility that *Palaeomicromenneus* may be the member of the family Uloboridae or of an undescribed family; a looped embolus exists in the Deinopidae and in the Uloboridae as well.

(5b) Family ULOBORIDAE

Cretaceous to today. – Three genera in Burmese amber; see the remark above (Deinopidae) on *Palaeomicromenneus* PENNEY 2003 in Cretaceous Lebanese amber.

In the Cretaceous spiders from Burma – which I studied more closely – I found some peculiar characters which I do not know from extant Uloboridae and which may be quite basal/ancestral characters of this family, e. g. the probable absence of femoral trichobothria in *Burmuloborus* n. gen., and metatarsus IV has a straight and not compressed shape in *Paramiagrammopes* n. gen. (fig. 120); compare fig. 116.

The pattern of these characters may indicate that a compressed and bent metatarsus IV and the existence of femoral trichobothria evolved at different times and not in the oldest taxa of this family. Apical cymbial bristles are also unknown in the single (!) male in Cretaceous ambers which is known today (a member of *Paramiagrammopes cretaceus* n. sp.). – In the new genera *Burmuloborus* and *Paramiagrammopes* exist further basal uloborid structures/characters like a recurved posterior eye row, a stout prosoma and opisthosoma as well as not or only very slightly modified anterior legs, see the figs. and photos. In *Burmoloborus* are the basal cheliceral articles large in contrast to the extant and remaining fossil taxa in amber. The dwarfism in *Paramiagrammopes* may be regarded as an advanced pattern. Advanced elongated anterior legs and opisthosoma were already present in the Cretaceous genus *Palaeomiagrammopes* (fig. 124, photos 107–108). The typically widely spaced lateral eyes which exist in all extant and Eocene taxa, were already present in the Cretaceous fossil spiders (figs. 115, 118, 123).

"Missing links" regarding number and position of the eyes: See above.

The Cretaceous members of the Uloboridae are smaller than Eocene or extant relatives; *Paramiagrammopes cretaceus* n. sp. – the body length of the male is 1.2 mm – is the tiniest known Uloboridae at all. Apparently there was/is a trend to a larger body size within the Uloboridae during fifty or even more than hundred million years of evolution, like e. g. in several other families of spiders as Palpimanoidea, Theridiidae and Araneidae/Zygiellidae. On the other hand dwarfism was apparently an old phenomenon in spiders, see the paper no. 3 on the family Theridiidae in this volume.

I did not find feathery leg hairs in the Burmese uloborid amber spiders; such hairs exist in extant Uloboridae except in the Uloborinae according to JOCQUE & DIPPENAAR-SCHOEMAN (2007).

Eocene taxa: Five uloborid genera were described by WUNDERLICH (2004: 851–886) from Eocene Baltic amber (only *Hyptiotes* WALCKENAER 1837 survived); they are all different from the Cretaceous genera which probably did not survive the K–T events.

Diagnosis of the family Uloboridae: Poison glands absent, femora – at least III–IV with very few to numerous trichobothria in 1–2 dorsal or lateral rows (figs. 119, 125–126) (*), wide eye field with the lateral eyes widely spaced from each other (figs. 115, 118, 123), usually with ventral tarsal and metatarsal bristles at least on the posterior legs (fig. 120) (**); cymbium usually with 2–3 apical or prodistal bristles at least in the extant taxa, frequently more than a single pair of receptacula seminis; orb-web basicly present (reported already in the fossils, see below).

(*) Similar to certain Tetragnathidae and the Cretaceous genus *Macryphantes* SELDEN 1990, see below ("Tetragnathidae"). Femoral trichobothria are reduced or even absent in the extinct genus *Burmuloborus* n. gen., and in the extant genus *Ariston* O. PICKARD-CAMBRIDGE 1896.

(**) According to SELDEN (1990) absent in the Lower Cretaceous genus *Palaeouloborus*). Such bristles exist also in the related Deinopidae as well as (e. g.) in the Oecobioidea and some Dictynidae.

Further characters: Cribellate, unpaired tarsal claw present, metatarsus IV usually distinctly compressed and bent in the basal part under the calamistrum (fig. 116) (but straight in the extinct genus *Paramiagrammopes* n. gen., fig. 120). Plumose hairs present, feathery hairs are absent in the Uloborinae (*). Posterior eye row – most often strongly – recurved, rarely straight, never procurved. Basal cheliceral articles usually small. Shape of prosoma and/or opisthosoma frequently modified; the opisthosoma is prolongated beyond the spinnerets in several taxa (figs. 117, 124). Frequently exists soft unpaired or paired outgrowths of the female genital area, but a strongly sclerotized epigynal plate is absent; in several taxa the femur of the male pedipalpus bears a ventral-basal outgrowth (figs. 121–122), a patellar outgrowth may exist, too.

(*) The determination of the Cretaceous genus *Palaeouloborus* SELDEN 1990 as a member of the Uloboridae was doubted by WUNDERLICH (2004: 854), but it actually may well be a member of this family, see below. SELDEN (1990: 262) excluded this genus from the Uloboridae e. g. by the absence of feathery hairs but feathery hairs are absent in certain Uloboridae (the subfamily Uloborinae).

Distribution: Cosmopolitical, mainly tropical; widely distributed already in the Early Cretaceous, three extinct genera in Burmese amber.

Key to the genera of the family Uloboridae in Burmese amber:

1 Spinnerets in a more anterior position (fig. 117), femoral trichobothria reduced or even absent, tarsal bristles absent, anterior legs not elongated. ?ad. ♀. . . . . . . *Burmuloborus*

- Spinnerets in a terminal or almost terminal position, femoral trichobothria present and long (figs. 119, 125), tarsus IV bears some ventral bristles in a row (fig. 120) 2

2(1) Opisthosoma short (oval), anterior legs not distinctly elongated, metatarsus IV straight and not compressed (fig. 120). ♂ . . . . *Paramiagrammopes*

- Opisthosoma long (fig. 124), anterior legs strongly elongated (photo 107), metatarsus IV dorsally distinctly compressed and bent (similar to fig. 116). ?ad. ♀. . . . . *Palaeomiagrammopes*

***Burmuloborus* n. gen.**

Diagnosis (?ad. and juv. ♀): Femoral trichobothria most probably strongly reduced or even absent, opisthosoma prolongated beyond the spinnerets (fig. 117), body and legs stout, eyes as in fig. 115, tarsal brisles absent, metatarsus dorsally strongly compressed (fig. 116).

Type species (by monotypy): *Burmuloborus parvus* n. sp.

Relationships: To my knowledge the femoral trichobothria in the Eocene and extant relatives are not reduced as strongly as in *Burmuloborus* (in the tiny spiders of the extant genus *Ariston* O. PICKARD-CAMBRIDGE 1896 these trichobothria are probably strongly reduced, too, may be due to their dwarfism). See the key to the Cretaceous genera and below.

Distribution: Mid Cretaceous Burmese amber forest.

***Burmuloborus parvus* n. gen. n. sp. (fig. 115–117, photo 105)**

Material (in Cretaceous Burmese amber): Holotypus ?ad. ♀, SMF (F2014/BU/AR/CJW); paratype, juv. ♀, OSU, G. POINAR coll. no. B-A-1-17.

Holotype:

Preservation and syninclusions: The spider is fairly well preserved, not darkened and almost not deformed, but slightly decomposed (the prosoma is slightly deformed); patella, tibia and the basal part of the metatarsus of the right leg I and dorsal parts of the right femur and patella II are cut off. – Remains of some probably cribellate threads and numerous tiny bubbles are preserved in the same piece of amber.

Diagnosis (?ad. ♀): See above.

Description (?ad. ♀):
Measurements (in mm): Body length 1.8, prosoma: Length 0.9, width 0.6; leg I: Femur >0.9, patella 0.32, tibia ~0.7, metatarsus ~0.8, tarsus 0.5, metatarsus II 0.62, metatarsus III ~0.4, metatarsus IV 0.53.
The colour of body and legs is mainly light brown.
Prosoma (fig. 115) 2/3 as wide as long, anteriorly with few long hairs, fovea low. 8 small eyes, the anteriors fairly protruding, posterior lateral eyes on low tubercles, the posterior row is recurved. Basal cheliceral articles large, teeth of the furrow hidden, fangs slender, labium apparently as wide as long, gnathocoxae not converging, coxae IV separated by less of their diameter. – Pedipalpus slender; a tarsal claw may exist (the apical part of the tarsus is hidden). – Legs fairly short, I longest, II and IV almost equal in length, III shortest. bristles thin, femora I–II a single one in the middle, patellae with a short basal and a long distal bristle, tibiae with 2 long dorsal bristles and shorter apicals, metatarsi III–IV bear apical bristles, the tarsi none. I did not recognize femoral trichobothria; apparently they are reduced or even absent. I regard retrodistal hairs of the left femur IV as normal hairs according to their tiny base/bothria. Metatarsi with a trichobothrium in about the middle, tarsal trichobothria absent. Metatarsus IV is dorsally strongly compressed (fig. 116), bent, bearing calamistrular hairs at almost its whole length. – Opisthosoma (fig. 117) oval, covered with short hairs, "epigyne" absent or hidden. Three pairs of spinnerets in a more anterior position, which are fairly close together, the anteriors large and fairly stout; the cribellum is hidden.

Paratype: This juvenile spider is incompletely preserved in a small piece of amber which contains numerous tiny bubbles which hide parts of body and legs of the spider; the anterior parts of the prosoma and leg articles are broken off with a part of the amber, tarsal tips are cut off, femoral trichobothria are not recognizable (the femora are difficult to observe). The body length is 1.1 mm, the opisthosoma is oval, the legs are short, the length of the calamistrum is about 3/4 of the length of metatarsus IV which is bent, and dorsally strongly compressed; three pairs of fairly stout spinnerets, their position as in the genus; the cribellum is not well preserved.

Relationships and distribution: See above.

Paramiagrammopes **n. gen.**

Diagnosis (♂; ♀ unknown): Tiny spiders, male only 1.2 mm long, prosoma (fig. 118) as wide as long, legs stout (photo 108), metatarsus IV straight and not compressed (fig. 120), pedipalpus (figs. 121–122): Femur with a ventral outgrowth, patella (?) with a long and claw-shaped prodorsal apophysis, cymbial bristles unknown (absent or hidden?), tegulum with a long distal apophysis.

Further characters: Stout body (photo 108), anterior leg not modified, femora with few trichobothria (fig. 119), feathery hairs apparently absent.

Type species (by monotypy): *Paramiagrammopes cretaceus* n. sp.

Relationships: According to the unmodified body and legs as well as the position of the posterior lateral eyes on only low tubercles *Paramiagrammopes* may be the member of a basal branch of the Uloboridae, probably of the Miagrammopinae. In the Cretaceous genus *Palaeouloborus* SELDEN 1990 (not preserved in amber; ♂ and eye position unknown) – according to SELDEN – a ventral "comb" of bristles of tarsus IV is absent (or only hidden?), leg I is powerful and the unpaired tarsal claws are strongly elongated. – In the Eocene genus *Eomiagrammopes* WUNDERLICH 2004 (preserved in Baltic amber) the eyes of the anterior row are strongly reduced (see the fig. B above), body and legs are long, and patellar as well as femoral outgrowths of the male pedipalpus are absent. Ventral femoral pedipalpal apophyses exist in several genera of the Uloboridae. – *Palaeomiagrammopes* n. gen. and *Burmuloborus* n. gen.: See the key. – In the derived extant genus *Miagrammopes* the four eyes of the anterior row have been lost (see the fig. C above); this genus may be related to the extinct genera *Paramiagrammopes*, *Palaeomiagrammopes*, *Palaeouloborus* and *Eomiagrammopes*. – The tiniest known extant uloborid species is the *Ariston mazolus* OPELL 1979; its body length is almost 1.4 mm in the male sex.

Distribution: Mid Cretaceous Burmese amber forest.

Paramiagrammopes cretaceus **n. gen. n. sp**. (figs. 118–122, photo 108)

Material: Holotypus ♂ in mid Cretaceous Burmese amber from Myanmar, OSU no. B-A-1-8, G. POINAR jr. coll.

Preservation and syninclusions: The spider is well and almost completely preserved in an orange-brown piece of amber which was heated; the tip of the left tarsus I is cut off. The right-basal side of the prosoma is depressed, tiny bubbles and an emulsion cover parts of legs and body. – A dragline is running below the opisthosoma from the spinnerets to the right coxa IV. Larger remains of a three-clawed – mygalomorph? –

spider are preserved at the corner of the piece of amber, furthermore few questionable spider's threads, stellate hairs, particles of detritus, tiny bubbles and small particles of insects' excrement.

Diagnosis (♂; ♀ unknown; see above): Position of the trichobothrium on metatarsus II in 0.19. Pedipalpus: Figs. 121–122.

Description (♂):
Measurements (in mm): Body length 1.2, prosoma: Length 0.5, width ~ 0.5; leg I: Femur almost 0.7 (0.12 high), patella 0.12, tibia 0.55, metatarsus 0.55, tarsus 0.3, tibia II 0.33, tibia III ~ 0.2 (?), tibia IV ~ 0.3 (?).
Colour yellow brown.
Prosoma (it is deformed and partly hidden) (photo 108, fig. 118) about as wide as long, eye field wide, eyes fairly large, posterior row (partly hidden) apparently strongly recurved, posterior lateral eyes on very low tubercles, clypeus long, chelicerae fairly small, sternum wide, separating the coxae IV by about their diameter. – Legs (photo, figs. 119–120) fairly stout, hairy, order I/II/IV/III, III distinctly the shortest. Femur I ventrally with numerous thin and erect hairs, otherwise not modified. Bristles thin, femora dorsally 1 near the end of the article, patellae dorsally 1/1, tibiae dorsally 1/1, metatarsus IV 1 ventrally-distally, tarsus IV 3 ventrally. Femoral trichobothria: I recognized at least three long ones in a single row on femur III (probably there are more). Feathery hairs and metatarsal trichobothria were not found. Metatarsus IV either bent nor compressed, calamistrum consisting of short hairs at least in the basal half of its length. – Opisthosoma (photo) oval, 1.5 times longer than wide, covered with short hairs, spinnerets in a terminal position; anterior spinnerets basally widely spaced, converging, cribellum partly hidden, apparently large. – Pedipalpus (figs. 121–122; it is partly deformed): Coxal files unknown, femur short, with a ventral apophysis, patella (really the patella – or the tibia?) with a long and pointed retrodorsal apophysis, apical cymbial bristles not recognizable (absent?), bulbus large, bearing a long tegular apophysis, embolus unknown/hidden, probably describing a wide loop.

Relationships: See above.

Distribution: Mid Cretaceous Burmese amber forest.

Paramiagrammopes **sp. indet**.

Material in mid Cretaceous Burmese amber from Myanmar: 1 subad. ♂, F1920/BU/AR/CJW.

The spider is completely and well preserved in a clear and yellow piece of amber; the prosoma is depressed on both sides, some femora are depressed laterally. A dragline and small particles of (insects?) excrement are also preserved. – Measurements (in mm): Body length 1.0, prosomal length 0.5; leg I: Femur 0.35, tibia ~0.27, metatarsus

+ tarsus ~0.35–0.4, tibia IV 0.21. The 8 – deformed – eyes are fairly large, the field is wide, the lateral eyes are widely spaced, the posterior row is distinctly recurved, the chelicerae are small. Legs fairly stout, hairy; bristles and metatarsal trichobothria probably as in the genus. Femoral trichobothria: 2 prolaterally on III and 1 long prolateral one on IV; they are finelly plumose and almost as long as the article. Tibiae III–IV bear a single prolateral trichobothrium. Metatarsus IV straight, calamistrum almost as long as 3/4 of the length of the article. – Relationships: *Paramiogrammopes cretaceus* is probably strongly related; its trichobothriotaxy is apparently different.

***Palaeomiagrammopes* n. gen.**

Diagnosis (?ad. ♀; ♂ unknown): Prosoma and opisthosoma long and slender (photos 106–107, figs. 123–124), opisthosoma at least two times longer than wide, in the holotype it is slightly elongated above the spinnerets (fig. 124); leg I distinctly the longest (photos), femora III–IV bear 6 trichobothria in a prodorsal row and a single retrodorsal trichobothrium as well (figs. 125–126).

Type species (by monotypy): *Palaeomiagrammopes vesica* n. sp.

Relationships: In *Paramiagrammopes* n. gen. the prosoma, the opisthosoma and the legs are stouter, leg I is not distinctly the longest, and the number of femoral trichobothria is lesser. *Burmuloborus* n. gen.: See the key. In the extant genus *Miagrammopes* O. PICKARD-CAMBRIDGE 1869 the eyes of the anterior row are absent.

Distribution: Mid Cretaceous Burmese amber forest.

***Palaeomiagrammopes vesica* n. gen. n. sp.** (figs. 123–126, photos 106–107)

Material (3 specimens in Cretaceous Burmese amber from Myanmar): OSU, G. POINAR coll.; holotypus: A questionable adult ♀, no. B-A-1-13; 2 paratypes ?juv. ♀, nos. B-A-1-18 and B-A-1-19.

Preservation and syninclusions: The holotype is completely preserved, prosoma, eyes and pedipalpi are strongly deformed, the opisthosoma has a fold at the left side, most leg articles are depressed laterally. Several threads – probably parts of the capture web of the spider – are preserved around the spider (photo); cribellate threads and remains of an attachment disc (questionable) may exist, too. Two larger Diptera are preserved just behind the spider together with few questionable cribellate threads; they are strongly deformed and partly cut off. A tiny wasp, some stellate hairs and long spiders' threads are also preserved. – Paratype no. 18 is almost completely preserved and deformed, parts of the left legs III and IV are broken off with a tiny piece of amber; parts of the opisthosoma are cut off within the amber, a large gas bubble is preserved within the opisthosoma, the right tarsus I is broken off and lying in an inverted position below the spider, remains of a questionable droplet of blood are preserved below the right coxa II (photo). Several long, thin spiders' threads in a partly parallel position are running through the piece of amber and have apparently been part of an ORB WEB. A large and thin hair, remains of a tiny arthopod and particles of detritus are also preserved. – Paratype no. 19 is completely preserved but badly deformed by natural heating and pressure, the opisthosoma is strongly flattened dorsoventrally, a stellate hair is preserved below the spider.

Diagnosis: See above.

Description (?ad. ♀, juv.):
Measurements (in mm): Holotype: Body length 1.8, prosoma: Length ~0.6, width ~0.45; leg I: Femur longer than the prosoma, patella 0.3, tibia 0.7, femur II 0.26, femur III 0.17, metatarsus + tarsus IV 0.34. – Paratype no. 18: Body length 1.5, prosomal length 0.52; leg I: Femur 0.7, patella 0.28, tibia 0.58, metatarsus 0.57, tarsus 0.26, femur II ~0.47, length of the free visible basal cheliceral article 0.25. – Paratype no. 19 has a body length of ~ 1.3.
Colour of the holotype: Prosoma and legs brown, opisthosoma yellow brown.
Prosoma (fig. 123) 1.33 times longer than wide (holotype), covered with short hairs, fovea unknown, 8 fairly small eyes in two wide rows, lateral eyes widely spaced from each other, posterior row distinctly recurved, clypeus fairly long, chelicerae robust (photo). The labium is free and longer than wide (paratype no. 18). – The pedipalpus (no. 18) bears a long and slender claw. – Legs (photo, figs. 125–126) slender, I distinctly the longest, III distinctly the shortest, hairs indistinct. Bristles thin, femur I 1 prodorsal in the basal half (holotype), patellae dorsally 1/1, tibiae dorsally 1/1 (long; III probably with a single bristle only), a ring of 3–4 apical bristles is preserved on metatarsus III in the holotype, tarsus IV with 4 short ventral bristles in a single row (no. 18) rsp. 7 bristles in the holotype. The position of the metatarsal trichobothria is unknown. The femoral trichobothria are difficult to recognize, II bears 2 prodorsally in the distal half (no. 18) or in the middle and more basally (no. 19), III and probably IV bear a prolateral row of 6 and a single retrodorsal one (holotype). The calamistrum occupies about 3/4 of the length of metatarsus IV, the tarsal claws are short. – Opisthosoma (photo, fig. 124) ca. 2 (no. 18) up to 3.25 (holotype) times longer than wide, elongated a bit beyond/above the spinnerets (holotype), spinnerets stout, cribellum well developed (holotype). The genital areas are hidden/deformed in all specimens.

Relationships and distribution: See above.

The ecribellate branch (= Araneoidea s. str.):

(5c) Family ARANEIDAE

The family has been reported at least from the Cretaceous to today.
Besides *Mesozygiella* (see the Zygiellidae below) I do not know a related adult male in Cretaceous ambers up to now. A juvenile spider indet. has been reported in Cretaceous Lebanese amber by WUNDERLICH (2004: 1864–1865). A probably juvenile specimen of the family Araneidae has been published by PENNEY (2004) in Upper Cretaceous amber from New Jersey. *Cretaraneus* SELDEN – preserved in Cretaceous limestones of NE-Spain – has been referred to the superfamily Araneoidea; according to the structures of its bulbus and embolus the genus is probably a member of the Nephilinae which is regarded as a family of its own by KUNTNER.

(5d) Family ZYGIELLIDAE (see also below: “Remark on a questionable member of the superfamily Araneoidea”)

Zygiellidae has been – and is – usually regarded as subfamily or only a tribus of the family Araneidae but as a family of its own by WUNDERLICH (2004). It surely is an old taxon in the geological sense: Members are known from the Cretaceous to today; they are not rare in Eocene Baltic ambers, too, see WUNDERLICH (2004: 924ff).
Recently PENNEY & ORTUNO (2006) described *Mesozygiella dunlopi* (n. gen. n. sp.) (figs. 127a–c) – without considering the relationships of Eocene genera, see WUNDERLICH (2004) – as the first member of this taxon (sub Araneidae) from Cretaceous amber of Alava, N-Spain.
Certain specimens from the Cretaceous of Santana (Brasil, not preserved in amber, see the photos 112–115) may be members of the Zygiellidae or Araneidae. The position of the eyes and the structures of the ♂-pedipalpus of the Brasilian spiders are still incompletely known.
See also the remark below, "Remark on a questionable member of the superfamily Araneoidea" in Lebanese amber, fig. 128.

Remark on the extant genus *Guizygiella* ZHU et al. 2003 from SE-Asia: Due to to the absence of a free sector of the capture web (P. JÄGER, person. commun. in 2007), the usually wide position of the eyes and the structures of the ♂-pedipalpus this genus is not a member of the Zygiellidae but probably of the Araneidae although the bulbus is not twisted retrolaterally.

(5e) Family PROTHERIDIIDAE WUNDERLICH 2004 (?)

The extinct family Protheridiidae WUNDERLICH 2004 was described only four years ago from Eocene Baltic amber; it is here reported (with some doubt) for Cretaceous amber for the first time. The existence of this family in the Cretaceous period has been suggested by the present author in 2004. Only the monotypic tribes Protheridiini WUNDERLICH 2004 and Praetheridiini WUNDERLICH 2004 were known up to now; a third tribus – Zarqaraneini n. trib. – is added in this paper. See also below: The paragraph “Remark on a questionable member of the superfamily Araneoidea”.

Diagnostic characters: The legs are spiny in the Protheridiidae, a retrobasal paracymbium exists which may stand widely out from the cymbium. I may add here to the diagnosis of the family that most PROBABLY ALL TARSAL CLAWS ARE TOOTHLESS, at least tibia I–II bear lateral bristles, dorsal metatarsal bristles are absent, and the prosomal profile is convex, see WUNDERLICH (2004: 1150, fig. 20). A sure proof of the female is absent, but see the report on a female below: “Remark on a questionable member of the superfamily Araneoidea”.

Relationships: According to the combined existence of a long cypeus and a large retrobasal/dorsal paracymbium the family Protheridiidae is one of the oldest known member of the orb weavers (see below) – or of the non orb-weavers – of the ecribellate branch of the superfamily Araneoidea.

The distribution of the family Protheridiidae is of peculiar interest: The genus *Praetheridion* WUNDERLICH 2004 is known from the Eocene Baltic amber forest, part of the former Laurasia, and the new and apparently related genus *Zarqaraneus* is known from the Lower Cretaceous Jordanian amber forest which was part of the Gondwanaland. So Protheridiidae may be an old Laurentian family which had a wide distribution in former times – in the Jura, Cretaceous and Early Tertiary (Eocene) –, and became extinct out probably in the Early Tertiary with the Oligocene cooling. See also above, the genus *Zamilia* n. gen. of the Oecobiidae: Mizaliinae, and p. 645.

ZARQARANEINI n. trib.

Diagnosis (♂; ♀ unknown, but see below: "Remark on a questionable member of the superfamily Araneoidea"): Metatarsi bristleless, all tibiae bear three long and strong apical bristles (figs. 129–130); ♂-pedipalpus (figs. 132–134): Patella with a dorsal-apical outgrowth, paracymbium: I regard this structure with little uncertainty as the "retrobasal paracymbium" of the superfamily Araneoidea – fixed to the cymbium, erect and horn-shaped, bulbus apparently simple, tegulum with a long apophysis which is directed anteriorly, embolus and conductor unknown.

Further characters: Profile of the prosoma convex – similar to *Protheridion bitterfeldensis* WUNDERLICH 2004: 1150, fig. 20) –, posterior eye row straight (fig. 129), femora and tibiae (fig. 130) with long bristles, "auxiliary hairs" of the tarsi present (fig. 131), tarsal claws tooth-less.

Type genus (by monotypy): *Zarqaraneus* n. gen.

Relationships: I suppose that the horn-shaped cymbial apophysis of *Zarqaraneus* is homologue to the retrolateral paracymbium of the ecribellate branch of the superfamily Araneoidea. The short spinnerets in a rosette-shaped position is typical for the Araneoidea. – Due to the toothless tarsal claws, the convex profile of the prosoma, the spiny legs including femoral and lateral tibial bristles, the absence of dorsal metatarsal bristles as well as the existence of a retrobasal paracymbium – which stands widely out and is fixed to the cymbium – I regard the Zarqaneini with some doubt as a member of the extinct family Protheridiidae WUNDERLICH 2004, which has been described from the Eocene Baltic amber forest. In the Praetheridiini of the Protheridiidae – which may be most related – position and shape of the paracymbium are similar, all metatarsal bristles are absent, too, and the tibiae bear a pair of apical bristles, but these bristles are stronger in the Zarqaraneini and an additional medial dorsal-apical bristle exists (fig. 130), a pedipalpal patellar outgrowth and a long tegular apophysis which stands out are absent in the Praetheridiini, the structures of the bulbus are quite different. – See also the family Salticoididae above.

Distribution: Lower Jordanian amber forest.

Zarqaraneus n. gen.

Diagnosis, relationships and distribution: See above.

Type species (by monotypy): *Zarqaraneus hudae* n. sp.

Ecology: The existence of auxiliary tarsal hairs (fig. 131) indicates that the members of *Zarqaraneus* were web builders.

Zarqaraneus hudae n. gen. n. sp. (figs. 129–135, photo 116)

Indet. spider in Jordanian amber. -- KADDUMI (2005): Amber of Jordan: 46, fig. 48 and (2007: 54–55, figs. 48.1 and 49).

Derivatio nominis: With pleasure I name this species after HUDA, who collected Cretaceous Jordanian fossils together with her father, HANI KADDUMI.

Material: Holotypus ♂ in Lower Cretaceous Jordanian amber from the Zarqa river canyon, ERMNH-ZRA no. 55.

Preservation and syninclusions: The spider is incompletely preserved, the dorsal-right parts of the prosoma and the opisthosoma are lost (cut off inside the amber), both body parts are empty and transparent, the right femur II is dorsally injured, eyes, legs and pedipalpi are well and completely preserved. – Numerous bubbles and particles of detritus are preserved in the same piece of amber which is partly slightly darkened by natural pressing and heating.

Diagnosis (♂; ♀ unknown): Pedipalpus (figs. 132–135) with a long tibia, a slightly divided paracymbium, and a long tegular apophysis.

Description (♂):
Measurements (in mm): Body length ~3.0, prosomal length 1.4; leg I: Femur 1.4, patella 0.43, tibia 0.9, metatarsus 1.25, tarsus 0.5; length of the pedipalpal tibia 0.3.
Colour: Body light brown, legs dark brown.
Prosoma (fig. 129) incomplete, longer than wide, covered with short hairs, dorsally convex, thoracal part highest. 8 eyes in two wide rows, posterior row straight, anterior median eyes slightly the largest, lateral eyes almost touching each other. Clypeus fairly long (partly hidden), basal cheliceral articles fairly small and slender, anteriorly

slightly concave; anterior margin of the cheliceral furrow with few teeth, fangs slender, gnathocoxae stout, labium wider than long, rebordered, not fused to the sternum which is longer than wide and small elongated between the coxae IV. – Legs (figs. 130–131) only fairly long, order I/II/IV/III, III distinctly the shortest, feathery hairs absent. Thin bristles exist on femora, patellae and tibiae (they are absent on metatarsi and tarsi): Femora with a mid-dorsal and an apical one, patellae dorsally with an inconspicuous basal and a longer distal one, tibiae usually 2 dorsally, I–II additionally with a mid-prolateral one, furthermore bear all tibiae 3 apical bristles. Tarsal trichobothria absent, metatarsi most probably with a single trichobothrium not far away from the base of the article. All tarsal claws are apparently toothless, unpaired claw large, paired "auxiliary hairs" existing. – Opisthosoma oval, covered with short hairs, scuta absent, anal tubercle small, spinnerets short, in a rosette-shaped position, tracheal spiracle small, its position near to the spinnerts. – Pedipalpus (figs. 132–135) (see also above): Femur fairly stout, patella short, tibia long, cymbium large, paracymbium horn-shaped, in an almost erect position and divided, tegulum with a long and slender apophysis which is directed anteriorly, embolus unknown.

Relationships: See above.

Distribution: Lower Cretaceous Jordanian amber forest.

(?) Araneoidea: Fam. indet. in Burmese amber (photo 118)

Material: Juv. ♀ in mid Cretaceous Burmese amber from Myanmar, OSU no. B-A-1-10, G. POINAR jr. coll.

Preservation and syninclusions: The spider is completely preserved in an orange piece of amber; numerous tiny bubbles are preserved in the fossil resin, and on body – e. g. on the eye lenses – and legs of the spider as well. Several thin threads of spider silk – apparently parts of a capture web of the spider – are preserved behind, below and right of the spider. The threads bear tiny bubbles but apparently no sticky droplets; one thread is divided. The threads start at the tips of the posterior tarsi and are in contact with the left tarsus III.

Description (juv. ♀):
Measurements (in mm): Body length 0.95, prosomal length 0.45; leg I: Femur 0.4, patella 0.17, tibia 0.28, metatarsus ca. 0.28, tarsus ca. 0.22; length of the basal bristle of patella I 0.14.
Prosoma hairy; 8 large eyes in two rows, covered with bubbles, clypeus at least as long as the eye field, vertical and not protruding; basal cheliceral articles partly hidden, longer than the prosomal height, mouth parts hidden. The sternum separates the

coxae IV by more than their diameter. – Legs only fairly long, III distinctly shorter than the remaining legs which are about equal in length (IV probably longest); covered with long hairs; 2 long, distinct and erect dorsal patellar and tibial bristles. Trichobothria unknown, most probably absent on the tarsi. Unpaired tarsal claw most probably existing, hard to recognize; calamistrum absent. – Opisthosoma oval and hairy, with at least two pairs of dorsal sigillae. Spinnerets covered with an emulsion, apparently short.

Relationships: According to the long, vertical and not protruding clypeus, the absence of tarsal trichobothria and the long patellaer and tibial bristles the spider may be a member of the superfamily Araneoidea (the "spineless femur-clade"? – but I do not want to exclude that it is a member of the scytodoid branch of the superfamily Dysderoidea s. l..

Distribution: Mid Cretaceous Burmese amber forest.

Remark on a questionable member of the superfamily Araneoidea (sub Linyphiidae sensu PENNEY & SELDEN (2002)) (fig. 128)

Material: 1♀ in Lower Cretaceous Lebanese amber, coll. D. AZAR no. 491 (sub Linyphiidae gen. et sp. indet.), MNHNP.

PENNEY & SELDEN (2002) published an adult female in Cretaceous Lebanese amber as a member of the family Linyphiidae but I doubt the correct determination. Recently I had the oppotunity to study the specimen. According to the stout legs, the wide labium (it is 3.4 times wider than long), and the absence of cheliceral stridulatory files – in contrast to almost all Linyphiidae: Linyphiinae – , I excluded a linyphiid membership of this specimen, and regarded it as "most probably" being a member of the Zygiellidae, see WUNDERLICH (2004: 1299, 1864–1865). Metatarsal leg bristles and teeth of the tarsal claws are absent (person. observ.). The epigyne has a wide opening and is strongly sclerotized; a scapus and a parmula are absent. – According to PENNEY & SELDEN (2002: 489) "Detailed structure and dentation of the cheliceae are non visible but appear unmodified..."). Actually few (at least two) long and slender teeth exist on the posterior margin of the cheliceral furrow (fig. 128) which are well observable and which shape is untypical in the Araneidae and Zygiellidae. According to the shape of the cheliceral teeth I am now quite unsure about the relationships of this taxon, but I do not want to exclude relationships to the Protheridiidae WUNDERLICH 2004, especially to the Praetheridiini and the Zarqaraneini n. trib. (see above), in which metatarsal bristles and teeth of the tarsal claws are absent, too. Due to the unknown male sex of the taxon in question as well as the unknown female sex of the Praetheridiini and Zarqaraneini the female in question may well be the member of an indet. higher taxon of the Araneoidea.

Remark on the family TETRAGNATHIDAE

The enigmatic Cretaceous genus *Macryphantes* SELDEN 1990 – not preserved in amber – has been described as a member of the Tetragnathidae but the determination was doubted, and the taxon was regarded as a member of another family – probably Uloboridae – by WUNDERLICH (2004: 854). Correctly determined taxa of the family Tetragnathidae have been described from Tertiary ambers, see WUNDERLICH (1988, 2004 and this volume) but not from the Cretaceous.

(6) RTA-clade

Remark: On the pretended report of a member of the family Zodariidae in French Cretaceous amber: See above, the chapter on “erroneous determinations...”.

In members of the large RTA-clade of higher evolved spiders the tarsi bear usually trichobothria (they are rarely strongly reduced in number and size), the metatarsi bear more than a single trichobothrium, the tibia of the ♂-pedipalpus bears usually at least a single apophysis (not in the Lycosidae), and one of these apophyses has – almost in all taxa – a retroapical position (= clade in which a **r**etrolateral **t**ibial **a**pophysis exists). The spiders are entelegyne, a sclerotized epigynal plate exists usually but is absent in various Dictynidae, cribellum/ calamistrum exist basicly but are very often lost. Three – very rarely two – tarsal claws are present in the branch of the “Trionycha” which members frequently are capture web dwellers. (Contrarily in hunting spiders frequently exist leg scopulae and only two tarsal claws (“Dioncha”); in this case the unpaired claw is lost and a claw tuft is most often present in its position).

SUPERFAMILY DICTYNOIDEA (photos 119–127)

Spiders of the RTA-clade are frequent in Tertiary/Eocene ambers but quite rare in Cretaceous ambers. Cribellum/calamistrum may exist or may be absent in this branch but they exist apparently always in the known Cretaceous taxa which may be members of the family Dictynidae or not; an adult male is needed. Certain of these Lower or mid Vretaceous taxa may be related to the root-group of the RTA-clade, and are therefore of very special interest.

Family DICTYNIDAE (a fairly questionable report in Cretaceous ambers!)

The family is known from the Cretaceous (questionable) to today. – Fossil Dictynidae have been described in diverse taxa from the Lower and Upper Tertiary (*) but the determinations of the reports of Cretaceous taxa – they all are juvenile specimens with a single exception of *Burmadictyna* – are unsure in my opinion and rare up to now, see PENNEY (2002: 717–720, pl. 3, figs. 1–3, text-fig. 6: Dictynidae indet. in amber from New Jersey). Specimens which are dealt with here are most probably members of various genera; their determination – even on the family level – is not sure; adult males of the Cretaceous taxa are needed for closer determinations. *Burmadictyna* n. gen. is one of the geological oldest described and named taxa of the RTA-clade if the determination is correct.

(*) See WUNDERLICH (1988: 178–196): Fossils in Dominican amber, and (2004: 1380–1482): Fossils in Baltic amber and remarks on extant genera as well as a discussion on the limits of the family and the possible/questionable subfamilies; p. 1429: Diagnosis of the Dictyninae s. str.). The (sub)recent family Copaldictyninae WUNDERLICH 2004 from Madagascar may be a family of its own.

Remark: In the Cretaceous members of questionable Dictynidae I found only a SINGLE row of metatarsal trichobothria, tarsal trichobothria are absent or hidden; see GRISWOLD (1990: 16–17). – I do not want to exclude that the RTA-clade is not a monophyletic taxon. According e. g. to the low – basicly low or reduced? – number of leg trichobothria the Dictynidae may be related to the Titanoecidae and few other families, and may represent an old branch of its own, the sister group to the RTA-clade.

Burmadictyna n. gen.

Diagnosis (probably ad. ♀): Chelicerae large (fig. 137), metatarsus III with a "preening comb" of strong bristles (fig. 138), calamistrum situated on a probably bent metatarsus IV (fig. 139) (the metatarsus is deformed by heating!), occupying more than 2/3 of this article, cribellum (fig. 139) very wide and undivided.

Further characters: Cephalic part narrow (fig. 136), unpaired tarsal claw long and bent in a right angle. I found no feathery hairs.

Type species (by monotypy): *Burmadictyna pecten* n. sp.

Relationships: According to the existence of cribellum and calamistrum, large basal cheliceral articles, the shape of the prosoma, the fairly small eyes as well as the trichobothriotaxy I regard *Burmadictyna* with some doubt as a member of the family Dictynidae, probably of the subfamily Dictyninae. Close relationships are unknown (a male is needed for further investigations). The existence of a ring of strong apical bristles on metatarsus III is not common within the subfamily Dictyninae. – See the taxa indet. below, too. – In the Uloboridae the femora bear usually trichobothria, the posterior eye row is not procurved, and the lateral eyes are widely spaced from each other, in the Deinopidae the legs I and II are very long and the posterior median eyes are larger.

Distribution: Mid Cretaceous Burmese amber forest.

Burmadictyna pecten n. gen. n. sp. (figs. 136–140, photos 119–121)

Material: Holotype ?ad. ♀ in Burmese amber from Myanmar, F769/BUR/AR/CJW.

Preservation and syninclusions: The spider is preserved in a small piece of amber which was heated. The left chelicera is cut off, the right legs I and II and the left leg I are lost beyond the coxa by autotomy, the left leg II is lost beyond the patella probably by autotomy. Body and legs are deformed, the left metatarsus IV (e. g.) is laterally compressed (fig. 139), the opisthosoma is dorsally strongly impressed (photo), emulsions (hyphae?) cover the ventral part of the opisthosoma incl. the genital area, some leg articles and dorsal parts of the prosoma. – Some ecribellate spider threads are preserved below and laterally of the spider, remains of a tiny Diptera: Nematocera are preserved at the margin of the piece of amber.

Diagnosis: See above.

Description (?ad. ♀):
Measurements (in mm): Body length 3.6, prosoma: Length 1.6, width 1.3; leg I: Femur 1.8, patella 0.6, leg II: Femur 1.5, patella 0.55, tibia 1.0, metatarsus 1.0, tarsus 0.65, femur IV ca. 1.55.
Colour dark brown (darkened by heating and pressure).
Prosoma (figs. 136–137) 1.23 times longer than wide, narrow anteriorly, fovea hidden, eyes fairly small, posterior row procurved, lateral eyes close together. Basal cheliceral articles large (deformed), teeth of the margins and most parts of the fangs are hidden. Gnathocoxae not distinctly converging, wide apically, labium most probably free, longer than wide, not rebordered. The sternum separates the coxae IV by about their

diameter. – Legs (figs. 138–139) fairly short, order I/IV/II/III, three legs – including both anterior legs – are lost beyond the coxa by autotomy, one leg II is lost beyond the patella (photo). Bristles are present on femora, patellae, tibiae, metatarsi and tarsi: Femora (I is lost) 2 retrolaterally, 1 ventrally and a mid-dorsal one, III–IV with an additional retrodistal one, patellae 2 dorsally, tibiae III 2 dorsally and few ventral-apical ones, metatarsi and tarsi III as in the figure, tarsus III bears 2 ventral bristles, metatarsus III bears apically-ventrally a "preening comb" of strong bristles. Femoral trichobothria are absent; the metatarsi bear several trichobothria which partly are difficult to recognize (fig. 138), I am not sure about the existence of tarsal trichibothria; paired tarsal claws with several long teeth, unpaired claws long and bent in a right angle. Calamistrum longer than 2/3 of the bent (deformed) metatarsus III. – Pedipalpus with long articles and a strongly toothed tarsal claw. – Opisthosoma deformed (photo) oval; spinnerets – especially the anteriors stout, anteriors close together; cribellum (fig. 140) wide and low, undivided, 0.33 mm wide, anal tubercle small, genital area hidden.

Relationships: See above (the genus) and Dictynidae indet. below.

Distribution: Mid Cretaceous Burmese amber forest.

?**Dictynidae indet**. **1**

Material: 2 juv. in Cretaceous Burmese amber from Myanmar, BMNHP, no. 20186.

The body length of both juveniles is 1.1 mm, in one of them the right leg is lost beyond the patella within the amber. The leg bristles are long, the calamistrum occupies almost the whole length of metatarsus IV. I will not exclude the conspecifity with *Burmadictyna pecten* n. gen. n. sp. In one of the spiders the right leg III is lost beyond the patella (by autotomy? See *B. pecten*).

?**Dictynidae indet**. **2** (fig. 141, photo 122)

Material: A probably ad. ♀ in mid Cretaceous Burmese amber from Myanmar, together with the holotype of *Pholcochyrocer guttulaeque* n. gen. n. sp., F1913/BU/ AR/CJW.

Preservation and syninclusions: The spider is incompletely and deformed preserved below a flattened part of another small spider; most articles of its left legs are cut off, legs and chelicerae are fairly, the opisthosoma is strongly deformed and partly lost. – Syninclusions: See above, *Pholcochyrocer guttulaeque* n. sp.

Description (?ad. ♀):
Measurements (in mm): Body length ca. 1.2, prosomal length ca. 0.6, tarsus I ca. 0.3, pedipalpal tarsus 0.3.
Prosoma (photo) strongly raised, cephalic part with 3 long medial hairs. 8 large eyes in a wide and long field (the anterior lateral eyes are smaller); anterior and posterior median eyes are widely spaced, the posterior row is slightly procurved, anterior and posterior lateral eyes are widely – ca. their diameter – spaced. The clypeus is short. Pedipalpus slender, with a long tarsus; tarsal claw absent. Legs slender, hairs fairly long. Tibia I bears a long probasal bristle (fig. 141); further bristles, trichobothria, calamistrum and tarsal claws unknown; an unpaired tarsal claw may exist. Opisthosoma hairy, spinnerets and genital area hidden.

The **relationships** are quite unsure. The area of the spinnerets and the metatarsus IV are deformed, hidden or absent, tarsal trichobothria are unknown. According to the shape of the raised prosoma and the position of the eyes I do not want to exclude close relationships to the family Dictynidae.

Distribution: Mid Cretaceous Burmese amber forest.

?Dictynidae indet. **3** (photo, fig. 142, photo 123)

Material: An ?ad. ♀ and a small piece of mid Cretaceous Burmese amber which has been separated, F1922/BU/AR/CJW.

The spider is well preserved, fairly heated and deformed; the tips of the left tarsi I and II are cut off, the dorsal-basal part of the prosoma is distinctly depressed. Numerous bubbles and remains of few stellate hairs are preserved in the same piece of amber. Measurements (in mm): Body length 1.15, prosoma: Length 0.5, width 0.45. The prosoma is not raised and bears 8 eyes, the posterior row is slightly recurved, the anterior median eyes are the smallest, lateral eyes well separated from each other (photo). Clypeus short, chelicerae deformed, of medium size. Legs fairly stout, bristles long and thin, patellae and tibiae dorsally 1/1, metatarsi IV bear apical bristles. Cribellum and calamistrum (ca. 2/3 the length of metatarsus IV) are well developed. Genital area (fig. 142) with a slender and sclerotized posterior margin and a pair of slit-like and bent lateral structures. – Probably a member of the Dictynidae.

?Dictynidae indet. 4 (photo 124**)**

Material: A juvenile or probably adult ♀ in Burmese amber, F2015/BU/AR/CJW.

The spider is darkened and strongly deformed (by natural pressing and heating), the opisthosoma is depressed, dorsally arises a large bubble. Parts of the left legs I and II are cut off.
The body length is almost 1.5 mm, tibia I is 0.6 mm long. The cephalic part is narrow; there are apparently 8 eyes which are strongly deformed, the chelicerae bear anterior humps in the basal half, they are long, slender and fairly diverging, the gnathocoxae are long and almost parallel (probably strongly deformed and not in their natural position), the pedipalpus is long, slender, spiny, and bears a long claw. The legs are long, slender, and bear numerous long and stronger bristles which stick widely out from their articles, tibia I bears 2 ventral pairs and apicals, metatarsus I bears 2 ventral pairs and apicals, too, tarsal bristles are absent. The unpaired tarsal claw is small, a metatarsal trichobothrium is long, its position on I is in 0.95, tarsal trichobothria may be absent. Metatarsus IV is straight, a calamistrum exists on almost its entire length and consists of bent hairs which are widely spaced. The opisthosoma is covered with short hairs, the epigaster with the genital area is strongly bulging, a sclerotized epigyne is absent, the cribellum is narrow, the deformed three pairs of spinnerets are long and slender. – According to the straight metatarsus IV which bears a calamistrum I regard this species as a – questionable – member of the family Dictynidae.

?Dictynidae indet. 5 (photo 125)

Material: 1 ?ad. ♀ in Burmese amber, F2016/BU/AR/CJW.

Preservation and syninclusions: The left side of the spiders' opisthosoma is broken off. The spider is preserved together with 2 ½ Diptera and some spiders' threads without droplets.

Description: Body length 1.6 mm, tibia I and the calamistrum are ca. 0.5 mm long each. The cephalic part is strongly narrow anteriorly, 6 eyes exist in two wide rows, the posterior row is slightly procurved, the basal cheliceral articles are large. Legs only fairly long, bristles long and thin, tibiae and metatarsi I–II almost bristle-less (short apical bristles are present), tarsal bristles are most probably absent. Tarsi relatively long, metatarsus IV almost straight, calamistrum almost as long as the article. Long opisthosomal hairs are absent, cribellum and spinnerets are hidden.

Relationships: Mainly because of the narrow cephalic part and the almost straight calamistrum I regard this specimen as a – questionable – member of the family Dictynidae.

Distribution: Mid Cretaceous Burmese amber forest.

Araneae indet. (RTA-CLADE?) (photo 117)

Material: Remains of a questionable exuvia in mid Cretaceous Burmese amber from Myanmar, OSA no. B-A-1-16, G. POINAR jr. collection.

Preservation: Only chelicerae (photo) and certain articles of two legs (one is almost complete) are preserved, tarsal claws are not preserved.

Description:
Measurements (in mm): Length of the basal cheliceral articles 0.55; articles of a loose leg: Femur (the basal part is cut off) 1.5 (width 0.4), patella >0.8, tibia >2.0, metatarsus probably ca. 1.6. – The body length of the spider may have been 4–5 mm.
The almost complete chelicerae bear three large teeth at the anterior margin of the furrow and tiny denticles posteriorly; lateral stridulatory files are absent. The legs are fairly long, there are numerous bristles which are distinct but not spine-shaped, unpaired, and standing out from the articles; probably more than a dozen bristles exist on the femur, the patella bears at least a dorsal-distal one, the tibia more than a dozen on all sides, the metatarsus at least a basal-lateral pair. Trichobothria: Absent on the femur, several on metatarsus and tarsus.

Relationships: According to the shape of the chelicerae, the teeth of their margins, the position of the leg bristles, and the number of tarsal (> 1) and metatarsal trichobothria the spider may well be a member of the RTA-clade, probably of the Trionycha. Unfortunately the number of the tarsal claws and the existence of a cribellum are not preserved.

Distribution: Mid Cretaceous Burmese amber forest.

REFERENCES, cited

Anonymous (2007): Cretaceous-Tertiary extinction event. -- Wikipedia, the free encyclopedia; http://en.wikipedia.org/wiki/Cretaceous-Tertiary_extinction_event.

BANDEL, K., SHINAQ, R. & WEITSCHAT, W. (1997): First insect inclusions from the amber of Jordan (Mid Cretaceous). -- Mitt. Geol.-Paläont. Inst. Univ. Hamburg, 80: 213–223.

DEELEMAN-REINHOLD, C. L. (1995): The Ochyroceratidae of the Indo-Pacific Region (Araneae). -- Raffles Bull. Zool., supplement No. 2: 1–103.

ENGEL, M. S. (2001): A Monograph of the Baltic Amber Bees and Evolution of the Apoidea (Hymenoptera). -- Bull. Amer. Mus. Nat. Hist., 259. 192 pp.

ESKOV. K. Y. (1987): A new archaeid spider (Chelicerata: Araneae) from the Jurassic of Kazakhstan, with notes on the so-called „Gondwanan“ ranges of recent taxa. -- N. Jb. Geol. Paläont. Abh., 175 (1): 81–106.

-- (1992): Archaeid spiders from Eocene Baltic amber (Chelicerata, Araneida, Archaeidae) with remarks on the so-called „Gondwanan“ ranges of Recent taxa. -- Neues Jahrbuch für Geologie und Paläontologie, Abh. 185: 311–328.

ESKOV, K. Y. & WUNDERLICH, J. (1995): On the spiders from Taimyr ambers, Siberia, with the description of a new family and with general notes on the spiders from the Cretaceous resins (Arachnida: Araneae). -- Beitr. Araneol., 4 (1994).

ETTER, W. (1994): Palökologie. 294pp.

GIRIBET, G. & DUNLOP, J. A. (2005): First identificable Mesozoic harvestman (Opiliones: Dyspnoi) from Cretaceous Burmese amber. -- Proc. R. Soc. B (2005), 272: 1007–1013.

GRIMALDI, D., ENGEL, M. S. & NASCIBENE, P. (2002): Fossiliferous Cretaceous amber from Burma (Myanmar): Its rediscovery, biotic diversity, and paleontological significance. -- Amer. Mus. Novit., 3361: 1–71.

GRISWOLD, C. E. (1990): A revision and phylogenetic analysis of the spider subfamily Phyxelidinae (Araneae, Amaurobiidae).-- Bull. Amer. Mus. Nat. Hist., 196: 1–206.

GROSSMANN, R. & JUNGHEIM, H. J. (2006): Landpflanzen im Verlauf der Erdgeschichte, Teil 1. Der Weg zur heutigen Flora. -- Fossilien, 1: 37–47.

-- (2007): Teil 2. Aus dem Wasser auf das Festland.-- Fossilien, 3: 170–185.

JOCQUE, R. & DIPPENAAR-SCHOEMAN, A. S. (2007): Spider Families of the World. Tervuren (Belgium). 336pp.

KADDUMI, H. F. (2005): Amber of Jordan. The Oldest Prehistoric Insects in Fossilized Resin. Publication of the Eternal River Museum of Natural History/Jordan (Amman). 224pp. Second ed. (2007).

MACALPINE, J. F. & MARTIN, J. E. H. (1969): Canadian amber – a palaeontological treasure-chest. -- Canadian entomologist, 101: 819–838.

MESQUITA, M. V. (1996): *Cretaraneus martinsnetoi* n. sp. (Araneoidea) da formacao Santana, Cretaceo Inferior da Bacia do Araripe. -- Rev. Univ. Guarulhos, Ser. Geoc., 1 (3): 24–31.

MOREAU, C. S., BELL, C. D., VILA, R., ARCHIBALD, S. B. & PIERCE, N. E. (2006): Phylogeny of the Ants: Diversification in the Age of Angiosperms. -- Science, 312: 101–104.

OPELL, P. D. (1979): Revision of the Genera and Tropical American Species of the Spider Family Uloboridae. -- Bull. Mus. Comp. Zool. Harvard University, 148 (10): 443–549.

-- & WARE, A. D. (1987): Changes in Visual Fields Associated With Web Reduction in the Spider Family Uloboridae. -- J. Morphology, 192: 87–100.

PAULUS, H. F. (1978): Co-Evolution zwischen Blüten und ihren tierischen Bestäubern. -- Sonderbd. naturwiss. Ver. Hamburg, 2: 51–81.

PENNEY, D. (2002): Spiders in Upper Cretaceous amber from New Jersey (Arthropoda: Araneae). -- Palaeontology, 45 (4): 709–724.

-- (2003): A new deinopid spider from Cretaceous Lebanese amber. -- Acta Palaeontol. Pol., 48 (4): 569–574.

-- (2003): *Afrarchaea grimaldii*, a new species of Archaeidae (Araneae) in Cretaceous Burmese amber. -- J. Arachnol., 31: 122–130.

-- (2004): Cretaceous Canadian amber spider and the palpimanoidean nature of lagonomegopids. -- Acta Palaeontol. Pol., 49 (4): 579–584.

-- (2004): A new genus and species of Pisauridae (Araneae) in Cretaceous Burmese amber. -- J. Syst. Palaeontology, 2 (2): 141–145.

-- (2004): New spiders in Upper Cretaceous amber from New Jersey in the American Museum of Natural History (Arthropoda: Araneae). -- Palaeontology, 47 (2): 367–375.

-- (2005): The fossil spider family Lagonomegopidae in Cretaceous ambers with descriptions of a new genus and species from Myanmar. -- J. Arachnol., 33: 439–444.

-- (2006): First fossil Huttoniidae (Arthropoda: Chelicerata: Araneae) in late Cretaceous Canadian amber. -- Cretaceous Research, 27: 442–446.

-- (2007): The oldest fossil pholcid and selenopid spiders (Araneae) in Lowermost Eocene amber from the Paris Basin, France. -- J. Arachnology, 34: 592–598.

-- (2007): A new fossil oonopid spider in lowermost Eocene amber from the Paris Basin, with comments on the fossil spider assemblage. -- African Invertebrates, 48 (1): 71–75.

PENNEY, D.D. (2008): Dominican Amber Spiders. 176 pp.

PENNEY, D. & ORTUNO, V. M. (2006): Oldest true orb-weaving spider (Araneae: Araneidae). -- Biol. Lett.: 1–4 (published online).

PENNEY, D. & SELDEN, P. A. (2002): The oldest linyphiid spider, in Lower Cretaceous Lebanese amber (Araneae, Lonyphiidae, Linyphiinae). -- J. Arachnology, 30: 487–493.

PENNEY, D., WHEATHER, C. P. & SELDEN, P. A. (2003): Resistance of spiders to Cretaceous-Tertiary extinction events. -- Evolution, 57 (11): 2599–2607.

PENNEY et al. (2007): First fossil Micropholcommatidae (Araneae), imaged in Eocene Paris amber using X-Ray Computed Tomography. -- Zootaxa, 1623: 47–53.

PERRICHOT et al. (2008): Fossil evidence for the early ant evolution. – Naturwissenschaften, 95: 85–90.

POINAR, G. O. & DANFORTH, B. N. (2006): A Fossil Bee from Early Cretaceous Burmese amber. -- Science, 314: 614.

POINAR, G. O. & SZADZIEWSKI, R. (2007): *Corethrella andersoni* (Diptera: Corethrellidae), a new species from Lower Cretaceous Burmese amber. -- Proc. entomol. Soc. Wash., 109 (1): 155–159.

RASNITSYN, A. P. & ROSS, A. J. (2000): A preliminary list of arthropod families present in the Burmese amber collection at the Natural History Museum, London. -- Bull. nat. Hist. Mus. Lond. (Geol.), 56 (1): 21–24.

SAUPE, E. E. & SELDEN, P. A. (in prep.): First fossil Mecysmaucheniidae (Arthropoda: Chelicerata: Araneae), from Lower Cretaceous (Upper Albian) amber from Charente-Maritime, France.

SCHAAL, S. & ZIEGLER, W. (1988): Messel – Ein Schaufenster in die Geschichte der Erde und des Lebens. 315pp.

SELDEN, P. A. (1990): Lower Cretaceous spiders from the Sierra de Montsech, North-East Spain. -- Palaeontology, 33 (2): 257–285.

SELDEN, P. A. et al. (1999): Fossil araneomorph spiders from the Triassic of South Africa and Virginia. -- J. Arachnology, 27: 401–414.

STORCH, V., WELSCH, U. & WINK, M. (2001): Evolutionsbiologie. 450pp.

WUNDERLICH, J. (1986): Spinnenfauna gestern und heute. 283pp. Publishing House Joerg Wunderlich, D–69493 Hirschberg.

-- (1988): Die fossilen Spinnen im Dominikanischen Bernstein. -- Beitr. Araneol., 2: 1–378. Publishing House Joerg Wunderlich, 69493 Hirschberg

-- (1995): On the biogeography of some so-called gondwanaland-spiders – new findings after investigation of fossil spiders (Araneae) in amber. -- Proc. 15th European Colloquium of Arachnology, Ceske Budejovice: 193–194.

-- (1995): Über “Ameisenspinnen” in Mitteleuropa (Arachnida: Araneae). -- Beitr. Araneol., 4: 447–470.

-- (2004): Fossil spiders in amber and copal. -- Beitr. Araneol., 3 (A, B): 1–1908. Publishing House Joerg Wunderlich, D-69493 Hirschberg.

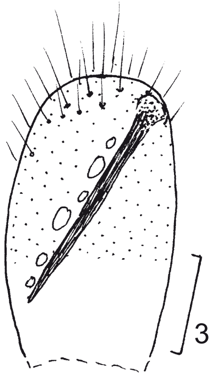
-- (2004): Report on spiders (Araneae) of the families Araneidae and Zygiellidae in Lebanese amber. -- Beitr. Araneol., 3 (B): 1864–1865.

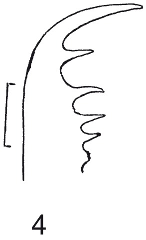
WUNDERLICH, J. & MILKI, R. (2004): Description of the subfamily Microsegestriinae n. subfam. (Araneae: Segestriidae) in Cretaceous Lebanese amber. -- Beitr. Araneol., 3: 1867–1873.

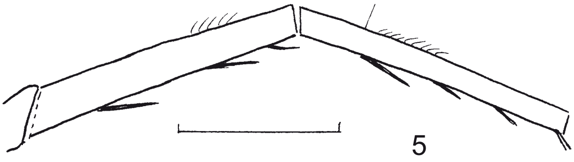
ZWÖLFER, H. (1978): Mechanismen und Ergebnisse der Co-Evolution von phytophagen und entomophagen Insekten und höheren Pflanzen. -- Sonderb. naturwiss. Ver. Hamburg, 2: 7–50.

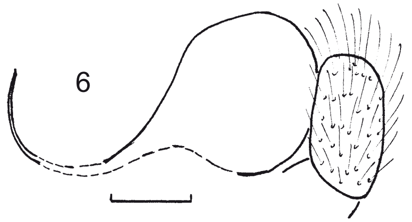
INDEX of the genera which are dealt with in this paper:

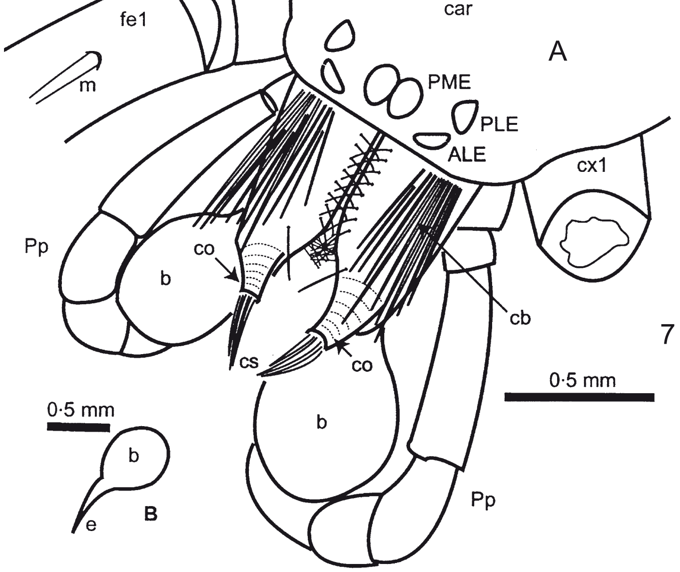
Index of the suprageneric taxa: See the appendix at the end of this volume.







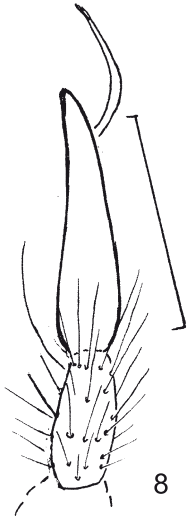


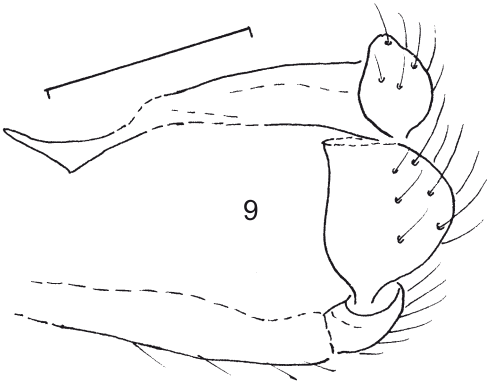


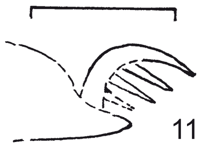
Figs. 3–4: Mygalomorpha indet.1, exuvia in Cretaceous Burmese amber, OSU no. B-A-1-6; 3) dorsal aspect of the basal article of the r. chelicera. The long and slender fang in its obloque longitudinal position and some teeth of the anterior margin of the cheliceral furrow are recognizable through the cuticula; 4) lateral aspect of the claw of a pedipalpal tarsus; scales lines 0.5 and 0.1 mm;

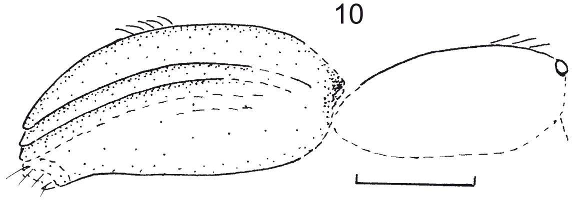
figs. 5–6: ?***Ariadna amissiocoli*** **n. sp**. (Segestriidae), ♂ holotype in Cretaceous Jordanian amber; 5) prolateral aspect of the r. anterior tibia and metatarsus I. Only few hairs are drawn; 6) retrolateral aspect of the l. pedipalpus (a part of the embolus is hidden); scale lines 1.0 and 0.2;

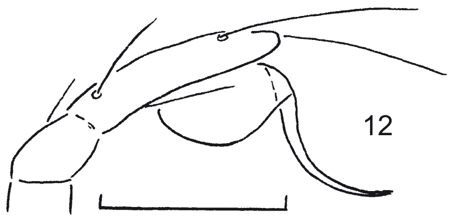
fig. 7: *Palaeosegestria lutzzii* PENNEY 2004 (Segestriidae), ♂, holotype, in Cretaceous amber from New Jersey (USA); A) Dorsal aspect of the anterior prosomal region and pedipalpi; B) bulbus with embolus. Note the brushes of cymbial bristle (cb). Taken from PENNEY (2004: Fig. 2);

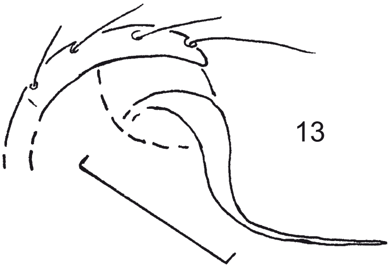

8

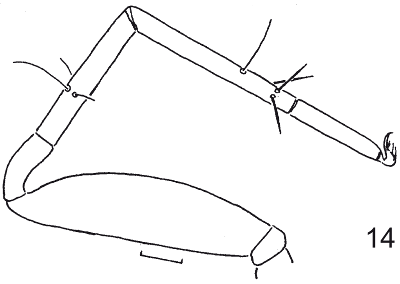

9


11


10


12

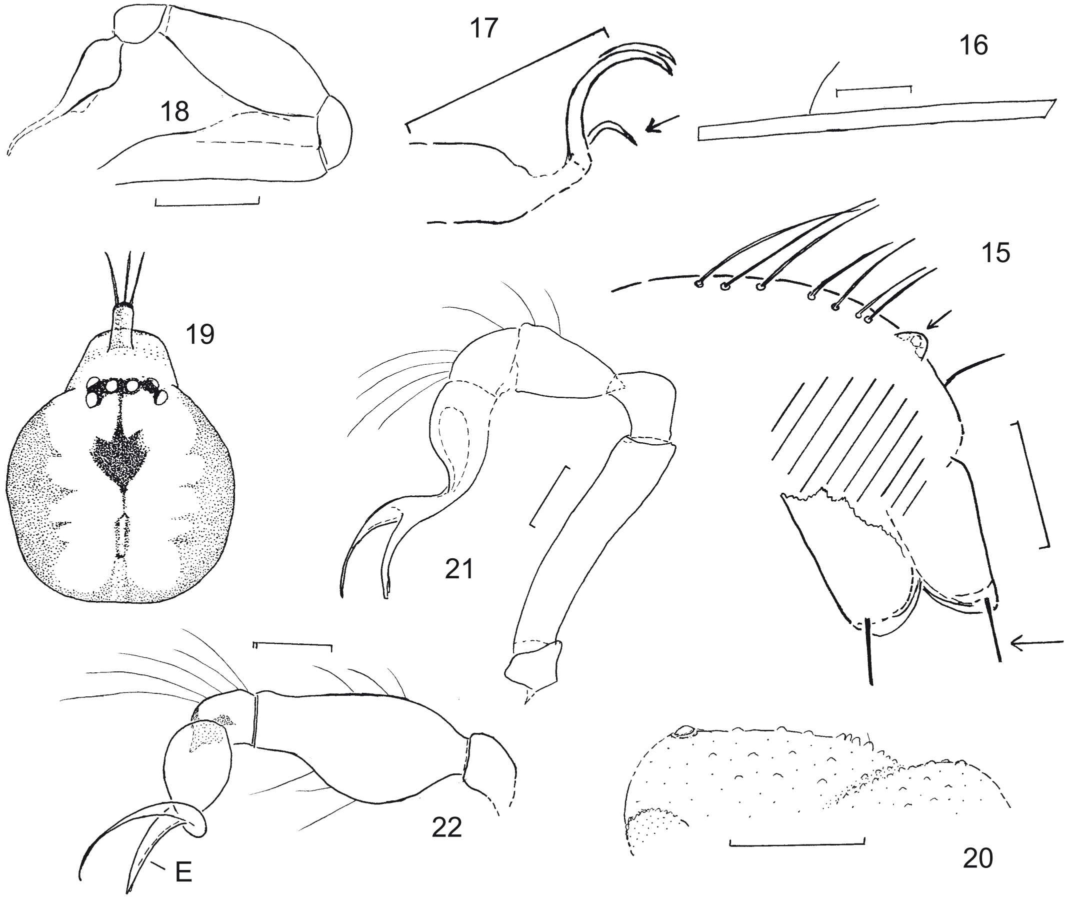

13


14

figs. 8–9: ***Lebansegestria azari* n. gen. n. sp**. (Segestriidae), ♂, holotype in Cretaceous Lebanese amber; 8) dorsal aspect of cymbium and bulbus with embolus of the r. pedipalpus; 9) retrolateral aspect of the l. pedipalpus which partly is deformed; scale lines 0.2;

figs. 10–13: ***Eogamasomorpha nubila* n. gen. n. sp**. (Oonopidae: Gamasomorphinae), ♂, holotype in Cretaceous Burmese amber; 10) outline of the body, lateral aspect; parts are hidden, only a single eye is drawn; 11) prolateral aspect of the retroclaw of the l. tarsus II; 12–13) retrodorsal/slightly basal and retrolateral aspect of the r. pedipalpus; scale lines 0.2 in fig. 10, 0.05 in fig. 11, 0.1 in figs. 12–13;

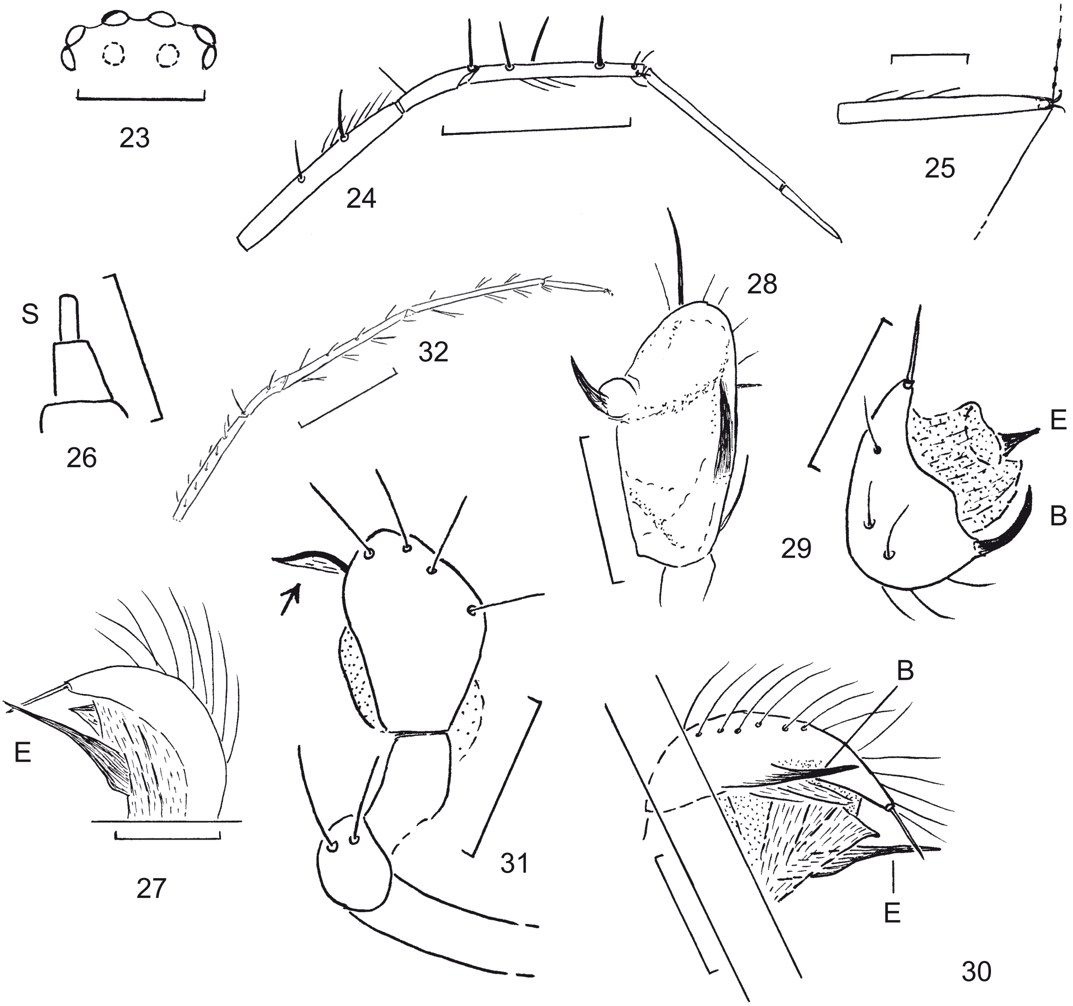
fig. 14) <u>Orchestininae sp</u>.: *Orchestina* (Oonopidae), ♀, prolateral aspect of the l. leg IV. Note the distinctly thickened femur; scale line 0.1;



figs. 15–18: ***Eopsiloderces loxosceloides* n. gen. n. sp**. (Eopsilodercidae n. fam.: Eopsilodercini), ♂ holotype in Cretaceous Burmese amber; 15) right-anterior aspect of the anterior part of the prosoma which is partly cut off. The long arrow indicates to the left cheliceral “clasping spine”, the short arrow indicates to a “hump” of most probably one two small eyes on the left side; 16) retrolateral aspect of the l. metatarsus III with its trichobothrium (hairs are not drawn); 17) retrolateral aspect of the tip of the r. tarsus IV. Teeth of the paired claws are not drawn and probably absent. The arrow points to the thin unpaired claw; 18) retrolateral aspect of the l. pedipalpus. The femur is deformed ventrally and flattened laterally; scale lines 0.1 in fig. 17, 0.2 in the remaining figs.;

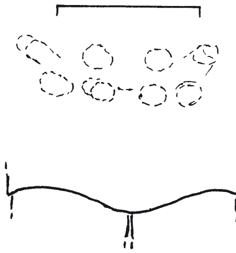
fig. 19) *Psiloderces enigmatus* DEELEMAN-REINHOLD 1995 (Psilodercidae, extant), ♂, dorsal aspect of the prosoma. Taken from DEELEMAN-REINHOLD (1995: Fig. 66);

figs. 20–22: ***Furcembolus andersoni* n. gen. n. sp**. (Eopsilodercidae n. fam.: Furcembolusini), ♂ holotype in Cretaceous Burmese amber; 20) outline of the prosoma, lateral-ventral aspect. Note the bulging thoracal part and the distinct wrinkles. The chelicerae are lost, parts like most eyes are hidden; 21) prolateral aspect of the loose r. pedipalpus which articles are slightly deformed; 22) retrolateral aspect of the l. pedipalpus. Only few hairs are drawn; scale lines 0.5 in fig. 20, 0.2 in the remaining figs;

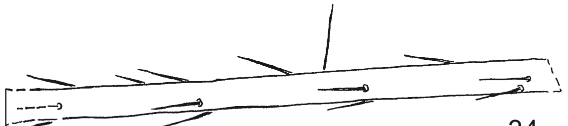


figs. 23–31: ***Preaterleptoneta spinipes* n. gen. n. sp.** (Praeterleptonetidae n. fam.: Praeterleptonetinae), ♂ holotype in Cretaceous Burmese amber; 23) dorsal aspect of the eyes, reconstruction of the partly deformed area; 24) retrolateral aspect of the r. leg) (only few hairs are drawn; 25) lateral aspect of the r. tarsus I with a thread which bears remains of three probable droplets. (Only three hairs are drawn); 26) lateral aspect of the r. median spinneret. Note the single large spigot (S); 27) distal part of the r. pedipalpus, prolateral aspect; 28) ventral aspect of the deformed r. pedipalpus; 29) apical aspect of the r. pedipalpus; 30) retrolateral aspect of the r. pedipalpus which is partly hidden by the r. femur I; 31) dorsal/prodorsal (femur) aspect of the l. pedipalpus. Note the deformed cymbial spine (arrow); B = cymbial bristle, E = embolus; scale lines 0.5 in fig. 24, 0.2 in fig. 23, 0.05 in fig. 26, 0.1 in the remaining figs.;

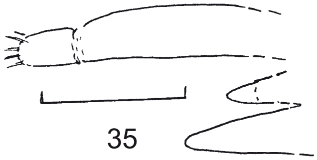
fig. 32) ?Praeterleptonetidae: Palaeohygropodini indet., exuvia in Cretaceous Burmese amber, retrolateral aspect of the r. leg I, HNMLP In. no. 20152. Hairs, trichobothria and deformations are not drawn; scale line 1.0;



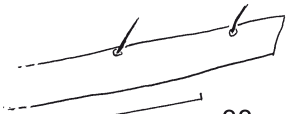
33



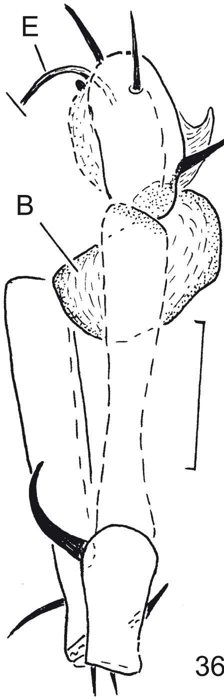
34



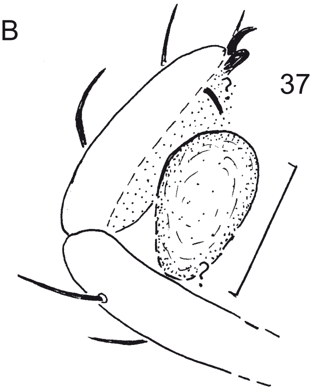
35



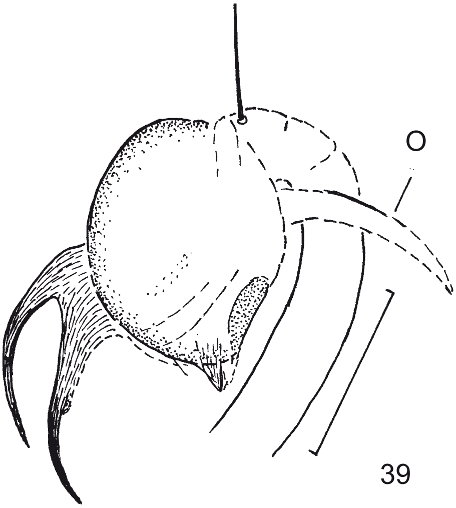
38



36



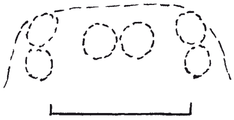
37



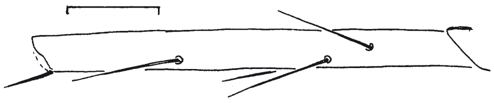
39

figs. 33–37: <u>*Palaeohygropoda myanmarensis*</u> PENNEY 2004 (Praeterleptonetidae n. fam.: Palaeohygropodini), ♂, holotype in Cretaceous Burmese amber; 33) anterior aspect of the prosoma (most eyes are deformed); 34) retroventral aspect of the r. tibia I. Not all of the bristles are well recognizable; 35) anal tubercle (below), l. posterior and r. anterior spinneret, left aspect; 36) dorsal aspect of the deformed r. pedipalpus; the cymbium is fairly bent ventrally. Note the prolateral patellar spur (“clasping spur”), the long tibia and the strong tibial bristles; 37) prolateral aspect of the l. pedipalpus; parts are hidden, see the question marks; B= bulbus, E = embolus (or artefact?); scale lines 1.0 in fig. 34, 0.5 in figs. 33, 36–37, and 0.1 in fig. 35;

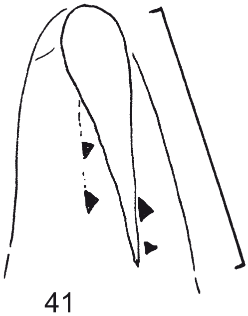
figs. 38–39: ***Pholcochyrocer guttulaeque* n. gen. n. sp**. (Praeterleptonetidae n. fam.: Pholcochyrocerini), ♂, holotype in Cretaceous Burmese amber; 38) oblique retrolateral aspect of the r. femur III which is basally hidden; 39) r. pedipalpus, prodorsal aspect of the bulbus but ventral aspect of the femur. (The pedipalpus is darkened by heating and pressure, most parts are partly deformed and difficult to recognize); O = outgrowth of the questionable cymbium; scale line 0.5;



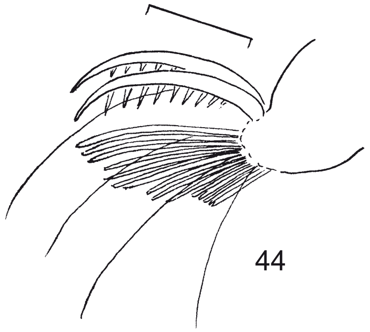
40



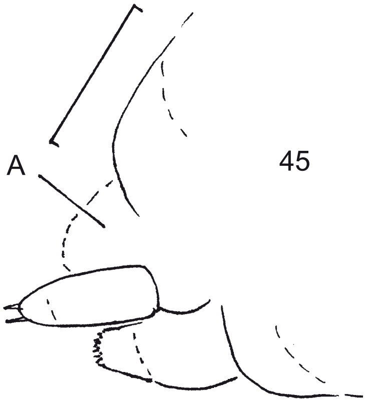
42



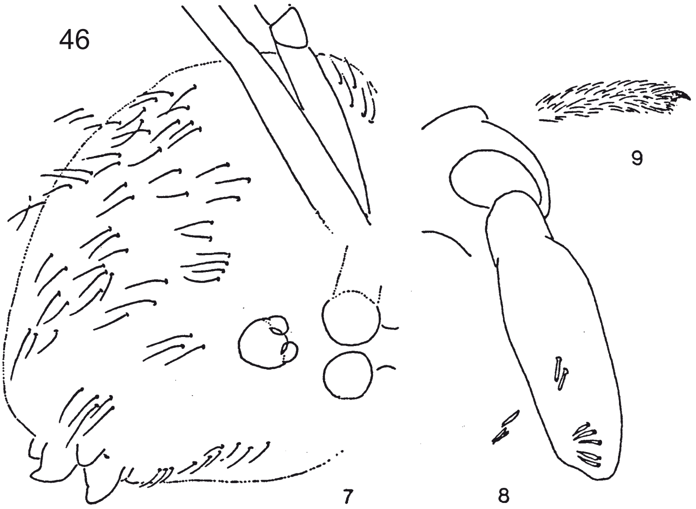
41



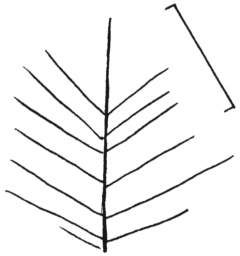
44



45



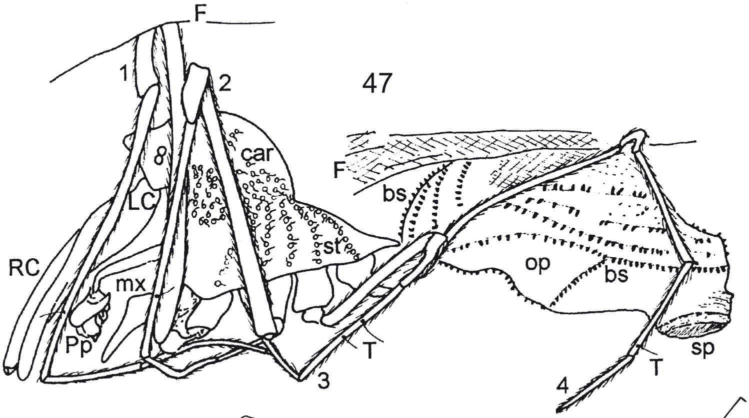
46

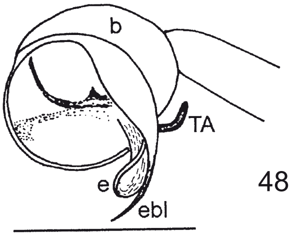


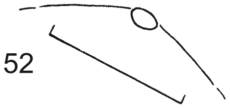
43

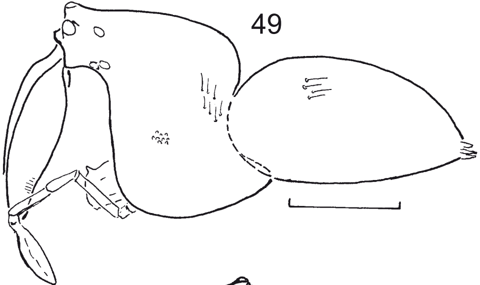
figs. 40–45: ***Plumorsolus gondwanensis* n. gen. n. sp**. (Plumorsolidae n. fam.), juv. in Cretaceous Lebanese amber, holotype fig. 44), paratype no. 724A figs. 40–41, 45), paratype no. 490 figs. 42–43; 40) reconstructed position of the eyes; 41) ventral and slightly posterior aspect of the distal part of the r. chelicera; 42) prolateral aspect of the r. tibia I; 43) feathery hair of a leg; 44) retrolateral aspect of the tip of the l. tarsus II; 45) left aspect of the spinnerets and the anal tubercle (A); scale lines 0.05 in figs. 43–44), 0.2 in the remaining figs.;

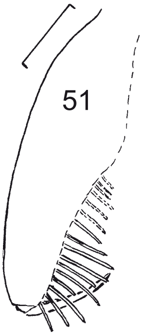
figs. 46: 7–9: *Jurarchaea zherikhini* ESKOV 1987 (Archaeidae), ♀ holotype from the Jurassic (not preserved in amber); (7) opisthosoma and some leg articles, ventral-right aspect; (8) l. chlicera, anterior-prolateral aspect; (9) prolateral aspect of the l. pedipalpus. Taken from ESKOV (1987: Figs. 7–9);

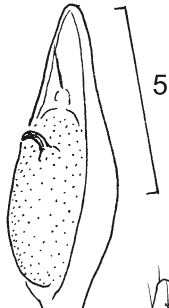


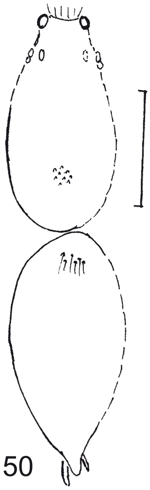


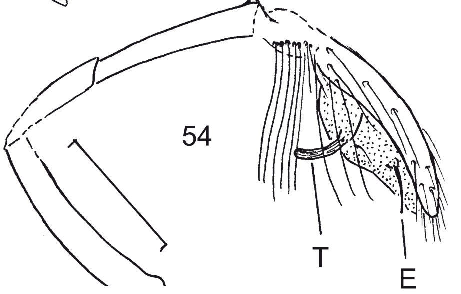


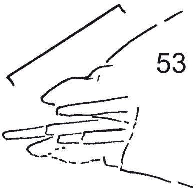


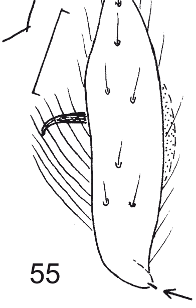






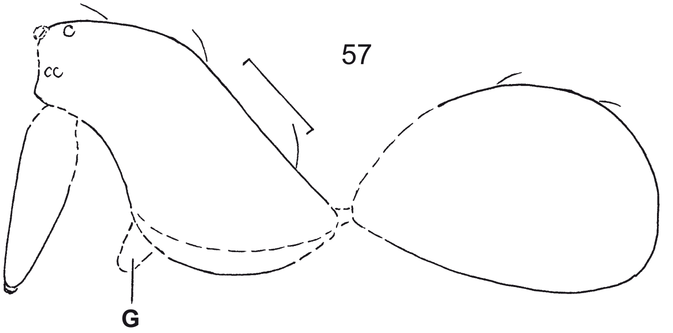


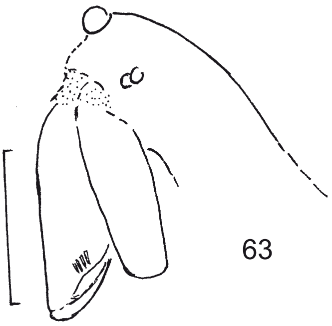


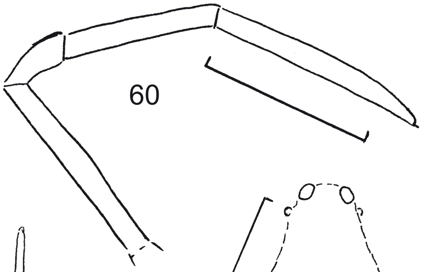


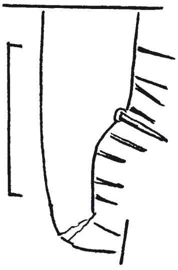
figs. 47–48: Burmesarchaea grimaldii (PENNEY 2003) (Archaeidae: Archaeinae), ♂ holotype in Cretaceous Burmese amber; 47) lateral aspect of the whole specimen; 48) retroventral aspect of the l. pedipalpus; scales 1.0 and 0.1. Taken from PENNEY (2003: Figs. 1, 3);

figs. 49–56: ***Lacunauchenius speciosus* n. gen. n. sp**. (Archaeidae: Lacunaucheniinae n. subfam.), ♂, holotype in Cretaceous Burmese amber; 49) lateral aspect of the specimen; 50) dorsal aspect of the body which is slightly deformed (only few hairs are drawn); 51) anterior aspect of the r. chelicera. Only anterior "peg teeth" are drawn; 52) retrolateral aspect of the membraneous "femoral organ" on the l. femur III which is depressed laterally; 53) outline of the fairly deformed spinnerets and anal tubercle, lateral aspect; 54) retrolateral aspect of the r. pedipalpus; 55) dorsal aspect of the l. cymbium and bulbus. The arrow points to the questionable stridulatory pick. (Only some hairs are drawn); 56) ventral (slightly retrolateral) aspect of bulbus and cymbium of the l. pedipalpus. (Hairs are not drawn); E = embolus, T = tegular apophysis; scale lines 0.5 in figs. 49–50, 0.2 in figs. 51, 53–54 and 56, 0.1 in figs. 52 and 55;

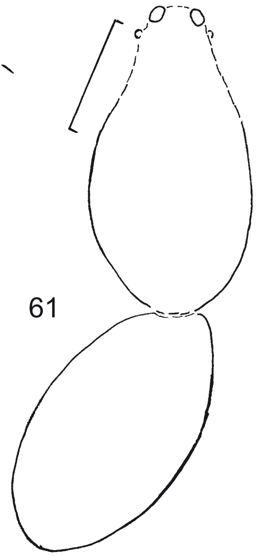

57

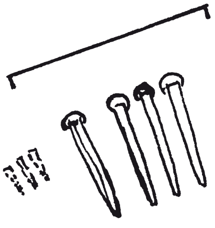

63


60


59


62

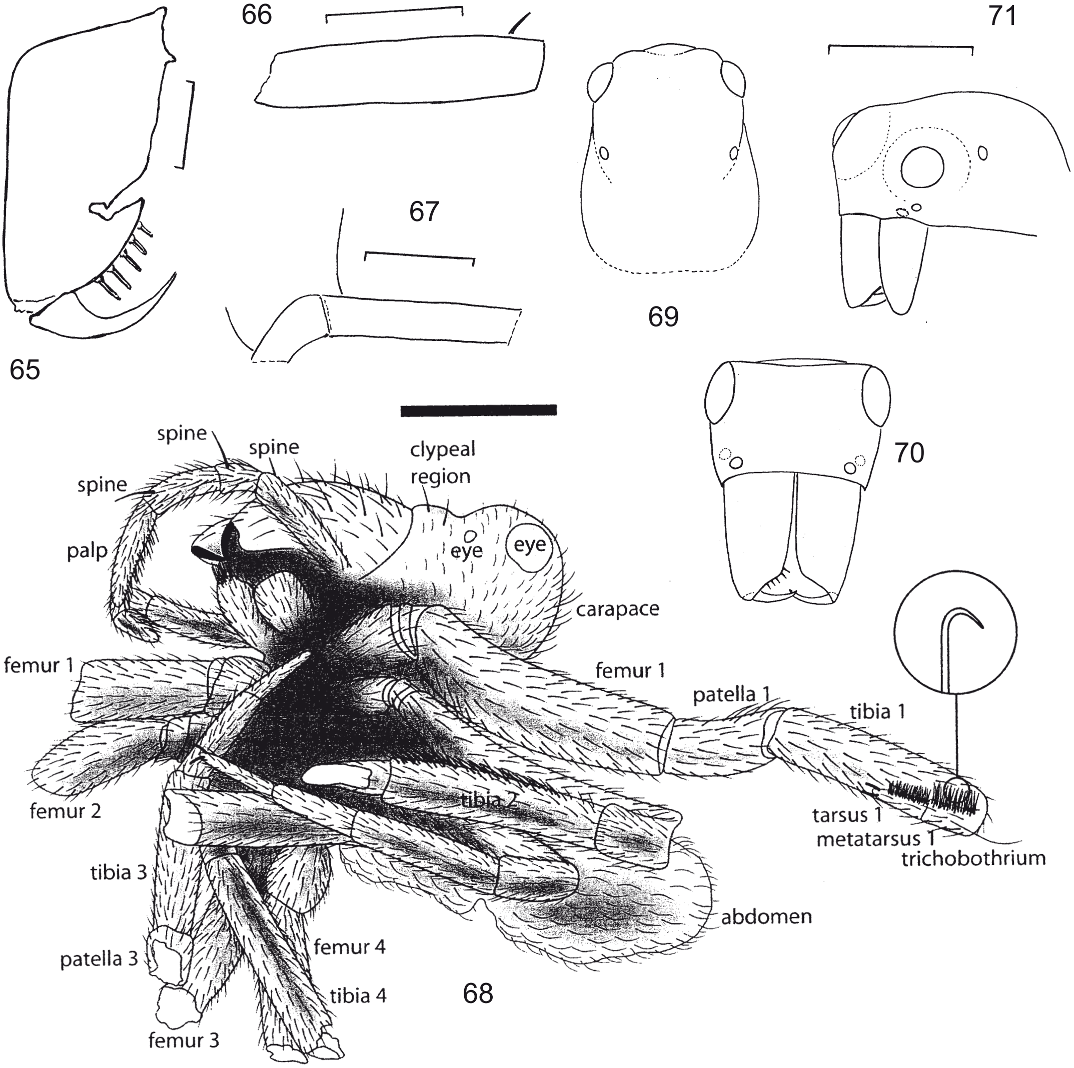

61


64


58

figs. 57–60: ***Eomysmauchenius septentrionalis* n. gen. n. sp**. (Archaeidae: Lacunaucheniinae n. subfam.), juv. ♀, holotype in Cretaceous Burmese amber; 57) lateral aspect of the body; 58) anterior-right and slightly apical aspect of the deformed prosoma; 59) anterior-prolateral aspect of the r. chelicera with long "peg teeth"; G = l. gnathocoxa; scale lines 0.1 in fig. 59, 0.2 in the remaining figs.;

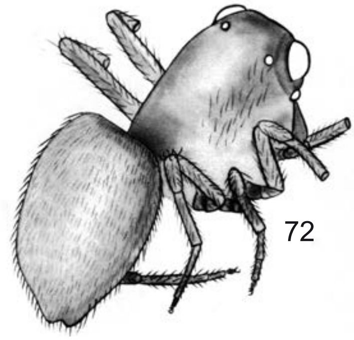
figs. 61–64: ***Filiauchenius paucidentatus* n. gen. n. sp**. (Archaeidae: Lacunaucheniinae n. subfam.), ♀, holotypus in Cretaceous Burmese amber; 61) dorsal aspect of the body which is fairly deformed; 62) dorsal aspect of patella, tibia and tarsus as well as the basal part of the femur of the r. pedipalpus; 63) lateral and slightly ventral aspect of the fairly deformed prosoma which partly is hidden; 64) "peg teeth" of the distal half of the r. chelicera, pro-frontal and slightly distal aspect; scale lines 0.5 in figs. 61–63, 0.1 in fig. 64;

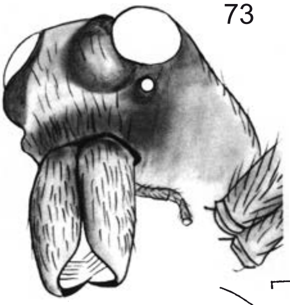


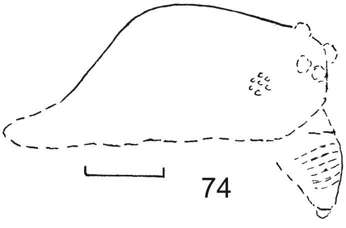
figs. 65–67: Burlagonomegops ?eskovi PENNEY 2004 (Lagonomegopidae), probably adult ♀, OSU no. B-A-1-2, and juvenile specimen F2017/CJW, both in Cretaceous Burmese amber; 65) anterior aspect of the slightly defect r. chelicera. Note the slender "peg teeth"; 66) retrolateral aspect of the r. femur II. Note the single dorsal bristle. (Hairs are not drawn); 67) prolateral aspect of the l. patella and tibia IV. Note the two long bristles; short hairs are not drawn; scale lines 0.2 and 0.5 (fig. 66);

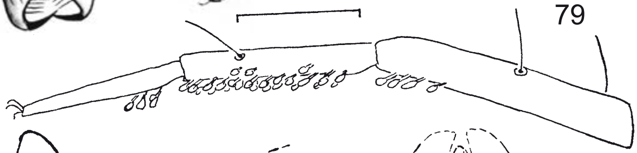
fig. 68) *Grandoculus chemahawinensis* PENNEY 2004 (Lagonomegopidae), ?adult ♀, holotype in Cretaceous Canadian amber, lateral-ventral aspect; scale line 1 mm. Taken from PENNEY (2004: Fig. 2B). Note the scopulae on the left tibiae I–II;

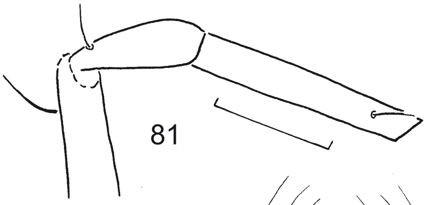
figs. 69–71: Lagonomegops sukatchevae ESKOV & WUNDERLICH 1995 (Lagonomegopidae), juvenile specimen in Cretaceous Siberian amber, dorsal, anterior and anterior-lateral aspects. Probably there exist 6 eyes; scale line 0.5;

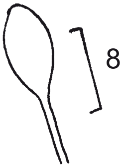

72

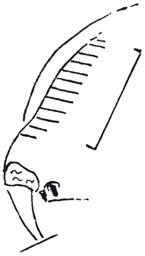

73

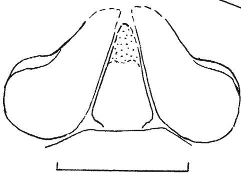

74

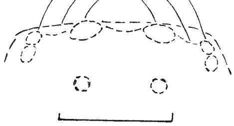

79

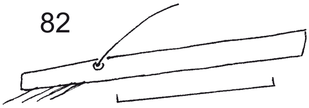

81

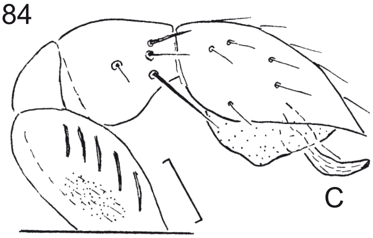

80

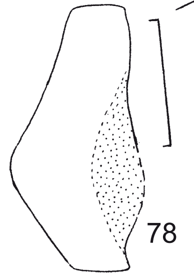

76

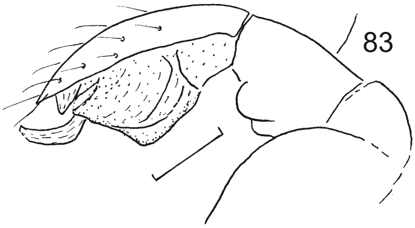

77


75


82


84

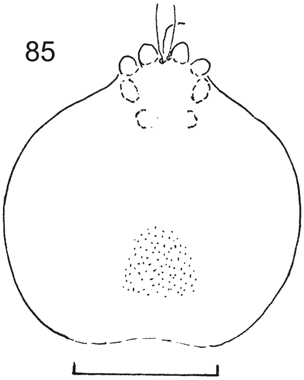

78

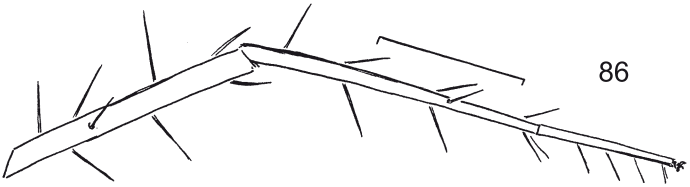

83

figs. 72–73: Zarqagonomegpops wunderlichi KADDUMI 2007, juvenile holotype in Cretaceous Jordanian amber; 72) retrodorsal aspect of the specimen, body length ca. 1.8 mm; 73) anterior-lateral and slightly ventral aspect of the prosoma. Drawings by HANI KADDUMI;

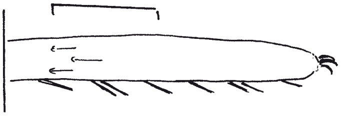
figs. 74–84: ***Micropalpimanus poinari* n. gen. n. sp.** (Micropalpimanidae n. fam.), ♂, holotype in Cretaceous Burmese amber; 74) lateral aspect of the prosoma; the eyes are partly hidden or deformed; 75) dorsal aspect of the eyes; 76) proapical aspect of the r. chelicera. Note the retrolateral stridulatory files and two “peg teeth”. (Hairs are not drawn); 77) labium and gnathocoxae (the apical parts are hidden); 78) ventral aspect of the r. femur I. Note the proventral depression; 79) prodorsal aspect of the r. leg II. Normal hairs are not drawn but spatulate hairs and at least two trichobothria; 80) spatulate hair of metatarsus I; 81) prolateral aspect of the l. tibia, patella and the distal part of femur I. Note the three thin (almost hair-shaped) bristles. Hairs are not drawn; 82) retrodorsal aspect of the l. metatarsus III. Note the long dorsal trichobothrium and the long ventral-distal hairs; normal hairs are not drawn; 83) retrolateral aspect of the l. pedipalpus; 84) prolateral aspect of the slightly deformed l. pedipalpus. Note the femoral stridulatory files. (Only few hairs are drawn); C = conductor; scale lines 0.1 in figs. 76, 83–84, 0.2 in the remaining figs.;

85



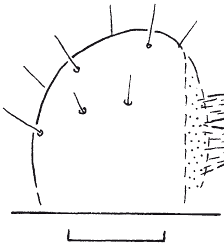


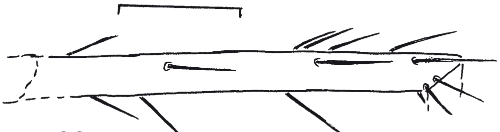
86



91

89

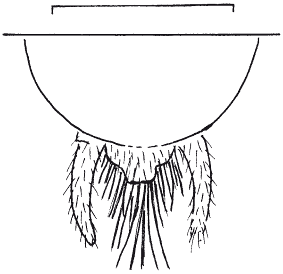


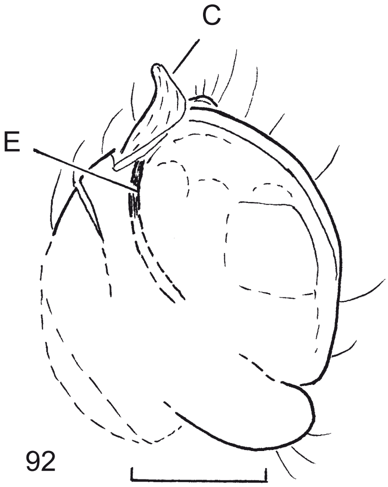


90

88

87

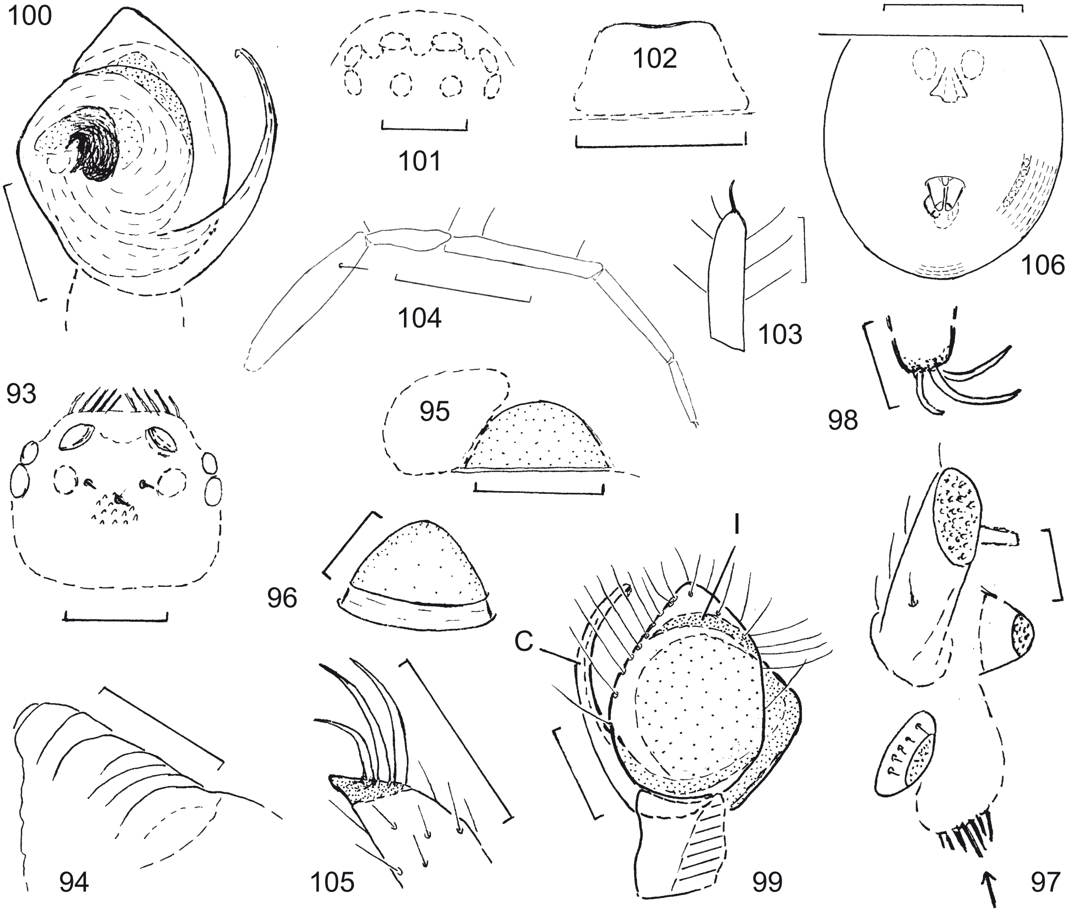




92

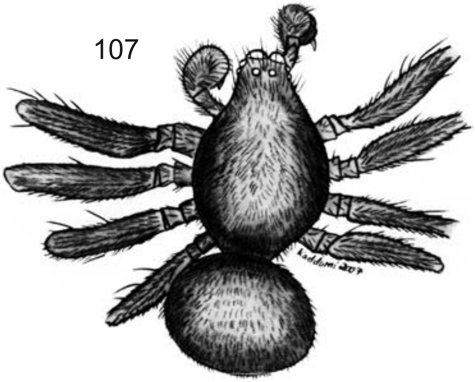
figs. 85–89: ***Zamilia antecessor* n. gen. n. sp.** (Oecobiidae: Mizaliinae), ♂ holotype in Cretaceous Burmese amber; 85) dorsal aspect of the slightly deformed prosoma. The position of the posterior median eyes is unsure; bubbles cover the eye lenses of the anterior row; 86) retrodorsal aspect of the r. leg IV (tibia, metatarsus and tarsus); 87) dorsal aspect of the posterior part of the opisthosoma. Note the long posterior spinnerets and the large anal tubercle with its fringe of hairs. (Hairs of the opisthosoma are not drawn); 93) dorsal aspect of the deformed left pedipalpus. Note the wide cymbium; 94) apical aspect of the r. pedipalpus (the basal part is hidden); scale lines 0.5 in figs. 85–87, 0.1 in figs. 88–89;

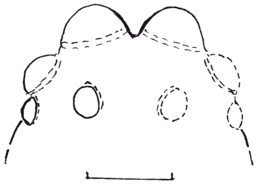
figs. 90–92: ?Oecobioidea indet., ♂ (F2006/CJW), Jordanian amber, 90) prolateral aspect of the l. tibia I; 91) retrolateral aspect of the r. tarsus I. (Only few hairs are drawn); 92) ventral aspect of the l. pedipalpus. (Parts are hidden by artefacts); C = conductor, E = questionable embolus; scale lines 0.5 in fig. 90, 0.1 in fig. 91 and 0.2 in fig. 92;



figs. 93–106: ***Burmascutum aenigma* n. gen. n. sp**. (Burmascutidae n. fam.) in Cretaceous Burmese amber; 93–100: ♂ holotype, 101–106: ♀ paratype; 93) reconstruction of the deformed/flattened prosoma, dorsal aspect. Only few wrinkles are drawn (in the centre); 94) retrolateral aspect of the deformed r. chelicera with folds which probably are artefacts; 95) labium and r. gnathocoxa which is partly hidden; 96) posterior aspect of the conique structure of the genital area; 97) retroaboral-apical aspect of the r. spinnerets which are deformed. Note the row of strong bristles on the deformed anal tuberctle (arrow) and the long prolateral artefact of the anterior spinneret; 98) prodorsal aspect of the claws of the r. tarsus II; 99–100) dorsal and ventral aspect of the r. pedipalpus. The conductor has probably an unnatural position, the retrolateral part of the tibia is deformed and partly hidden. (Hairs are not drawn in fig. 100); 101) reconstruction of the approximate position of the eyes, dorsal aspect; 102) ventral aspect of the slightly deformed labium; 103) retrodorsal aspect of the pedipalpal tarsus; 104) prolateral aspect of the l. leg I. The leg articles are deformed, the femur is flattened laterally; 105) prolateral aspect of the r. tarsal claws II; 106) ventral aspect of the opisthosoma (anteriorly hidden). The left half of the epigynal plate is reconstructed, some parts of the scutate furrows are faintly marked. Note the anterior position of the spinnerets; C = conductor, I = internal cymbial structure; scale lines 0.5 in figs. 104 and 106, 0.03 in figs. 96–98, 0.05 in fig. 105, 0.2 in figs. 93 and 101, 0.1 in the remaining figs.;

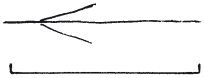
107



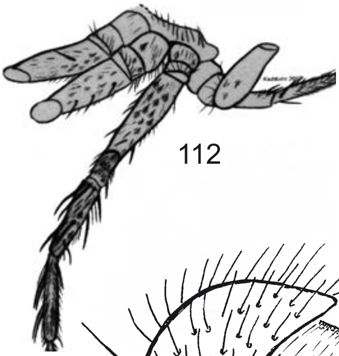


108

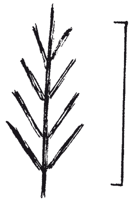
109



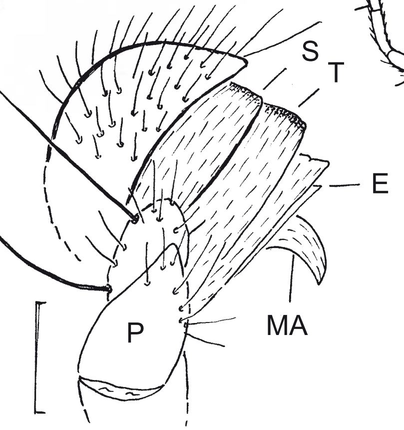
110



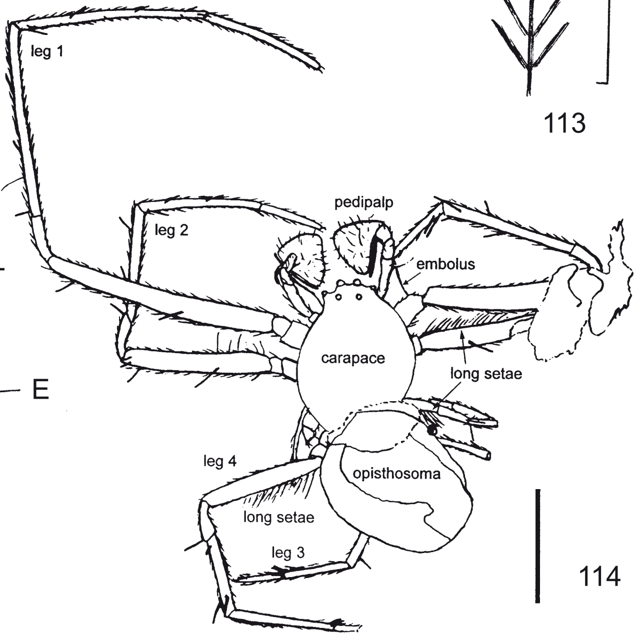
112



113



111

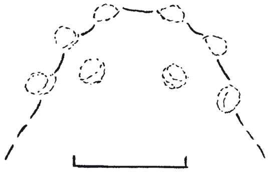


114

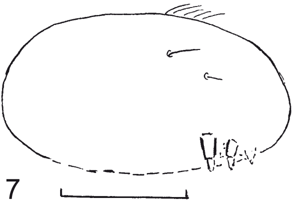
figs. 107–111: ***Salticoididus kaddumiorum* n. gen. n. sp.** (Salticoididae n. fam.), ♂ holotype in Jordanian amber; 107) dorsal aspect of the specimen, body length 2.6 mm (drawing by HANI KADDUMI); 108) dorsal aspect of the eyes; 109) thin (incomplete?) feathery hair of the r. femur IV; 110) dorsal aspect of the l. femur I; 111) dorsal (patella and tibia) and retrodorsal (cymbium and bulbus) aspect of the r. pedipalpus; E = questionable embolus, MA = median apophysis, S = subtegulum, T = tegulum; scale lines 0.1 in fig. 109), 0.2 in the remaining figs.;

figs. 112–113) ?Salticoididae indet., juv.; 112) part of the specimen (drawing by HANI KADDUMI); 113) feathery hair of a leg; scale = 0.05;

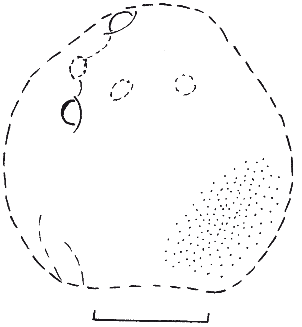
fig. 114) *Palaeomicromenneus lebanensis* PENNY 2003 (Deinopidae), ♂ holotype in Lebanese amber, dorsal aspect of the spider; scale line 1 mm. Taken from PENNEY (2003: Fig. 3);



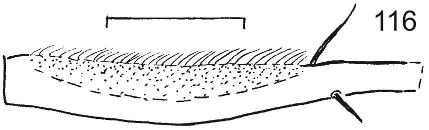
115



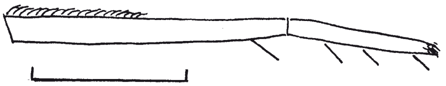
117



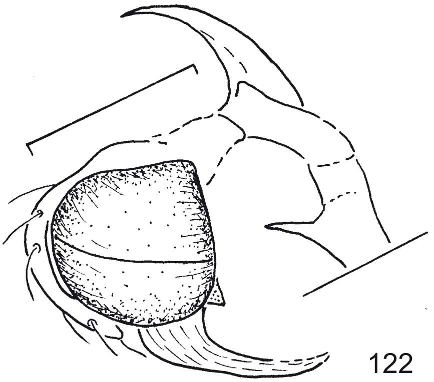
118



116

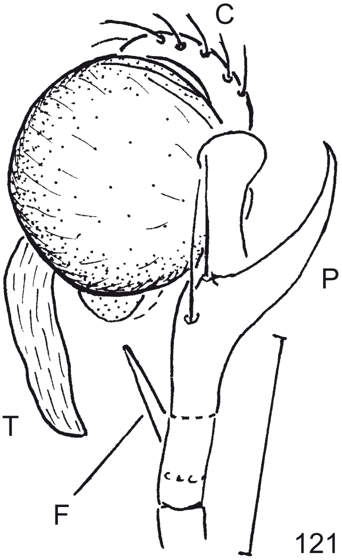


120



122

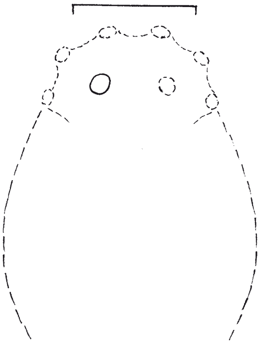
119



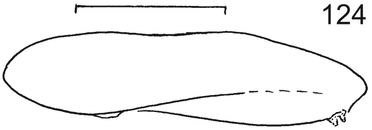
121

figs. 115–117: ***Burmuloborus parvus*** **n. gen. n. sp.**, ?ad. ♀, holotype in Cretaceous Burmese amber; 115) position of the fairly deformed eyes which are partly covered with bubbles or an emulsion; 116) prodorsal aspect of the l. metatarsus IV. The calamistral hairs are difficult to recognize. Normal hairs are not drawn; 117) left retroventral aspect of the opisthosoma. Only few hairs are drawn, the cribellum is hidden; scale lines 0.2 in figs. 115–116, 0.5 in fig. 117;

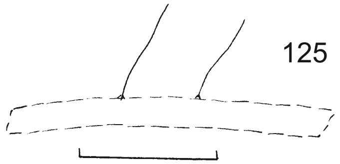
figs. 118–122: ***Paramiagrammopes cretaceus*** **n. gen. n. sp**. (Uloboridae), ♂ holotype in Cretaceous Burmese amber; 118) dorsal aspect of the prosoma which is slightly deformed. Some eyes are more or less hidden by tiny bubbles and an emulsion, a depression exists on the right side; 119) dorsal aspect of the r. femur III with three long prolateral trichobothria. (Normal hairs are not drawn); 120) prolateral aspect of the l. metatarsus and tarsus IV. Note the ventral bristles and the metatarsal calamistrum. (Normal hairs are not drawn); 121–122) dorsal and retrolateral aspect of the l. pedipalpus. The articles are slightly to fairly deformed; bubbles are not drawn; C = cymbium, F = ventral femoral apophysis, P = prodorsal patellar apophysis, T = tegular apophysis; scale lines 0.2;



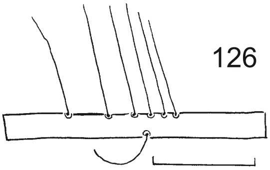
123



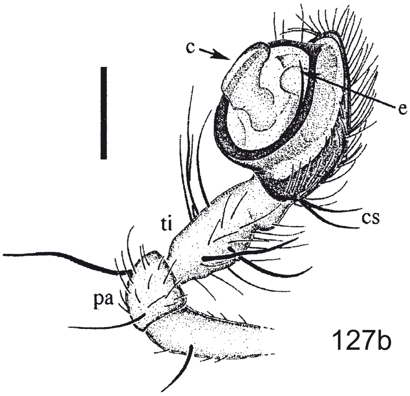
124



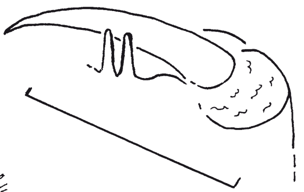
125



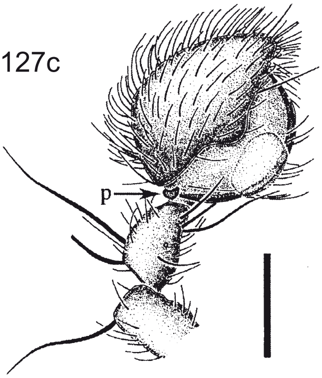
126



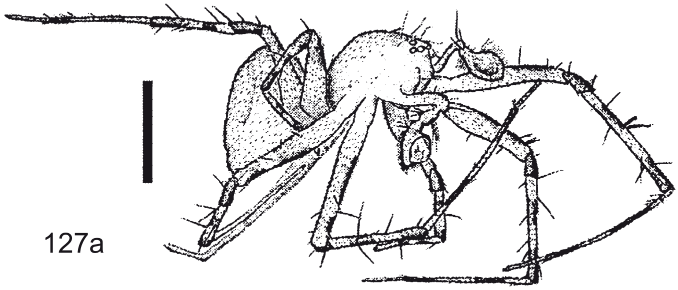
127b



128



127c

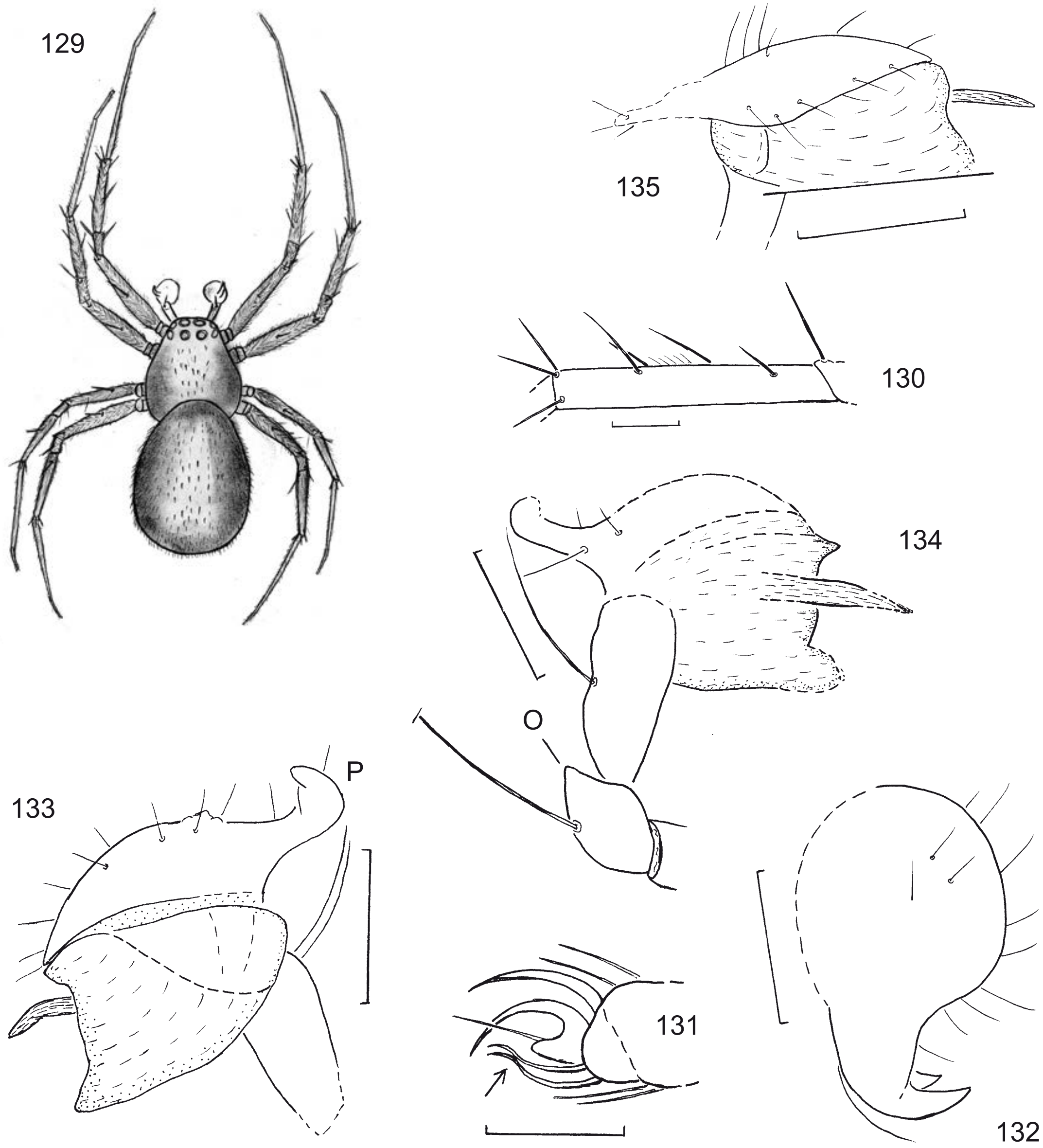


127a

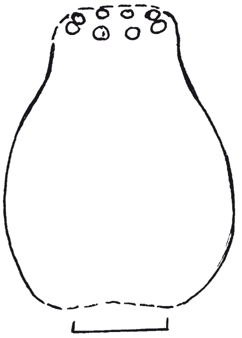
figs. 123–126: ***Palaeomiagrammopes vesica* n. gen. n. sp**. (Uloboridae) in Cretaceous Burmese amber; 123–124, 126: ?ad. ♀, holotype, 125: ?juv. ♀, paratype OSU no. B-A-1-19; 123) reconstruction of the deformed prosoma, dorsal aspect; 124) dorsal-left aspect of the deformed opisthosoma (outline), with artificial fold; 125) prodorsal aspect of the deformed l. femur II. (Normal hairs are not drawn); 126) dorsal aspect of the l. femur III with long trichobothria; scales: 0.5 in fig. 124, 0.2 in the remaining figs.;

fig. 127a–c: Mesozygiella dunlopi PENNEY & ORTUNO 2006 (Zygiellidae; sub Araneidae), ♂ in Cretaceous amber from N-Spain (Alava); a) lateral aspect of the holotype; b) proventral aspect of the l. pedipalpus of the holotype; c) probably retrolateral aspect of the r. pedipalpus of the paratype (according to PENNEY "left pedipalp of paratype, medial view"); c = median apophysis (according to PENNEY "conductor"), e = embolus, p = paracymbium; scale lines 1.0 in fig. a, 0.2 in figs. b–c. Taken from PENNEY & ORTUNO (2006, Fig. 1);

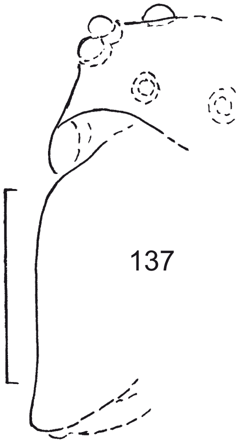
fig. 128) Araneoidea indet., ♀ in Cretaceous Lebanese amber, coll. D. AZAR no. 491, MNHNP (Linyphiidae gen. & sp. indet. sensu PENNEY & SELDEN (2002)), retroposterior aspect of the l. chelicera. Note the two long and slender teeth of the posterior cheliceral margin; scale line 0.1 mm;



figs. 129–135: ***Zarqaraneus hudae* n. gen. n. sp**. (?Protheridiidae WUNDERLICH 2004: Zarqaraneini), ♂, holotype in Cretaceous Jordanian amber; 129) dorsal aspect of the specimen, body length 3 mm; 130) retrodorsal aspect of the l. tibia I; 131) prolateral aspect of the tip of the r. tarsus II. The arrow points to the paired "auxiliary hairs". Note the large unpaired claw. (Only few hairs are drawn); 132) dorsal aspect of the r. cymbium. (Only few hairs are drawn); 133) retrodorsal aspect of the l. pedipalpus; 134) prolateral and slightly dorsal aspect of the l. pedipalpus. (Parts of the bulbus are hidden); 135) retroapical aspect of the r. pedipalpus. (Parts of the bulbus are hidden); O = apical outgrowth of the patella, P = paracymbium; scale lines 0.05 in fig. 131, 0.2 in the remaining figs.;

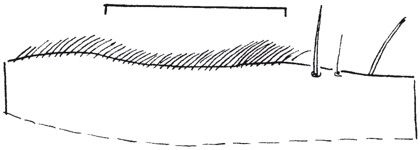


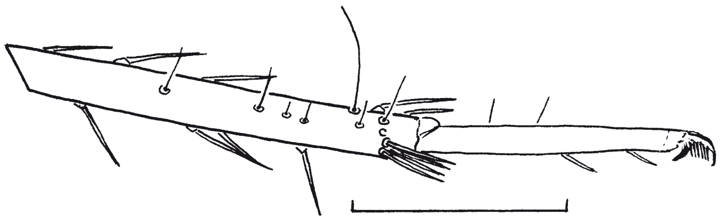
136



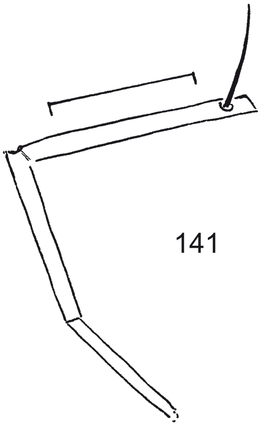
137

139

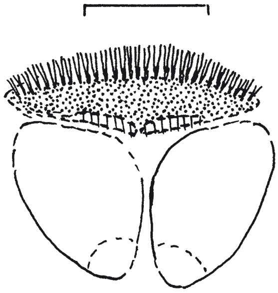




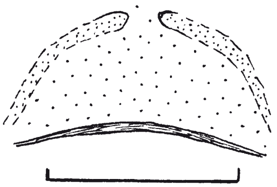
138



141



140



142

fig. 136–140: ***Burmadictyna pecten*** **n. gen. n. sp**., (?Dictynidae), ?ad. ♀, holotype in Cretaceous Burmese amber; 136) dorsal aspect of the prosoma. A fovea is absent or hidden (hairs are not drawn); 137) anterior aspect of the r. half of the deformed prosoma; 138) prolateral aspect of the l. tarsus and metatarsus III. (Not all trichobothria and no normal hairs are drawn); 139) fairly deformed left metatarsus IV with the calamistrum; 140) cribellum and outline of the anterior spinnerets. A pair of lamellar structures in front of the spinnerets may be artefacts; scale lines 0.2 in fig. 140, 0.5 in the remaining figs.;

fig. 141) ?Dictynidae indet. sp. 2, ?ad. ♀ (F1913/BU/AR/CJW) in Cretaceous Burmese amber, oblique proapical aspect of the three distal articles of the r. leg I. Note the long probasal bristle of the tibia (hairs are not drawn); Scale line 0.2.

fig. 142) ?Dictynidae indet. sp. 3, ?ad. ♀ (F1922/BU/AR/CJW) in Cretaceous Burmese amber, genital area; scale line 0.1.

Über die paläontologischen Ereignisse am Ende der Kreidezeit

(z. T. in Anlehnung an UDO LINDENBERG)

Vor 65 Millionen Jahren
– am Ende der Kreidezeit –
da war es soweit:
nach dem Aufprall eines Meteoriten,
verschwanden die Ammoniten,
und die Dinosaurier
wurden zunehmend „ trauriger“,
(die plazentalen Säugetiere
taten dazu das ihre),
nur die fliegenden Dinosaurier
– die Vögel – hoben flugs ab
und entkamen so knapp
der Konkurrenz bodenständiger Säugetiere.
Ähnliches geschah bei den Spinnen:
Viele Gruppen der urtümlichen Haplogynen
konnten dem Aussterben nicht entrinnen;
dagegen die „cleveren“ Entelegynen
– so Baldachin-, Kugel- und springende Spinnen –
konnten im Tertiär sich voll erst entfalten,
im Gegensatz zu den Taxa, den alten!
Fossilien vom Eozän unschwer beweisen
die Früh-Tertiäre Radiation
der Völker geselliger Ameisen
und ihre Verknüpfung mit der Spinnen-Evolution.

JW

BEITR. ARANEOL., 5 (2008)

REVISION OF THE EUROPEAN SPECIES OF THE SPIDER GENUS *HYPTIOTES* WALCKENAER 1837 (ARANEAE: ULOBORIDAE)

JOERG WUNDERLICH, 69493 Hirschberg, Germany.

Abstract: The European species of the genus *Hyptiotes* WALCKENAER 1837 (Araneae: Uloboridae) are revised, *H. gerhardti* WIEHLE 1929 is regarded as a junior synonym of *H. flavidus* (BLACKWALL 1862) (**n. syn**.), *H. dentatus* **n. sp**. is described from Southern France (its adult female remains unknown).

Institutions: CJW = private collection of J. WUNDERLICH in the Laboratory of Arachnology, D-69493 Hirschberg; SMF = Senckenberg-Museum Frankfurt a. M.

Material besides *Hyptiotes dentatus* n. sp.:
(1) *H. paradoxus* (C. L. KOCH 1834): ♂♀ from Central and Southern Europe, SMF;
(2) *H. flavidus* (BLACKWALL 1862): ♂♀ Madaira, Canary Islands, SMF; S-France: Provence, 8 km S Valensole, SMF 33270;
(3) *H. gerhardti* WIEHLE 1929: Russia (Sochi), 1♂ syntype, SMF 13096/1.

In contrast to the Central and North European spider fauna is the fauna of Southern Europe still only incompletely known. To my knowledge more than 4200 species of European spiders have been described up to 2007 but a greater number of dubious names exists, and an unknown number of synonyms.

During the last two decades almost 400 European spider species were described for the first time, mainly from the Canary Islands, and the number of named European spiders rose by about 10%. Due to dozens of undescribed species from Southern Europe including the Canary Islands (SMF, CJW) – which are known to me and which will probably be described by me in the future – I suppose that only about 90% of the European spider species have already been described. European taxa of the family Lycosidae, e. g. of the Macaronesian Islands, urgently need a revision.

Descriptions of new species frequently require a revision of their related species. An example is the here for the first time described Triangle spider – see below –; the discovery of this exciting species was a great surprise to me. The Provence / the Sea Alps in Southern France are known as regions which contains numerous endemic species of arthropods; here apparently survived certain species the last glaciation. Furthermore the Provence is the only known region in which the three European species of Triangle spiders exist together. Is *H. dentatus* a relict species or has it overlooked previously? Further studies will find out if it may have a wider distribution.

Triangle spiders (German name: “Dreiecksspinnen”) – the genus *Hyptiotes* – are widely spread in the Northern Hemisphere, and are probably absent in the Southern Hemisphere. These cribellate spiders (see photo 46) are of special interest for several reasons:

(1) The BODY and unusual structures: The shape of the stout body and legs, and the very wide eye field (figs. 1–3, photo 383) with the position of the posterior lateral eyes at the prosomal margin (arrow in fig. 1) of these spiders are unique within the European fauna. The femora bear long sensory hairs (trichobothria, fig. 6) like almost all other spiders of this family. The male pedipalpus (fig. 7, photo 383) possesses complicated structures and a very long embolus; it has an enormous size, the cymbium is as long as the prosoma or the anterior femur (!).

(2) POISON GLANDS are absent in these spiders as in all other species of the family Uloboridae, a unique character in “higher” spiders. The – sexually dimorphic – TINY CHELICERAE in the male sex (fig. 2) may possess a connection to the absence of poison glands.

(3) Waiting for a prey these spiders – see fig. 3 – look like a “bud of a spruce” (*Picea*), see HEIMER (1988: 66); this is a special kind of CAMOUFLAGE, imitating a part of a plant (mimesis). (Most spiders of *Hyptiotes* live in forests of *Picea*, and can be found in Germany usually about 1 to 2 m above the ground. The spiders are not too rare but frequently overlooked).

(4) The CAPURE WEB AND CAPTURING BEHAVIOUR (figs. 3–4) are unique: The spider holds its reduced triangle capture web (a sector of an orb web!) with its anterior legs (the web contains “sticky” dry cribellate threads mainly between the radial threads). If the spider is alarmed with the help of the “signal line” by a prey – e.g. by a fly which has been entangled, in the capture web – the spider lengthens the dragline from its anterior spinnerets, the web collapses around the prey, and the prey will be wrapped after that by further threads of the spider. So the spider’s “throw-away”capture web can be used only a single time.

(5) Uloboridae are mainly tropical spiders, and so it is not astonishing that their PERIOD OF MATURATION in Europe is relatively late in the year, to my knowledge July/August until November; the specimens of the new species *Hyptiotes dentatus* were collected as subadults in mid August, and the mature moulting of the male was at the end of August in the laboratory. (The subadult females were already preserved in alcohol during collecting). On the Canary Islands I collected adult specimens of *H. flavidus* already in April.

(6) *Hyptiotes* is an “old” and “LONG-LIVING GENUS” which has existed for at least 50 million years, and were present already within the subtropical Eocene European amber forests, see WUNDERLICH (2004: 856–861, photos 99–102); the number of five described extinct species was higher in the Eocene than the number of only three species in Europe today. In contrast to the extant species (arrow in fig. 2) the lenses of the anterior lateral eyes were not reduced in the fossil spiders, see WUNDERLICH (2004: 878, fig. 5).

Remarks on the species-groups of *Hyptiotes*:

The Eocene fossil spiders possess a furcate “median apophysis” according to WUNDERLICH (2004: 858, fig. 4) but now I am not sure: Both “branches” of the “median apophysis” may be different apophyses (*); a large and plate-shaped conductor is absent in contrast to the extant taxa.
In the males of the nearctic species a LONG AND PROTRUDING apophysis exists which is widened distally (fig. 14). The epigyne (fig. 15) is strongly protruding similar to certain structures of female primates.
The remaining species may build more than a single group. In the European species the sternum bears a posterior hump (fig. 5).

(*) Remark on the bulbus sclerites in *Hyptiotes*: The terms of these sclerites are only provisional; the homology of the “median apophysis” with a “similar” apophysis in related genera appears unsure to me.

Synonymy: *Hyptiotes gerhardti* WIEHLE 1929 is – due to the structures of the male pedipalpus of a syntype – a junior synonym of *H. flavidus* (BLACKWALL 1862) (**n. syn**.). I cannot confirm the differences which exist in the male pedipalpi of *gerhardti* and *flavidus* sensu WIEHLE (1929: Figs: 8 and 9). Has the position of the pedipalpi changed during the drawings? Have they been deformed by the preparation?

Hyptiotes dentatus n. sp. (figs. 2, 5–10, photo 383)

Material: Southern France, Provence, W Grasse, at the brook La Siagnole (upper part) near Mons, taken from a needle bush above the brook, 1 subad. male (holotype), 2 subad. females (paratypes), JW leg. mid August 2007, mature moulting of the male 26. August 2007; male and exuvia CJW R10/AR/CJW, paratypes R11/AR/CJW.

Diagnosis (♂): Pedipalpus: The embolus bears two angles and points (arrows in fig. 7), and originates almost in the middle of the bulbus (fig. 9); a tegular apophysis 2 (fig. 8) exists.

Description:
Measurements (in mm) (♂): Body length 3.0, prosoma: Length 1.4, width 1.4; leg I: Femur 1.5, patella 0.5, tibia 0.9, metatarsus 1.4, tarsus 0.5, tibia II 0.6, tibia III 0.4, leg IV: Femur 1.0, patella 0.45, tibia 0.8, metatarsus 0.75, tarsus 0.45; length of the cymbium 1.4; subad. ♀: Body length 4.2–4.4, prosoma: Length 1.4–1.5, width 1.4; leg I: Femur 1.0, patella 0.5, tibia 0.6, metatarsus 0.65, tarsus 0.35, tibia IV 0.7.
Colour (photo 383) mainly dark grey brown, legs mainly dark brown, tibia IV light brown in the male and yellow brown near the base, metatarsus and tarsus I–II medium brown, opisthosoma dorsally with light brown and yellow patches.
Prosoma (fig. 2, similar to fig. 1) as wide as long, bearing a wide and deep fovea (hidden in fig. 1; it is lower in the female), clypeus distinctly protruding (especially medially), feathery hairs are present, they are similar to fig. 26 in the book of WUNDERLICH (2004: 882). 8 eyes in a wide field, the posterior laterals are situated on distinct humps, the anterior lateral have reduced lenses. Basal cheliceral articles very small in the male, larger in the subadult females, fangs long, labium long and triangular, gnathocoxae large and widened distally, sternum with a posterior hump (fig. 5). – The ♀-pedipalpus bears a large and toothed tarsal claw. – Legs (figs. 1, 6, photo 383) stout, order I/IV/II/III, bearing numerous strong bristles namely on the male tibiae, the ♂-tibia I bears – mainly prolaterally – 12 strong – clasping (?) – bristles (they are absent in the female), femur IV bears only 1/1 dorsal bristles, the short femur IV bears about 12 trichobothria in two irregular rows (fig. 6) in both sexes (and few coxal trichobothria exist as well). The metatarsal trichobothria are tiny, its position on I (male) is in 0.15. Metatarsus IV dorsally distinctly depressed and concave; the calamistrum covers almost 5/6 of its length. Most tarsi and metatarsi bear strong short ventral bristles whose number is higher on III–IV; in the female tarsus and metatarsus IV bear a larger number of ventral bristles, tarsus IV bears 7 – 8 ones in an irregular row (they are abselnt in the male on this article). – Opisthosoma (photo 383) almost oval in the male, stout, high and widened in the middle in the female (like in fig. 1), and almost triangular, protruding beyond the spinnerets in both sexes; a pair of hairy dorsal humps is more distinct in the female; cribellum (see fig. 46) large, wide and undivided, colulus large and hairy, anterior spinnerets large, widely spaced basally, strongly converging. – ♂-pedipalpus (figs. 7–10): Patella and tibia bear a dorsal bristle, median apophysis long and pointed, two slender tegular apophyses and a wide and almost scinny (translucent) terminal apophysis are present, conductor consisting of a long and sclerotized lateral part and a wide and scinny medial part, embolus very long, originating in the

middle of the bulbus, having two angles/points (arrows in fig. 7) which are absent in other congeneric species.

Relationships (see the tab. 1 below): According to the structures of the male pedipalpus (figs. 11–12) *H. paradoxus* (Palaearctic) is most related; most structures of the bulbus are quite similar, e. g. the pointed tip of the median apophysis – but not the embolus –, in both species exists a tegular apophysis 2 of the same size and position (see the figs.) in contrast to *flavidus* in which it is absent. *H. paradoxus* may be slightly larger than dentatus, the origin of the embolus is more basally, and embolic angles/points are absent, the basal part of the conductor (near the pedipalpal tibia) is larger and has a different shape. – *H. flavidus* (Mediterranean, Russia) is the smallest European species, the prosoma is relatively longer, the clypeus is more protruding, the shape and the origin of the embolus are similar to *paradoxus* (angles/points are absent, too) but a distinct tegular apophysis 2 is absent, the tip of the median apophysis is widened apically (fig. 13), the terminal apophysis (not drawn) is slender and has a pointed pit in contrast to the wide terminal apophysis in *dentatus* (fig. 8) and *paradoxus*, and the shape of the tegular apophysis 1 (not drawn) is different.

Distribution: Southern France (Provence).

Character		*flavidus*	*paradoxus*	*dentatus*
usual body length	♂	2.2–3.0	3.0–4.5	~3.0
	♀	2.7–4.3	4.5–6.0	4.2–4.4(*)
prosomal length	♂	1.0–1.25	~1.6	~1.4
	♀	1.1–1.5	~1.8	~1.5 (*)
ratio of prosomal length to width		~1.2 (**)	~1.0	~1.0
length of the cymbium		0.9–1.0	~1.6	~1.4
shape of the terminal apophysis		slender, pointed	wide and scinny, fig. 8	
tegular apophysis 2		absent	present similar fig. 8	present (fig. 8)
embolic angles and points		absent	absent	present (fig. 7)
origin of the embolus		basally, similar to fig. 12	basally (fig. 12)	near the middle of of the bulbus (fig.9)
distribution		Mediterranean, Russia	Palaearctic	S-France

(*) subad. ♀.
(**) clypeus stronger protruding than in the other species.

Tab. 1. Comparison of selected characters and the distribution of the three European species of the genus *Hyptiotes*. (Measurements in mm)

REFERENCES

HEIMER, S. (1988): Wunderbare Welt der Spinnen. 103 pp.

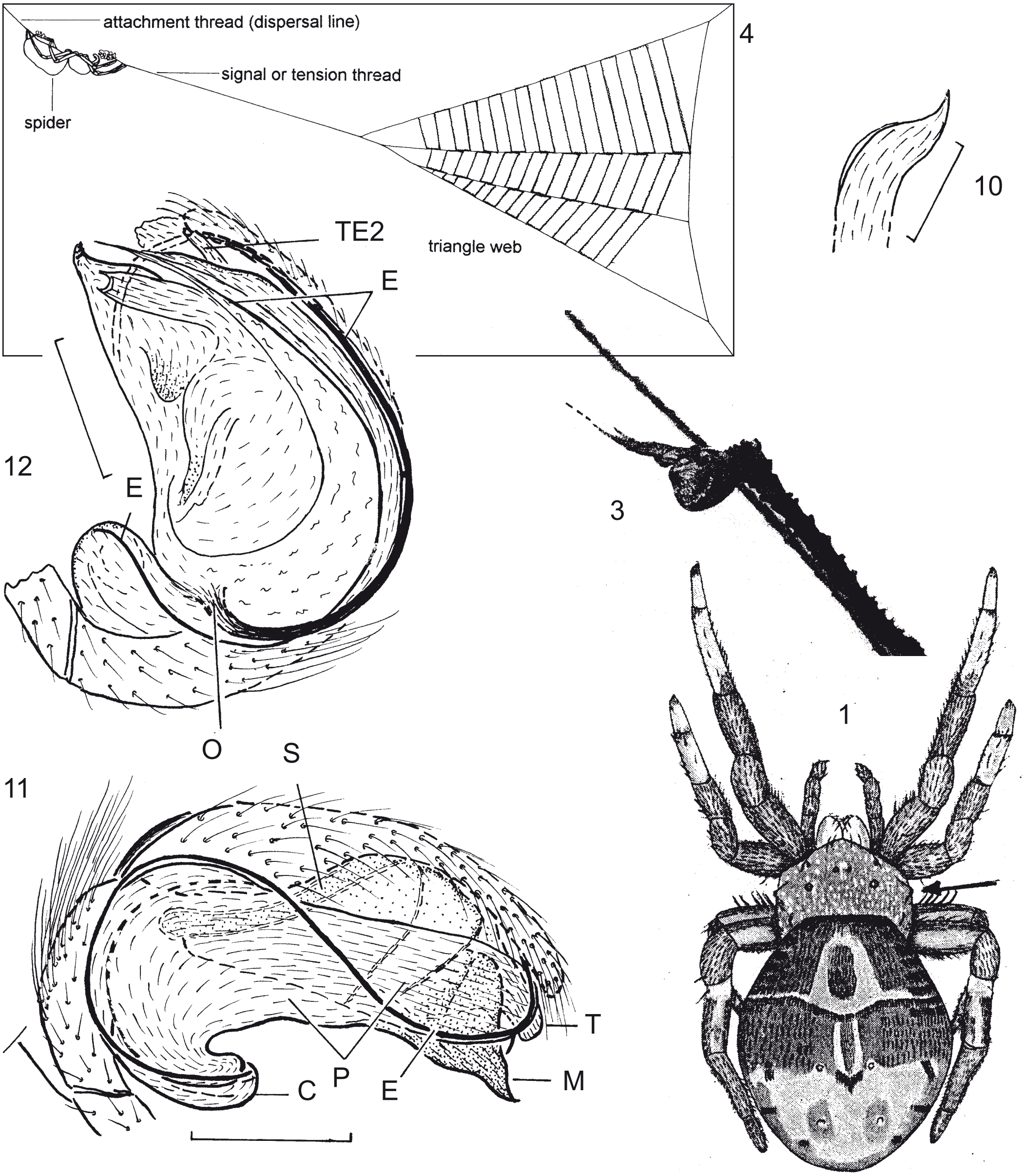
MUMA, M. H. & GERTSCH, W. J. (1964): The Spider Family Uloboridae in North America North of Mexico. – Amer. Mus. Novit., 2196: 1–43.

OPELL, B. D. (1979): Revision of the Genera and Tropical American Species of the Spider Family Uloboridae. – Bull. Mus. Comp. Zool., 148 (10): 443–549.

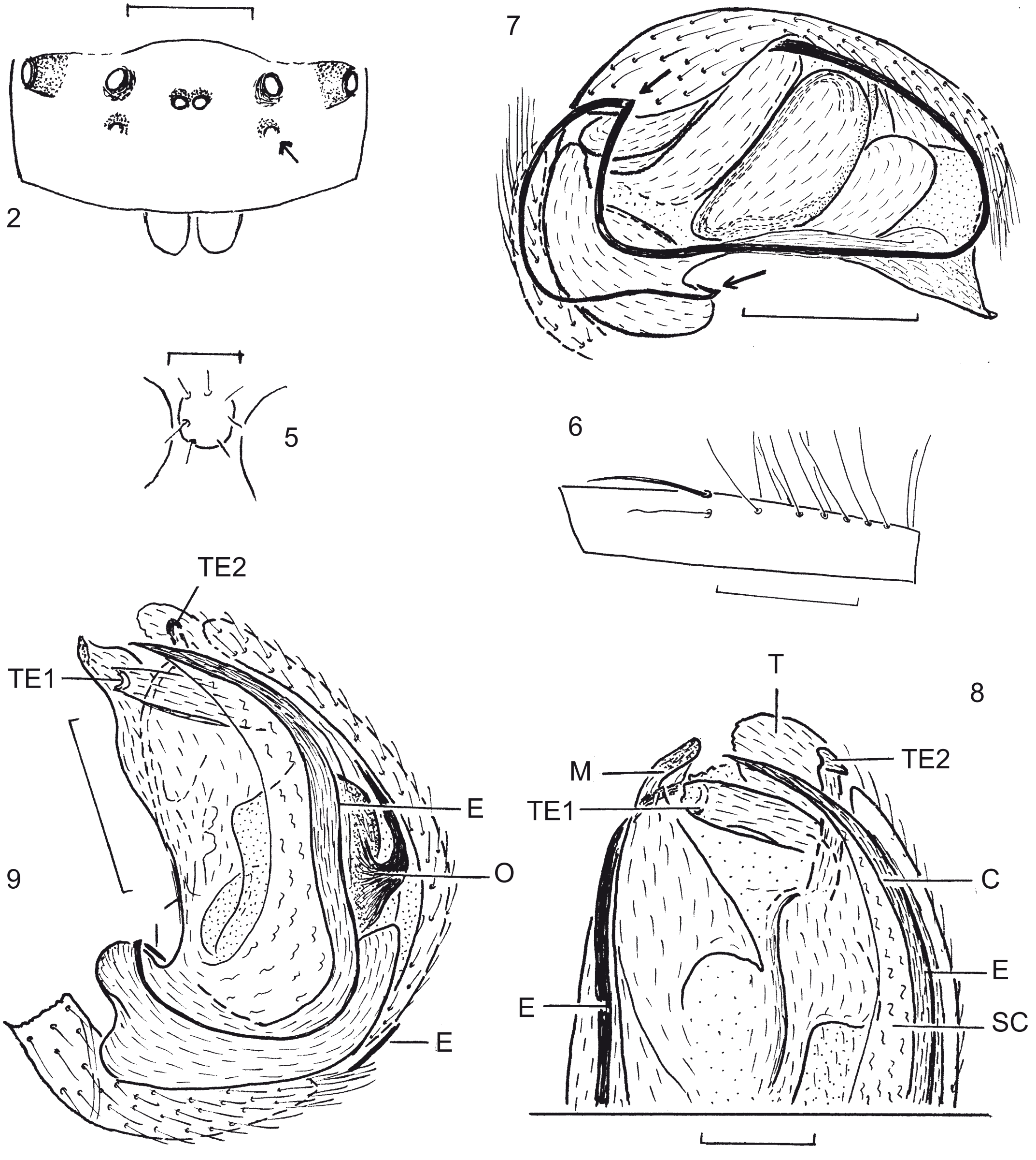
WIEHLE, H. (1964): Über *Hyptiotes gerhardti* WIEHLE (Arach., Araneae). – Senckenbergiana biol., 45 (1): 81–85.

-- (1953): Uloboridae, in DAHL, F. (ed.): Die Tierwelt Deutschlands, 42: 113–124.

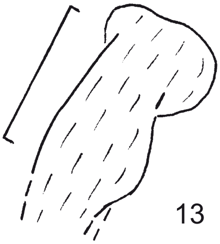
WUNDERLICH, J. (2004): Fossil Spiders in Amber and Copal. – Beitr. Araneol., 3 (vol. A, B), 1908 pp.

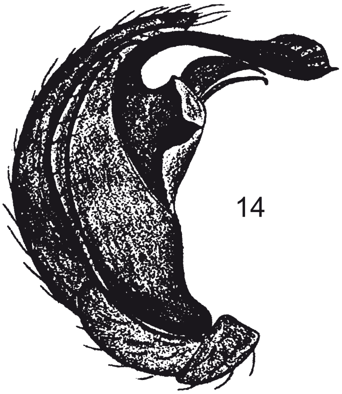


Figs. 1, 3–4, 10–12: *Hyptiotes paradoxus* (C. L. KOCH 1834); 1) dorsal aspect of a female. The arrow points to the right posterior lateral eye which is situated on a hump; 3) lateral aspect of a female at the top of a twig, holding the signal thread (dotted) with its anterior legs (see fig. 4). Note the upside-down position of the spider which is about 5 mm long; 4) female with its capture web. The spider functions as a “living bridge” between an attachment point at a twig or an attachment thread (left) and a signal thread which lead to the triangle capture web; 10) male, ventral aspect of the distal part of the r. median apophysis which has the same shape as in *dentatus*;11–12) male from Germany, retrolateral and prolateral aspect of the r. pedipalpus;



figs. 2, 5–10: *Hyptiotes dentatus* **n. sp.**, male; 2) anterior aspect of the prosoma. Note the tiny chelicerae and the reduced lenses of the anterior lateral eyes (arrow); 5) hump of the sternum between the posterior coxae; 6) prolateral aspect of the r. femur III which bears a single long dorsal bristle and a dozen trichobothria; 7) retrolateral aspect of the r. pedipalpus. Note the position of the long and bent embolus; the arrows point to the embolic angles/points; 8) retroventral aspect of the distal part of the r. pedipalpus which is like in *paradoxus*; 9) prolateral aspect of the r. pedipalpus; 10) ventral aspect of the distal part of the r. median apophysis which has the same size, position and shape as in *paradoxus* (see previous page);


13


14

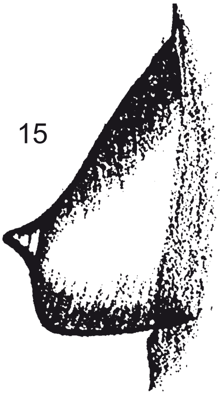

15

fig. 13) *Hyptiotes flavidus* (BLACKWALL 1862), ventral aspect of the r. median apophysis; compare fig. 10) of the other two European species;

fig. 14) *Hyptiotes puebla* MUMA & GERTSCH 1964 (USA), retrolateral aspect of the r. ♂-pedipalpus;

fig. 15) *Hyptiotes puebla* MUMA & GERTSCH 1964 (USA), female, lateral aspect of the genital area of the spider.

Abbreviations: C = stronger sclerotized part of the conductor, E = embolus, M = median apophysis, O = origin of the embolus, S = sperm duct, SC = scinny and wide part of the conductor, T = terminal apophysis, TE1, TE2 = tegular apophyses 1 and 2.

Scale lines 0.5mm in figs. 2), 6–7), 9), 11–13), 0.1 in figs. 5), 10) and 13), 0.2 in the remaining figs.

Figs. 1) and 3) (from a photo) are taken from WIEHLE (1953), fig. 4) from HEIMER (1988), figs. 14) and 15) from MUMA & GERTSCH (1964).

BEITR. ARANEOL., 5 (2008)

DESCRIPTIONS OF NEW TAXA OF EUROPEAN DWARF SPIDERS (ARANEAE: LINYPHIIDAE: ERIGONINAE)

JOERG WUNDERLICH, D-69493 Hirschberg.

Abstract: The following taxa of European spiders (Araneae: Linyphiidae: Erigoninae) are described: *Nusoncus* **n. gen**., *Trichopternoides* **n. gen**., *Trichoncyboides* **n. gen**., *Mecopisthes pumilio* **n. sp**., and Erigoninae gen. & sp. indet. *Metapanamomops* MILLIDGE 1979 is regarded as a junior synonym of *Elaphopus* MENGE 1878 (**n. syn**.).

Key words: Araneae, Erigoninae, Linyphiidae, new taxa, new synonyms, spiders.

The generic revision of European Erigoninae is still in progress, see WUNDERLICH (1995: 643–654); the relationships of some species are still unsure, *Pelecopsis alpica* THALER 1991 and *Pelecopsis/Minyriolus medusa* SIMON 1884 are two examples. In this paper I describe three new genera of this linyphiid subfamily: *Nusoncus* (type species *Troxochrus nasutus* SCHENKEL 1925), *Trichopternoides* (type species *Trichopterna thorelli* WESTRING 1862), and *Trichoncyboides* (type species *Gongylidiellum simoni* LESSERT 1904); furthermore described are *Mecopisthes pumilio* n. sp. from Switzerland (thanks to the attention of A. HÄNGGI), the female and the hithero unknown male of *Micrargus pervicax* DENIS 1947, and an unnamed dubious taxon from Berlin; the new synonymy of the European genus *Metapanamomops* MILLIDGE 1979 with the older name *Elaphopus* MENGE 1878 is proposed.

(1) ***Nusoncus* n. gen.** (figs. 1–4)

The gender of the name is masculine.

Diagnosis and description: Sequence of the dorsal tibial bristles 1/1/1/1, metatarsus IV without trichobothrium, position of the trichobothrium on metatarsus I a bit distally of the middle, clypeus with a “nose” which is larger in the male (figs. 1–2), ♂-prosoma with a lobe and lateral depressions. ♂-pedipalpus (figs. 3–4): Tibia with a long apophysis, cymbium with a retrodorsal hook and a larger probasal outgrowth, paracymbium in an unusual more anterior position, and with a long posterior outgrowth, suprategulum large, embolus strongly bent, and with a tooth near its tip. ♀: Epigyne posteriorly with a pair of strongly sclerotized structures which bear the introducing openings, vulva with semicircular glandular ducts, and large, thick-walled, oval receptacula seminis.

Relationships: In *Troxochrus* SIMON 1884 – which may be related – the tibiae bear a single dorsal bristle, too, but a clypeal “nose” and modifications of the cymbium are absent, the paracymbium is sickle-shaped and originates in a more basal position, the structures of the bulbus are different, especially exists a complicated radix apophysis, the epigyne is a plate-shaped structure which is widened posteriorly, and the shape of the receptacula seminis is circular.

Type species (by monotypy): *Troxochrus nasutus* SCHENKEL 1925 (figs. 1–4).

Ecology: The spiders are dwellers of the bark of needle trees, e. g. of *Pinus*, where they may build their capture webs in a high number. I observed a population in spring time on the bark of dead needle-trees which were deposited on the ground of a mixed forest near Pforzheim (SW-Germany). Bark beetles (Scolytidae) is one of the prey of the spiders.

Distribution: Europe.

(2) ***Trichopternoides* n. gen.** (figs. 5–9)

The gender of the name is neuter.

Diagnosis and description: All ♀-tibiae with a single dorsal bristle/spine which is shorter than the diameter of the tibia, but no bristle on the ♂-tibiae. Metatarsal trichobothrium present on IV, its position on I–II in 0.92–0.95. The anterior cheliceral margin bears 5 (♂) or 6 (♀) teeth (more than in related genera), the second one is by far the largest, the posterior cheliceral margin bears usually 5 teeth (♀) or 4 (♂). Opisthosoma without a dorsal scutum but leathery hardened in the male. ♂-prosoma with a large lobe which bears the posterior median eyes, anteriorly with a grove and hanging over (fig. 5). ♂-pedipalpus (figs. 6–7): Patella longer than the tibia, bearing a retrodorsal apophysis, bulbus simple, subtegulum large, radical part short, suprategular apophysis disc-shaped, with a tooth. ♀: Epigyne (fig. 8) with a large transparent/scinny area posteriorly, vulva: Fig. 9.

Relationships: The genus *Trichopterna* KULCZYNSKI 1894 – type species *Erigone cito* O. PICKARD-CAMBRIDGE, O. – is polyphyletic, see e. g. HOLM (1979), PLATNICK (1993: 361). *Erigonoplus* lacks a trichobothrium on metatarsus IV, the position of the trichobothrium on metatarsus I–II is in about 0.45, the males of almost all species bear long ventral bristles or spines on femur I, their embolic division is composed of a massive sickle-shaped radical part, the epigyne is divided by a “rim”. In *Trichopterna* the position of the trichobothrium on metatarsus I is in 0.7–0.75, the ♂-opisthosoma bears most often a dorsal scutum, the ♂-prosoma lacks an anterior grove, the embolus is long and thin, and the ducts of the vulva are coiled.

Type species (by monotypy): *Erigone thorelli* WESTRING 1862 (= *Trichopterna t.*, *Entelecara t.*). According to LEHTINEN (person. commun. ca. 30 years ago) *Hypselistes paludicola* TULLGREN 1955 is a junior synonym.

Distribution: Europe.

(3) *Elaphopus* MENGE 1878

Synonym: *Metapanamomops* MILLIDGE 1979 (**n. syn**.).

Material: Germany, Niederlausitz, 8♂, H. WIEHLE det. *Trichoncus hackmani*, SMF 18257.

Fourteen years ago I discussed the synonymy in question with K.THALER; the synonymy has not yet been published because of so many other projects of both authors. – The descriptions and the figures of the original descriptions of both genera indicate the synonymy of the monotypic genera *Elaphopus* MENGE 1878 (type species *Elaphidion flagelliferum* MENGE 1869) and *Metapanamomops* MILLIDGE 1979 (type species *Micrargus kaestneri* WIEHLE 1961). The original genus name *Elaphidion* MENGE 1869 (praeocc.) was replaced by MENGE (1879) by *Elaphopus* and – probably erroneously – by *Elaphipus* in the index. BONNET – Bibliographia Araneorum (1945–1959: 1650) – selected the name *Elaphipus* for this genus, but already SCUDDER (1882) used the name *Elaphopus*. Refering to art. 23.9 of the Internat. Code of Zool. Nomenkl. the name *Elaphopus* has to replace the name *Metapanamomops*. – See also PROSZYNSKI & STAREGA (1971: 150–151) and WOZNY (1978) with the description of the female.

Distribution: Central Europe.

(4) ***Mecopisthes*** **SIMON 1926**

MILLIDGE (1977) revised the species of the genus *Mecopisthes*. After my work on the Central European species of *Mecopisthes* (1972) I recognized that the size of the scutum on the ♂-opisthosoma – at least in *M. peusi* and *silus* – varies strongly within these species and may even be completely absent. The position of the radix and the shape of the teeth of the suprategular apophysis are distinctly variable, too. THALER (in litt. 1993) supposed that *M. peusi* WUNDERLICH 1972 may be a junior synonym of *M. pictonicus* DENIS 1949 (♂ unknown); see MILLIDGE (1977: 13).
Remark on the chaetotaxy of *M. latinus* MILLIDGE 1977: After MILLIDGE (1977: 116) are tibial bristles absent, but due to my observation all tibiae bear an indistinct dorsal bristle.

Key to the males of the Central European species of *Mecopisthes*:

1 Length of the prosoma 0.55–0.6 mm; pedipalpus figs. 12–13. – Switzerland . . . . *pumilio* n. sp.

- Length of the prosoma 0.6–0.9 mm; pedipalpus very similar in *silus* but the “fleshly” apophysis is more slender fig. 15). 2

2(1) Dorsal tibial apophysis of the pedipalpus longer than the retrolateral one, its tip claw-shaped (fig. 17). – Austria . . . . *alter* THALER

- Dorsal tibial apophysis not longer than the retrolateral one, similar to fig. 12, its tip not claw-shaped 3

3(2) Prosoma with a distinct lobe (fig. 18). – Switzerland . . . . *latinus* MILLIDGE

- Prosoma without a distinct lobe, similar to fig. 10 4

4(3) Without a posterior suprategular apophysis, but with a small tooth (5 in fig. 15) . . . . *peusi* WUNDERLICH

- With a posterior suprategular apophysis as in *pumilio* (4 in fig. 13), without an additional tooth . . . . *silus* O. PICKARD-CAMBRIDGE

Mecopisthes pumilio **n. sp.** (figs. 10–14; compare figs. 15–18)

Material (captured in pit falls): Switzerland, (1) Mte. Generoso, Pree, meadow which is in a extensive REGULAR use; 2♂, holotype and paratype, A. HÄNGGI leg. in XII–I; (2) Valle della Giasca, 880m, mixed forest with *Castanea, Corylus* and *Fagus*, 1 questionable ♀, A. HÄNGGI leg. in V; 1 questionable ♀ Bedretto; Naturhistorical Museum Bale, Switzerland.

Remark: The conspecifity of the two females with the holotype is unsure; see the colour of the prosoma and the position of the posterior median eyes.

Diagnosis: Smallest species of the genus in Central Europe, prosomal length only 0.55 – 0.6 mm (♀), posterior median eyes separated by 1 1/2 of their diameter (only 1 1/6 in the ♀), ♂-prosoma as in figs. 10–11. ♂-pedipalpus (figs. 12–13): Tibia with two apophyses of medium length, length of the cymbium 0.22 mm, posterior suprategular apophysis (4 in fig. 13) present (as in *silus*), "fleshly" apophysis (1 in fig. 13) wide. Epigyne as in *M. peusi*, vulva: Fig. 14.

Description:
Measurements (in mm): Body length 1.0–1.2, prosoma: Length 0.55–0.6 (♀), width 0.42–0.47 (♀); leg I (♂): Femur 0.3, patella 0.15, tibia 0.31, metatarsus 0.24, tarsus 0.22, tibia IV 0.32; ♀: Tibia I 0.28, tibia IV 0.3.
Colour: Prosoma dark brown in the ♂, medium brown in the ♀, legs yellow brown, opisthosoma medium to dark grey.
Prosoma with an indistinct thoracal fissure. ♂-prosoma (figs. 10–11) with the clypeus protruding; ♀ as in *peusi*. Eyes fairly large, posterior row procurved, posterior median eyes separated by 1 1/2 (♂) (fig. 11) or 1 1/6 (♀) of their diameter. Cheliceral stridulatory files strongly reduced, the anterior margin of the cheliceral furrow bears 4 teeth, the posterior margin bears 4–5 teeth in the ♂ but only 3 in the ♀. The wide sternum is separated by the coxae IV almost by their diameter. – Legs short, bearing short hairs; sequence of the short dorsal tibial bristles 1/1/1/1, their position on I–II in 0.08, on IV in 0.18, their length on tibia I 1/5 of the tibial diameter in the ♂, 2/5 in the ♀, on tibia IV 1/3 tibial diameter (the bristle is rubbed off in the ♀). Position of the metatarsal trichobothrium I in 0.5–0.55, trichobothrium on metatarsus IV absent. – Opisthosoma oval, hairs short, scutum absent in both sexes.

Relationships (see the key; *pumilio* is the smallest species in Central Europe): In respect to the similar shape of the prosoma and the structures of the bulbus *M. silus* (O. PICKARD-CAMBRIDGE 1872) (fig. 16) is most related, see WUNDERLICH (1972: 302–303, figs. 24–28) and WIEHLE (1960: 87–91) (remarks regarding two figs. in this paper: (a) the profile of the ♂ (fig. 145) may be only slightly concave, (b) fig. 149 refers to the right pedipalpal tibia, not to the left one); *silus* is larger, the clypeus is more narrow, more protruding, its profile is slightly more concave, the copulatory organs are slightly different, the shape of the "fleshly" apophysis is a bit different (fig. 16). *M.*

pumilio and *M. peusi* are closely related, too, their bulbi are different, see the key and the figs. 13 and 15.

Distribution: Switzerland.

(5) ***Trichoncyboides* n. gen**. (figs. 19–21)

The gender of the name is feminine.

Diagnosis: All tibiae bear a single short dorsal bristle, metatarsus IV without a trichobothrium; ♂-pedipalpus (figs. 19–20): Radix with a pointed lamellar apophysis, embolus long and tape-shaped. ♀: Epigyne with a groove, vulva (fig. 21) with wide ducts near the oval receptacula.

Further characters: Position of the bristle on tibia I in 0.1, position of the metatarsal I trichobothrium in ca. 0.45, body length ca. 1.1 mm, furrows of the ♂-prosoma absent, colour of the body yellow brown, posterior eye row distinctly procurved, posterior median eyes separated by 1.6–2 diameters. Chelicerae with numerous lateral stridulatory files, the anterior margin bears 5 teeth. ♂-prosoma dorsally convex, without lobe or furrows. ♂-pedipalpus (figs. 19–20) (see above): Tibia with two short apophyses.

Type species (by monotypy): *Gongylidiellum simoni* LESSERT 1904; see MILLIDGE (1977: 25) and THALER (1973: 54–58, figs. 46–55) (= *Trichoncus s*., *Tapinocyboides s.*).

Relationships: The genus *Trichoncus* SIMON 1884 – a revision of the European species is in preparation by the present author – has turned out to be not monophyletic; see *Heterotrichoncus* WUNDERLICH 11970, *Trichoncoides* DENIS 1950, and the new genus. – MILLIDGE (1977: 25) regarded *simoni* as a member of *Trichoncus*, but the colour of the body of ALL species of *Trichoncus* is dark- to blackbrown, all spiders are larger, the profile of the ♂-prosoma is slightly concave, the posterior eye row is straight, the bristles of the legs are long, and their position more distally, the tibia of the ♂-pedipalpus bears several long apopyses, one of these apopgyses is a prolateral slender and long one which is lying on the cymbium; the receptacula seminis are multisectional. – Some authors regarded *simoni* as a member of *Tapinocyboides* WIEHLE 1960, but in this genus bears the ♂-prosoma glandular furrows, the embolic division is different and the position of the slender introducing ducts of the epigyne is far more posteriorly.

Distribution: Europe incl. Germany.

(6) ***Micrargus pervicax*** (DENIS 1947) (figs. 22–27)

1947 ?*Blaniargus pervicax* DENIS, -- Rev. fr. ent., 14: 153, figs. 8–9 (♀).

Material: Probably near Purgstall in Austria; 1♂ 1♀ SMF, 1♂ 1♀ CJW. The material has been collected more than 30 years ago; the name of the collector and the place of discovery are unsure and probably lost.

Remarks: (1) BRIGNOLI (1983: 346) placed *pervicax* correctly in the genus *Micrargus* DAHL 1886. – (2) The male of the species is described here for the first time.

Diagnosis: Sequence of the thin dorsal tibial bristles 2/2/1/1, trichobothrium on metatarsus IV absent; ♂-pedipalpus (fig. 23–25): Tibia with a very long and slender prolateral and a short retrolateral apophysis; ♀: Epigyne (fig. 26) with a large groove which is widened posteriorly, vulva: Fig. 27.

Further characters: Position of the trichobothrium on metatarsus I in 0.4–0.45, ♂-prosoma (fig. 22) dorsally distinctly convex, bearing a pair of hole-shaped depressions; ♂-pedipalpus (figs. 23–25) with a long embolus; ♀ (figs. 26–27): Epigynal margin partly strong sclerotized, receptacula seminis oval and two-partite, well recognizable in the epigyne.

Description:
Measurements (in mm): Body length 1.4–1.55 (♀), prosoma: Length 0.6, width 0.47; leg I (♂): Femur 0.48, patella 0.18, tibia 0.38, metatarsus 0.32, tarsus 0.29, tibia II 0.27, tibia IV 0.43; ♀: Tibia I 0.35, tibia IV 0.38.
Colour: Prosoma dark brown, legs light to medium brown, opisthosoma dark grey.
Profile of the prosoma slightly raised in the ♀ but distinctly raised and with a pair of small depressions behind the lateral eyes in the ♂ (fig. 22). Eyes only fairly large, posterior row straight or only slightly recurved, posterior median eyes separated by one diameter in the ♀, a bit less in the ♂. Basal cheliceral articles fairly stout, lateral stridulatory files well developed, anterior/posterior margins of the cheliceral furrow with 5–6/5 teeth; the sternum separates the coxae IV by their diameter. – Legs only fairly long, hairs indistinct. Bristles and trichobothria: See above, length of the basal tibial bristle I (♂/♀) 1.25/1.4 tibial diameters. – Opisthosoma oval, hairs short. Genital organs (see above): The pedipalpal tibia bears two trichobothria and long dorsal hairs, the shape of the paracymbium is simple, an outgrowth is absent.

Relationships: In the males of the related species is the prolateral tibial apophysis shorter, and the anterior part of the epigyne is wider if compared with the posterior part.

Distribution: France (Vendee), Austria?

(7) Erigoninae gen. & sp. indet. (figs. 28–31)

Material: Berlin, Köpenick, Kleines Fenn (fen, bog), 1♂ R. PLATEN leg. 15 or more years ago, coll. R. PLATEN.

Remarks: (1) The single male is in a fairly bad condition: The left pedipalpus is lost, the right one – its bulbus is expanded – exists in two parts, the left leg I is cut through the tibia, its distal part is lost. – (2) I send drawings of this species to several colleagues; no one knows this taxon.

Diagnosis (♂; ♀ unknown): Sequence of the dorsal tibial bristles 2/2/1/1, a trichobothrium on metatarsus IV is absent, its position on metatarsus I is in 0.34; the basal cheliceral articles bear an anterior tooth (arrow in fig. 28); ♂-pedipalpus (figs. 29–31): Tibia retroapically with a sclerotized tooth, paracymbium with a longitudinal furrow, embolus in a circular position, a large and scinny conductor exists.

Description:
Measurements (in mm): Body length 1.55, prosoma: Length 0.9, width 0.72; leg I: Femur 0.71, patella 0.21, tibia 0.6, metatarsus 0.52, tarsus 0.42, tibia II 0.5, tibia III 0.4, tibia IV 0.55.
Colour: Prosoma dark brown, with a distinct stellate spot, sternum black brown, legs yellow brown, partly grey darkened, opisthosoma dark grey.
Prosoma distinctly longer than wide, low, smooth, with a distinct thoracal ridge. Clypeus slightly shorter than the field of the median eyes. Eyes of medium size, all of about the same size, posterior row straight, posterior median eyes separated by slightly more than their diameter. Basal cheliceral articles large, lateral stridulatory files well developed, anteriorly with a larger tooth (arrow in fig. 28), anterior and posterior margin of the cheliceral furrow bear 4 teeth each. The sternum is widely prolongated between the posterior coxae. – Legs long and fairly hairy, sequence of the tibial bristles 2/2/1/1, bristles long and thin, length of the basal one on tibia I 1.2 tibial diameters. Metatarsal trichobothria: See above. – Opisthosoma oval, covered scarcely with short hairs; colulus slightly longer than wide. – Pedipalpus (figs. 29–31; see also above): Patella and tibia slightly longer than wide, tibia with two trichobothria, cymbium basally-ventrally with an outgrowth.

The **relationships** are unsure; the species may be a member of the Erigoninae. The anterior tooth of the ♂-chelicerae is a bit similar to the tooth in *Lessertia* F. P. SMITH 1908; but in *Lesertia* bears tibia III 2 dorsal bristles, a trichobothrium on metatarsus IV is absent, and the pedipalpal tibia bears a long apophysis.

Distribution: Germany, Berlin.

Selected **REFERENCES**

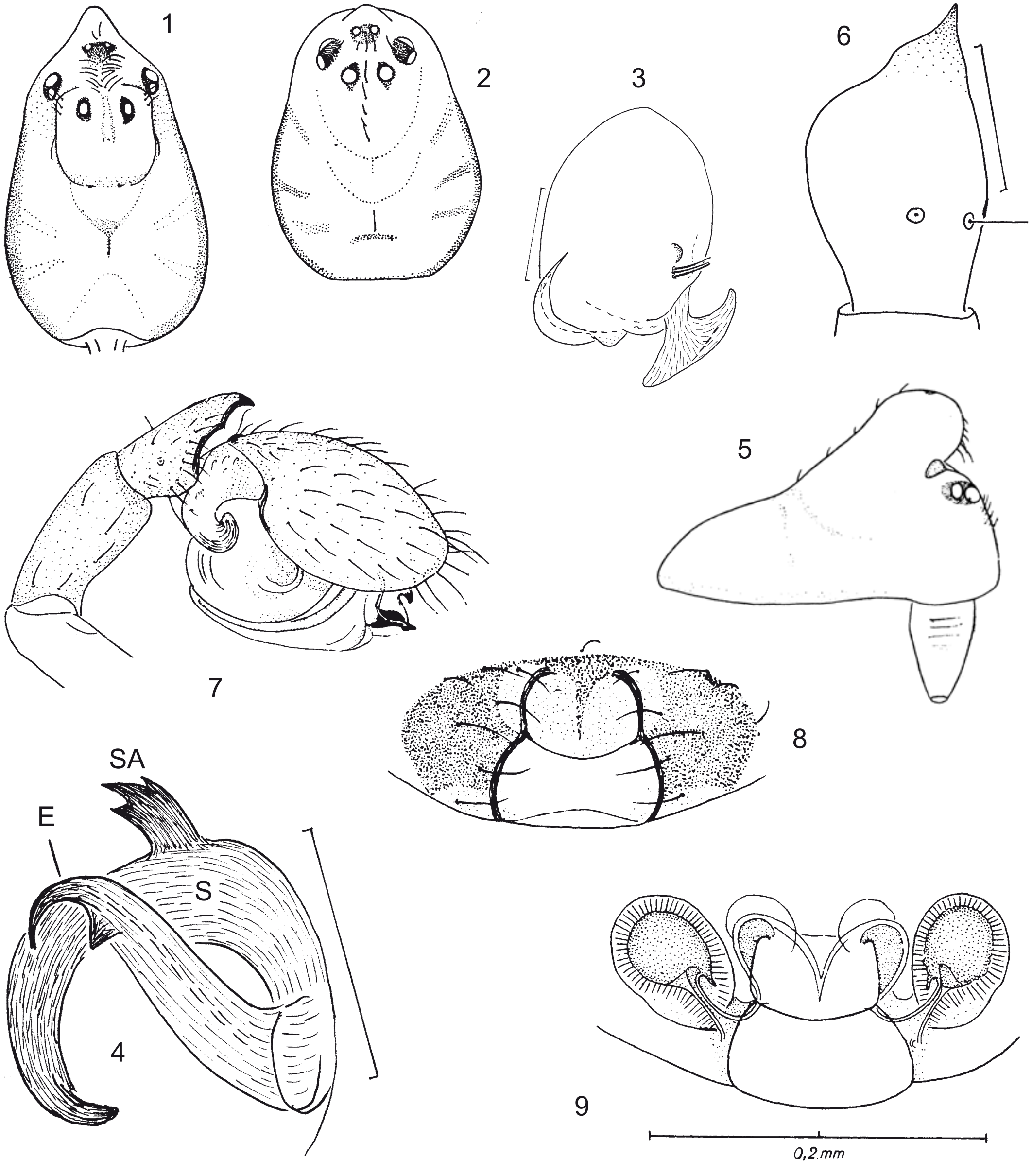
HÄNGGI, A. (1990): Beiträge zur Kenntnis der Spinnenfauna des Kt. Tessin III – für die Schweiz neue und bemerkenswerte Spinnen (Arachnida: Araneae). -- Mitt. schweiz. ent. Ges., 63: 153–167.

WIEHLE, H. (1960): Micryphantidae – Zwergspinnen. -- In DAHL (ed.): Die Tierwelt Deutschlands, 47 (11): 1–620.

-- (1963): Beiträge zur Kenntnis der deutschen Spinnenfauna III. -- Zool. Jb. (Syst.), 90: 227–298.

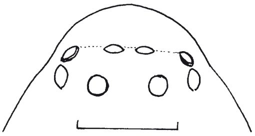
WUNDERLICH, J. (1972): Zur Spinnenfauna, XII. Neue und seltene Arten der Linyphiidae und einige Bemerkungen zur Synonymie (Arachnida: Araneae). -- Senckenbergiana biol., 53 (3/4): 291–306.

-- (1995): Zur Taxonomie Europäischer Gattungen der Zwergspinnen (Arachnida: Araneae: Linyphiidae: Erigoninae). -- Beitr. Araneol., 4 (1994): 643–654).

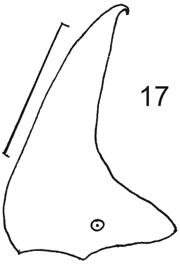


Figs. 1–4: *Nusoncus nasutus* (SCHENKEL 1925) (**n. gen**.); 1–2) dorsal aspects of the ♂- and ♀-prosoma, taken from WIEHLE (1963) (no scale bars); 3) ♂, dorsal-basal aspect of cymbium and paracymbium (tibia removed); 4) ♂, embolus (E), suprategulum (S) and suprategular apophysis (SA) of the r. pedipalpus; scale bars 0.1 in figs. 3–4;

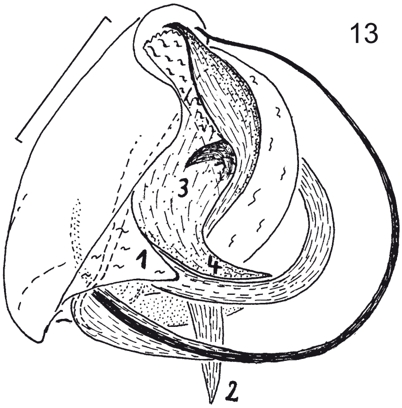
figs. 5–9: *Trichopternoides thorelli* (WESTRING 1862) (**n. gen**.); 5) lateral aspect of the ♂-prosoma; 6) dorsal aspect of the tibia of the r. ♂-pedipalpus; 7) retrolateral aspect of the r. ♂-pedipalpus; 8–9) ♀, epigyne and vulva; scale bars: 0.1 in fig. 6, 0.2 in figs. 8–9, no scale bars in figs. 5 and 7. Figs. 5 and 7–9 are taken from WIEHLE (1960).



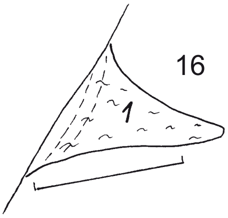
11



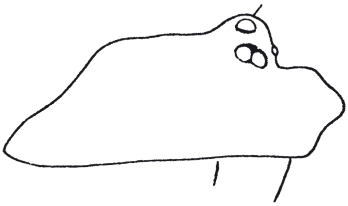
17



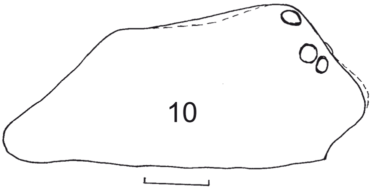
13



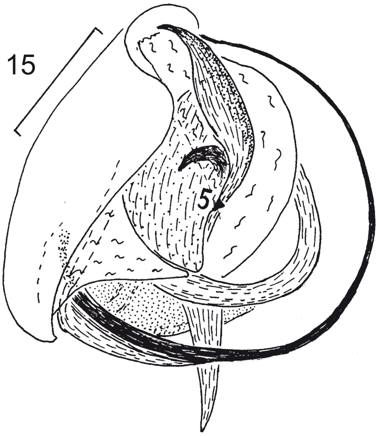
16



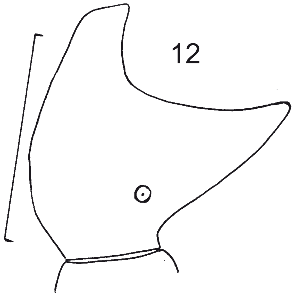
18



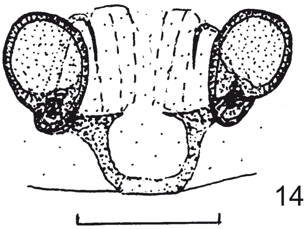
10



15



12



14

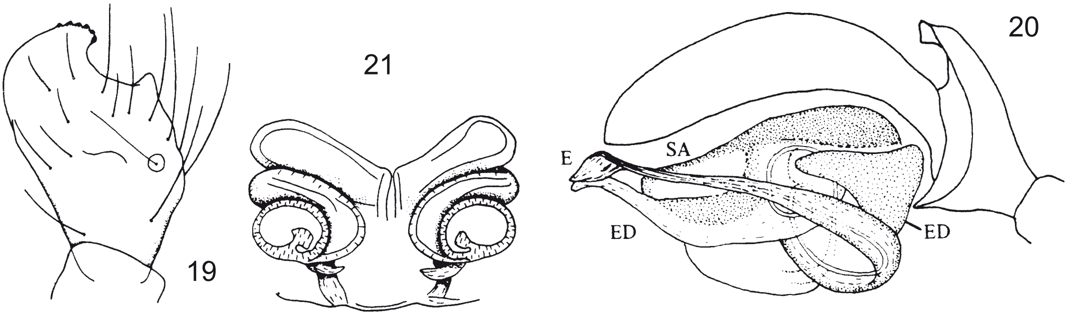
figs. 10–14: <u>*Mecopisthes pumilio*</u> **n. sp**.; 10) ♂, lateral aspect of the prosoma, variability; 11) ♂, dorsal aspect of the anterior part of the prosoma; 12) ♂, dorsal aspect of the tibia of the r. pedipalpus; 13) retroapical aspect of the l. pedipalpus; 14) questionable ♀ of *M. pumilio* n. sp., dorsal aspect of the vulva, taken from HÄNGGI (1990: fig. 13); 1 = "fleshly" apophysis, 2 = radical part of the embolus, 3 = suprategulum, 4 = posterior suprategular apophysis; scale bars: 0.2 mm in fig. 10, 0.1 in the remaining figs.;

fig. 15) <u>*Mecopisthes peusi*</u> WUNDERLICH 1972, ♂, retroapical aspect of the l. pedipalpus; 5 = tooth of the suprategular apophysis; scale bar: 0.1;

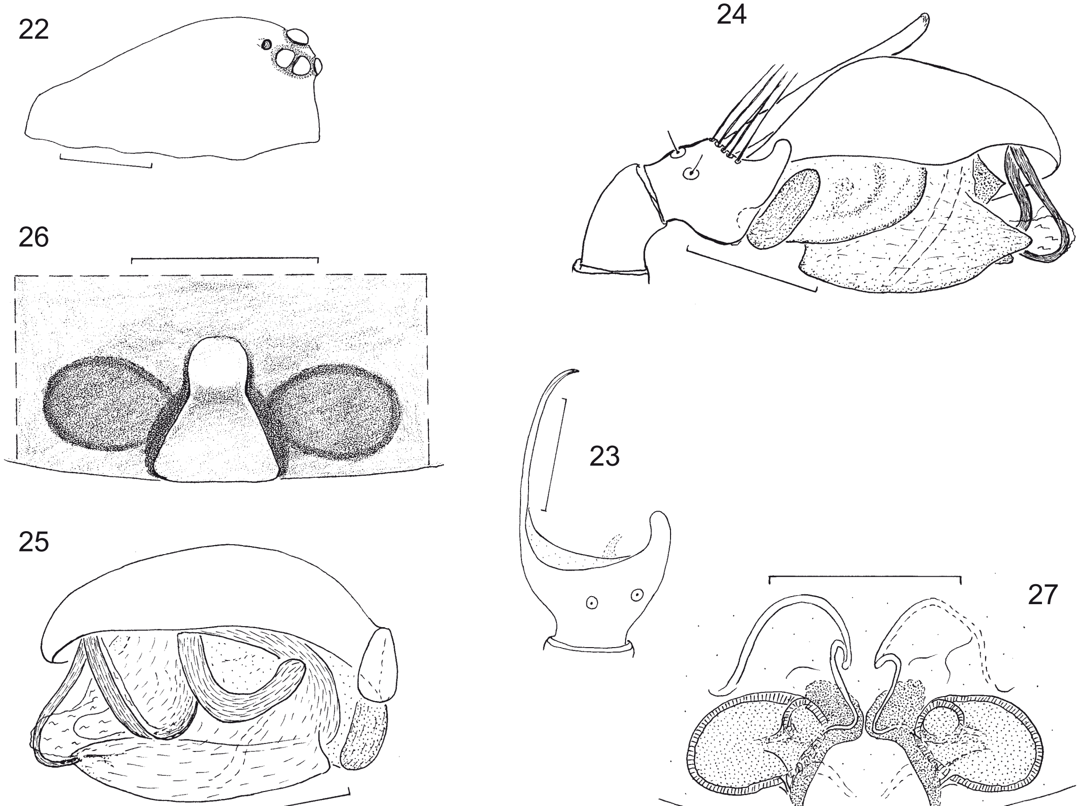
fig. 16) <u>*Mecopisthes silus*</u> (O. PICKARD-Cambridge 1872), ♂, "fleshly" apophysis of the l. pedipalpus, retrolateral aspect; scale bar: 0.1;

figs. 17) <u>*Mecopisthes alter*</u> THALER 1991, ♂, dorsal aspect of the r. pedipalpal tibia; taken from THALER (1991); scale bar: 0.1;

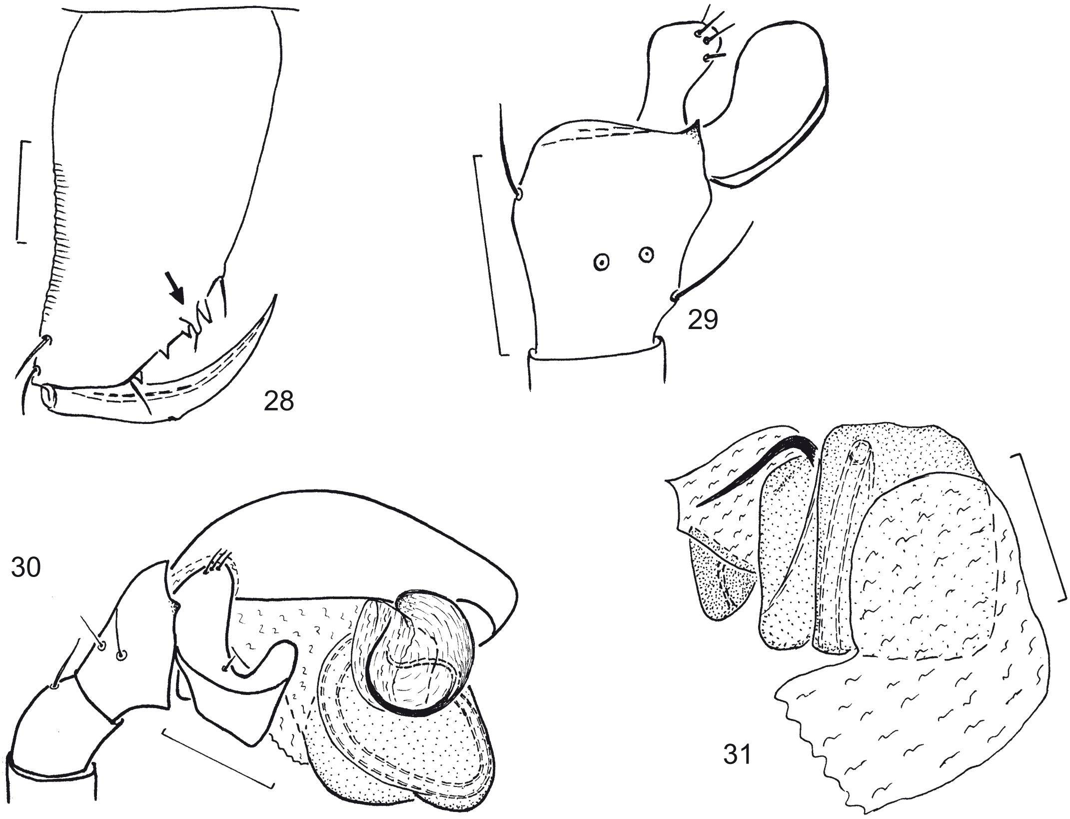
fig. 18) <u>*Mecopisthes latinus*</u> MILLIDGE 1978, ♂, lateral aspect of the prosoma; no scale bar;



figs. 19–21: *Trichoncyboides simoni* (LESSERT 1904) (**n. gen.**); 19) dorsal aspect of the tibia of the r. ♂-pedipalpus; 20) prolateral aspect of the r. ♂-pedipalpus; 21) ♀, vulva; no scale bars. Figs. 19 and 21 are taken from THALER (1973), fig. 20 from MILLIDGE (1977);



figs. 22–27: *Micrargus pervicax* (DENIS 1947); 22) lateral aspect of the ♂-prosoma; 23) dorsal aspect of the tibia of the r. ♂-pedipalpus; 24–25) retrolateral and prolateral aspects of the r. ♂-pedipalpus; 26–27) ♀, epigyne and dorsal aspect of the vulva; scale bars: 0.2 in fig. 22, 0.1 in the remaining figs.;



figs. 28–31: Linyphiidae: Erigoninae gen. & sp. indet., ♂; 28) anterior apsect of the r. chelicera; 29) dorsal aspect of the pedipalpal tibia and paracymbium; 30) retrolateral aspect of the r. pedipalpus with the bulbus expanded; 31) prolateral aspect of the structures of the r. bulbus; scale bars 0.1.

BEITR. ARANEOL., 5 (2008)

IDENTIFICATION KEY TO THE EUROPEAN GENERA OF THE JUMPING SPIDERS (ARANEAE: SALTICIDAE)

JOERG WUNDERLICH, D-69493 Hirschberg.

ABSTRACT: An identification key is presented to the European genera of the Jumping Spiders (Araneae: Salticidae). Few taxonomical remarks are added.

Key words: Jumping Spiders, identification key, Salticidae, Europe.

Acknowledgements: I thank very much H. METZNER for leaving me some figures (nos. 1, 11, 17a), 20, 26a), 31, 32, 38, 47, 49, 50) for publication, T. BLICK for the copy of papers, C. ROLLARD and P. JÄGER for the loan of material, GALINA AZARKINA for some comments.

According to their powerful anterior median eyes which are directed forward (fig. 4), and their extraordinarily long and wide eye field (figs. 2, 11) in three or four rows spiders are easily recognized as Jumping Spiders (family Salticidae). The most frequent way of their locomotion – jumping – is the reason for their name; with the remarkable exception of members of the genus *Ballus* all European salticids jump occasionally. (Wolf Spiders (Lycosidae), Sac Spiders (Clubionidae) and members of numerous other non web-building spider families jump, too, but less frequent, when disturbed). Like Sac Spiders members of the Salticidae spin sac-shaped "buildings" in which they hide for certain time. European salticids build no capture webs in contrast to certain tropical members of this family.

The European Jumping spiders are quite diverse, about 40 genera are known, 10 of these – *Bianor, Cyrba, Habrocestum, Heliophanillus, Mogrus, Phidippus*, *Plexippoides, Plexippus, Saitis* and *Thyene* – occur in Southern Europe but not (some exceptionally) in Central or Northern Europe.

The identification – especially of the females of certain genera – remains difficult; see e.g. the keys of SIMON (1937) and METZNER (1999). Certain characters which are used most often in the keys – e.g. the number of teeth of the posterior cheliceral furrow in dark coloured chelicerae (one has to use a strong light and a dark subsoil), the questionable stridulatory organ between prosoma and femur I (no. 29), the exact position of the eyes and the "rings" of spines of certain leg articles – are frequently hard to recognize. Therefore I use these characters only rarely and/or in combination with other characters.
After the distinctly ant-shaped spiders – *Leptorchestes, Myrmarachne* and *Synageles*, nos. 2–3 in the key – I put the diverse genera *Heliophanus* and *Salticus* (which possess peculiar characters) near the beginning of the key.

Selected characters which are used in the key:
Occasionally I use the habitat and/or the distribution of the spiders in the key, see *Yllenus* (no. 22), *Pseudicius* (no. 30) and *Phidippus* (appendix). Notes on the distribution in the key may help to identify spiders from Central and Northern Europe.
I use the term "megaspine" for strong/thick bristles or spines (e. g. fig. 5). The legs in their sequence are marked from I to IV.
The smallest/tiny spiders are treated within the nos. 15–18. The largest spiders are members of the genera *Carrhotus, Hasarius*, *Marpissa canestrinii*, *Philaeus* and *Phidippus*., see nos. 8, 11, 12, and the appendix.
The posterior cheliceral margin is toothless in *Ballus, Chalcoscirtus*, *Sitticus* and *Yllenus*; in *Hasarius* exists a "keel" (fig. 25), in *Ballus* it bears 2–3 larger teeth (fig. 12), in *Cyrba* 3–5 small teeth (fig. 16); a single tooth exists in the remaining genera. (*Neon* was erroneously regarded as toothless by METZNER (1999: 20)).
(?Stridulatory) bristles on femur I (figs. 7, 27–28) exist in both sexes in *Heliophanillus, Heliophanus, Icius, Phintella* and *Pseudicius,* see METZNER (1999: 20).
Questionable stridulatory cheliceral organs in the male sex: See e. g. *Chalcoscirtus* (no. 16, fig. 15) and *Icius* (no. 30, fig. 29).
The most distinct prosomal wrinkles exist in *Ballus, Bianor* and *Sibianor* (see nos. 9 and 14 in the key).
The presence/number of the leg's trichobothria of the Salticidae are only insufficiently studied; a comprehensive study is needed. In the Euophrydini (fig. 22) and in *Synageles* (no. 3) I found only a single – long – one on tarsus I–III and two ones on tarsus IV but a higher number of trichobothria in the remaining genera, see e. g. figs. 40, 48.
A single bristle-shaped hair at the tip of the ♀-pedipalpus exist in *Marpissa* (fig. 34) and *Synageles*, a pair at the end of the pedipalpus in *Heliophanillus* and *Heliophanus* (no. 5 in the key, fig. 6), a small tooth ventrally at the tip in *Cyrba* (not figured).
The cymbium bears in certain taxa – *Aelurillus v-insignitus*, some *Pseudicius*, *Saitis* and *Thyene* (fig. 52) an apical depression and hairs which are directed to the centre. I

suppose that this may be a secretory or olfactory organ.
See also below: Sexual dimorphism and variability.

Convergently evolved structures and losses exist in numerous structures of the Salticidae and may complicate the determinations as well as do their sexual dimorphism and intraspecific variability, see below. The bristles of leg I–II are strongly reduced e. g. in *Icius* and *Salticus*; they are also reduced in ant-shaped spiders (nos. 1–3 in the key). An ant-shaped body evolved two times in European Salticidae: (a) in the ancestor of the related genera *Leptorchestes* and *Synageles* and (b) in *Myrmarachne*. A reduced number of tarsal trichobothria exist in *Synageles* and in the Euophrydini; retromarginal cheliceral teeth are convergently lost in several taxa, see above. Extremly long basal articles of the male chelicerae exist in *Myrmarachne* (in an anterior parallel position, figs. 1–2) and *Salticus* (in an oblique and diverging position, fig. 3). A circular embolus is known in European genera from *Euophrys, Mogrus, Pseudeuophrys, Saitis, Sitticus, Talavera* and other genera; a very long – circular/spirally – embolus exist in *Ballus* (in a vertical position) as well as in *Myrmarachne* and in *Thyene* (in a horizontal position). Bristle-shaped hairs of the female pedipalpal tarsus evolved in *Heliophanus* (fig. 6), *Marpissa* (fig. 34) and *Synageles*. A special depressed and hairy structure of the cymbial tip evolved in *Aelurillus* sp. (e.g. in *v-insignitus*), some *Pseudicius*, *Saitis* and *Thyene* (fig. 52), see above.

Sexual dimorphism, intrageneric and intraspecific variability. In most species exist a distinct sexual dimorphism mainly in the colour of body and legs, in structures of leg I and of the chelicerae (both may be enlarged in the male sex, see *Heliophanus* (no. 5 in the key), and *Myrmarachne* (no. 2) or may be otherwise modified (stridulatory structures?): See *Chalcoscirtus* (no. 16) and *Icius* (no. 30). Leg I may be powerful and more hairy in the male sex, e. g. in *Sibianor*); in the male of *Saitis* leg III is enlarged and covered with very long hairs (figs. 47–48). Males of *Philaeus chrysops* and *Pellenes ostrinus* (photo 387) possess a mainly red or redbrown opisthosomal dorsum – in contrast to the inconspicuous females –, which is probably a “warning colour” similar to males of certain species of the genus *Eresus* (Eresidae). In *Cyrba algerina* the females possess a distinctly lighter colour than males. In the tiny members of *Talavera* exist only a weak sexual dimorphism in the colour of body and legs. Males of numerous salticid species possess a leathery or scutate dorsal part of the opisthosoma; this character is variabe within several genera and occasionally within the same species. Within certain genera the prosoma is more or less wrinkled or even smooth, e. g. in *Heliophanus*. Leg IV is usually longest (as a jumping leg), but in *Habrocestum*, *Neaetha* and *Pellenes* leg III – especially the femur – is longer than IV, and in certain (!) species of the genera *Aelurillus* and *Phlegra* the leg III – especially the articles patella + tibia – is also longer than IV; in members of *Mogrus, Thyene* and *Saitis*-♂ legs III and IV are almost equal in length or III is longer. The relative length of certain legs may be different in the sexes, e. g. in *Aelurillus, Saitis* and *Sibianor*. In members of *Aelurillus* exist usually a dorsal megaspine on tibia III and IV (see fig. 39) but – especially in females – it may be absent on some (!) tibiae of the same specimen as an intraspecific variability, see no. 24 in the key.

Taxonomy, subgenera. *Dicroneon* is regarded as a subgenus of *Neon*; see the paper on the tribus Euophrydini in this volume. *Asianellus* has characters common to *Aelurillus*; it may be regarded as a genus of its own or a subgenus of *Aelurillus*. *Heliopha-*

nillus is very close to *Heliophanus* and may also be regarded as a subgenus only. In Europe occurs furthermore – besides *Heliophanus* – the subgenus *Helafricanus* (only *H*. *edentatus* SIMON), see METZNER (1999: 98); similar cases are *Pellenes*: *Pellenes* and *Pelmultus*, see ALICATA & CANTARELLA (2000). – See also below: "*Hyllus*" (appendix) and *Afraflacilla*: Key no. 30 (*Pseudicius*). The relationships of ?*Pseudicius epiblemmoides* (*Afraflacilla*?) are unsure, see DOBRORUKA (2001).
According to LOGUNOV (2001) *Asianellus leiopoldae* METZNER 1999 is actually a member of *Aelurillus* and *Pseueuophrys sengleti* METZNER 1999 is actually a member of *Saitis*. In *Bianor albobimaculatus* and *Sibianor aurocinctus* the tables 83 and 84 in METZNER (1999) have been interchanged erroneously.

Key to the genera of European Jumping Spiders :

It is a pleasure for me to draw attention to the important work of H. METZNER (1999) on the Salticidae of Greece in which most European genera are treated; only *Yllenus* and the recently to the Azores introduced genus *Phidippus* are lacking, see no. 22 and the appendix. In most genera I citate pages and tables (t) of the work of METZNER. See the index at the end of this paper.
If not otherwise noted the spiders have a medium body size of 3–4 or 5 mm and occur in Central Europe. Tiny spiders are treated in the nos. 15–20, and 26.

1 Spiders distinctly ant-shaped (few hairs, slender body and legs, usually shining body, opisthosoma frequently with a saddle-shaped inclination and a white band crossover, e. g. fig. 1). Legs quite slender, tibiae III–IV usually without thick megaspines (in *Leptorchestes* occasionally few short distal-ventral ones may exist) 2

- Spiders not distinctly ant-shaped (*Heliophanus* – no. 5 – slightly ant-shaped and with shining body). Legs more stout, hairy and usually more spiny, tibiae III–IV with or without megaspines, in *Heliophanus* and *Heliophanillus* with megaspines (similar to fig. 39). . 4

2(1) Anterior part of the prosoma raised like a step (fig. 2), tibia II ventrally with megaspines. ♂: Chelicerae stongly and almost horizontally protruding in a parallel position (figs. 1–2) (chelicerae strongly diverging and obliquely protruding in *Salticus*-♂, no. 6, fig. 3). Opisthosoma with a dorsal shield (scutum). ♀: Apical article of the pedipalpus strongly thickened. Body length 5–6.5 mm. Only *M. formicaria*. METZNER: 79, t. 44 . . . . *Myrmarachne*

- Anterior part of the prosoma not raised, tibia II without ventral megaspines. ♂: Chelicerae not horizontally protruding, opisthosoma without a scutum. ♀: Apical article of the pedipalpus only slightly thickened. Body length usually 3–6 mm. See METZNER: t. 2–5 3

3(2) Body length up to 4 mm, all coxae ventrally light/yellow, embolus thin, tip of the ♀-pedipalpus with a well developed bristle-shaped hair similar to fig. 34. METZNER: 38–39. t. 5 . . . . *Synageles*

- Body length most often 4–6 mm, coxa III – and occasionally I – ventrally black, embolus thick, tip of the ♀-pedipalpus without bristle-shaped hair. In Central Europe only *L. berolinensis*. METZNER: 36–38, t. 2–4 . . . . *Leptorchestes*

4(1) Femur of the ♂-pedipalpus in almost all species ventrally in some distance from its base with a large outgrowth which stands widely out and may be divided) (figs. 8–9) (exceptions are *Heliophanus edentulus* and *Heliophanillus fulgens*, see below). Tarsus of the ♀-pedipalpus at its end (**LATERALLY** of the tip) with a pair of thin black bristle-shaped hairs (fig. 6) which are **S-SHAPED** bent in contrast to the light hairs which are bent only once; the prolateral hair is usually weakly developed. Similar tiny special hairs exist at the end of the cymbium. Medium sized spiders, body frequently "metallic" shining, white markings of the body very variabel 5

- Ventral femoral outgrowth of the ♂-pedipalpus absent or smaller and usually near to the base of the femur (figs. 35, 55) (a blunt outgrowth in the distal half exists in *Aelurillus v-insignitus*, no. 36). End of the ♀-pedipalpus (and the end of the cymbium) without a pair of small bristle-shaped hairs, with normal hairs only or with a single bristle-shaped hairs directly at its tip (fig. 34) but never laterally of its tip. Tiny to large spiders 6

5(4) ♂: Femur of the pedipalpus ventrally in some distance from the base with a large outgrowth which stands out and may be divided (figs. 8–9) or – rarely – with a retroapical apophysis, see METZNER: t. 63 (*H. edentulus*) (photos 385–386). . . *Heliophanus*

- ♂: Femur and patella of the pedipalpus without apophyses, tibia of the pedipalpus with 2 retrolateral apophyses which are widely spaced at their base. Only *H. fulgens* (= *Heliophanus f.*). METZNER: 96, t. 62. Southern Europe . . . . *Heliophanillus*

6(4) ♂♀: Tibia I without megaspines, metatarsus I bears at most a single megaspine at its end. Opisthosoma with more or less distinct transverse white bands on a dark ground, never with longitudinal white bands. ♂: Chelicerae unusually long, distinctly diverging and obliquely protruding (fig. 3) (compare *Myrmarachne*, no. 2). METZNER: 111–118, t.77–82 . . . . *Salticus*

- ♂: Chelicerae not unusually long. ♀: Tibia/metatarsus I with several megaspines, pattern of the opisthosoma differend. – Note: Except *Ballus* (no. 9) are the members of the following seven genera only known from Southern Europe. If not *Ballus* go on with spiders from Central and Northern Europe to no. 13 7

7(6) Prosoma in both sexes anteriorly with a brush of hairs which is directed forward and may be rubbed off to black stumps (arrow in fig. 51), laterally frequently strongly convex, opisthosoma frequently long and slender, similar to *Marpissa* (no. 23, photo 384). Copulatory organs of the common *T. imperialis* (figs. 52–54): Cymbium apically with a hairy depression, embolus long and widely spirally. Southern Europe. METZNER: 132–134, t. 97–98 . . . . *Thyene*

- No such prosomal brush of hairs, copulatory organs different, apical cymbial depression absent or present, embolus not coiled in this way. 8

8(7) The posterior cheliceral margin bears 2–5 teeth (figs. 12, 16) which are well observable on their light background. 9

- Posterior cheliceral margin smooth or with a single tooth. 10

- Posterior cheliceral margin with a keel (fig. 25). ♂-pedipalpus (fig 26): Tibia with long white prolateral hairs, longer than the small cymbium/bulbus. ♀: Epigyne fig. 26a. Only *H. adansoni*. In Central Europe only in warm houses. . . . . *Hasarius*

9(8) Body length usually 4–5 mm, prosoma not wrinkled, cheliceral retromargin with 3–5 tiny teeth (fig. 16), body not flattened, opisthosoma anteriorly convex. ♂-pedipalpus (fig. 17) with 2 patellar and 2 long tibial apophyses. ♀: Epigyne fig. 17a; posteriorly with a w-shaped sclerotized structure. The tip of the pedipalpal tarsus bears a claw. The female is distinctly lighter coloured than the male. Only *C. algerina*, Southern Europe. . . . . *Cyrba*

- Body length usually 3–4 mm, prosoma distinctly wrinkled, cheliceral retromargin with 2–3 larger teeth (fig. 12), body flattened, anterior opisthosomal margin wide and straight or even concave (fig. 11). ♂-pedipalpus: No patellar and a single tibial apophysis, embolus spirally and in a distal-vertical (!) position. Both sexes dark coloured. These spiders never jump. METZNER : 40–41, T. 6–7 . . . . *Ballus*

10(8) Prosoma widest anteriorly, smaller at the second eye row (fig. 47). ♂: Leg III distinctly enlarged, metatarsus, tibia and occasionally patella and femur dorsally and ventrally with a conspicuous seam of long hairs (fig. 47a) and larger than IV. Embolus circular, in a distal position. ♀: Epigyne with a pair of larger depressions. Southern Europe. METZNER: 57–60, t. 22–24 . . . .*Saitis*

- Shape of the prosoma different, articles of the ♂-leg III without a seam of long hairs, of different length. Copulatory organs different 11

11(10) Opisthosoma dorsally in the male red with a black longitudinal band in the middle, in the female very variable, usually black with a pair of 2 longitudinal white bands or spots. Cymbium very long and strongly bent. Only *C. chrysops*. Largest Jumping Spiders in Central Europe, body length 7–8 mm. METZNER: 14o, t. 105–106 . . . . *Philaeus*

- Colour of the opisthosoma and cymbium different 12

12(11) Tibia of the ♂-pedipalpus (dorsal aspect) as long and voluminous as the cymbium (fig. 13) (compare *Hasarius* no. 8). Epigyne: Fig. 14. Body length 4–6 mm. Only *C. xanthogramma* . . . . *Carrhotus*

- Tibia of the ♂-pedipalpus distinctly smaller than the cymbium. Epigyne different. Body length frequently less than 4 mm. 13

13(12) Prosoma strongly wrinkled (similar to fig. 11) and almost hairless. Body length 2.7–4 mm. ♂-opisthosoma with a dorsal shield. 14

- Prosoma in few species weakly wrinkled (e. g. in *Icius hamatus*, no. 30), usually hairy. ♂-opisthosoma with or without a dorsal scutum. 15

14(13) Body length usually 3.2–4 mm. ♂: Tibia I fairly thickened, bulbus flat. Southern Europe, *B. albobimaculatus*. METZNER: 119, t. 84 (sub *aurocinctus*) . . . . *Bianor*

- Body length usually 2.7–3.5 mm. ♂: Tibia I strongly thickened, the bulbus stands distinctly out. ♀: Epigyne with a u-shaped structure. In Central Europe only *S. (= Bianor) aurocinctus* (= *aenescens*). METZNER: 118, t. 83 (sub *Bianor albobimaculatus)*. . . . . *Sibianor*

15(13) Tarsi I–III dorsally with only a single – long – trichobothrium (arrow in fig. 22) (it is longer than the surrounding hairs and usually in a more erect position), tarsus IV with two trichobothria. Retrolateral tibial apophysis of the ♂-pedipalpus – with the exception of *Chalcoscirtus* – usually long, slender and straight (fig. 13), in *Talavera* completely absent. Small or most tiny salticid spiders of Europe, body length 1.3 – ca. 3 mm. See the paper on the tribus Euophrydini in this volume. 16

- Tarsi I–III with two or more trichobothria in a row (fig. 40), IV with more than two ones (the trichobothria are best recognizable on light coloured tarsi). Body length not less than 2 mm, usually more than 3 mm. Tibial apophysis of the ♂-pedipalpus always present, very variable, in some taxa divided (figs. 42, 55). 21

16(15) Cheliceral retromargin toothless. Body almost black, shining. ♂: Chelicerae retrofrontally near the middle with a corniculate (stridulatory?) hump (fig. 15), opisthosoma in almost all males covered with a large and smooth shield. Prosomal length usually 1–1.2 mm METZNER: 45–47, t. 11–12 . . . . *Chalcoscirtus*

- Cheliceral retromargin with a small tooth which may be indistinct. Body not almost black and shining. ♂-opisthosoma without a large and glancing shield, in certain males leathery or with a small shield. 17

17(16) Eyes of the two posterior rows surrounded by large black rings (fig. 20). Prosomal length usually 1–1.4 mm. *Neon* 18

- No such rings around the two posterior eye rows 19

18(17) Basal part of the embolus with a non-sclerotized light structure which bears numerous denticles (arrow in fig. 21). Vulva with large receptacula, medially with a pair od thick-walled glands. Subgenus *Neon* . . . . *Neon*

- Basal part of the embolus without such structure. Vulva with tube- or sac-shaped structures. METZNER: 65–66, t. 30–31. Subgenus *Dicroneon*. . . . . *Neon*

19(17) Paired retrolateral tarsal claws IV with at least a single large tooth. Prosoma dark brown, medially with a light spot or band. Tibial apophysis of the ♂-pedipalpus usually of normal size. Prosomal length usually 1.5–2 mm. METZNER: 53–57, t. 18–19, 21. Photo 389 . . . . *Pseudeuophrys*

- Paired tarsal claws IV toothless. Prosomal colour variable. Tibial apophysis of the ♂-pedipalpus thin or completely absent (*Talavera*) 20

20(19) Legs not annulated but usually with longitudinal lateral dark bands. ♂-tibia I usually thickened and ventrally with numerous long hairs. Tibia of the ♂-pedipalpus retrolaterally with an apophysis which may be very thin and indistinct (fig. 23) (the investigation can be more difficult by hairs which cover cymbium and tibia), tegulum without an lobe, shape of the embolus almost circular. Prosomal length usually 1.5–2 mm. METZNER: 47–52, t. 13–17 . . . . *Euophrys*

- Legs usually distinctly annulated at least in the female and on the male tibia, metatarsus and tarsus III and IV. ♂-tibia I not thickened, with few short hairs. Tibia of the ♂-pedipalpus without retrolateral apophysis, tegulum with a distal lobe (L in fig. 24). Prosomal length 0.8–1.3 mm. METZNER: 64, t. 29 . . . . *Talavera*

21(15) Opisthosoma in both sexes soft and stout (fig. 49), usually with a pair of light spots in the posterior half, rarely with a single spot or unicoloured. Cheliceral retromargin toothless, promargin with 2–6 teeth. ♂-pedipalpus usually similar to fig. 50, with a non-divided tibial apophysis and a flat bulbus. (= *Attulus*). METZNER: 80–87, t. 45–52. . . . *Sitticus*

- Combination of characters different, ♂-opisthosoma soft, leathery or scutate. Cheliceral retromargin – with the exception of *Yllenus*, no. 22 – with a tooth 22

22(21) Both margins of the cheliceral furrow toothless. *Y. arenarius*: ♂-pedipalpus (figs. 55–56) very particularly shaped, with stout articles, a small ventral outgrowth at the femoral base (arrow), tibia apophysis in *arenarius* very long, cymbium modified. ♀: Epigyne fig. 57. Body length usually 5–6 mm. At sandy localities like dunes near the sea. In Germany only *Y. arenarius* . . . . *Yllenus*

- Cheliceral retromargin with a tooth. Copulatory organs different; the articles of the ♂-pedipalpus may be stout (e. g. in *Menemerus*, no. 32, fig. 35) 23

23(22) Sternum strongly elongated between the anterior coxae und so NARROW in this position that they are separated by only less than half of their diameter (arrow in fig. 33). Opisthosoma (photo 384) long, slender and flattened. Tip of the ♀-pedipalpus with a small bristle-shaped hair (fig. 34). (Incl. *Mendoza canestrinii*). METZNER: 137–140, t. 102–104; photo 384 . . . . *Marpissa*

- Sternum anteriorly not prolongated, anterior coxae separated usually by their diameter or more. Opisthosoma most often stouter and not flattened 24

24(23) Tibia III and IV always without a dorsal megaspine (lateral tibial megaspines may exist). Chelicerae longer. Usually a single tibial apophysis of the ♂-pedipalpus but two apophyses exist in some species of *Pseudicius.* (In doubt go both ways) 25

- Tibia III and IV bear in the basal half most often a dorsal megaspine (fig. 39), variable in certain members – especially females! – of the diverse genus *Aelurillus* in which the chelicerae are shorter than the prosomal height (fig. 4) and in Phlegra; the tibia of the ♂-pedipalpus bears two apophyses and a scinny conductor exist (figs. 10–10a) . . . 33

25(24) Leg III longer than IV. Epigyne with a medial cap 26

- Leg III shorter than IV 27

26(25) ♂-opisthosoma dorsally with a longitudinal narrow white band which may be fragmented similar to *Phlegra*, no. 34; it is indistinct in *ostrinus* (photo 387). Embolus guided by a wide apophysis. Epigyne usually with a longitudinal medial ridge. METZNER: 121–131, t. 86–96; photo 387 . . . . *Pellenes*

- No such band of the ♂-opisthosoma, no apophysis of the embolus, the epigyne may be similar. In Central Europe only *N. membranosa*, body length usually 3–3.5 mm METZNER: 120, t. 85 . . . . *Neaetha*

27(25) ♂: Position of the long and bent left embolus **COUNTERCLOCKWISE** (fig. 31) (unusual in European Salticidae), with a large basal part. Chelicerae retroanteriorly with a depression and in the distal half retrofrontally with an edge (both may be indistinct). ♀: Epigyne with a pair of small pits in an anterior position (e. g. fig. 32). In Central Europe only *M. nidicolens*. METZNER: 42–44, t. 9–10. Photo 390. . . . . . . *Macaroeris*

- ♂: Left embolus straight or in a clockwise position (fig. 30); a cheliceral edge exist in certain members of *Icius*. ♀: Epigyne different 28

28(27) Embolus very short (fig. 37). Epigyne fig. 38. Eyes of the 2. and 3. row surrounded by large black rings (similar to *Neon*, no. 18, fig. 20, *Pellenes*, no.26 and *Pseudicius*, no. 30). In Central Europe only *P. castriesiana* (= *Icius c.*, *Telamonia c.*). METZNER: 88, t. 53 . . . . *Phintella*

- Eyes similar or different, embolus longer, epigyne different 29

29(28) ♂♀: Femur I usually prodistally with 1–2 rows of thin bristles (e. g. figs. 27–28) or a single one, which may be hard to recognize on the dark femur on certain species like *Icius subinsermis*; prosoma slender lateral margins almost parallel 30

- No such bristles on femur I in this position; prosoma different, wider 31

30(29) ♂-chelicerae retrofrontally with a sharp (stridulatory?) edge (carina) (fig. 29). In Central Europe *I. hamatus*. METZNER: 96, t. 61 . . . . *Icius*

- ♂-chelicerae without carina. In Central Europe *P. encarpatus* and ?*P*. (= *Afraflacilla*) *epiblemmoides*. METZNER: 88–95, 54–60 . . . . *Pseudicius*

31(29) ♂: Gnathocoxae retrodistally with a small hook (arrow in fig. 18) (similar to *Heliophanus*, no. 5). Embolus short, with a strongly sclerotized, slender and rectangular basal outgrowth (fig. 19). ♀: Epigyne anteriorly with an arched structure. METZNER: 41–42, t. 8 . . . . *Dendryphantes*

- ♂: Gnathocoxae without such hook, embolus and epigyne different, epigyne with a pair of conspicuous pits 32

32 (31) ♂-pedipalpus (e. g. figs. 35–36) with stout articles, femur strongly bent, near the base with a ventral outgrowth or hook, tegulum with a longitudinal furrow (arrow), embolus thick. In Central Europe *M. falsificus*, epigyne fig. 36a). METZNER: 143–146, t. 108–110. Photo 388 . . . . *Menemerus*

- ♂-pedipalpus: Articles more slender, femur not strongly bent nor with a ventral outgrowth near to the base, tegulum without longitudinal furrow, embolus long, its position in a wide loop near the cymbium. Southern Europe. METZNER: 150–152, t. 116–117. . . . . *Mogrus*

33(24) Metatarsus I and II usually prolaterally and retrolaterally (dorsally of the ventral megaspines) without a megaspine except at the end. Leg III most often shorter than IV. METZNER: 67, t. 33 34

- Metatarsus I and II prolaterally and retrolaterally (dorsally of the ventral megaspines) with an additional megaspine in the basal half (arrow in fig. 5). Length of legs III and IV: See no. 35. 35

- See the appendix: “*Hyllus*” and *Phidippus*.

34(33) Scopula of tarsus I and II only near the tarsal claws. Tibia of the ♂-pedipalpus with a single apophysis. METZNER: 146–150, t. 111–114 . . . . *Evarcha*

- A scopula exists in the distal half of tarsus I and II (fig. 40). ♂: Prosoma and opisthosoma dorsally with1–4 longitudinal light bands. Two tibial apophyses of the ♂-pedipalpus (fig. 41; similar to *Aelurillus*, fig. 10a) or with a divided tooth. Epigyne posteriorly with a large sclerotized plate. METZNER: 67–71, t. 32–35 . . . . *Phlegra*

35(33) Opisthosoma short/stout (similar to fig. 40). Leg III in *Habrocestum* distinctly longer than IV, in most ♂ and some ♀ of *Aelurillus* leg III is not shorter or even longer than IV 36

- Opisthosoma longer. Leg III always shorter than IV. Southern Europe 37

36(35) ♂: Opisthosoma: Anterior margin with a semicircular white band crossover, femur III much longer than femur IV, pedipalpus with a single tibial apophysis and a long embolus, conductor present or absent. Southern Europe. METZNER: 60–64, t. 25–28.. . . . . *Habrocestum*

- ♂: Opisthosoma never with a white band in this position but frequently with white spots or one or three longitudinal white median band(s), pedipalpus (e.g. figs. 10a–b) usually with two tibial apophyses (the retrodorsal one may be hidden by hairs), a short and thin embolus and a scinny conductor. ♀: Introductory openings in an anterior position. METZNER: 73–79, t. 37–43; 71 . . . . *Aelurillus*

- ♂: Opisthosoma similar, pedipalpus with two tibial apophysis, but femur I dorsally-apically with 4 bristles and a medial **HAIR** in a transverse row (in *Aelurillus* with 5 bristles in this position. ♀: Introductory openings in a posterior position. METZNER: 71, t. 36 (*A. festivus*) . . . . *Asianellus*

37(35) Opisthosoma dorsally mainly dark. ♀: Legs distinctly annulated, epigyne e. g. as in fig. 44. ♂-pedipalpus (fig. 43) with extremely long light hairs, cymbium with a pointed retrobasal apophysis which is directed to a pointed tibial apophysis, embolus long and thin, originating in the basal half of the bulbus. Two species in Southern Europe. METZNER: 134 (sub *Hyllus)*, 155, t. 99, 115 (sub *Hyllus*) . . . . *Plexippoides*

- Opisthosoma dorsally with a longitudinal light medial band within a pair of dark bands. ♀: Legs not annulated, epigyne e. g. as in fig. 46. ♂-pedipalpus (fig. 45) with wide cymbium and bulbus, retrobasal cymbial apophysis absent, embolus basally thick, originating in the distal half of the cymbium. Two similar species in Southern Europe. METZNER: 135–137, t. 100–101 . . . . *Plexippus*

Appendix on two additional taxa from Southern Europe and the Acores:

“*Hyllus*” *insularis* METZNER 1999: 150, t. 115. Body length ca. 5.5–6.5 mm, copulatory organs figs. 58–59. Southern Europe. According to LOGUNOV (2001) *insularis* is not a member of the genus *Hyllus* and its relationships are unclear. See the key no. 37.

Phidippus. This is a genus of the new world. *P. audax* (HENTZ 1848) (figs. 60–62) was recently introduced from North America to the Azores; BORGES & WUNDERLICH (in prep.). These spiders are the largest Jumping Spiders in Europe, body length usually 6–15 mm (♀), very hairy; their chelicerae are anteriorly iridescent (blue and green), the distal part of the tegulum bears numerous tiny furrows, the epigyne possesses a large depression and a deep posterior inclination.

Index of the genera and subgenera which are treated in the book of METZNER (1999); numbers to the genera in the key above, the figures of the genera, and few photos (384–390):

Aelurillus: 72–79, t. 37–43; no. 36, figs. 4–5, 10a–10b,
Afraflacilla: 88, t. 54; see *Pseudicius,* no. 30,
Asianellus: 71, T. 36 strongly related to *Aelurillus*, no 35,
Attulus: See *Sitticus*,

Ballus: 40–41: t. 6–7; no. 9, figs. 11–12,
Bianor: 119, t. 84 (not 83!) (see *Sibianor*); no. 14,

Carrhotus: 142, t. 107; no. 12, figs. 13–14,
Chalcoscirtus: 45–47, t. 11–13; no 16, fig. 15,
Cyrba: 35, t. 1; no. 9, figs. 16–17a,

Dendryphantes: 41–42, t. 8; no. 31, figs. 18–19,
Dicroneon: 65–66, t. 30–31 (subgenus of *Neon*); no. 18,

Euophrys: 47–52, t. 13–17; no. 20, figs. 20–21,
Evarcha: 146–150, t. 111–114; no. 34,

Habrocestum: 60–64, t. 25–28; no. 35,
Hasarius: 152, t. 118; no. 8, figs. 25–26a,
Heliophanillus: 96, t. 62; no. 5,
Heliophanus (and subgenus *Helafricanus*): 97–111, t. 63–76; no. 5, figs. 7–9, photos 385–386,
“*Hyllus*”: 150, T. 115, no. 37; see the appendix, figs. 58–59,

Icius: 96, t. 61; no. 30, figs. 27–30,

Leptorchestes: 36–38, t. 2–4; no. 3,

Macaroeris: 42–44, t. 9 –10; no. 27, figs. 31–32, photo 390,
Marpissa s. l. (incl. *Mendoza canestrinii*), 137–140, t.102–104; no. 23, figs. 33–34, photo 384,
Mendoza: See *Marpissa*,
Menemerus: 143–146, t.108–110; no. 22, figs. 35–36a, photo 388,
Mogrus: 150–152, t. 116–117; no. 32,
Myrmarachne: 79, t. 44; no. 2, figs. 1–2,

Neaetha: 120, t. 85; no. 26,
Neon (incl. the subgenus *Dicroneon*): 65–66, t. 30–31; no. 17–18, figs. 20–21,

Pellenes: 121–131, t. 86–96; no. 26 (incl. subgenus *Pelmultus*), photo 387,

REFERENCES cited

ALICATA, P. & CANTARELLA, T. (2000): I Salticidi di Sicilia: stato della conoscenza e descrizione di nuove specie (Araneae Salticidae). –- Mem. Soc. entom. ital., 78 (2): 485–498.

DOBRORUKA; L. J. (2001): *Pseudicius epiblemmoides* (Araneae: Salticidae) in Central Europe. -- Arachnol. Mitt., 22: 50–54.

KASTON, B. J. (1981): Spiders of Connecticut. 1020pp. Revised edition. State Geol. Nat. Hist. Survey Connect.

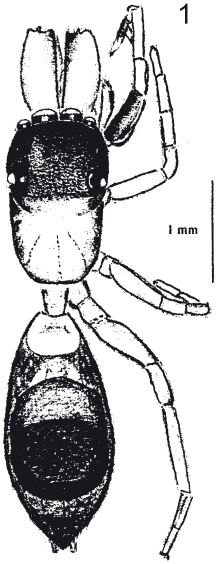
LOGUNOV, D. V. (2001): New and poorly known species of the jumping spiders (Aranei: Salticidae) from Afghanistan, Iran and Crete. -- Arthropoda Selecta, 10 (1): 59–66.

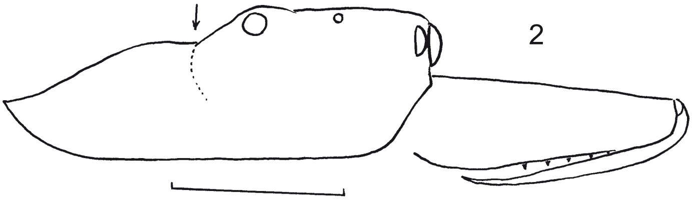
-- & MARUSIK, Y. M. (2003): A revision of the genus Yllenus Simon, 1868 (Arachnida, Araneae, Salticidae). -- KMK Scientific Press Ltd. 168pp.

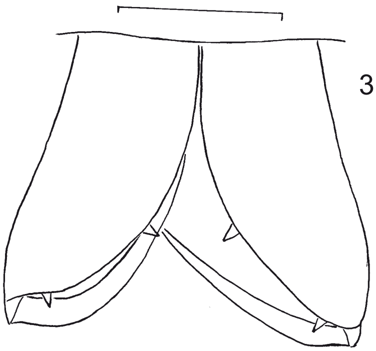
PROCZYNSKI, J. (1992): Salticidae (Araneae) of the Old World and Pacific Islands in several US collections. -- Ann. Zool., 44 (8): 87–279.

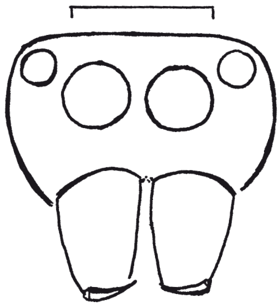
METZNER, H. (1999): Die Springspinnen (Araneae, Salticidae) Griechenlands. -- Andrias, 14: 1–279. Staatliches Museum für Naturkunde Karlsruhe.

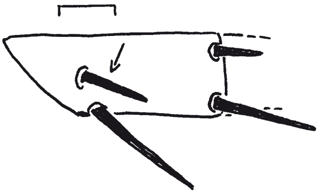
SIMON, E. (1937): Salticidae. – Les Arachnides de France, 6 (5): 1146–1272.


1


2


3

4



5

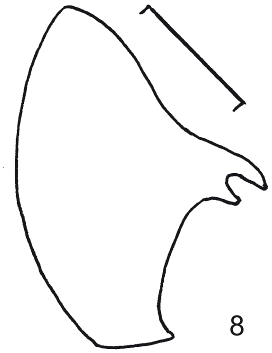
Figs. 1–2: Myrmarachne formicaria (DE GEER 1778), ♂; 1) dorsal aspect of the body; 2) lateral aspect of the prosoma. Note the anterior part of the prosoma which is raised like a step (arrow). Scale bar = 1.0 mm;

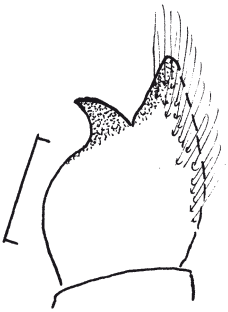
fig. 3: Salticus sp., ♂, anterior aspect of the chelicerae. Scale bar = 0.5;

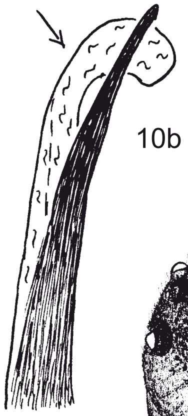
figs. 4–5: Aelurillus sp., ♂♀; 4) anterior aspect of the prosoma; 5) prolateral aspect of the r. metatarsus I, with lateral megaspine (arrow). Scale bar = 0.5 and 0.2;


6

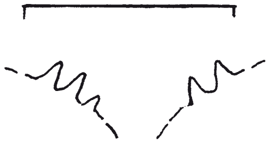

7

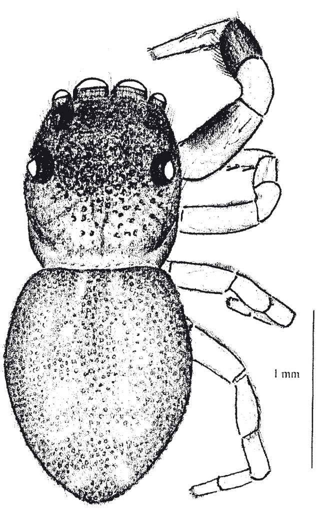

8


10a


10b


9


12



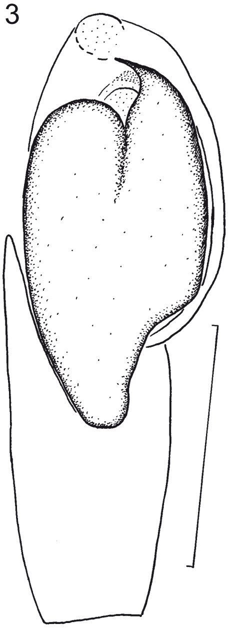
11

figs. 6–9: *Heliophanus* sp.; 6) ♀, distal part of the pedipalpus with two bristle-shaped hairs (black); 7) ♂♀, anterior-basal aspect of the thin bristles of femur I (arrow); 8–9) retrolateral aspect of the r. pedipalpal femur with their ventral outgrowths. Scale bars = 0.2;

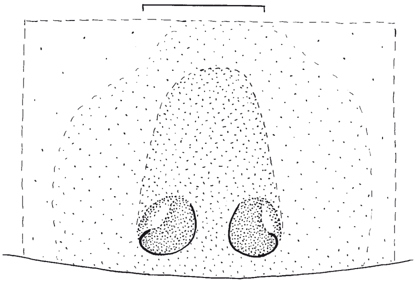
figs. 10a–b: *Aelurillus v-insignitus* (CLERCK 1757), ♂; 10a) retrolateral aspect of the left pedipalpal tibia (only few hairs are drawn); 10b) embolus and conductor (arrow) of the l. pedipalpus. Scale bar = 0.2 in fig. 10a);

figs. 11–12: *Ballus* sp., 11) dorsal aspect of the male; 12) posterior aspect of the ♂♀-cheliceral retromargins. Note the variable number of teeth. Scale bars = 1.0 and 0.1;

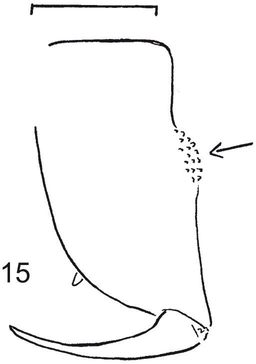
13



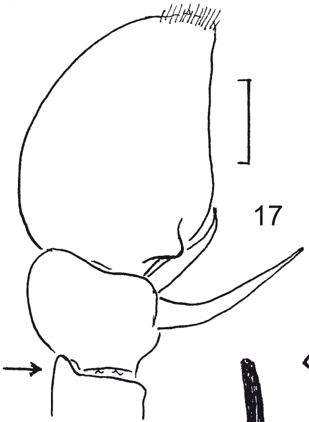
14



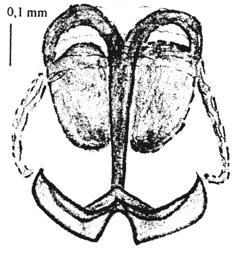
15



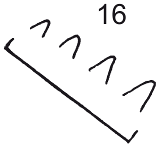
17



17a

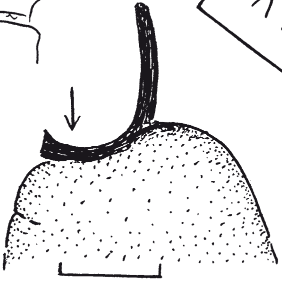


16

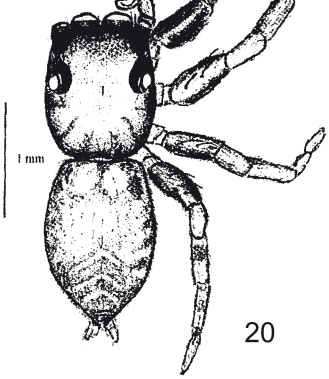


18

19



20



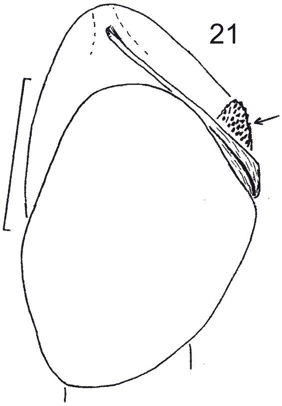
figs. 13–14: <u>*Carrhotus xanthogramma*</u> (WALCKENAER 1805); 13) ventral aspect of the r. ♂-pedipalpus; 14) ♀, epigyne. Scale bars = 0.5 and 0.2 mm;

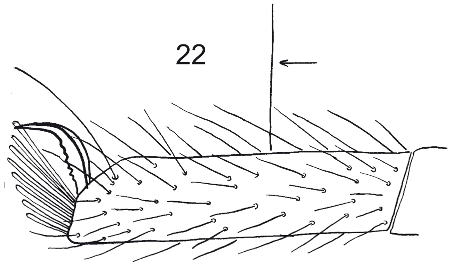
fig. 15: <u>*Chalcoscirtus*</u> sp., ♂, anterior-medial aspect of the left chelicera. The arrow indicates to the corniculate ?stridulatory lateral hump. Scale bar = 0.2;

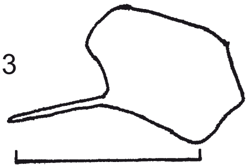
figs. 16–17a: <u>*Cyrba algerina*</u> (LUCAS 1846); 16) posterior aspect of the teeth of the r. cheliceral retromargin (there may be 3–5 teeth on the posterior margin); 17) ♂, dorsal aspect of the r. pedipalpus (the arrow indicates to the patellar apophysis); 17a) ♀, epigyne. Scale bars = 0.1, 0.2 and 0.1;

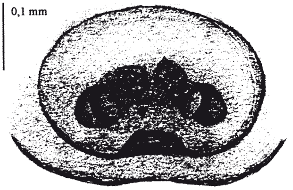
figs. 18–19: <u>*Dendryphantes*</u> sp., ♂; 18) ventral aspect of the r. gnathocoxa (the arrow indicates to the small retrolateral gnathocoxal outgrowth); 19) ventral aspect of the embolus of the r. pedipalpus (the arrow indicates to the strongly sclerotized slender basal outgrowth of the embolus). Scale bars = 0.2 and 0.1;

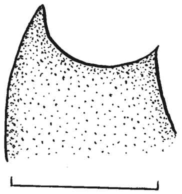
fig. 20: <u>*Neon levis*</u> (SIMON 1871), dorsal aspect of the male;

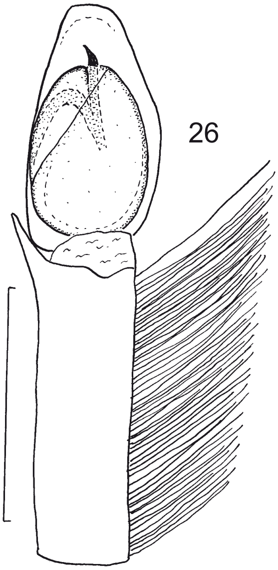

21

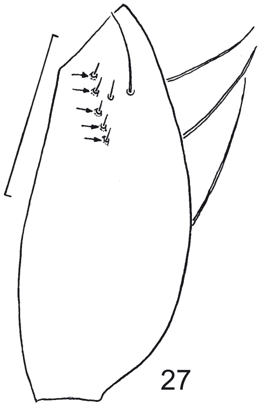

22

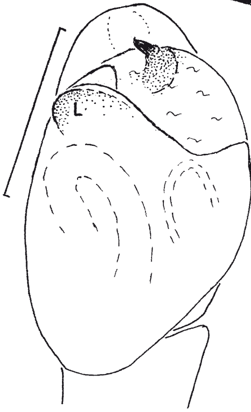

23


26a


25


26


27


24

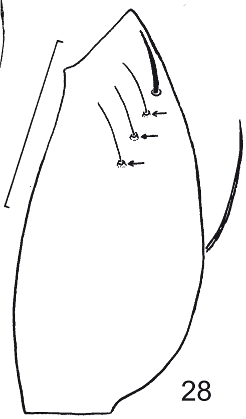

28

fig. 21: Neon reticulatus (BLACKWALL 1853), ♂, ventral aspect of the r. pedipalpus (the arrow indicates to the corniculate basal structure of the embolus). Scale bar = 0.2;

figs. 22–23: Euophrys sp.; 22) ♂♀, lateral aspect of the l. tarsus I with trichobothrium (arrow); 23) retrolateral aspect of the l. pedipalpal tibia. Scale bar = 0.2;

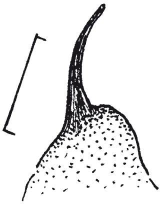
fig. 24: Talavera sp., ventral aspect of the r. ♂-pedipalpus (L = distal tegular lobe). Scale bar = 0.2;

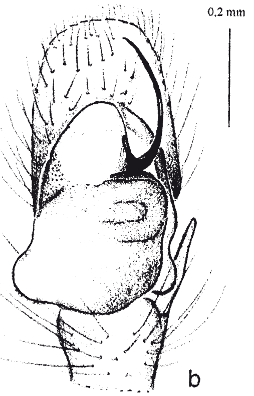
figs. 25–26a: Hasarius adansoni (AUDOUIN 1827); 25) ♂♀, keel-shaped tooth of the l. cheliceral retromargin; 26) ♂, ventral aspect of the r. pedipalpus; 26a) ♀, epigyne. Scale bars = 0.1 in fig. 25), 0.5 in fig. 26;

figs. 27–28: Icius ssp., ♂♀, prolateral aspect of femur I with thin ?stridulatory bristles. Scale bar = 0.5;

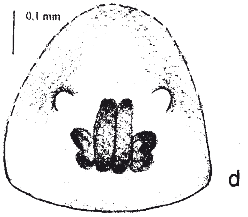
29

30

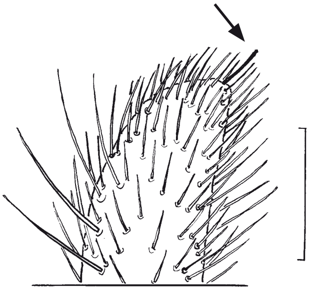




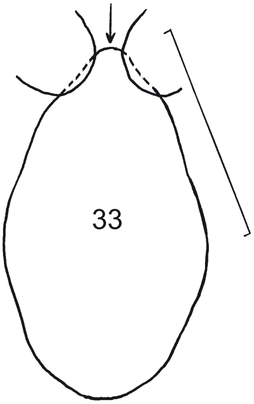
31



32

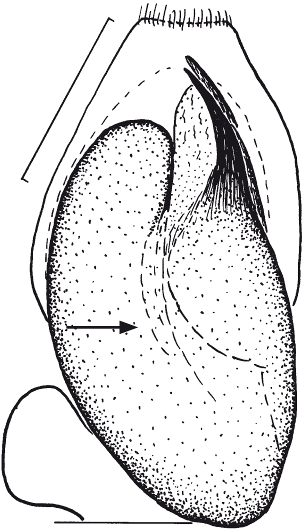


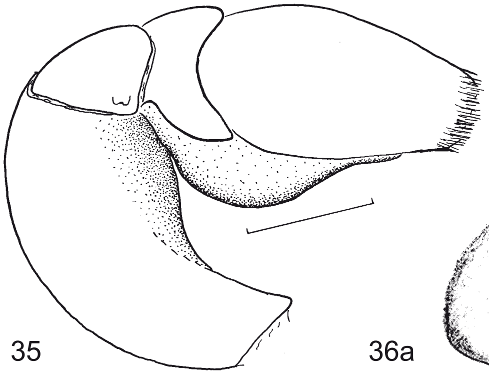
34



33

36





35

36a

fig. 29: <u>Icius hamatus</u> (L. KOCH 1846), ♂, retrofrontal and slightly dorsal aspect of the r. chelicera. (The arrow indicates to the retrofrontal edge (carina) of the chelicera). Scale bar = 0.2;

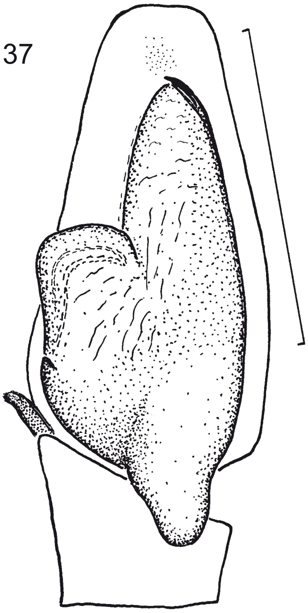
fig. 30: <u>Icius</u> sp., ♂, ventral aspect of the embolus of the r. pedipalpus. Scale bar = 0.1;

figs. 31–32: <u>Macaroeris nidicolens</u> (WALCKENAER 1802); 31) ♂, ventral aspect of the l. pedipalpus; ♀, epigyne;

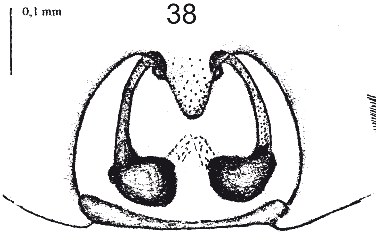
figs. 33–34: <u>Marpissa muscosa</u> (CLERCK 1757); 33) ♂♀, sternum with the position of coxae I and the anteriorly prolongated part of the sternum (arrow); 34) ♀, retrolateral aspect of the distal part of the pedipalpal tarsus with the tiny bristle at the tip (black) (arrow). Scale bars = 1.0 and 0.2;

figs. 35–36a: <u>Menemerus falsificus</u> SIMON 1868; 35–36) ♂, retrolateral and ventral aspect of the r. pedipalpus; taken from PROSZYNSKI (1997); 36a) ♀, epigyne. Scale bars = 0.5;

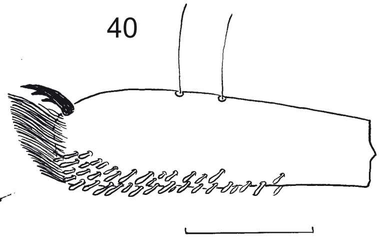
37



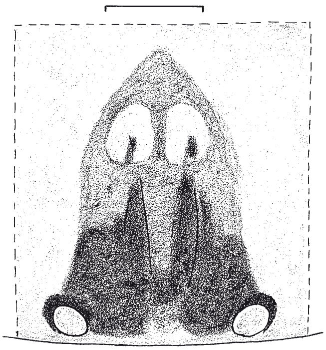
38



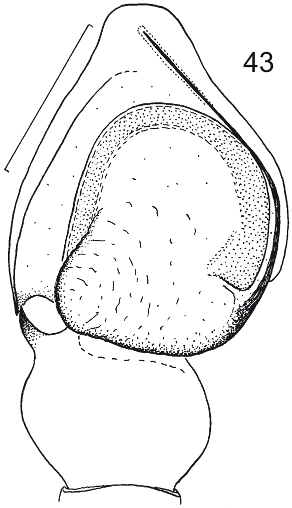
40



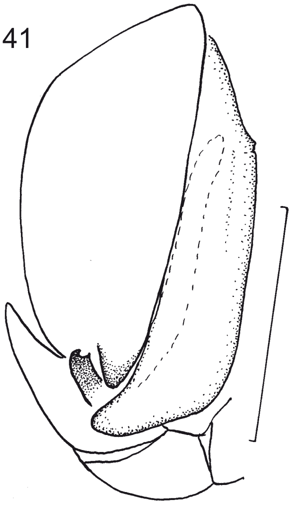
44



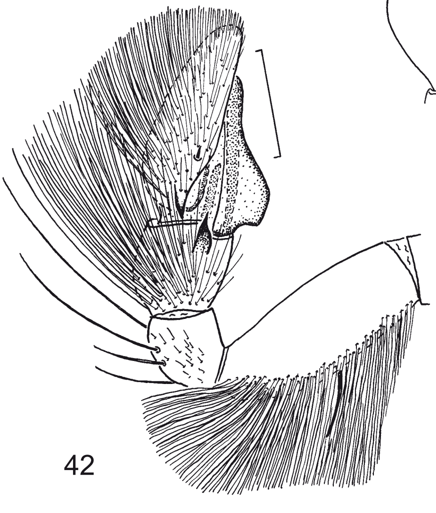
43



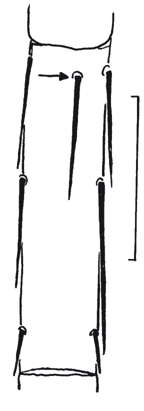
41



42



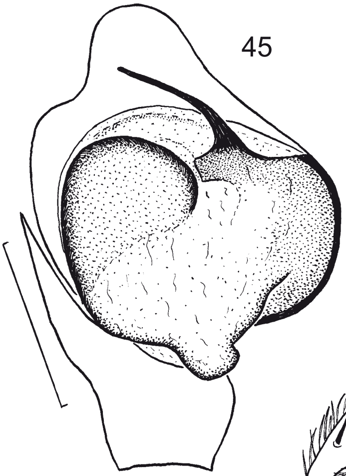
39

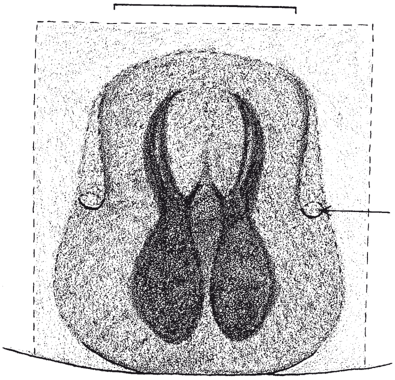


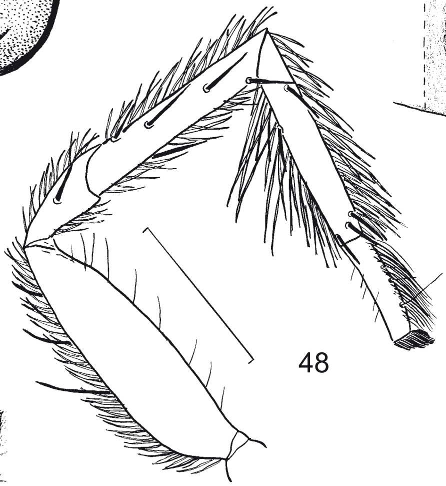
figs. 37–38: Phintella castriesiana (GRUBE 1861); 37) ♂, ventral aspect of the r. pedipalpus. Scale bar = 0.5; 38) ♀, epigyne;

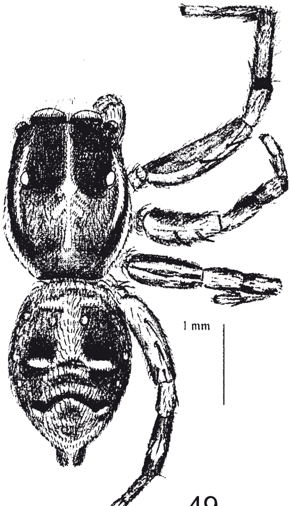
figs. 39–41: Phlegra fasciata (HAHN 1826); 39) ♂♀, dorsal aspect of the r. tibia IV with the megaspine near to the base (arrow); 40) ♂♀, prolateral aspect of the r. tarsus I with scopula, claw tuft and dorsal trichobothria (further hairs are not drawn); 41) ♂, retrolateral aspect of the r. pedipalpus. Scale bars = 0.5, 0.2 and 0.5;

figs. 42–44: Plexippoides gestroi (DALMAS 1920); 42–43) ♂, retrolateral and ventral aspect of the r. pedipalpus; 44) ♀, epigyne. Scale bars = 0.5, 0.5 and 0.2;

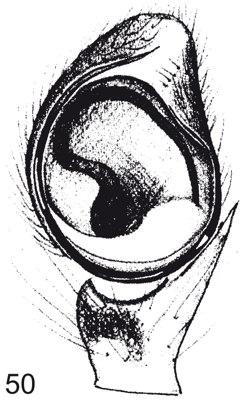

45

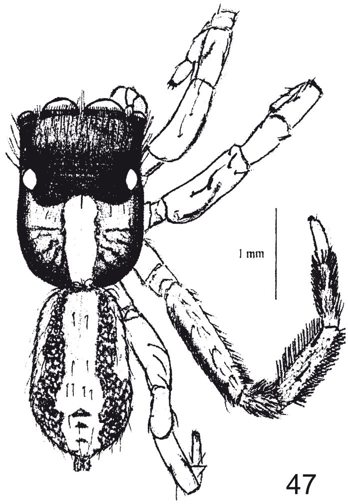

46


48



49


50

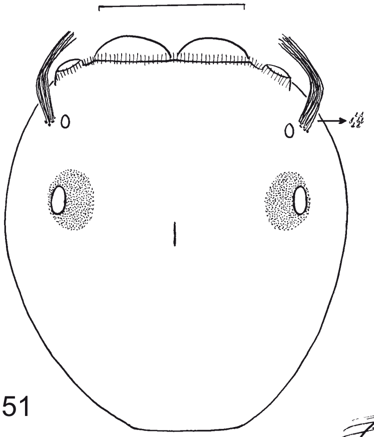


47

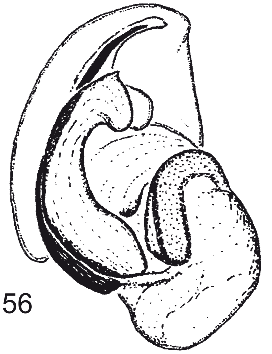
figs. 45–46: <u>*Plexippus paykulli*</u> (AUDOUIN 1827); 45) ♂, ventral aspect of the r. pedipalpus; 46) ♀, epigyne (the arrow indicates to the left introducing opening). Scale bar = 0.5;

figs. 47–48: <u>*Saitis barbipes*</u> (SIMON 1868), ♂; 47) dorsal aspect of body and r. legs, 48) retrolateral aspect of the r. leg III. Note the conspicuous dorsal and ventral hairs. Scale bar = 1.0 in fig. 48);

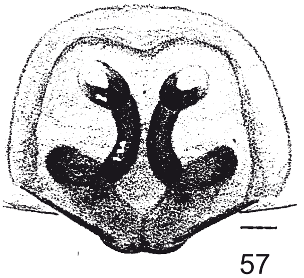
figs. 49–50: <u>*Sitticus floricola*</u> (C. L. KOCH 1837), ♂; 49) dorsal aspect of body and r. legs; 50) ventral aspect of the l. pedipalpus;



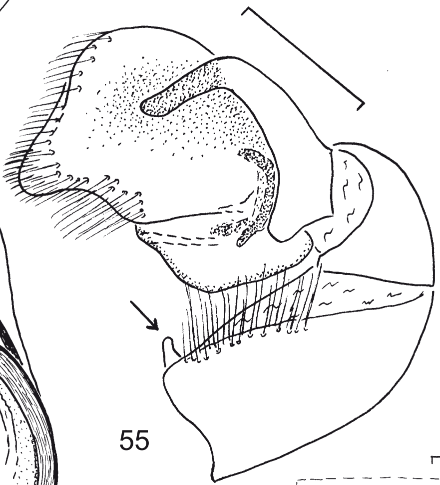
51



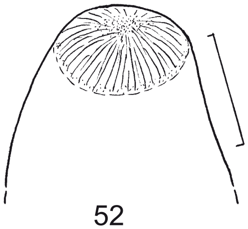
56



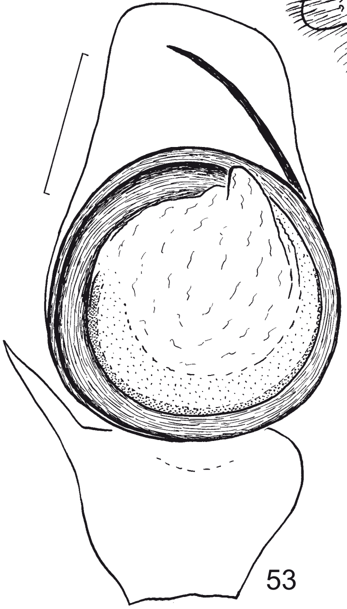
57



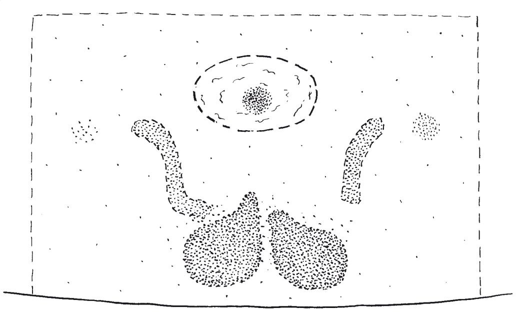
55



52



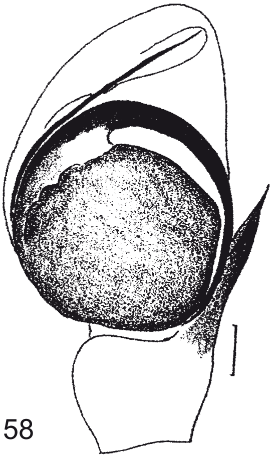
53



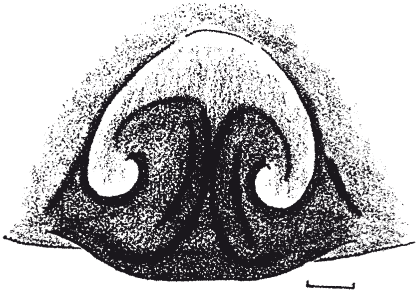
54

figs. 51–54: Thyene imperialis (ROSSI 1846); 51) dorsal aspect of the ♂♀-prosoma. Note the long hairs laterally of the eyes of the second row which can be rubbed off to stumps (arrow); 52) ♂, retrodorsal aspect of the tip of the r. cymbium. Note the hairs which are centered within a depression; 53) ♂, ventral aspect of the r. pedipalpus; 54) ♀, epigyne. Scale bars = 1.0 in fig. 51, 0.2 in the remaining figs.;

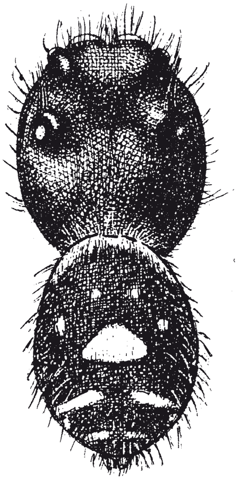
figs. 55–57: Yllenus arenarius MENGE 1868; 55–56) ♂, retrolateral and ventral aspect of the l. pedipalpus (the arrow in fig. 55 points to the ventral-basal outgrowth of the femus); 57) ♀, epigyne. M = 0.5, 0.2, 0.2. Figs. 56–57 are taken from LOGUNOV & MARUSIK (2003: 301 and 304);



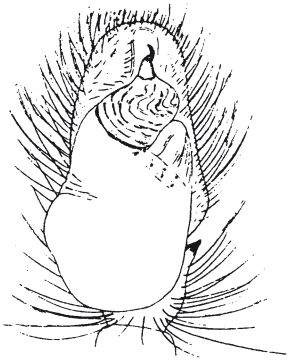
58



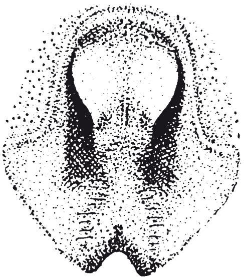
59



60



61



62

figs. 58–59: *“Hyllus” insularis* METZNER 1999; 58) ♂, ventral aspect of the l. pedipalpus; 59) ♀, epihyne. M = 0.1. Taken from LOGUNOV (2001: figs. 4, 6);

figs. 60–62: *Phidippus audax* (HENTZ 1848); 60) ♀, dorsal aspect of the body; 61) ♂, ventral aspect of the l. pedipalpus; 62) ♀, epigyne. No scle bars. Taken from KASTON (1981: Figs. 1770, 1787 and 1785).

BEITR. ARANEOL., 5 (2008)

ON THE IDENTIFICATION AND TAXONOMY OF THE CENTRAL EUROPEAN JUMPING SPIDERS (ARANEAE: SALTICIDAE) OF THE TRIBUS EUOPHRYDINI, WITH SPECIAL REFERENCE TO *TALAVERA*

J. WUNDERLICH, D-69493 Hirschberg.

ABSTRACT: Keys are given to the identification of the European genera of the tribus Euophrydini: *Chalcoscirtus* BERTKAU 1880, *Euophrys* C. L. KOCH 1834, *Neon* SIMON 1876, *Pseudeuophrys* DAHL 1912, and *Talavera* PECKHAM & PECKHAM 1909; the Central European species of the genus *Talavera* are treated in more detail. *Talavera milleri* (BRIGNOLI 1983) is regarded as a junior objective synonym of *T. brevipes* (MILLER 1971) (sub *Euophrys*).

Key words: Chalcoscirtus, Euophrydini, *Dicroneon*, *Euophrys*, Jumping Spiders, *Neon, Pseudeuophrys*, Salticidae, *Talavera*, taxonomy.

INTRODUCTION

Especially the tiny Jumping Spiders are difficult to differentiate, and there are numerous errors and wrong determinations of Central European spiecies, e. g. in the book of HEIMER & NENTWIG (1991); some corrections were published in the papers of CHVATALOVA & BUCHAR (2002), LOGUNOV & KRONESTEDT (2003) and METZNER (1999).
Fifteen years ago a “Workshop zur Taxonomie mitteleuropäischer Spinnen” on selected tiny Jumping Spiders was hold in Germany (Erlangen), see BAUCHHENSS et al. (1994); several of the previous findings are published in the present paper. Few additional tiny Central European members of the genus *Talavera* have been published in the meantime: *T. inopinata* WUNDERLICH 1993 and *T. parvistyla* LOGUNOV & KRONESTEDT 2003; *Talavera brevipes* (MILLER 1971) (= *milleri* BRIGNOLI 1983) – see BAUCHHENSS (1994) – and *Neon robustus* LOHMANDER 1945 were reported from Germany during the last years.

TAXONOMY

The small or even tiny spiders of the taxa *Chalcoscirtus* BERTKAU 1880, *Dicroneon* LOHMANDER 1944, *Euophrys* C. L. KOCH 1834, *Neon* SIMON 1877, *Pseudeuophrys* DAHL 1912 and *Talavera* PECKHAM & PECKHAM 1909 are members of the tribus Euophrydini (= Chalcoscirtini); they possess only a single trichobothrium on tarsus I–III (fig. 43) and 2 trichobothria on tarsus IV, the embolus has a distal and basicly circular position, and they have a mainly holarctic distribution. The same sequence – and reduced number – of trichobothria exist also in members of other small salticid genera like the ant-shaped genus *Synageles* – apparently a convergent loss of trichobothria – in contrast to most of the remaining salticid genera of Central Europe (and most salticid genera of other regions) in which their number is higher. – The status as a subfamily or a tribus – which I prefer –, and the limitation of the Euophrydini are unsure.

Key to the Central European genera and subgenera of the Euophrydini:

1 Posterior margin of the cheliceral furrow tooth-less. Body almost uniformly black, glancing. ♂-opisthosoma most often covered with a large and "glancing" scutum. Prosomal length ca. 1–1.2 mm . . . . *Chalcoscirtus*

- Posterior margin of the cheliceral furrow with a small tooth which may be indistinct. Body not uniformly black and glancing, the opisthosoma bears usually distinct markings. ♂-opisthosoma without large and "glancing" scutum, in some males leathery or with a weak scutum 2

2(1) Eyes surrounded by large and conspicuous black rings (fig. 42). Metatarsus III bears only a single ring of strong bristles near its end (arrow in fig. 43). Position of the eyes of the posterior row in the middle of the prosomal length (fig. 42). Prosomal length usually 1–1.4 mm. *Neon.* See also below (3) 3

- Eyes not surrounded by conspicuous black rings. Metatarsus III bears additional strong bristles. Position of the eyes of the posterior row in front of the middle, in ca. 0.4 4

3(2) Position of the embolus in the basal half, it bears a white (unsclerotized) structure which is covered with numerous tiny denticles (thin arrow in fig. 46). Vulva with large receptacula, additionally with a pair of most often small and thick-walled glandular structures near the middle (glands or secondary receptacula) . . . . . . Subgenus *Neon*

- Base of the embolus without a spiculate structure. Vulva with tube- or sac-shaped structures. . . . . Subgenus *Dicroneon*

4(2) Paired tarsal IV claws toothed (prolateral claw with several long teeth, retrolateral claw with 1–2 teeth). Prosoma dark brown, medially with a light spot or band at/behind the thoracal fissure (fig. 47). Tibial apophysis of the ♂-pedipalpus usually of normal size (thick at least at the base). Prosomal length usually 1.5–2 mm. Photo 389 . . . .*Pseudeuophrys*

- Both paired tarsal IV claws smooth. Colour of the prosoma otherwise. Tibial apophysis of the ♂-pedipalpus thin and indistinct or even completely absent (*Talavera*) 5

5(4) Legs not annulated but laterally usually with dark longitudinal bands. ♂-tibia I usually thickened and ventrally with numerous long hairs. Tibia of the ♂-pedipalpus with an – frequently very thin and indistinct – retrolateral apophysis (figs. 38–39), tegulum without a distal lobe, embolus almost circular. Prosomal length usually 1.5–2 mm . . . . *Euophrys*

- Leg annulation (figs. 3–4) usually distinct in the female as well as at least on tibia, metatarsus and tarsus III and IV of the male. ♂-tibia I not thickened, bearing few normal (short) hairs. Tibia of the ♂-pedipalpus without an apophysis (for an investigation in *petrensis* one has to rub off numerous long hairs which partly cover tibia and cymbium), tegulum with a strongly sclerotized distal lobe (figs. 1, 9). Embolus circular in *petrensis*, tiny and corkscrew-like in *aequipes* and *poecilopus*, and only slightly bent in the remaining species. Prosomal length usually 0.8–1.3 mm . . . . *Talavera*

(1) ***Talavera***

This rather diverse genus has a holarctic distribution, see LOGUNOV & KRONESTEDT (2003). From Central Europe are more species described than from other parts of the world; only a single species is known from North America: *T. minuta* (BANKS 1895), the generotype.

Most species of *Talavera* were formerly listed sub *Euophrys* which is strongly related. Distribution, habitat and additional diagnostic characters of *Talavera* – which are not noted in the key above – are listed in the paper of LOGUNOV & KRONESTEDT (2003) but *T. milleri* is lacking. – Remarks on the diagnostic characters: A modification of the male pedipalpal trochanter exist in most species but is absent in some species like *parvistyla*; a tegular lobe – “sclerite” sensu LOGUNOV & KRONESTEDT – exist in all species of the genus including *petrensis* (person. observ.).

LOGUNOV & KRONESTEDT (2003) transfered *Euophrys petrensis* for the first time – and correctly – to *Talavera*. *Petrensis* is the largest known species of *Talavera*; it possesses “still” the long and coiled embolus (fig. 1) as members of its sister group *Euophrys*, and represents therefore in my opinion the only known Central European member of the most basal branch of *Talavera*. The shortening of the more straight embolus in *Talavera* may be a result of dwarfism and is (“still”) only fairly developed in *aequipes* (figs. 5–6).

The species in Central Europe:

aequipes (O. PICKARD-CAMBRIDGE 1871) (figs. 3–8),
aperta (MILLER 1971) (figs. 22–27),
brevipes (MILLER 1971) (= *Euophrys milleri* BRIGNOLI 1983) (figs. 17–21),
inopinata WUNDERLICH 1993 (figs. 28–32),
monticola (KULCZYNSKI 1884) (figs. 13–16),
parvistyla LOGUNOV & KRONESTEDT 2003 (= *poecilopus* auct, *westringi* auct.) (figs. 9–12),
petrensis (C. L. KOCH 1837) (figs. 1–2),
thorelli (KULCZYNSKI 1891) (figs. 33–37).

Remarks on the synonymy:

Attus westringi SIMON 1868 (= *Attus laetabundus* WESTRING 1851) and *Talavera* (= *Euophrys*) *poecilopus* (THORELL 1873):
The species which is dealt with sub *westringi* by MILLER (1971) and PROSZYNSKI in HEIMER & NENTWIG (1991) is in my opinion actually *Talavera parvistyla*. – 5♂ and 1♀ from SW-Germany (Kaiserstuhl), which were published sub *Euophrys* ?*westringi* by WUNDERLICH in 1975 (Entomologica Germanica, 1: 385) are actually members of *Talavera brevipes*. – *Westringi* has – according to the original description – a body length of 3 3/4 mm and is larger than all species of *Talavera*, the legs are not annulated and SIMON compared the species with *Euophrys frontalis*. Therefore *westringi* is surely not a member of *Talavera* and not an older synonym of *poecilopus*. I suppose that the description of SIMON (1868) regards probably to more than a single species. Material has not been found in the MNHN (person. commun. C. ROLLARD in II 1993). – According to THORELL (1873: 403) SIMON's *westringi* is not identical with *laetabundus* for which THORELL (1873:403) created the new name *poecilopus*. – See also LOGUNOV & KRONESTEDT (2003: 1132) which regarded *poecilopus* and *westringi* as nomina dubia and created the new name *parvistyla* for *Euophrys poecilopus* sensu LOHMANDER 1944.

Talavera milleri (BRIGNOLI 1983) (sub *Euophrys*) = *Talavera brevipes* (MILLER 1971) (**nov. syn**.):
Euophrys brevipes MILLER 1971 was regarded as a secondary homonym of *Salticus brevipes* HAHN 1831 which is a junior synonym of *Ballus chalybeius* (WALCKENAER 1802), see BAUCHHENSS (1994: 47). Contrarily – according to O. KRAUS (person. commun. in VII 2006) – art. 59.2 and 59.4 of the IRZN has ruled this case clearly: The temporary homonymy of *brevipes* MILLER 1971 with *brevipes* HAHN 1831 is not given anymore; *E. milleri* BRIGNOLI 1983 has to be regarded as a younger objective synonym of *brevipes* MILLER 1971 (**nov. syn.**).
Talavera milleri sensu CHVATALOVA & BUCHAR (2002) may be *parvistyla*, in my opinion more likely than *brevipes*.

Key to the Central European species of the genus *Talavera*:

Males

Remark: In *petrensis, milleri* and *parvistyla* the clypeus is usually covered with numerous thick and orange hairs; in the remaining species exist most often few thin and white hairs in this position, but in some males of *aequipes* exist numerous yellow hairs.

1 Prosomal length usually 1.2–1.5 mm. The embolus forms a free, large and complete circle (fig. 1). . . . .*petrensis*

- Prosomal length usually 0.8–1.3 mm. The embolus forms not a free and large circle, it may have a corkscrew shape (fig. 5) or it is almost straight (figs. 9, 14) 2

2(1) The embolus – in ventral aspect – forms a tiny corkscrew-like spiral at the margin of a seam (figs. 5–6), cymbium yellow, femur of the pedipalpus yellow, rarely retrolaterally with a dark patch. . . . .*aequipes*

- the embolus – in ventral view – does not form such a corkscrew-like spiral (e. g. fig. 18) (in *parvistyla* it is fairly similar but distinctly smaller, fig. 10), cymbium usually darkened at least in the distal half (except *milleri*), pedipalpal femur distinctly darkened 3

3(2) Embolus broad and flat, the tiny tip bent ventrally in the not-expanded bulbus (figs. 13–15). – Alps, Tatra (1100–2200 m) . . . . *monticola*

- Embolus more slender, tip in the not-expanded bulbus not bent ventrally (e. g. figs. 18, 24, 29) 4

4(3) Clypeus covered with numerous thick orange hairs. Embolus tiny (figs. 9–11, 18) 5

- Clypeus covered with some thin white hairs. Embolus larger (figs. 24, 28, 33) 6

5(4) Embolus almost straight (figs. 17–18). Cymbium: Length most often 0.22–0.28 mm, yellow with white hairs, distally slightly darker. – At hot and dry localities (= *milleri*) . . . . *brevipes*

- Embolus at first view similar (fig. 9), in higher magnification a very small spiral (fig. 10) with the tiny tip bent to the tip of the cymbium. Cymbium: Length usually 0.33–0.35 mm; its colour shows a distinct contrast: Yellow (and with white hairs) in the basal half but dark in the distal half. – At humid localities like bogs (= *poecilopus* auct., *westringi* auct.) . . . . *parvistyla*

6(4) Embolus directed retrolaterally (figs. 28–29) . . . .*inopinata*

- Embolus directed prolaterally (figs. 24, 33). 7

7(6) Embolus in the distal half slightly thicker and bent at two points, in the basal half and distally (figs. 22– 25). – At warm/hot and dry localities. . . . . *aperta*

- Embolus continually more slender, bent only once and more distally (figs. 33–35) (seen in exactly the same position). – Not at hot/dry localities . . . . *thorelli* (*)

Females

1 Length of the prosoma usually 1.3–1.6 mm. Epigyne (fig. 2): Anterior vulva ducts long, spirally and heavily sclerotized, with a pair of large pits in front of the receptacula. . . . . *petrensis*

- Length of the prosoma 0.9–1.3 mm. Epigyne (e. g. figs. 7, 16, 36) with shorter ducts of the vulva which may be indistinct 2

2(1) Epigyne with a wide, usually hairy and darkened structure, vulva (fig. 19–21) with spiral introducing ducts . . . . *brevipes*

- Epigyne anteriorly with a distinct narrow and sclerotized border/rim crossways (e. g. figs. 26, 31, 36) 3

- Epigyne without a border (e. g. figs. 7, 12, 16) 5

3(2) Position of the border is 2/3 to 1 diameter of a receptaculum in front of the receptacula which are relatively small; pit large, distinct and heart-shaped with the position of the introducing ducts at their margin (figs. 36–37) . . . . *thorelli* (*)

- Position of the border only up to half a diameter in front of (or even above) the large receptacula, pit shallow(er), not heart-shaped (figs. 26–27, 31) 4

4(3) Epigyne with a shallow pit in front of the border; inserting openings separated by 1 – 1 1/2 diameters of the inserting area (figs. 31–32) . . . . *inopinata*

- Epigynal pit shallow, its position behind the border; inserting openings separated by ca. 1 diameter of the inserting area (figs. 26–27) . . . . *aperta*

5(2) Ducts of the vulva long and spirally (figs. 7–8) (in some ♀ of *parvistyla* these ducts are similar and only slightly shorter). Femur of the pedipalpus usually annulated dark brown and yellow. . . . . *aequipes*

- Ducts of the vulva short(er), spirally or not (figs. 12, 16). 6

6(5) Position of the sclerotized areas of the introducing openings near the anterior margin of the receptacula, the ducts of the vulva have a characteristic course (fig. 12). Femur of the pedipalpus darkened . . . . *parvistyla*

- Position of the sclerotized areas of the introducing openings distinctly in front of the anterior margin of the receptacula and more close together (fig. 16). Femur of the pedipalpus yellow. Alps, Tatra, 1100–2200 m . . . . *monticola*

(*) Related *is T. esyunini* LOGUNOV 1992 from Northern Europe in which the receptacula seminis are distinctly larger.

(2) Differentiation of two species: *Euophrys frontalis* (WALCKENAER 1802) and *E. herbigrada* (SIMON 1871*)*

The coloration is quite different in both sexes:
Female: Clypeus conspicuously covered with white hairs in *herbigrada*,
male: Legs dark in *herbigrada*, only tarsi light whereas in *frontalis* light, only leg I dark (except the tarsus). – The epigynal pit is distinct in *herbigrada* but shallow in *frontalis*.
Male copulatory organs: The thin tibial apophysis of the male pedipalpus is ca. 0.1 mm long in *herbigrada* (fig. 38) and shorter than the tibial hight, but ca. 0.15 mm long in *frontalis* (fig. 39) and longer than the hight of the tibia, and furthermore usually hidden under long white hairs. In *frontalis* furthermore the loop of the embolus is distinctly larger.

Remark: In the chaotic key of HEIMER & NENTWIG (1991) are the figs. of the male pedipalpi exchanged: 1333.1 and 2 show *frontalis*, 1334.1 (erroneously sub 1134.1) and 1342.2 show *herbigrada*.

(3) *Neon* and *Dicroneon*

Dicroneon LOHMANDER 1945 was published as a subgenus of *Neon* SIMON 1877; this status was accepted by GERTSCH & IVIE (1955) and METZNER (1999), and I agree in this assess. Diagnostic characters: See the key to the genera above. In both subgenera the position of the eyes of the second row (fig. 40) is closer to the first row in contrast to *Euophrys* and *Talavera* (fig. 41). The colour of the body varies strongly within some species. The patellae and femora bear long and thin bristles but no spines (as in numerous other salticid genera). The “secondary receptacula” sensu LOGUNOV in *Neon* may be glandular, see WIEHLE (1967). Both subgenera have a mainly holarctic distribution.
Avalonus GERTSCH & IVIE 1955, *convolutus* DENIS 1937 (= *pusio* SIMON 1937), *kovblyuki* LOGUNOV 2004, *levis* SIMON 1871, *pixii* GERTSCH & IVIE 1955, *rayi* SIMON 1875, and *sumatranus* LOGUNOV 1998 are members of *Dicroneon*, the remaining species which were described sub *Neon* are members of the subgenus *Neon*.

The species in Central Europe are:

Neon (Dicroneon) levis (SIMON 1871) (= *laevis* auct.) (fig. 42),
Neon (Dicroneaon) rayi SIMON (1875),
Neon (Neon) reticulatus (BLACKWALL 1853) (fig. 46),
Neon (Neon) robustus LOHMANDER 1945 (fig. 45),
Neon (Neon) valentulus FALCONER 1912 (figs. 43–44).

Key to the species of the subgenus *Neon* in Central Europe:

1 ♂: Embolus distinctly bent distally (fig. 44). ♀: Epigynal pits and loops of the introducing ducts of the same size as the receptacula. . . . . *valentulus*

- ♂: Embolus slightly bent (figs. 45–46). ♀: Epigynal pits and loops smaller 2

2(1) ♂: Origin of the embolus in a more distal position, denticulate structure larger (fig. 46). ♀: Receptacula much larger than the pits and loops . . . . *reticulatus*

- ♂: Origin of the embolus in a more basal position, denticulate structure smaller (fig. 45). ♀: Receptacula not much larger than the pits and loops . . . . *robustus*

REFERENCES cited

BAUCHHENSS, E. (1994): Nachweise von *Euophrys milleri* in Deutschland (Araneae: Salticidae). -- Arachnol. Mitt., 8: 47–48.

BAUCHHENSS, E., GACK, C., HARMS, K.-H., V. HELVERSEN, O., KOBEL-LAMPARSKI, A. & WUNDERLICH, J. (1993): „Workshop zur Taxonomie mitteleuropäischer Spinnen“ in Erlangen (8.–10.01.1993): Taxonomie und Faunistik der kleinen *Euophrys*-Arten und der Gattungen *Neaetha* und *Pellenes* (Salticidae). -- Arachnol. Mitt., 5: 52–53.

CHVATALOVA, I. & BUCHAR, J. (2002): Distribution and habitat of *Talavera aperta, T. milleri* and *T. thorelli* in the Czech Republic (Araneae: Salticidae). -- Acta Soc. Zool. Bohem., 66: 3–11.

GERTSCH, W. J. & IVIE, W. (1955): The Spider Genus *Neon* in North America. -- Am. Mus. Novitat., 1743: 1–17.

LOGUNOV, D. V. (1992): Definition of the spider genus *Talavera* (Araneae, Salticidae), with a description of a new species. -- Entomologie, 62: 75–82.

-- (1998): The spider genus *Neon* Simon, 1876 (Araneae, Salticidae) in SE Asia, with notes on the genitalia and skin pore structures. -- Bull. Br. arachnol. Soc., 11 (1): 15–22.

-- (2004): Notes on new and poorly known Palaearctic species of the genera *Neon, Sitticus* and *Synageles* (Araneae: Salticidae). -- Bull. Br. arachnol. Soc., 13 (2): 33–40.

LOGUNOV, D. V., CUTLER, B. & MARUSIK, Y. M. (1993): A review of the genus *Euophrys* C. L. KOCH in Siberia and the Russian Far East (Araneae: Salticidae). -- Ann. Zool. Fennici, 30: 101–124.

LOGUNOV, D. V. & KRONESTEDT, T. (2003): A review of the genus *Talavera* PECKHAM & PECKHAM, 1909 (Araneae, Salticidae). -- J. Nat. Hist., 37: 1091–1154.

LOHMANDER, H. (1944): Die Salticiden-Gattung *Neon* SIMON in Südschweden. -- Göteborg Vetensk Vitterh. Handl. (6b) 3 (9): 31–75.

-- (1997): Salticidae of Middle Asis. 4. A review of the genus *Euophrys* (s. str.) C. L. KOCH (Araneae, Salticidae). -- Bull. Br. arachnol. Soc., 10 (9): 344–352.

METZNER, H. (1999): Die Springspinnen (Araneae, Salticidae) Griechenlands. 279pp. -- Andrias, 14, Staatliches Museum für Naturkunde Stuttgart, Germany.

SIMON, E. (1868): Monographie des esp. europ. de la fam. Attides. -- Ann. Soc. Ent. France (4) 8: 11.72, 529–726.

THALER, K. (1981): Bemerkenswerte Spinnenfunde in Nordtirol (Österreich). -- Veröffentlichungen Mus. Ferninandeum (Innsbruck), 61: 105–150.

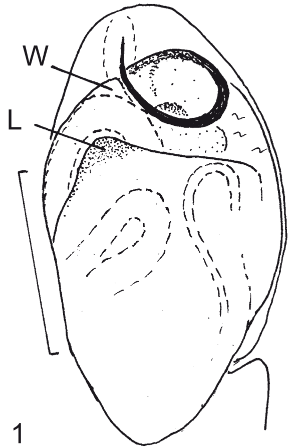
THORELL, T. (1873): Remarks on Synonyms of European Spiders. -- Nova Act. Reg. Soc. Sci. Upsaliae (3) 7: 375–644.

WESTRING, N. (1851): Förteckning öfver till närvar. tid kända, i Svärige förek. spindearter. -- Göteborg Vet. Handl., 2: 25–62.

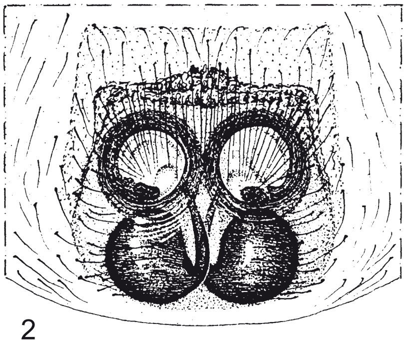
WIEHLE, H. (1967): Beiträge zur Kenntnis der deutschen Spinnenfauna, V (Arach., Araneae). -- Senckenbergiana biologica, 48 (1): 1–36.

WUNDERLICH, J. (1975): Spinnen vom Kaiserstuhl (Arachnida: Araneae). -- Entomologica Germanica, 1: 53–58.

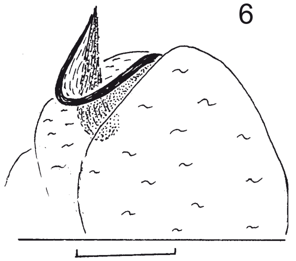
-- (1993): Beschreibung der Springspinne *Talavera inopinata* n. sp. aus Mitteleuropa (Arachnida: Araneae: Salticidae). -- Entomol. Z., 103 (6): 109–112.



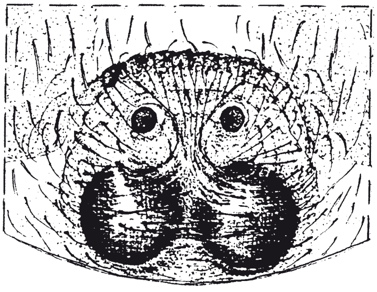
1



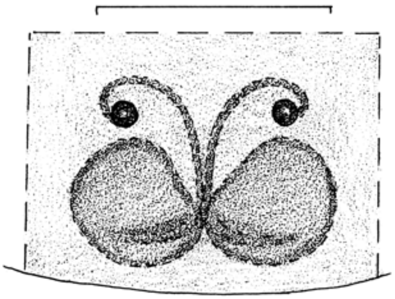
2



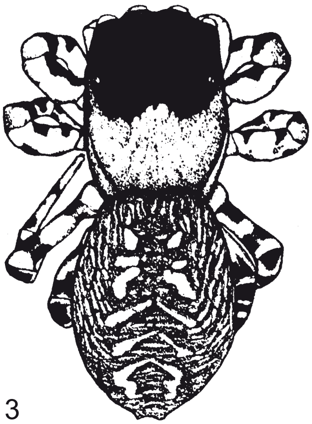
6



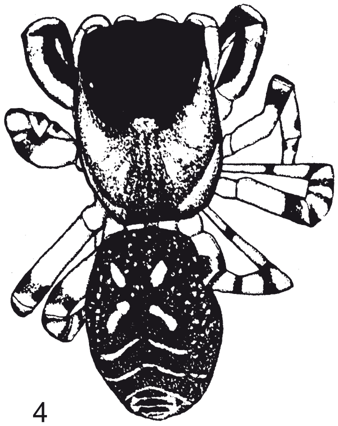
8



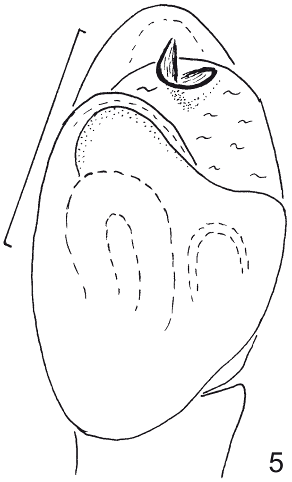
7



3



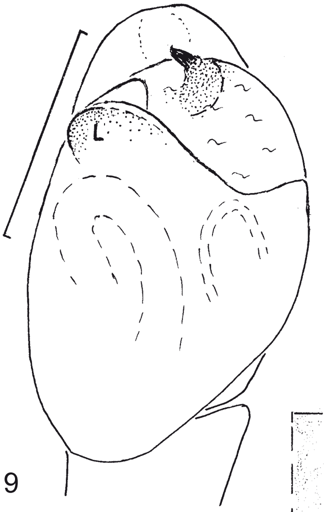
4



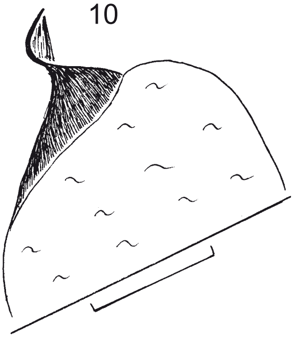
5

Figs. 1–2: Talavera petrensis (C. L. KOCH 1837); 1) ♂, ventral aspect of the r. pedipalpus. L = strongly sclerotized tegular lobe, W = weakly sclerotized tegular lobe, scale bar 0.2 mm; 2) ♀, epigyne (taken from ROBERTS, no scale bar).

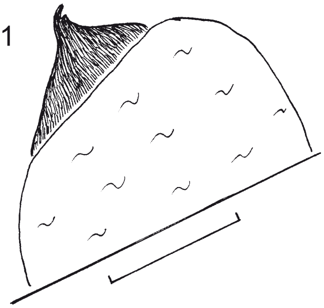
Figs. 3–8: Talavera aequipes (O. PICKARD-CAMBRIDGE 1871); 3–4) dorsal aspects of ♀ and ♂, body length ca. 2.5 mm; 5–6) ventral aspect of the ♂-pedipalpus, enlarged in fig. 6; 7–8) ♀, epigyne (paired depressions not shown in fig. 7, hairs are only drawn in fig. 8); scale bar 0.05 mm in fig. 6, 0.2 mm in figs. 5 and 7. Fig. 8 after ROBERTS, no scale bar; drawings 3–4 by H. PIEPER.



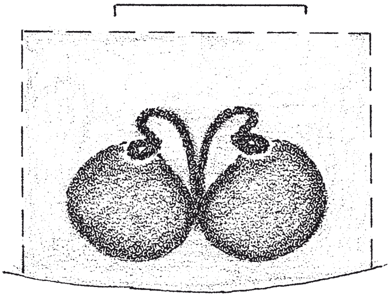
9



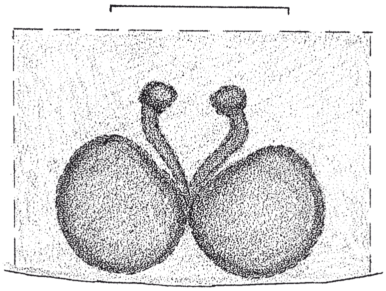
10



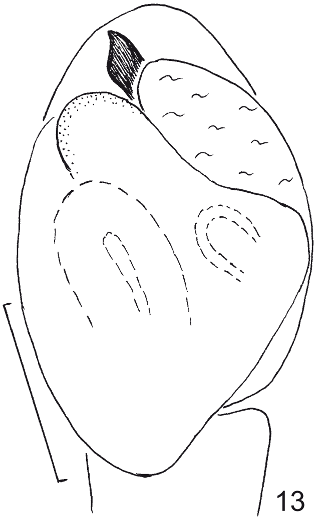
11



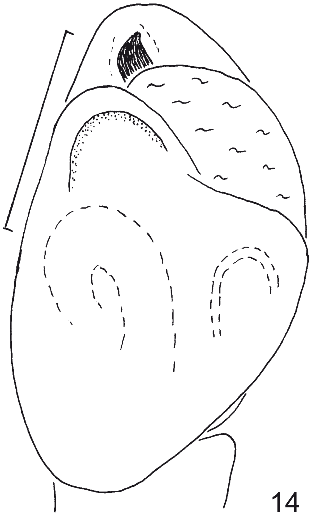
12



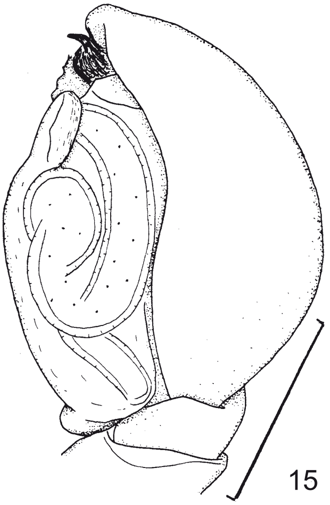
16



13



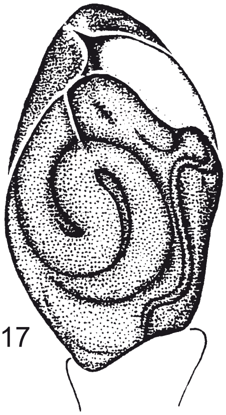
14

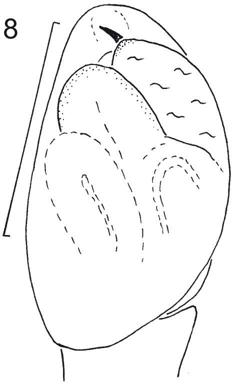


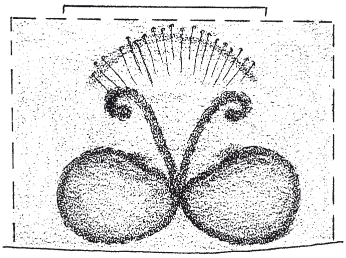
15

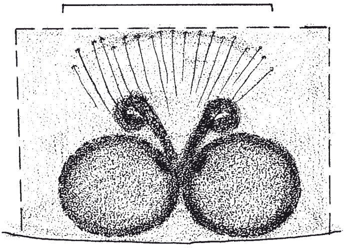
Figs. 9–12: *Talavera parvistyla* LOGUNOV & KRONESTEDT 2003; 9) ventral aspect of the ♂-pedipalpus (L = strongly sclerotized tegular lobe); 10–11) proventral aspect of the tip of the embolus, usual and rare form; 12) ♀, epigyne. Scale bars 0.2 mm in figs. 9 and 12, 0.05 mm in figs. 10–11.

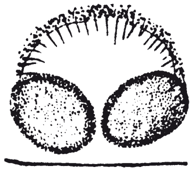
Figs. 13–16: *Talavera monticola* (KULCZYNSKI 1884); 13–14) ventral aspects of the ♂-pedipalpus in slightly different positions; 15) retrolateral position of the l. pedipalpus; taken from THALER (1981: Fig. 70); 16) ♀, epigyne. Scale bar 0.2 mm.

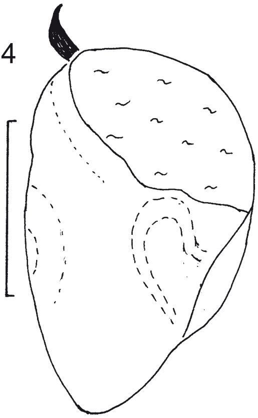

17

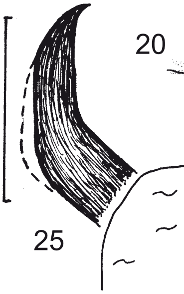

18

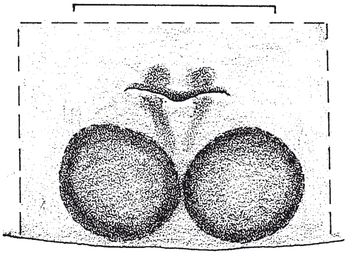

19

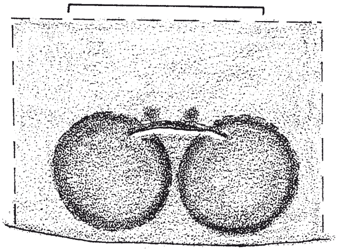

20

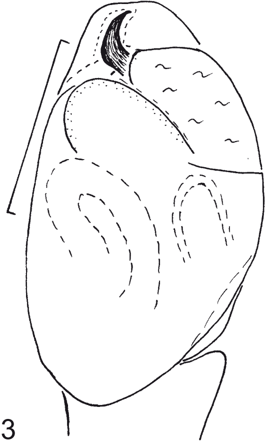

21

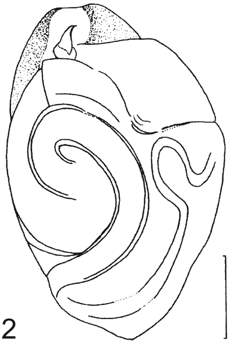

24


25


26


27

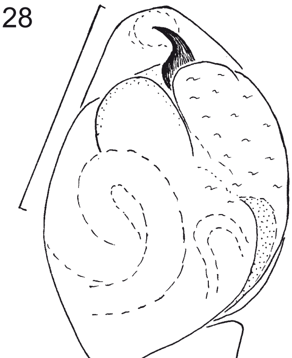

23


22

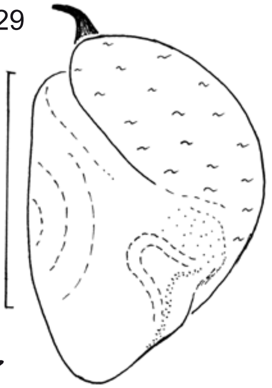
Figs. 17–21: Talavera brevipes (MILLER 1971); 17–18) ventral aspect of the r. ♂-pedipalpus (fig. 17 was drawn by H. PIEPER); 19–21) ♀, epigyne, 19) from Bavaria, 20) from Baden-Württemberg, Kaiserstuhl, 21) holotype of *Euophrys brevipes* MILLER, from Czech Republic, taken from MILLER (1971: T. 20, fig. 20). Figs. 17) and 21) no scale, the remaining figs. 0.2 mm.

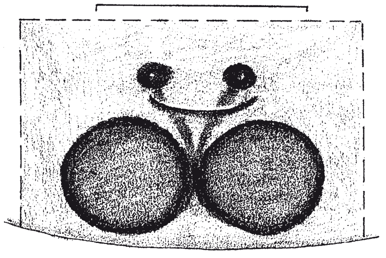
Figs. 22–27: Talavera aperta (MILLER 1971); 22–23) ventral aspect of the ♂-pedipalpus, fig. 22) taken from CHVATALOVA & BUCHAR (2002: Fig. 1); 24) proventral aspect of the bulbus of the r. pedipalpus; 25) proventral aspect of the r. embolus; dotted line: thicker embolus in ventral-basal aspect; figs. 26–27) ♀, epigyne, 26) frequent form, 27) rare form. Scale bar 0.1 mm in fig. 22), 0.05 mm in fig. 25), 0.2 mm in the remaining figs.

28

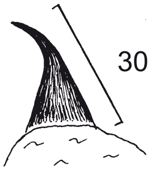


29



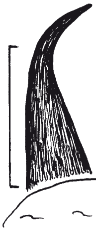


31

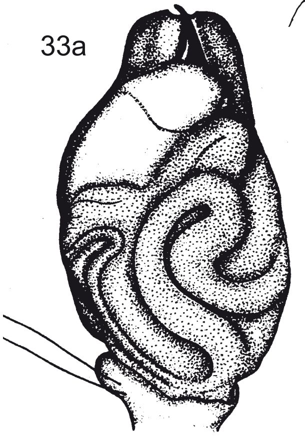


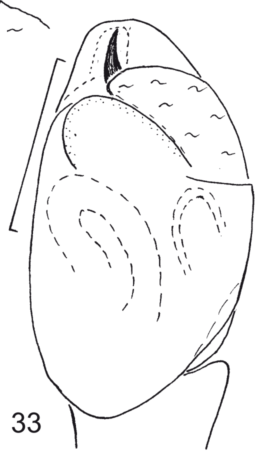
30

35



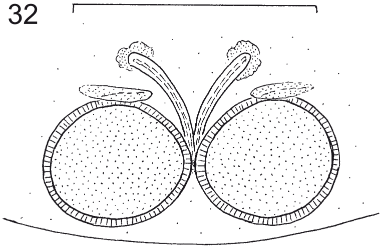
33a

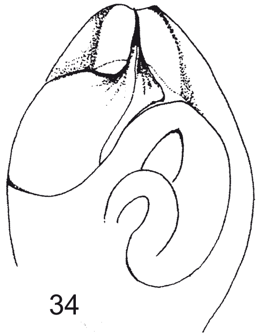




33

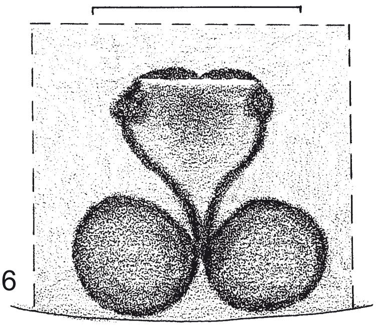
32



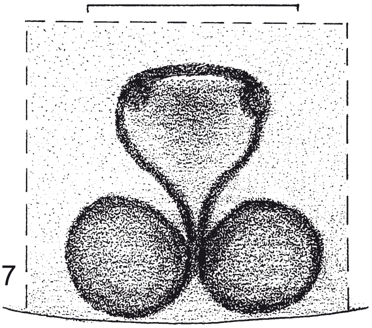


34

36



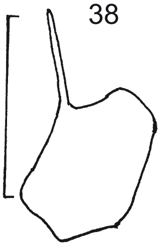
37



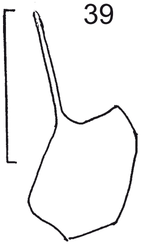
Figs. 28–32: Talavera inopinata WUNDERLICH 1993; 28) ventral aspect of the r. pedipalpus; 29) proventral aspect of the r. bulbus; 30) probentral aspect of the r. embolus; 31) ♀, epigyne, 32) ♀, dorsal aspect of the vulva. Scale bars 0.05 mm in fig. 30), 0.2 mm in the remaining figs.

Figs. 33–37: Talavera thorelli (KULCZYNSKI 1891); 33–33a) ventral aspect of the r. pedipalpus, fig. 33a) drawn by H. PIEPER without scale bar; fig. 34) taken from CHVATALOVA & BUCHAR (2002: Fig. 3); 35) proventral aspect of the r. embolus; 36–37) ♀, epigyne. Scale bars 0.05 mm in fig. 35), 0.1 mm in fig. 34), 0.2 mm in the remaining figs.

38

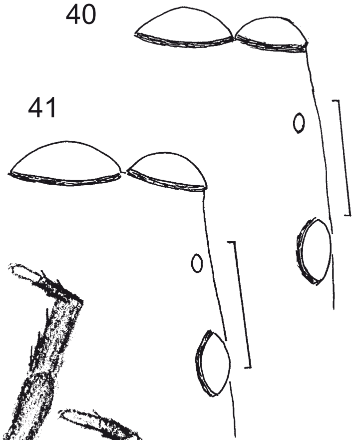


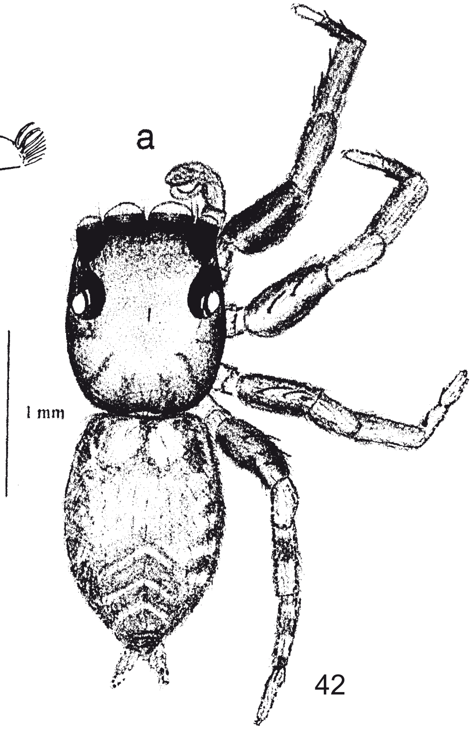
39



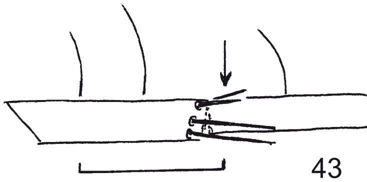
40

41





42



43

44

Fig. 38) Euophrys herbigrada (SIMON 1871), retrolateral aspect of the tibia of the l. pedipalpus. Scale bar 0.2 mm.

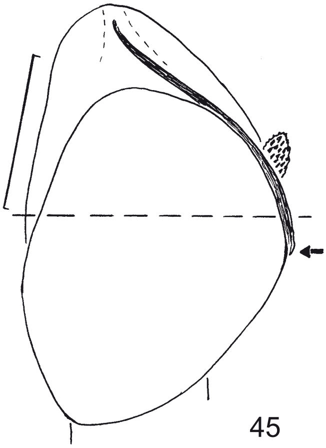
Fig. 39) Euophrys frontalis (WALCKENAER 1802), retrolateral aspect of the tibia of the l. pedipalpus. Scale bar 0.2 mm.

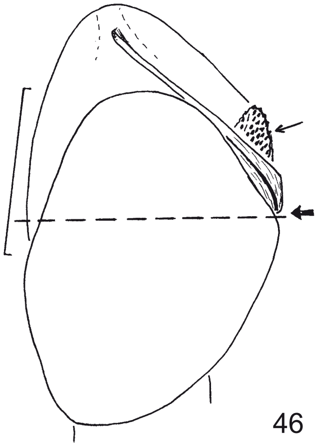
Fig. 40) Neon sp., dorsal aspect of the right eyes. Scale bar 0.2 mm.

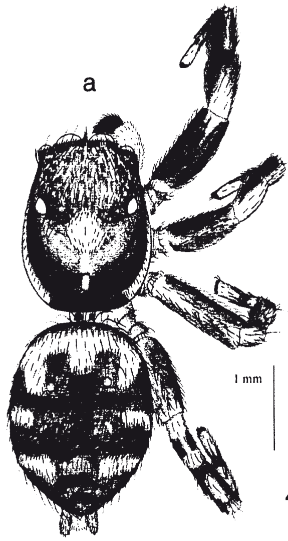
Fig. 41) Euophrys and Talavera sp., dorsal aspect of the right eyes. Scale bar 0.2 mm.

Fig. 42) Neon levis (SIMON 1871), dorsal aspect of the male. Taken from METZNER (1999: T. 30, fig. a).

Figs. 43–44: Neon valentulus FALCONER 1912; 43) ♀, prolateral aspect of the l. tarsus and metatarsus IV; 44) ♂, ventral aspect of the r. pedipalpus (sperm ducts not drawn). Scale bar 0.2 mm.


45


46



47

Fig. 45) *Neon robustus* LOMANDER 1945, ♂, ventral aspect of the r. ♂-pedipalpus (sperm ducts not drawn). Scale bar 0.2 mm.

Fig. 46) *Neon reticulatus* (BLACKWALL 1853), ♂, ventral aspect of the r. ♂-pedipalpus (sperm ducts not drawn). Scale bar 0.2 mm.

Fig. 47) *Pseudeuophrys erratica* WALCKENAER 1826), dorsal aspect of the body. Taken from METZNER (1999: T. 18, fig. a).

BEITR. ARANEOL., 5 (2008)

NOTES ON THE RECENT NORTHWARDS SPREADING OF THE JUMPING SPIDER SPECIES (SALTICIDAE) *MACAROERIS NIDICOLENS* (WALCKENAER 1802)

JOERG WUNDERLICH, 69493 Hirschberg.

ABSTRACT: The second record of the southern European Jumping Spider species *Macaroeris nidicolens* (WALCKENAER 1802) (Araneae: Salticidae) in Germany is discussed: The spreading of this species into and within Germany is most probably a recent one, it well may be in connection with the global warming, the way of its spreading probably runs along the river Rhine valley.

Key words: Area enlarging, climate change, global warming, Jumping Spiders, *Macaroeris nidicolens*, Salticidae.

Numerous – probably more than 20 – species of non-synanthropic and non-urbane species of spiders have been introduced into Germany during the last decades, see WUNDERLICH (1995). Two species have to be added to this list: *Eperigone trilobata* (EMERTON 1882) (Linyphiidae) from North America as well as *Cicurina japonica* (SIMON 1886) (Dictynidae) from SE-Asia. The three species which are listed as *Euophrys* were transferred to *Talavera*.
The genus *Macaroeris* WUNDERLICH 1992 is distributed mainly in the Mediterranean, most species are reported from the Macaronesian Islands. A generic revision is prepared by LOGUNOV. *M. nidicolens* (photo 390) is the only species of the genus which has been found north of the Alps up to now.
Only twelve years ago a population of the Jumping Spider (Salticidae) *Macaroeris nidicolens* (WALCKENAER 1802) (= *Dendryphantes n*., *Eris n.*) was reported from a large town in Germany at the river Rhine, Colonia, leg. in May 1995, see JÄGER (1995).
In July 2005 the present author collected a male (now SMF) of this species in 69493 Hirschberg-Leutershausen at the eastern margin of the river Rhine valley, somewhat 10 km north of Heidelberg, below an apple tree within a S-exposed meadow, about half a km outside of the next village. This region is known to have a warm climate.
Members of this species mainly live in higher strata of the vegetation, not only in the

crowns of needle trees as erroneously reported by some authors. Its range reaches from Central Asia to the Mediterranean, South Europe, Western Europe (Great Britain: London, in 2002, see MERRETT & MILNER (2004)) and Central Europe: Austria, the Czech Republic, Belgium and – recently – Germany.

The first record of *nidicolens* in Colonia was an urbane locality (as the one in England) but the record in Hirschberg is not. The only proofs of *nidicolens* in Germany up to now are located within the river Rhine valley.

Almost all reports of *nidicolens* north of the Alps are younger than 15 years except the one from Belgium which is older than 1882; the report in England is only 4 years old; so surely the spreading or introducing of this species to the north happened independently at least three times and took place into England and Germany most probably only recently.

The spreading of this "expansive species" may well be connected with the climate change and the warming in Central Europe up to ca. 0.1° C every decade nowadays, see WUNDERLICH (1995).

Has the species been introduced to Germany by man? Trains and cars along the river Rhine valley could have transported spiders of *nidicolens* to the north fifty or even more than a hundred years ago but apparently they did not. Why not? Has it been too cold in former times? – The spiders probably colonized this valley in a "natural way" and this may go on to the north step by step in the direction to Belgium if it has not come from Belgium or France. The area of Hirschberg near Heidelberg may have been something like a "stepping stone" along the Rhine valley; it is situated almost 200 km away from Colonia, the northernmost known point of the spiders areal in Germany. Probably specimens arrived in Germany from Switzerland – where the origin of the Rhine is – but *nidicolens* has not yet been reported from Switzerland.

A similar way of spreading along the Rhine valley existed apparently in several species of spiders, e. g. in *Eperigine trilobata* (Linyphiidae) (see above), *Cicurina japonica* (Dictynidae) (see above) (these species were introduced from North America rsp. Japan), as well as the Salticidae *Pseudeuophrys lanigera* (SIMON 1871) and *Heliophanus tribulosus* SIMON 1868; *trilobata* and *japonica* invaded Germany – and the continent of Europe – not earlier than in the second half of the 20th century, and *lanigera* invaded Germany apparently also only in the second half of the 20th.

REFERENCES cited

JÄGER, P. (1995): Erstnachweise von *Macaroeris nidicolens* und *Icius subinermis* für Deutschland in Köln (Araneae: Salticidae). -- Arachnol. Mitt., 9: 38–39.

MERRETT, P. & MILNER, E. (2004): *Macaroeris nidicolens* (Walckenaer, 1802) in Britain (Araneae: Salticidae). -- Bull. Br. arachnol. Soc., 13 (2): 63–64.

WUNDERLICH, J. (1995): Spinnen (Araneae) als mögliche Indikatoren für Auswirkungen von Klima-Veränderungen in Deutschland? -- Beitr. Araneol., 4: 441–445 (1994).

BEITR. ARANEOL., 5 (2008)

ON SOME HEALING EVENTS OF INJURED LEGS IN EXTANT SPIDERS (ARANEAE)

JOERG WUNDERLICH, D-69493 Hirschberg.

Abstract: Healed/closed wounds of legs of four extant spiders (Araneae: Clubionidae, Linyphiidae, Sparassidae, and Zodariidae) are reported and shortly discussed.

Key words: Araneae, China, healing events, injured legs, spiders.

The **material** of the spiders – which are preserved in alcohol – is deposited in the Zoological Institute of the Chinese Academy of Sciences in Beijing, coll. ZHENG GUO.

Acknowledgements: I thank Li SHUQIANG for kind supply of instruments in his Zoological Institute as well as a helpful discussion, and ZHENG GUO who collected the spiders alive in a tropical rain forest of S-China, and took the photos of the spiders.

Only very few informations about healing processes of injured/amputated spiders are available. Seemingly an injured area of the cuticula can not or only hardly “heal” in spiders but the stumps of legs which are amputated THROUGH an article of a leg and apparently are closed – partly by sclerotization (?) – may indicate a peculiar “healing mechanism" especially in members of the families Theridiidae and Zodariidae, which attack ants, may feed on ants, and are attacked by ants which may be dangerous to spiders. So these spiders may not bleed to death. See the remarks (1) and (2). In this paper I report in short on possible healing events in extant chinese members of the families Clubionidae, Linyphiidae, Sparassidae (first reports in this matter), and of the Zodariidae (photos 1–7):

(1) "Healed" leg of a juvenile member of the family Sparassidae indet., photos 1–2. The prosomal length of the spider is 4.2 mm. The left metatarsus II is "cut through" (cross), the wound has been closed probably by darkened blood.

(2) Two injuries of a juvenile member of the Linyphiidae: Erigoninae indet., body length 1.4 mm (photo 3): (a) an autotomy between a patella and a tibia, and (b) a cut through the left femur III with darkened parts inside and empty. The spider apparently survived these injuries.

(3) A female of the family Clubionidae, body length 1 cm, shows an oblique fissure on the left coxa II which is dark brown, and apparently is closed/healed. Photo 4.

(4) An indet. female of the family Zodariidae (photos 5–7), body length about 6 mm, ventral aspect. Three injuries/cuts of legs are apparently healed (the spider was captured alive!): (a) through the right metatarsus I (photo 5), (b) through the left patella I near the end (photo 6), and (c) through the left metatarsus III (darkened) (photo 7).

Remarks:

(1) Injuries and probable healing events – mainly of FOSSIL spiders of the family Zodariidae – are reported by WUNDERLICH, Beitr. Araneol., 3 (2004: 154–157, figs. 1–7, photos 351, 473, 607–610).

(2) Healing events in FOSSIL theridiid spiders of the genera *Clavibertus* n. gen., *Eomysmena* PETRUNKEVITCH, *Hirsutipalpus* n. gen., and *Lasaeola* SIMON: See the paper no. 3 on the family Theridiidae in this volume; e. g. the photos 8–11 in the present volume.

BEITR. ARANEOL., 5 (2008)

ON THE FUNCTIONS OF THE MALE PEDIPALPUS IN SPIDERS (ARANEAE)

ÜBER DIE FUNKTIONEN DES MÄNNLICHEN KIEFERNTASTERS (PEDIPALPUS) BEI SPINNEN (ARANEAE)

JOERG WUNDERLICH, D- 69493 Hirschberg.

Abstract: More than a dozen different functions of the male pedipalpus of spiders (Araneae) are listed and briefly discussed. A peculiar kind of ant-mimicry is reported.

Keywords: Araneae, behaviour, ant mimicry, fossils, spiders, male pedipalpus.

Acknowledgements: My great thanks go to JASON DUNLOP who kindly translated the German text into English.

Remarks: The excellently preserved and the numerous “preparations” of fossil spiders in amber – cf. WUNDERLICH (2004) – have prompted me to write this review and in this study I make particular reference to the fossil spiders treated in this book.

The pedipalps or "feelers" (Figs. 1–6) – the extremities in front of the first pair of walking legs in spiders – play a special role, particularly in males. Here, they serve to take up sperm and are the most common means by which the sperm cells are transported to the female genital opening, a process in which the "sperm web" forms an intermediate station for these cells after their release from the genital opening on the underside of the abdomen. Most arachnids – male spiders included – lack a penis, and such an organ was probably not present in their aquatic ancestors. Harvestmen and certain mites are the only arachnids that have a true penis. This means that spiders require a special mechanism to transport the sperm. The pedipalps act in sense as a "penis alternative", a secondary sexual organ and – being in their own way unique – as a new development for this group of animals (Figs 1, 3, 6).

Spider pedipalps have six segments, unlike the seven-segmented walking legs. The pedipalps of both male and female spiders lack the second to last segment: the metatarsus. At the base of the palps are the gnathocoxae (which belong functionally to the **MOUTHPARTS**) and are usually widely separated. At the end of the **MALE** palp sits the cymbium which bears the bulbus (Figs. 1, 3, 6) (*).

In female spiders and juvenile males the pedipalps are still leg-like, as in spider ancestors, but are smaller than the legs (Fig 4). In females of the dwarf spiders of the family Anapidae s. l. they are reduced or even missing completely. In primitive spiders, like tarantulas, they are quite long and distinctly leg-like. In the males of some araneomorph spiders at a development stage before they moult to maturity the pedipalps are sac- or pear-shaped, although the cymbium is still missing (Fig. 5). During walking the pedipalps play only a minor role, but they may have an important function in orientation (see No. 1 below).

In adult males the tip of the pedipalp – the still hairy cymbium, effectively the modified tarsus – carries the most important organ for copulation (Figs 1, 3, 6). In most spiders this lies under the cymbium, but is frequently on the end in primitive forms. This bulbus is a more-or-less rounded and hairless structure, which can carry – particularly in highly advanced spiders – complicated projections. One of these, the embolus ("intromittant organ"), serves to transport the sperm cells. It can be short and insignificant or extremely long and coiled.

In all male spiders the pedipalps, in particular the modified cymbium, can have functions other than the transport of sperm cells; functions which may not be particularly associated with reproduction. Among the most unusual uses and changes in the role of the male pedipalp are for signalling – see Nos. 4, 5 and 10 below). A difference between the sexes is generally absent in functions 1, 6 and 7–10. Changes in the size – both increases and decreases – are dealt with in Nos. 4 and 10; elongation of the embolus in 11.

(*)The spider pedipalps are paired, thus male spiders usually have two such appendages. Exceptions are members of the cobweb spider genera *Echinotheridion* and *Tidarren*, in which mature males have only one pedipalp; either the left or right with equal frequency. One pedipalp is amputated before the moult to maturity – an extremely unusual form of self-amputation! Also in some hermaphrodites – the one part feminine – a male pedipalp is formed only on one side, the other being female. An asymmetrical male pedipalp occurs exceptionally in the pholcid species *Metagonia mariguitarensis*, cf. HUBER et al. (2007: 651).

Summaries of the functions of the male pedipalp are detailed below (mouthpart functions are not considered further):

(1) as carriers of sensory organs (the cymbium),
(2) as reproductive organs (for transporting sperm: various segments of the palp with their projections, the cymbium and in particular the bulbus and its structures),
(3) for the production of mating plugs (bulbus),
(4) in courtship displays (femur, patella, tibia, cymbium or the whole pedipalp),
(5) in threat displays (antagonistic behaviour) (to ward off predators or against rivals of the same species) (whole pedipalp),
(6) in prey capture (particularly the femur) and the transport of prey,
(7) in feeding (particularly the coxae),
(8) for cleaning, especially of the mouthparts (cymbium and bulbus),
(9) for digging tunnels or retreats (cymbium),
(10) in association with ant-mimcry (cymbium and bulbus),
(11) unkown functions (cymbium and bulbus).

(1) As carriers of sensory organs on the cymbium (equivalent to the leg tarsus), the pedipalps bear, for example, mechanoreceptive hairs for feeling (hence the common name for the palps of “feelers”), hairs that can “hear” air movements (trichobothria) and chemosensory organs for “smelling” like the tarsal organs or chemosensory hairs. Some of these chemosensory hairs – e.g. in wolf spiders – help the male follow a line of silk leading to a reproductively-receptive female (FOELIX 1996: fig.163). The cymbium also plays a role in detecting water.

(2) In copulation (sperm transfer by the embolus, fig. 1) (see above and FOELIX 1992: 207–209) the pedipalps have a generally well-known function during mating – with their many adaptations for the form of the female genitalia and the mating position – and this needs not be considered further here. Apophyses projecting from the segments of the pedipalp – primarily tibial apophyses (mostly at the end), and the (ventral) femur, as well as projections from the cymbium, mostly “paracymbiums” laterally at the base or (dorsal) modifications of the cymbium – play a role here. Mostly they help to fix the position of the partner or the pedipalp. In numerous orb-weaving spiders (Araneidae and some Zygiellidae) this is achieved with the help of a lateral hook on the gnathocoxa, or in many mygalomorphs by a growth at the front of the gnathocoxa.

(3) Mating plugs are hardened secretions from special glands in the bulbus which, after a successful mating, can close the external opening of the female genitalia; typically a groove in the epigyne. In this way sperm-transfer by a rival male can be prevented. Mating plugs are well known from various families of araneomorph spiders. In fossils they are known from Theridiidae, Synotaxidae, Dictynidae and Trochanteridae; see WUNDERLICH (2004: 172–173, fig. 24, 1725, fig. 11). Blockage of the opening to the epigyne can be achieved through broken-off remains of the emboli. This is not uncommon in certain orb-weavers or widow spiders like *Latrodectus*.

(4) Courtship (see also 5 and 11)

(a) Stridulatory teeth (sometimes a single tooth, an elongate margin or series of teeth) can occur anteriorly on a segment of the pedipalp; in araneomorph spiders usually in the basal half of the femur (see e.g. WUNDERLICH 2004: 719, fig. 12, 800–801, figs 15, 19). They are associated with washboard-like lateral ridges on the chelicerae, along which the teeth can be rubbed to produce vibrations (see e.g. WUNDERLICH 2004: 162, 798–802, photo 261). Thanks to the occurrence of such files in fossil spiders we can conclude that such courtship behaviour developed by at least the early Cretaceous over 100 million years ago, see the paper no. 5 in this volume. Typically such files or ridges occur in both sexes (in females they can be more weakly expressed) in various families like mesotheles, money spiders, spitting spiders and their relatives. In many mygalomorphs (e.g. tarantulas) stridulatory organs also occur on the gnathocoxae of the pedipalps.

(b) Prominent long and/or colourful and often erect cymbial hairs give the appearance of a larger cymbium. They are found in many large-eyed, visually acute, vagrant spiders which do not build a web for prey capture, such as wolf- or jumping spiders.
These hairs are part of a “visual courtship” in males of these spiders involving clear movements of the pedipalps und sometimes also the front legs. These movements are often accompanied by an “acoustic courtship”: a “circling” movement of the pedipalps (Fig. 2) in wolf spiders is followed by “drumming” on the ground or dry leaf litter; see below and FOELIX (1992: 201–202). In Baltic amber fossil spiders I found suitably prominent hairs on the cymbium of the jumping spider *Almolinus ligula* (see WUNDERLICH 2004: photo 414). Such hairs in a fossil species suggest optical courtship displays like those of modern spiders (“waving movements”) and this would be the oldest – indirect – geological evidence of this courtship behaviour; coming from the Eocene, 40–50 million years ago.

(c) In some male spiders, e.g. orb-weavers, the males “pluck” the webs of females they wish to woo using the pedipalps and sometimes also the forelegs, doing so in a species-specific way and often tugging on special “courtship threads”. In many mygalomorphs the males drum in a species-specific way on the catching web or the trapdoor of the female. Drumming with the pedipalps is also described from various other spider families like wolf spiders (on the ground in which a stridulation organ on a joint in the pedipalp is involved) and in Amaurobiidae in the capture web. In some spider species the males stroke the females during courtship using the pedipalps.
In many, mostly small, web-building spiders such as Anapidae the bulbi are highly voluminous. These structures – simply by virtue of their size – do not play a role in courtship as far as I am aware. See also No. 10. In primitive spiders – the mygalomorphs through to the six-eyed spiders and their relatives (Dysderoidea) – one or more segments of the male pedipalp can be unusually large. In many mygalomorphs the pedipalps are, in both sexes, almost leg-like.
It is notable that in some male spiders with unusually large chelicerae, the end segment of the pedipalp is usually small; see e.g. Wunderlich (2004: photo 292), or some males of the jumping spider genus *Myrmarachne*.

(d) In some spiders, like members of the genus *Pisaura* or *Meta*, the males use their pedipalp to wrap and transport their “nuptial gift”. This is given to the female before copulation and is usually consumed while this act takes place. In this way the female is “distracted” from showing aggressive behaviour.

(5) Antagonistic or threat behaviour is used against predators or rivals. When threatened, spiders of both sexes in some species (particularly mygalomorphs) raise their whole cephalothorax, spread their jaws, and the forelegs – and in many species also the pedipalps – are held up in a typical defensive posture. Threat behaviour in some male jumping spiders competing for females is similar to their courtship displays.

(6) Prey capture and transport. In some female spiders particular segments have long spines which aid in prey capture, even forming a type of "catching basket". For example the tiba and tarsus of the linyphiid *Drapetisca socialis* bear strong spination. In males of this species, however, the spines are absent and the function of the pedipalps is thus different between the genders (i.e. it is sexually dimorphic), and in males the palps play little or no role in prey capture. The situation is different in many examples of the Leptonetidae: long spines are present in both sexes of some species (Figs 3–4). The lack of differentiation between the sexes in these spiders suggests a function related to feeding rather than reproduction.

(7) Feeding. Spiders cannot ingest their food in pieces. They liquefy their prey in front of the mouth opening and filter out large particles with the help of the mouthparts in general. In this context the filtering hairs on the pedipalpal gnathocoxa play, in both sexes, a particular role. The "serrula" on the gnathocoxa in araneomorph spiders functions rather like a "saw". There are also spines on the gnathocoxae in both sexes of mygalomorphs which may act as possible mechanoreceptors.

(8) Cleaning. "Against dry particles of dirt brushing is sufficient. However spiders use, like many other animals, the effect of their saliva with its digestive enzymes. The whole body is thoroughly rubbed with saliva using the legs and pedipalps. This small amount of liquid has, firstly, a dirt-releasing function. Secondly, few bacteria or fungi can resist the aggressive digestive juices…The body areas which can't be reached by the mouth are cleaned with special combs and spines on the legs and feelers [pedipalps]" HEIMER (1988: 134–135) See also No. 11(a).

(9) Digging burrows and retreats. Spiders of numerous families dig burrows in the earth or construct retreats and spend at least part of their time underground. Examples include many mygalomorphs, like trap-door and purse-web spiders, many zodariids and various wolf spiders. For digging they use spines and hairs on the cephalothorax, the jaws (chelicerae), various leg segments and the cymbium. Spines on the cymbium can be seen even in fossil trapdoor spiders (Ctenizidae) and zodariids; see WUNDERLICH (2004: 624–625, figs 8, 8d, 1605, fig. 13).

(10) Ant mimicry. Unusually large – e. g. in numerous Anapidae s. l.: Mysmeninae and some Theridiosomatidae – or unusually small pedipalps – e. g. in the genus *Hylyphantes* (Linyphiidae) – could be, among other things, adaptations associated with ant mimicry, but their function is unknown. The adoption of the shape and behaviour of ants has been described from numerous spider families: e.g. Theridiidae, Zodariidae, Corinnidae, Gnaphosidae, and Salticidae. In the course of evolution these spiders have "camouflaged" themselves with the "warning form" of an ant (Batesian mimicry). Unlike spiders, ants are generally avoided as prey by birds because of their foul taste. Thus ant-mimicking spiders enjoy a certain degree of protection.

There are various ways in which the "typical" shape of the spiders body – with its two body parts and often robust and hairy legs – can be made to resemble the three-part and often slender ant shape.
(a) The most common way to look like an ant is to "thin out" the body, legs and pedipalps and to develop a saddle-like abdominal constriction which gives the impression here of two body parts. An example is the fossil genus *Eomazax* in Baltic amber in which this shape is slightly expressed; see WUNDERLICH (Fig. 6, p. 192, photo 376). Unusually slender, much more slender than in related genera, are the pedipalps of males of the highly ant-like gnaphosid *Micaria* (Fig. 6) and in Corinnidae of the subfamily Castianerinae in which the tip of the pedipalp (i.e. cymbium and bulbus) in examples of these spiders are unusually small. Such behaviour occurred in fossil spiders some 40–50 million years ago; see WUNDERLICH (2004, 480, fig. 376).
(b) In terms of the size of the pedipalps some cobweb spiders (Theridiidae) have taken an alternative evolutionary path. In some species of *Steatoda* and – even more so – in *Neottiura* the end segments of the male pedipalp are enormous (Fig. 5); much larger than in related genera. A particular role for these huge pedipalps is not apparent in specimens preserved in alcohol, but becomes clear when the spiders are observed in their natural habitat. These ca. 2 mm long spiders live in upper layers of vegetation where they would be easy prey for birds. In southern France I watched a male *Neottiura herbigrada* (see WUNDERLICH 2004: 196). He stretched his pedipalps almost together in front of the cephalothorax in such a way that the large bulbi and cymbia looked remarkably like the head of an ant and the spider appeared to have a three-part body! Through these huge pedipalps held before the prosoma these spiders seem to create an "illusionary head". Furthermore, the front pair of legs move alternately up and down similar to the antennae of an ant; apparently forming "illusionary antennae". Whether such mimicry also occurs in closely-related species and whether it also protects them from attack by ants is not yet known. These days scientists barely know the living animals; more often they know their DNA instead.
Interestingly, in the above-mentioned species this mimicry is sexually dimorphic, since *Neottiura* females possess only small pedipalps which are inappropriate for this sort of camouflage. Why are males so protected? The answer lies in the biology of these spiders. Females are pretty much protected for most of the time within their webs. Males, by contrast, go in search of receptive females in spring, during which time they would be easy prey for animals like songbirds. This type of ant mimicry has not yet been recorded in the literature and experiments about its actual effectiveness – in relation to birds – have yet to be carried out.

(11) Evolution. The noticeable (often spiral) extension of the embolus – through which sperm cells are sucked from the sperm web into the bulbus and by which the cells are later released – apparently plays a "stimulating" role in the "diversification" of species in various genera of numerous spider families. Examples include the huntsman spiders (Sparassidae) and cobweb spiders (see the study of Theridiidae in this volume) and this role is currently the subject of intensive discussion.

Unknown or little-known functions (a brief selection; a-d concern the cymbium):

(a) Outgrowths and strong spines on the segments of the pedipalps in Linyphiidae include, for example, the spines on a projection of the pedipalp patella in *Floronia* (here

on the tibia too) and in *Bolyphantes*. Other examples include spines on the patella in *Microneta*, “feather-like” spines on the tibia of *Centromerita* and on the tibia and cymbium of *Maso gallica*, tibial spines modified at the tip in *Allomengea*, spines on the cymbium of *Drapetisca* and modified spines on an outgrowth of the cymbium in *Sintula*.
Spines also exist on the cymbium in males of numerous other families, e.g. Leptonetidae, Zodariidae (see above) and some Lycosidae (here at the cymbium end).These spines may play a role in cleaning behaviour, as well as in copulation (in Leptonetidae?) or in digging (Zodariidae, Lycosidae); see Nos 8 and 9.

(b) Hair bushes are often small, brush-like and occur usually at the distal end of the cymbium in various groups of spiders, like Zodariidae, wolf spiders (Lycosidae) and jumping spiders (Salticidae); see WUNDERLICH 2004: 1608m fig. 32, 1621). They may play a role in courtship/copulatory behaviour.

(c) In a fossil male of the family Zodariidae (*Anniculus balticus*) in Baltic amber the cymbium and bulbus have a very unusual form. The cymbium is very extensive and the bulbus is flat, even concave; see WUNDERLICH (2004: Photos 348, 632). Because of its form and position, the distal articles of the pedipalps antero-laterally can be fitted exactly against the jaws and part of the cephalothorax, such that the delicate parts of the bulbus are protected to some extent against the bites of ants. Otherwise the strongly armoured spiders (Photo 348) are pretty well protected against the defensive bites of their prey; although as Photo 611 shows, they occasionally fall victim to the ants. See also the genus *Borboropactus*, paper no. 4 in this volume.

(d) The meaning of outgrowths/modifications of the cymbium, as in numerous anapids is unknown. In some theridiids the outer margin of the cymbium acts as a guide for the embolus (conductor) and can carry a row of stout hairs, as per the article on cobweb spiders in this volume.

(e) The meaning of the special position of the pedipalp in some spiders has not been resolved. An example is the peculiar position of the final article of the pedipalp in male representatives of the Dictynidae genus *Mastigusa*, in which the bulbus is small but the embolus in some species forms an extremely extended loop which can lie across the entire prosomal length, see WUNDERLICH (2004: Photo 276),

(f) Autonomy: The occasional loss of a pedipalp – e.g. at the coxa in a fossil male of the genus *Eomatachia* – indicates the occurrence of autonomy in some spiders involving the occasional amputation of particular parts of the limb, usually after the coxa; see WUNDERLICH (2004: 146–148).

ÜBER DIE FUNKTIONEN DES MÄNNLICHEN KIEFERNTASTERS (PEDIPALPUS) BEI SPINNEN (ARANEAE)

Zusammenfassung: Mehr als ein Dutzend verschiedene Fuktionen des „multifunktionellen" männlichen Kieferntasters (Pedipalpus) bei Spinnen (Araneae) werden aufgeführt und kurz behandelt. Eine besondere Art von Ameisen-Mimikry wird beschrieben.

Anmerkung: Die hervorragend und in großer Anzahl existierenden „Präparate" fossiler Spinnen im Bernstein – vgl. WUNDERLICH (2004) – haben mich zu dieser Zusammenstellung veranlasst, und ich beziehe mich daher mehrfach auf in dieser Arbeit behandelte fossile Spinnen.

Die Pedipalpen oder „Kieferntaster" (Abb. 1–6) – die Extremitäten vor dem ersten Beinpaar der Spinnen – haben im männlichen Geschlecht vor allem eine ganz besondere Funktion: Sie dienen – bevor eine erfolgreiche Paarung stattfinden kann! – der Aufnahme der Samenzellen, die gewöhnlich mit ihrer Hilfe in die weibliche Geschlechtsöffnung transportiert werden, wobei ein „Spermanetz" als „Zwischenstation" bei der Weitergabe der Samenzellen nach ihrer Abscheidung aus der Geschlechtsöffnung am Bauch des Spinnen-Männchens dient.
Die meisten männlichen Spinnen-Verwandten – so auch die Spinnen-Männchen – besitzen keinen Penis, und bei den wasserbewohnenden Vorfahren der Spinnentiere fehlte er vermutlich bereits. Weberknechte und manche Milben gehören zu den wenigen Spinnentieren, bei denen dagegen ein Penis existiert. (Andere mänliche Spinnentiere – z. B. die Pseudoskorpione – setzen Samenpakete ab, die vom Weibchen aufgenommen werden). Bei den Spinnen sind daher für eine Samenübertragung vom Männchen zum Weibchen besondere Lösungen gefordert. Die Pedipalpen fungieren gewissermaßen als „Ersatzpenis", als „sekundäres Geschlechtsorgan"; sie sind eine – in dieser Weise einzigartige – „Neuentwicklung" bei dieser Tiergruppe (Abb. 1, 3, 6). (*)
Der Kieferntaster der Spinnen besitzt sechs Glieder (im Gegensatz zu den siebengliedrigen Beinen fehlt dem Pedipalpus in beiden Geschlechtern immer das vorletzte Glied, der Metatarsus); am Grunde sitzen die Gnathocoxen (sie besitzen eine Funktion von Mundteilen (!)), die meist deutlich verbreitert sind, am Ende sitzt **IM MÄNNLICHEN GESCHLECHT** das Cymbium, das den Bulbus trägt. Abb. 1, 3, 6.
Bei weiblichen Spinnen und bei männlichen Jungspinnen sind die Pedipalpen noch beinähnlich wie bei den Vorfahren der Spinnen; sie sind aber kleiner (Abb. 4) (bei den Weibchen der Zwerg-Kugelspinnen (Anapidae s. l.) sind sie reduziert oder fehlen sogar). Bei ursprünlichen Spinnen – wie den Vogelspinnen – sind sie allerdings relativ lang und beinähnlich. – Bei männlichen Querkieferspinnen im Entwicklungsstadium unmittelbar vor der Häutung zur Geschlechtsreife sind die Pedipalpen blasen- oder birnenförmig verdickt und ein Cymbium fehlt noch (Abb. 6). Bei der Fortbewegung

spielen die Pedipalpen eine ganz untergeordnete Rolle; bei der Orientierung können sie allerdings eine wichtige Funktion besitzen, siehe unten, Nr. 1.

Bei adulten männlichen Spinnen trägt der letzte Teil des Pedipalpus – das stets behaarte Cymbium, es handelt sich um das umgewandelte Fußglied – unten (bei ursprünglichen Spinnen befindet es sich meist am Ende) den für die Kopulation wichtigsten Abschnitt (Abb. 1, 3, 6): Einen mehr oder weniger kugelförmigen und unbehaarten Abschnitt, den Bulbus, der seinerseits – vor allem bei den meisten hochentwickelten Gruppen der Spinnen – komplizierte Anhänge trägt. Einer dieser Anhänge, der Embolus („Eindringer") (Abb. 1) dient der Übertragung der Samenzellen; er kann unscheinbar und kurz oder auch extrem lang und spiralig eingerollt sein.

Bei allen männlichen Spinnen besitzen die Pedipalpen – z. B. das in vielfältiger Weise modifizierte Cymbium – neben der Übertragung von Samenzellen noch weitere, recht verschiedenartige Funktionen, von denen einige mit dem Fortpflanzungsverhalten in keinerlei Zusammenhang stehen. Zu den bemerkenswerten Erweiterungen der Funktion und zum bemerkenswerten Funktionswandel von Strukturen des männlichen Pedipalpus – etwa zu einer Signalfunktion – siehe unten die Nr. 4, 5 und 10. Ein Unterschied bei den Geschlechtern fehlt überwiegend bei Nr. 1, 6 und 7–10. Abwandlungen der Größe – Vergrößerungen wie Verkleinerungen – werden bei den Nr. 4 und 10 behandelt, die Verlängerung des Embolus in Nr. 11.

(*) Die Pedipalpen der Spinnen sind paarig ausgebildet, somit besitzen Spinnen-Männchen gewöhnlich zwei dieser Extremitäten. Ausnahmen sind Kugelspinnen der Gattungen *Echinotheridion* und *Tidarren*, bei denen die geschlechtsreifen Männchen nur einen einzigen Kiefertaster besitzen, den rechten oder den linken etwa gleich häufig. Einer der Pedipalpen wird vom Männchen vor der Häutung zur Geschlechtsreife amputiert – eine ganz ungewöhnliche Form der Selbst-Amputation! Sie belegt, dass sich Spinnen im Prinzip auch mit nur einem Pedipalpus fortpflanzen können. – Auch bei bestimmten Zwittern – den Halbseiten-Gynandern – ist ein männlicher Pedipalpus nur auf einer Seite ausgebildet, der andere ist „weiblich". – Ein asymmetrischer ♂-Pedipalpus existiert ausnahmsweise bei der Zitterspinnenart *Metagonia mariguitarensis*, siehe HUBER et al. (2007: 651).

Der unten stehenden Übersicht über die Funktionen des männlichen Pedipalpus sind einige Erläuterungen angefügt (die oben erwähnte Funktion von Mundteilen wird hier nicht wiederholt):

(1) Als Träger von Sinnesorganen (das Cymbium),
(2) als Begattungsorgan (zur Samenübertragung): Verschiedene Glieder des Pedipalpus mit Apophysen, das Cymbium und insbesondere der Bulbus mit seinen Strukturen, insbesondere der „Eindringer" (Embolus),
(3) bei der Herstellung des „Begattungszeichens" (Bulbus),
(4) bei der Balz (Femur, Patella, Tibia, Cymbium oder gesamter Pedipalpus),
(5) beim Drohverhalten (antagonistischem Verhalten) (gegenüber Feinden und artgleichen Konkurrenten) (gesamter Pedipalpus),
(6) beim Beutefang (vor allem das Femur) und beim Beutetransport,
(7) bei der Nahrungsaufnahme (vor allem die Coxa),
(8) beim Putzen, beim Reinigen der Mundwerkzeugen (Cymbium und Bulbus),
(9) beim Graben von Wohnröhren und Verstecken (Cymbium),
(10) im Zusammenhang mit Ameisenmimikry (Cymbium und Bulbus),
(11) unbekannte Funktionen (Cymbium und Bulbus).

(1) Träger von Sinnesorganen auf dem Cymbium (entsprechend den Tarsen der Beine), z. B. von „Tasthaaren“ (daher der deutsche Name „Kieferntaster“ für Pedipalpus), von „Hörhaaren“ (Trichobothrien) und Geruchsorganen wie Tarsal-Organen und „Geruchshaaren“. Bestimmte „Geruchshaare“ besitzen – etwa bei Wolfspinnen – eine Funktion bei der Leitung des Männchens entlang des Wegfadens als „Richtschnur“ zu einem paarungsbereiten Weibchen, siehe FOELIX (1996: Abb. 163). Auch beim Aufspüren von Wasser spielen Sinnesorgane des Cymbiums eine Rolle.

(2) Kopulation (Samenübertragung): Siehe oben und FOELIX (1992: 207–209). Die allgemein bekannte Funktion des männlichen Pedipalpus bei der Paarung – mit ihren zahlreichen Anpassungen an die Ausbildungen der weiblichen Sexual-Organe und an die Paarungs-Stellung – wird hier nicht näher behandelt. Apophysen der Glieder des Pedipalpus – vor allem Apophysen der Tibia (meist am Ende) und des Femur (unten) – sowie Auswüchse des Cymbiums – vor allem seitlich-basale „Paracymbia“ oder weitere (meist obere) Modifikationen des Cymbiums – spielen in diesem Zusammenhang – etwa bei der Fixierung der Geschlechtspartner oder des Pedipalpus – ebenso eine Rolle wie ein zur Seite gerichteter Höcker auf den Gnathocoxen bei zahlreichen Radnetzspinnen (bei Araneidae und manchen Zygiellidae) oder ein Auswuchs vorn am Ende der Gnathocoxen bei zahlreichen Längskieferspinnen.

(3) „Begattungszeichen“ sind erhärtete Sekrete spezieller Drüsen des Bulbus, die – nach erfolgter Begattung – die äußeren Öffnungen des weiblichen Genitalorgans (gewöhnlich eine Grube der Epigyne) verschießen können. Dadurch kann eine weitere Sperma-Übertragung (konkurrierender Männchen!) verhindert werden. Begattungszeichen sind von zahlreichen Familien der Querkieferspinnen bekannt; fossil wurden sie z. B. bei Kugelspinnen (Theridiidae), Kugelhöhlenspinnen (Synotaxidae), Kräuselspinnen (Dictynidae) und Schenkelring-Spinnen (Trochanteriidae) nachgewiesen, siehe WUNDERLICH (2004: 172–173, Abb. 24, 1725: Abb. 11). – Ein einseitiger Verschluß der Einführungs-Öffnung der Epigyne wird durch abgebrochene und stecken gebliebene Teile oder Anhänge der Emboli („Eindringer“) erreicht; er findet sich nicht selten z. B. bei einigen Radnetzspinnen, Baldachinspinnen und Kugelspinnen (etwa den Witwen, Gattung *Latrodectus*).

(4) Balz. (Siehe auch Nr. 5 und 11)

(a) Stridulationszähne (gelegentlich nur ein einzelner Zahn, eine Leiste oder Rillen) vorn auf einem Glied des Pedipalpus, bei Querkieferspinnen meist in der ersten Hälfte des Femurs, siehe z. B. WUNDERLICH (2004: 719, Abb. 12, 800–801, Abb. 15, 19). Sie stehen in Verbindung mit waschbrettartigen seitlichen Rillen der Kiefer (Cheliceren), auf denen die Zähne entlang gerieben werden und auf diese Weise Vibrationen erzeugen, siehe z. B. WUNDERLICH (2004: 162, 798–802, Foto 261). Aus der Existenz dieser Rillen bei fossilen Spinnen ist zu schließen, dass ein derartiges Balzverhalten bereits in der Kreidezeit vor mehr als 100 Millionen Jahren entwickelt war, siehe die Arbeit Nr. 5 in diesem Band. Gewöhnlich existieren derartige Rillen in beiden Geschlechtern – beim Weibchen können sie schwächer ausgebildet sein – bei zahlreichen Spinnenfamilien, etwa bei Urspinnen, Baldachinspinnen sowie Speispinnen und ihren Verwandten. Bei zahlreichen Längskieferspinnen (z. B. Theraphosidae) existieren ebenfalls Stridulationsorgane, so z. B. auf den Gnathocoxen der Pedipalpen.

(b) Auffällige – farbige und/oder lange und meist abstehende – Haare des Cymbiums, das auf diese Weise scheinbar vergrößert wird. Sie existieren bei zahlreichen sich optisch orientierenden (großäugigen) vagilen Spinnen wie Wolfspinnen und Springspinnen, nicht dagegen bei Spinnen, die Fangnetze herstellen (bei diesen existiert eher eine „mechnische“ Balz durch Zupfen der Männchen an Signalfäden des Fangnetzes der Weibchen, siehe c).
Diese Haare stehen in Verbindung mit einer „optischen Balz“ dieser Spinnen-Männchen: Auffälligen Bewegungen der Pedipalpen und oft auch der Vorderbeine. Diese Bewegungen sind nicht selten verknüpft mit einer „akustischen Balz“: Zunächst erfolgt ein „Pedipalpenkreisen“ (Abb. 2), dann „Pedipalpentrommeln“ etwa bei Wolfspinnen, „winkende“ und auf den Boden – etwa auf trockenes Laub – trommelnde Bewegungen der Pedipalpen, siehe unten und FOELIX (1992: 201–202). – Bei fossilen Spinnen im Baltischen Bernstein fand ich entsprechende auffällige Haare auf dem Cymbium der Springspinne *Almolinus ligula*, siehe WUNDERLICH (2004: Foto 414). Derartige Haare bei einer fossilen Spinnenart lassen auf ein den heutigen Spinnen entsprechendes optisches Balzverhalten („winkende Bewegungen“) schließen; damit handelt es sich um den geologisch ältesten – indirekten – Nachweis dieses Balz-Verhaltens; er stammt aus dem Eozän vor 40–50 Millionen Jahren.

(c) bei manchen Spinnen – z. B. Radnetzspinnen – zupfen die Männchen mit den Tastern – auch mit den Vorderbeinen – in arttypischer Weise am Fangnetz (oft an speziellen „Balzfäden“) des umworbenen Weibchens. Bei zahlreichen Längskieferspinnen trommeln die Männchen in arttypischer Weise am Fangnetzt oder an der Falltür des umworbenen Weibchens. Ein Trommeln mit den Pedipalpen ist auch von verschiedenen anderen Spinnenfamilien beschrieben worden, so von Wolfspinnen (auf dem Untergrund, wobei ein Stridulationsorgan an einem Gelenk des Pedipalpus betätigt wird) und Finsterspinnen (Amaurobiidae) (am Fangnetz). Bei manchen Spinnenarten berühren („streicheln“) die Männchen die Weibchen während der Balz mit den Pedipalpen.

Bei zahlreichen, überwiegend kleinen Netzspinnen – wie den meisten Zwerg-Kugelspinnen (Anapidae), aber auch bei Dreiecksspinnen (*Hyptiotes*) – sind die Bulbi voluminös entwickelt. Diese Strukturen spielen allerdings – allein aufgrund ihrer Größe – bei der Balz meines Wissens keine besondere Rolle. Siehe auch Nr. 10. – Bei ursprünglichen Spinnen – den Längskieferspinnen bis hin zu den Sechsaugenspinnen-Verwandten (Dysderoidea) sind ein Glied oder vielfach mehrere Glieder des männlichen Pedipalpus ungewöhnlich groß, bei zahlreichen Längskieferspinnen sind sie – in beiden Geschlechtern nahezu beinartig.
Es fällt auf, dass bei manchen Spinnen-Männchen, die ungewöhnlich große Kiefer besitzen, die Endglieder der Pedipalpen besonders klein sind; siehe z. B. WUNDERLICH (2004: Foto 292), manche Springspinnen-Männchen der Gattung *Myrmarachne*.

(d) Bei manchen Spinnen – etwa bei Vertretern von Jagdspinnen der Gattung *Pisaura* und Herbstspinnen der Gattung *Meta* (Familie Streckerspinnen) – setzen die Männchen ihre Pedipalpen beim Umspinnen und beim Transport ihres „Brautgeschenks“ ein, das sie vor der Paarung dem Weibchen übergeben, und das von diesen gewöhnlich während der Paarung verzehrt wird. (Auf diese Weise wird das potentiell aggressive Verhalten des Spinnen-Weibchens vom Partner „umgelenkt“).

(5) Antagonistisches Verhalten, Drohverhalten (gegenüber Feinden und Konkurrenten). Bei einer Bedrohung richten die Spinnen beider Geschlechter mancher Arten – insbesondere der Längskieferspinnen – den Vorderkörper in die Höhe, wobei die Kiefer weit gespreizt und die Vorderbeine – bei zahlreichen Arten auch die Pedipalpen – in einer typischen Abwehrstellung aufgerichtet werden. Das Drohverhalten mancher männlicher Springspinnen, die um Weibchen konkurrieren, ähnelt ihrem Balzverhalten.

(6) Beutefang und Beutetransport. Bei manchen Spinnen-Weibchen sind bestimmte Glieder der Pedipalpen mit langen Borsten versehen und besitzen eine Funktion beim Beutefang; es kann sogar ein regelrechter „Fangkorb" ausgebildet sein. Beispielsweise tragen Tibia und Tarsus bei der Baldachinspinnenart *Drapetisca socialis* starke Borsten. Beim Männchen dieser Art fehlen aber derartige Borsten; die Aufgabe der Pedipalpen in dieser Hinsicht ist bei den Geschlechtern dieser Art somit ungleichartig (Sexual-Dimorphismus), und die männlichen Pedipalpen haben offenbar keine Funktion beim Beutefang. – Anders ist die Situation bei zahlreichen Vertretern der Schlankbein-Spinnen (Leptonetidae): Lange Borsten sind bei einigen Arten gleichstark ausgebildet (Abb. 3–4). Der fehlende Unterschied beider Geschlechter deutet bei diesen Spinnen eher auf eine Funktion – auch des männlichen – Pedipalpus beim Beutefang als auf einen Zusammenhang mit dem Fortpflanzungsverhalten.

(7) Nahrungsaufnahme. Spinnen können ihre Beute nicht stückweise als Brocken hinunterschlucken; sie verflüssigen ihre Nahrung vor der Mundöffnung und filtern grobe Bestandteile mit Hilfe ihrer Mundwerkzeuge heraus. Dabei spielen – in beiden Geschlechtern gleichermaßen – vor allem filternde Haare auf den Gnathocoxen eine Rolle. In diesem Zusammenhang ist auch die Funktion der „Serrula" der Gnathocoxen bei Querkieferspinnen als „Säge" von Beuteteilen zu sehen und auch die Stacheln auf den Gnathocoxen beider Geschlechter als mögliche Mechanorezeptoren zahlreicher Längskieferspinnen.

(8) Putzen. „Gegen trockene Schmutzteilchen genügt einfaches Abbürsten. Aber Spinnen nutzen wie viele andere Tiere auch die Wirkung ihres Speichels mit ihren Verdauungsenzymen. Sehr gründlich wird der gesamte Körper unter Einsatz der Beine und Taster mit Speichel eingerieben. Einmal hat die geringe Flüssigkeitsmenge schmutzlösende Funtion, zum anderen dürften nur wenige Bakterien und Pilze den aggressiven Verdauungssäften gewachsen sein....Die vom Mund nicht erreichbaren Körperstellen werden mit besonderen Putzkämmen und Stacheln der Beine und Taster <Pedipalpen> gereinigt." HEIMER (1988: 134–135). Siehe Nr. 11 (a).

(9) Graben von Wohnröhren und Verstecken. Spinnen vielerer Familien graben Erd-Röhren oder Verstecke und leben wenigstens zeitweise unterirdisch, z. B. zahlreiche Vertreter der Längskieferspinnen – etwa Falltürspinnen und Tapezierspinnen –, viele Ameisenjäger (Zodariidae) und verschiedene Wolfspinnen. Zum Graben benutzen sie Stacheln und Borsten des Vorderkörpers, der Kiefer (Cheliceren), verschiedener Beinglieder und des Cymbiums. Bereits bei fossilen Spinnen sind Borsten oder Stacheln des Cymbiums bei Vertretern der Falltürpinnen (Ctenizidae) und der Ameisenjäger (Zodariidae) nachgewiesen worden, siehe WUNDERLICH (2004: 624–625, Abb. 8, 8d, 1605, Abb. 13).

(10) Ameisenmimikry. Besonders mächtig entwickelte – z. B. bei zahlreichen Zwerg-Kugelspinnen (Anapidae s.l.: Mysmeninae) und einigen Zwerg-Radnetzspinnen (Theridiosomatidae) – und besonders kleine Pedipalpen – z. B. bei der Gattung *Hylyphantes* (Linyphiidae) – können unter anderem als Anpassungen im Zusammenhang mit Ameisenmimikry gesehen werden; ihre Funktion is aber unbekannt. – Die Nachahmung von Gestalt und Verhalten der Ameisen ist von Vertretern zahlreicher Familien beschrieben worden, z. B. von Kugelspinnen, Ameisenjägern, Ameisen-Sackspinnen, Plattbauchspinnen und Springspinnen. Diese Spinnen haben zur „Tarnung" ihre Spinnengestalt gegen eine „Warntracht" in Ameisengestalt im Verlaufe ihrer Evolution „eingetauscht" (Bates'sche Mimikry). Im Gegensatz zu Spinnen werden Ameisen von den meisten Vögeln als Beutetiere gemieden – sie schmecken ihnen nicht -, und so genießen ameisen-ähnliche Spinnen einen gewissen Schutz.

Es existieren verschiedene Möglichkeiten, die „typische" Spinnengestalt – mit ihrem zweiteiligen Körper und den oft robusten und stärker behaarten/beborsteten Beinen – der dagegen dreiteiligen und meist schlanken Ameisengestalt anzunähern:

(a) Die bei weitem häufigste Art, eine Ameisenähnlichkeit zu erreichen besteht darin, dass der Körper, die Beine und die Pedipalpen „verschlanken" und der Hinterkörper eine sattelförmige Einschnürung entwickelt, wobei eine scheinbare Zweiteilung desselben resultiert, wie es bei der fossilen Gattung *Eomazax* der Familie Ameisen-Sackspinnen im Baltischen Bernstein – hier noch wenig ausgeprägt – zu beobachten ist, siehe WUNDERLICH (Abb. 6 S. 192, Foto 376). Ungewöhnlich schlank – deutlich schlanker als bei verwandten Gattungen – sind die Pedipalpen bei Männchen der sehr ameisenähnlichen Plattbauchspinnen-Gattung *Micaria* (Abb. 6) und bei Ameisen-Sackspinnen der Unterfamilie Castianeirinae, wobei die Endabschnitte (Cymbium und Bulbus) bei den Vertretern dieser Spinnen besonders klein sind. Derartige Verhältnisse existieren bereits bei fossilen Spinnen von 40–50 Millionen Jahren, siehe WUNDERLICH (2004: 480, Abb. 376).

(b) Hinsichtlich der Größe der Pedipalpen hat die Evolution bei einigen Kugelspinnen den entgegengesetzten Weg eingeschlagen: Bei einigen Arten der Gattung *Steatoda* und – noch ausgeprägter – bei *Neottiura* besitzen die Endglieder der männlichen Pedipalpen eine enorme Größe (Abb. 5); sie sind deutlich größer als bei verwandten Gattungen. Eine besondere Bedeutung dieser voluminösen Pedipalpen ist den in Alkohol verkrümmt konservierten Spinnen nicht anzusehen; bei sich in ihrer natürlichen Umgebung bewegenden Spinnen ist sie aber zu erahnen. Diese gut 2 mm langen Spinnen leben in höheren Vegetations-Schichten, wo sie eine leichte Beute von Vögeln werden könnten. In Süd-Frankreich beobachtete ich ein sich auf den Zweigen eines Busches bewegendes Männchen von *Neottiura herbigrada*; siehe WUNDERLICH (2004: 196): Es streckte seine Pedipalpen nahe beisammen vor den Vorderkörper, so dass die großen Bulbi und Cymbia dem Kopf einer Ameise verblüffend ähnelten und die Spinne einen dreiteiligen Körper zu besitzen schien! Mittels ihrer voluminösen Pedipalpen, die direkt vor dem Vorderkörper gehalten wurden, zeigte sie offensichtlich eine „Kopf-Illusion". Daneben bewegte sie das vordere Beinpaar abwechselnd auf und ab, ähnlich den Antennen einer Ameise, offenbar eine „Antennen-Illusion". Ob diese Art der Mimikry auch bei verwandten Arten existiert und ob sie vielleicht sogar vor Angriffen von Ameisen schützen kann, ist unbekannt. Heutige wissenschaftliche Bearbeiter kennen kaum noch die lebendenTiere selbst, eher sind sie dagegen mit deren DNA vertraut.

Interessanterweise liegt bei der oben erwähnten Spinnenart eine sexual-dimorphe Mimikry vor, denn die *Neottiura*-Weibchen besitzen nur einen kleinen Pedipalpus, der für eine derartige Tarnung nicht geeignet ist. – Wieso existiert dieser Schutz lediglich bei den Männchen? Die Anwort könnte in der Biologie dieser Spinnen liegen: Die Weibchen sind die überwiegende Zeit ihres Lebens in ihrem Fangnetz eher geschützt; die Männchen dagegen begeben sich im Frühjahr auf die Suche nach paarungsbereiten Weibchen, bei der sie leicht eine Beute – zum Beispiel von kleinen Singvögeln – werden können. – Ein derartiges Beipiel vermutlicher Ameisen-Mimikry ist mir aus der Literatur nicht bekannt. Experimente zu ihrer tatsächlichen Wirksamkeit – etwa auf Vögel – stehen aus.

(11) Evolution: Die auffällige (oft spiralige) Verlängerung des Embolus – über ihn werden die Samenzellen aus dem Spermanetz in den Bulbus eingesaugt und er überträgt später die Samezellen – bei bestimmten Gattungen zahlreicher Spinnen-Familien wie zum Beispiel bei Riesen-Krabbenspinnen (Sparassidae) und Kugelspinnen – (siehe die Bearbeitung der Theridiidae Nr. 3 in diesem Band, die Gattung *Clya*), spielt vermutlich eine „stimulierende“ Rolle bei der „Vervielfältigung“ von Arten und wird zur Zeit intensiv diskutiert.

Unbekannte oder wenig bekannte Funktionen (eine kleine Auswahl; a–d betreffen das Cymbium):

(a) Auswüchse und starke Borsten auf Gliedern des Pedipalpus bei Linyphiidae: Zum Beispiel die starke Borste auf einem Auswuchs der Patella des Pedipalpus bei *Floronia* (auch auf der Tibia) und bei *Bolyphantes* sowie die Borsten auf der Patella bei *Microneta*; „gefiederte“ Borsten auf der Tibia bei *Centromerita* sowie auf Tibia und Cymbium bei *Maso gallica*, an ihrer Spitze modifizierte Tibia-Borsten bei *Allomengea*, Borsten auf dem Cymbium bei *Drapetisca*; modifizierte Borsten auf einem Auswuchs des Cymbiums bei *Sintula*.
Borsten und Stacheln auf dem Cymbium existieren auch bei Männchen zahlreicher weiterer Familien, z. B. bei Schlankbeinspinnen (Leptonetidae), zahlreichen Ameisenjägern (Zodariidae) (siehe oben) und einige Wolfspinnen (Lycosidae), (bei diesen am Ende). Diese Borsten und Stacheln könnten beim Putzverhalten wie auch beim Fortpflanzungs-Verhalten (bei den Leptonetidae?) und beim Graben in der Erde (Zodariidae, Lycosidae) eine Rolle spielen, siehe oben, Nr. 8 und 9.

(b) Haarbüschel – oft kurz, bürsten-ähnlich – meist im letzten Abschnitt auf dem Cymbium beim Männchen zahlreicher Gruppen von Spinnen, z. B. Ameisenjägern, Wolfspinnen und Springspinnen; siehe WUNDERLICH (2004:1608, Abb. 32, 1621) könnten mit dem Fortpflanzungs-Verhalten zusammen hängen.

(c) Bei einem fossilen Männchen der Familie Ameisenjäger (*Anniculus balticus*) in Baltischem Bernstein besitzen Cymbium und Bulbus eine ganz ungewöhnliche Form: Das Cymbium ist sehr großflächig und der Bulbus ist flach, ja sogar konkav; siehe WUNDERLICH (2004: Fotos 348, 632). Aufgrund ihrer Form und Position konnten die Endglieder der Pedipalpen vorn seitlich offenbar genau passend an die Kiefer und Teile des Vorderkörpers angelegt werden, so dass die empfindlichen Teile des Bulbus vor Bissen von Ameisen einigermaßen geschützt waren. Ansonsten waren die stark gepanzerten Spinnen (Foto 348) gegen die Agriffe ihrer wehrhaften Beutetiere zwar recht gut geschützt; wie Foto 611 zeigt, fielen sie den Ameisen gelegentlich aber doch zum Opfer. (Siehe auch die Gatung *Borboropactus*).

(d) Die Bedeutung von Auswüchsen/Modifikationen des Cymbium wie bei zahlreichen Zwerg-Kugelspinnen (Anapidae s. l.) ist unbekannt. Bei gewissen Kugelspinnen fungiert der äußere Rand des Cymbiums offenbar als Führung des Embolus (Conductor) und kann eine Reihe starker Haare tragen, siehe den Beitrag über die Kugelspinnen (Nr. 2) in diesem Band.

(e) Die Bedeutung der besonderen Position des Pedipalpus mancher Spinnen ist ungeklärt. Ein Beispiel ist die besondere Position der Endglieder des Pedipalpus bei männlichen Vertretern Kräuselspinnen-Gattung *Mastigusa* (Widderhornspinnen), bei denen der Bulbus klein, der Embolus sich aber bei einigen Arten mit einer extrem weiten Schleife sogar auf den gesamten Vorderkörper legen kann, siehe WUNDERLICH (2004: Foto 276).

(f) Autotomie: Der gelegentliche Verlust eines Pedipalpus – z. B. nach der Coxa bei einem fossilen Männchen der Gattung *Eomatachia* – belegt das gelegentliche Vorkommen von Autotomie bei einigen Spinnen, das der Abstoßung bestimmter Beinabschnitte – vielfach nach der Coxa – entspricht; siehe WUNDERLICH (2004: 146–148). – Siehe auch oben: Selbst-Amputation bei Kugelspinnen.

REFERENCES; cited

BRIGNOLI, P. M. (1974): Araignees de Grece VIII. Quelques Leptonetidae de la Laconie et de l'ile de Crete (Arachnida, Araneae).--Ann. Speleol., 29 (1): 63–70.

BRISTOWE, F. S. (1941) The comity of spiders, 1, 2. Ray Society, London. Reprint 1968 by Johnson Reprint Corporation.

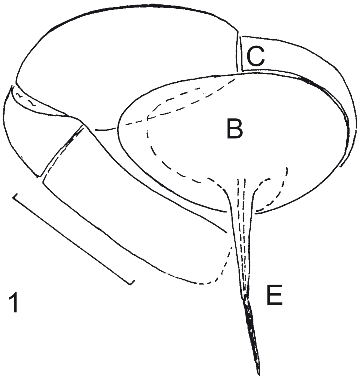
FOELIX, R. F. (1992): Biologie der Spinnen. 331 S.; Georg Thieme Verlag, Stuttgart.

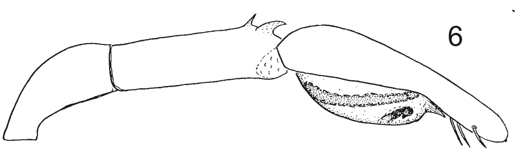
-- (1996) (second edition): Biology of Spiders. 330pp.

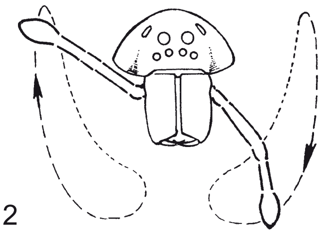
HEIMER, S. (1988): Wunderbare Welt der Spinnen. 188 S., Urania-Verlag.

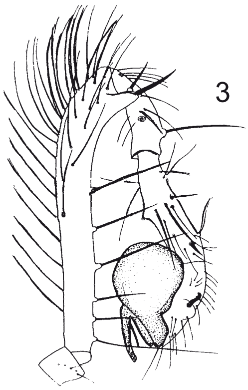
HUBER, B. A. et al. (2007): The evolution of asymmetric genitalia in spiders and insects. -- Biol. Rev., 82: 647–698.

WUNDERLICH, J. (2004): Fossil spiders in amber and copal – Fossile Spinnen in Bernstein und Kopal. -- Beitr. Araneol., 3 (A, B): 1–1908. Joerg Wunderlich Verlag, 69493 Hirschberg.









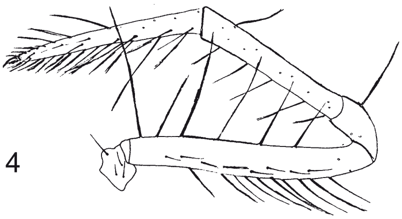


Fig. 1) Simple male pedipalpus (family Oonopidae) with the cymbium (C), bulbus (B) and embolus (E);
Abb. 1) Einfach gebauter männlicher Kieferntaster (Pedipalpus) einer Zwerg-Sechsaugenspinne, mit Cymbium (C), Bulbus (B) und Embolus (E);

Fig. 2) Rotating “pedipalp-waving” (courtship movements) in a male wolf spider (Lycosidae), frontal view. From FOELIX (1992: Fig. 153 b);
Abb. 2) Rotierendes „Pedipalpenwinken“ (Balzbewegungen) bei einer männlichen Wolfspinne, Vorderansicht. Aus FOELIX (1992: Abb. 153 b);

Figs. 3–4) “Spiny” ♂-pedipalpus (fig. 3) and ♀-pedipalp (fig. 4) from spiders of the family Leptonetidae. After BRIGNOLI (1974);
Abb. 3–4) “Borstiger” ♂-Pedipalpus (Abb. 3) und ♀-Pedipalpus von Spinnen der Familie Leptonetidae. Nach BRIGNOLI (1974);

Fig. 5) Outline of the prosoma and unusually large right pedipalpus of the male cobweb spider (Theridiidae) *Neottiura bimaculata*. After WIEHLE (1953: Fig. 71).
Abb. 5) Umriss von Vorderkörper und ungewöhnlich großem rechten Pedipalpus der männlichen Kugelspinne *Neottiura bimaculata*. Nach WIEHLE (1953: Fig. 71);

Fig. 6) Unusually slender ♂-pedipalpus of an ant-mimicing gnaphosid spider of the genus *Micaria*;
Abb. 6) Ungewöhnlich schlanker ♂-Pedipalpus einer Ameisen imitierenden Plattbauchspinne der Gattung *Micaria*.

BEITR. ARANEOL., 5 (2008)

DIFFERING VIEWS OF THE TAXONOMY OF SPIDERS (ARANEAE), AND ON SPIDERS' INTRASPECIFIC VARIABILITY

ON "LUMPERS" AND "SPLITTERS", SUPERTAXA AND SUBTAXA, INTRA-SPECIFIC VARIABILITY, AND DISAGREEMENTS ABOUT FOSSIL TAXA, WHICH MAY LEAD TO INSUFFICIENT DIAGNOSES AND INCORRECT CONCLUSIONS

JOERG WUNDERLICH, 69493 Hirschberg, Germany.

Key words: Araneae, Azores, Archaeidae, Borboropactidae, biogeography, Canary Islands, caves, chrono-superspecies, cladogram, Clubionidae, Cheiracanthium, *Clya*, *Dysdera*, Eutychurinae, fossils, "frozen microevolution", hybrids, intermediates, intraspecific variability, islands, Linyphiidae, Liocranidae, "lumpers", malformation, Mecysmaucheniidae, *Micaria*, *Minicia*, Miturgidae, Nephilinae, phylogeny, *Prochora,* Salticidae, speciation, spiders, "splitters", Stephanopinae, subspecies, subtaxa, Synotaxidae, taxonomy, Theridiidae, Thomisidae, Zoridae.

ABSTRACT: Different aspects of the biogeography and diagnoses of certain spider (Araneae) taxa and subtaxa caused by differing opinions of various authors regarding spider taxonomy are briefly discussed. Fossil taxa may be very important for explaining today's distribution of higher spider taxa, as well as their diagnoses and their phylogenetic relationships. Some remarks and ideas are given on various subtaxa at different levels in spiders; the present author argues for the use of subgenera e.g. in *Lepthyphantes* MENGE (Linyphiidae). A few indications about the existence of subspecies in – mainly European – spiders from islands, from the Alps, and from a cave are discussed as well as the existence of subspecies and "chrono-superspecies" in Eocene members of the genus *Clya* KOCH & BERENDT 1854 of the family Theridiidae. The intraspecific variability of selected species is briefly discussed. *Walckenaeria quarta* WUNDERLICH 1972 (Linyphiidae) is regarded as a junior synonym of *W. antica* (WIDER 1834), *Centromerus ensifer* (SIMON 1884) and *C. unidentatus* MILLER 1958 are regarded as junior synonyms of *C. arcanus* (O. PICKARD-CAMBRIDGE 1873) (**n. syn**.), *Zora palmgreni* HOLM 1939 (Zoridae) is regarded as a species of its own (upgraded from a subsp. of *nemoralis* BLACKWALL 1861) (**n. stat**.). *Textrix intermedia* **n. sp**. (Agelenidae) is described as a species in its own right, rised to a species level from a putative hybridization of *T. caudata* L. KOCH 1872 and *T. pinicola* SIMON 1875.

Acknowledgement: I thank very much JASON DUNLOP who corrected most parts of the English text, and THEO BLICK for comments and for the copies of some papers.

INTRODUCTION

The beginner in araneology will respectfully look at the sytems and cladograms of spiders which are published e.g. by GRISWOLD et al. (1999) or JOCQUE & DIPPENAAR-SCHOEMAN (2007). No question marks are usually noted with such impressive/suggestive systems or cladograms, but (a) they are far from being definitive or “objective” in several respects, and (b): we have to keep in our mind that suprageneric taxa are no natural categories (!).

It is well-known to “insiders” that the limits, diagnoses, and relationships of numerous spider subfamilies, families – and even various superfamilies – are still quite unsure and discussed controversially, see e.g. JOCQUE & DIPPENAAR-SCHOEMAN (2006, 2007), SCHÜTT (2000), WUNDERLICH (2004). One may distinguish (a) the subjective view of “splitters” and “lumpers” (*) – e. g. in the family Anapidae (Symphytognathidae) sensu lato or sensu stricto (**) and in the Archaeidae s. l., or s. str. – and (b) differing supposions on the relationships of certain higher taxa which may well be clarified in the future, see e. g. below (2), the relationships of the families Pimoidae and Pumiliopimoidae. The consequences of this situation are greatly differing aspects/opinions/conclusions regarding the biogeography and the diagnoses of such families. In the following I will (**A**) give some notes on a few examples of higher fossil and extant spider taxa which are usually grouped into pairs, and which are – or were previously – regarded as single families or as subfamilies. Numerous further families are problematical in this respect; examples are Araneidae s. l. (including Nephilinae and Zygiellinae?), Argyronetidae/Cybaeidae, Clubionidae (including Cheiracanthinae?), Dictynidae s. l. (including, e.g., Copaldictyninae and Hahniinae?), Gnaphosidae (including Prodidominae?), Loxoscelidae/Sicariidae, Mimetidae s. l. (including Malkarinae?), Plectreuridae s. l. (including Diguetinae?), Zodariidae s. l. (including Homalonychinae?), Zoridae s.l. (see Liocranidae), and Zoropsidae s. l.: See WUNDERLICH (2004). I will (**B**) shortly discuss differing opinions and open questions, note the subjective view of the present author on subtaxa in spiders, give remarks on the intraspecific variability of selected spider species, and on teratological structures.

(*) According to "lumpers" about 53 spider families occur in Europe today in contrast to up to 62 families which are recognized by "splitters". These proportions – a difference of about 20% (!) – are quite similar regarding the fossil spider families which are preserved in the Eocene European ambers.

(**) "Splitting" Anapidae s. l. will cause the "existence" of six families: Anapidae, Comaromidae, probably Micropholcommatidae, Mysmenidae, Symphytognathidae, and Synaphridae; see WUNDERLICH (2004: 1031) (Micropholcommatinae most probably has to include; its exact position in the cladogram p. 1031 is unsure).

A. CONSIDERING FOSSIL AND EXTANT TAXA REGARDING SELECTED FAMILIES AND SUBFAMILIES

(1) Archaeidae s. l.: Archaeinae and Mecysmaucheniinae

Archaeinae and Mecysmaucheniinae are closely related and are regarded as subfamilies of Archaeidae s. l. by WUNDERLICH (2004: 768ff) and other authors, but as families in their own right by most recent authors like PLATNICK – a matter of opinion. Archaeidae s. l. is restricted today to the Southern Hemisphere: South America, South Africa, and the Australian Region. Its taxa occur on all continents of the Southern Hemisphere except the Antarctic (see the map of the distribution of the family Archaeidae s. l. in the paper no. 5 on Cretaceous spiders in this volume):
(a) Archaeinae (= the „split" Archaeidae s. str.) is restricted today to South Africa, Madagascar, and the Australian Region, but is absent in South America; (b) Mecysmaucheniinae (= the „split" Mecysmauchiniidae s. str.) is restricted today to South America and the Australian Region, but absent in South Africa (most probably extinct). Thus Archaeidae s. l. occurs in South America but Archaeinae s. str. do not.
Fossil reports: Archaeidae s. l. is reported from Eocene Baltic amber (Archaeinae), and in Cretaceous Burmese amber (Archaeinae and a subfamily near the Mecysmaucheniinae) as well as in Cretaceous European (France) amber (a subfamily near the Mecysmaucheniinae). So spiders from both groups are reported from the Southern <u>and</u> the Northern Hemisphere as well; they demonstrate an almost worldwide distribution in the Mesozoic era, and these reports support the theory of "ousted relicts" contra "mobilistic biogeography", see the paper on spiders in Cretaceous ambers in this volume.

The number of spinnerets is one of the most important diagnostic characters to distinguish archaeid subfamilies: Archaeinae has six pairs, the plesiomorphic number for the superfamily Archaeoidea. By contrast all the – extant – Mecysmaucheniinae possess a single pair of spinnerets only. New finds of Cretaceous taxa (paper no. 5 of this volume) show that the Lacunaucheniinae n. subfam. – they are related to the Mecysmaucheniinae, see SAUPE & SELDEN (2008) – had still 2 or even 3 pairs of spinnerets at that time, doubtless a plesiomorphic pattern. The diagnosis of the Archaeidae s. l. has to include the Cretaceous taxa, and therefore it has to be changed and completed.

(2) Pimoidae and Pumiliopimoidae

Pimoidae is a spider family which is only known from the Northern Hemisphere: *Weintrauboa* HORMIGA 2003 from SE-Asia, and *Pimoa* from North America and Eurasia. Fossils of this family – the genus *Pimoa* – have been reported from the Eocene Baltic amber forest by WUNDERLICH (2004). HORMIGA et al (2005) included the new genus *Nanoa* from North America in the Pimoidae. The inclusion of *Nanoa* in the family Pimoidae would change the diagnosis of this family strongly but in *Nanoa* the most important diagnostic characters of the Pimoidae are absent, and therefore I regard this genus not as a member of the Pimoidae but of the new family Pumiliopimoidae, which is also known from Eocene Baltic amber, see the papers on these families in this volume (no. 2), on the Pimoidae, and on the "linyphoid branch".

(3) Zoridae s. l.: Liocraninae and Zorinae

Liocranidae and Zoridae were previously split off from the family Clubionidae, but are united in a single family – the Zoridae s. l. – by the present author, see paper no. 4 in this volume (family Zoridae). The limits and the diagnostic characters of Liocraninae and Zoridae are discussed controversially, see e. g. JOCQUE & DIPPENAAR-SCHOEMAN (2007). In my opinion one has to focus on the type genera of the (sub)families. In respect to ventral stridulatory structures in the male sex and the strongly recurved posterior eye row certain FOSSILS in Baltic amber may be "morphological links" to and between extant members; they are extremely helpful in the discussion on phylogenetic relationships.

(4) Clubionidae, Miturgidae and Eutichurinae

Miturgidae is quite insufficiantly diagnosed, see e. g. JOCQUE & DIPPENAAR-SCHOEMAN (2007: 174), RAMIREZ et al. (1997). It may be mainly a family of the Australian/Oriental region. Certain authors recently regarded the genus *Cheiracanthium* C. L. KOCH 1839 erroneously as a member of the family Miturgidae, see e. g. JOCQUE & DIPPENAAR-SCHOEMAN (2007: 174 and 2007), contra (e. g.) WUNDERLICH (2004: 1613), and this opinion was quickly accepted by PLATNICK in his Catalog of spiders. Cheiracanthinae WAGNER 1888 is an older synonym of Eutichurinae LEHTINEN 1967, see paper no. 4 in this volume. Miturgidae would be a family of the European fauna if *Cheiracanthium* is placed within this family, but *Cheiracanthium* is doubtless a member of the Clubionidae, see DEELEMAN-REINHOLD (2001: 85, 223) and WUNDERLICH (2004: 1613), and therefore the family Miturgidae is absent from the European fauna; see the remarks on *Prochora* in the paper on the family Zoridae in this volume (no. 4). (*)

(*) *Prochora* SIMON 1885 from Sicily and Israel has been regarded as a member of the Liocranidae by SIMON, and is regarded as a member of the family Zoridae by me; see the paper no. 4 on the Zoridae/Liocranidae in this volume. The taxon was transferred to Miturgidae by LEHTINEN (1967: 260), accepted by PLATNICK; a revision is needed. This spiders are about 1 cm long, the colour of the body is medium brown, agnathocoxal serrula is absent. ♂: the cymbium bears a long retrolateral furrow. ♀: the epigyne possesses a small anterior helm-shaped structure. 1 ♂ 1 ♀ coll. G. LEVY (Israel).

(5) Borboropactidae and Thomisidae

Borboropactidae WUNDERLICH 2004 has been split off from the Thomisidae: Stephanopinae; see the paper on this family in this volume. The family is distributed in SE-Asia and Africa, and reported from the Eocene Baltic amber forest as well; see p. 479ff.
LEHTINEN in 2007 (17th Internat. Congress of Arachnology in Brasil, abstract, “Redefinition of *Stephanopis*...”) regards Borboropactidae – based mainly by the existence of strong anterior setae apically on the chelicerae – as a tribus of the Thomisidae: Stephanopinae. This downgrading may be justified or not, but strong setae in this position may well be a plesiomorphic character of Borboropactidae + Thomisidae. The powerful raptorial anterior legs of the Borboropactidae are similar to Thomisidae but their leg position is prograde, and the size as well as the position of the eyes are quite different. If Borboropactidae is regarded as a member of the Thomisidae the most important diagnostic family characters “laterigrade leg position”, “wide eye field with large lateral eyes on humps”, and “pedipalpal tibia with ventral apophysis” would have to change dramatically, see JOCQUE & DIPPENAAR-SCHOEMAN (2007: 258).

B. SUBTAXA: THEIR RELATIONSHIPS AND THEIR LIMITS; VARIABILITY WITHIN CERTAIN TAXA

Remarks on CONVERGENCES, LOSSES, MULTIPLICATIONS, and REVERSALS (= restaurations of previous conditions during the evolution): Short/strict diagnoses are an important help to recognize a peculiar taxon. Problems within diagnoses are frequently caused by the high number of "exceptions", regarding various structures, which may be caused, e.g., by losses (well-known are the numerous losses of the cribellum or of stridulatory files within the family Linyphiidae), convergences (e.g. numerous independent evolutions of cheliceral stridulatory files), multiplications or – usually questionable! – reversals. I report in the following on four examples within the superfamily Araneoidea: (a) Femoral bristles are usually absent in the "bristle-less femur clade" of the Araneoidea but in a single species of the extinct species – *Balticoroma gracilipes* (Anapidae: Comarominae) – the anterior femur bears a prolateral bristle (not a "clasping spine"), see WUNDERLICH (2004: Fig. p. 1036) – a reversal? (b) Metatarsal bristles are usually absent within the genus *Porrhomma* (Linyphiidae) but in *P. errans* a bristle exists on all metatarsi – apparently a reversal. (c) feathery hairs originated as an old (synapomorphic) pattern of the araneomorph spiders but were lost several times, see LEHTINEN (1967: 283). In the genus *Tegenaria* (Agelenidae) and strongly related taxa exist feathery hairs in contrast to other taxa of this familiy – probably a case of reversal. (d) Almost all members of the superfamily Araneoidea possess at most only a single metatarsal trichobothrium but in *Allomengea scopigera* (Linyphiidae) exists more than a single trichobothrium on the metatarsi (in contrast to the related *M. warburtoni*), and also in several species of *Pimoa* (Pimoidae) exist several metatarsal trichobothria – apparently cases of multiplications of this structure in these taxa.

In the following I will shortly discuss the use of some further subtaxa of spiders at different levels.The subjective suggestions on taxa at the level of subfamilies and subgenera may be of greatest importance for practical use; the more objective investigations on SUBSPECIES – which are urgently needed – are more important in a scientific respect.

History: About a century ago the famous araneologist E. SIMON already used tribus and subtaxa (*) like subfamilies. LEHTINEN (1967) raised numerous subtaxa for one level, tribus to subfamilies and subfamilies to families, and the overwhelming part of these changes are accepted today. In their cataloges of spiders BRIGNOLI and ROEWER used subfamilies but PLATNICK did/does not.

(*) The artificial division in former times into the two large "branches" of spiders – "Cribellatae" and "Ecribellatae" – has been taken over by SIMON from the discoveries of BERTKAU (1882); it caused numerous errors regarding the relationships of spider taxa, before the cribellum was recognized as an "old" structure of spiders, which has been LOST numerous times within superfamilies, families, tribus, and even within certain genera. There does not actually exist two branches like "Cribellatae" and "Ecribellatae", but numerous cribellate and ecribellate taxa which may be related to each other. An example is the family Dictynidae in a wide sense, which includes many cribellate and ecribellate taxa, see WUNDERLICH (2004), but parts of this taxon in the sense of the present author – for example the Copaldictyninae WUNDERLICH 2004 – is most probably the member of a different family, and the relationships and the level of the Hahniinae are not sure.

(1) Suborders and Infraorders

As generally accepted today the order Araneae (spiders) is divided into two suborders:

(1) Mesothelae (spiders with a segmented opisthosoma) and the
(2) Opisthothelae (opisthosoma not segmented); it is is divided into the infraorders
    (a) Mygalomorpha (they have the fangs in a longitudinal position), and the
    (b) Araneomorpha (which have the fangs in a transverse position) (*).

(*) Mygalomorpha (= Mygalomorphae) was previously called “Orthognatha”, and Araneomorpha (= Araneomorphae) was called “Labidognatha”; both were/are regarded as suborders in former times and by certain recent authors.

(2) “Clades” and superfamilies

Large groups of families are frequently allied to “branches” or “clades”, e. g. Araneoclada, Entelegynae, Orbiculariae, RTA-clade, Dionycha, see e. g. GRISWOLD et al. (1999). Some of these “clades” are subject to controversy; e. g. the Dionycha and the Orbiculariae may be nothing more than superfamilies, and the RTA-clade (= clade in which a **r**etrolateral **t**ibial **a**pophysis exists) is probably not a monophyletic taxon (e. g. the Nicodamidae and the Titanoecidae may be excluded). I regard the term “Orbiculariae” – its spiders build basically an orb web, its spinnerets have a converging “rosette-shaped” position (although the anteriors are widely spaced in the cribellate taxa) – as superfluous, and I include a cribellate branch (Deinopidae and Uloboridae) as well as an ecribellate branch (Araneidae and the remaining related families). Both branches were united to the enlarged superfamily Araneoidea (s. l.) by WUNDERLICH (2004: 1112ff, 1127).
In some cases the relationships of the nominate superfamily are unsure. An example is the superfamily Eresoidea: If the Oecobiidae and the Hersiliidae are strongly related to the Eresidae this name for the superfamily can be accepted, but if the Eresidae is more related to Archaeidae and Palpimanidae we would have a quite different assembly of families, see WUNDERLICH (2004: 747), and the paper on Cretaceous spiders in this volume (no. 5). – Another example is the superfamily Dysderoidea s. l. sensu WUNDERLICH (2004: 644-645), which may include the “dysderoid branch”, the “scytodoid branch” as well as the branch of the “ecribellate tube dwellers” and/or even the cribelate family Filistatidae, too, a further branch. Does this “assambly of families” include three or even four superfamilies?

(3) Families, subfamilies and tribus

Numerous subfamilies are regarded as families in their own right by "splitters" – like FORSTER and LEHTINEN – or are combined to families in a wide sense by "lumpers", see the remark on the number of European spider families in the introduction and under (A). Examples are the families Agelenidae, Amaurobiidae, Araneidae, Archaeidae, Argyronetidae, Dictynidae, Miturgidae, Nephilidae, Oecobiidae, Synotaxidae, Zodariidae, Zoridae, and Zygiellidae. The Oecobiini changed their position over four levels (!) from a superfamiliar taxon to the level of a tribus, see above. The Nephilinae/Nephilidae – in my opinion a subfamily of the Araneidae, see WUNDERLICH (2004: 963-967), PAN et al. (2004) – shifted from a tribus or subfamiliar level of the Araneidae to the Tetragnathidae, and back, and recently – sensu KUNTNER – to the rank of an independent family, contra PAN et al., WUNDERLICH.
"As is evident from the example of the Acarina, an excessive multiplication of the families obscures the relationships between the different groups." (BRIGNOLI (1983: 12)). Most divergent views may be subjective but more objective criteria in this respect may be found in the future.
Remarks on five spider (sub)families: (1) The limits and the relationships of the family Dictynidae s. l. are controversially discussed, see above, WUNDERLICH (2004: 1380ff) and SPAGNA & GILLESPIE (2007). Early Cretaceous taxa may give important indications to the phylogeny of the Dictynidae and the Dictynoidea in the future. – (2) According to a genetical study the Cybaeinae is placed back again in the Agelenidae (from the Amaurobiidae s. l.), see SPAGNA & GILLESPIE (2007). – (3) The number of subfamilies of the Theridiidae may be 6 or even 9, see the paper (no. 3) on this family in this volume; Hadrotarsinae has been regarded as an independent family for some time. – (4) The number of subfamilies of the Linyphiidae is not sure, there may be three or even half a dozen. The subfamily Ipainae SAARISTO 2007 is downgraded to tribus rank in this volume, see the paper no. 2 in this volume, the "linyphioid branch". – (5) The number of subfamilies of the Salticidae "exploded" to more than twenty, although BRIGNOLI (1983) in his "Catalogue of the Araneae) listed only two (Salticidae sensu str. and Lyssomaninae), and also the number of another young family (in the geological sense), the Lycosidae, was still growing recently. In my opinion there may be ten or far less subfamilies of the Salticidae – see WUNDERLICH (2004: 1761ff) – but numerous tribes.

(4) Genera and subgenera

On this matter "splitters" and "lumpers" are fighting most hard: "Lumpers" regard numerus genera as species-groups only. A striking example is the recent splitting of *Lepthyphantes* MENGE (Linyphiidae) by TANASEVITCH in various papers. K. THALER (person. commun.) was not happy with this splitting which he regarded as superfluous (he prefered the use of species-groups); I basicaly agree with him, but I prefer subgen-

era. Although no cladogram of the new genera was presented – and most of their close relationships are unclear – the names of these genera were accepted immediately by PLATNICK, and adopted in his cataloge of spiders (*).
In my opinion one has (a) to split off the basal taxa of this "branch", and may regard these taxa as genera of their own – these taxa are *Megalepthyphantes* WUNDERLICH, *Midia* SAARISTO & WUNDERLICH as well as probably *Canariphantes* WUNDERLICH -, and (b) best regard the remaining groups/taxa as species-groups or subgenera. I prefer subgenera of *Lepthyphantes* as it is used in numerous orders of insects.
– Complicated is the splitting of *Agyneta* s. l. and *Centromerus* s. l. (**) (Linyphiidae).
– See the subgenera of the Theridiidae (within the genera *Achaearanea, Argyrodes*, *Euryopis, Lasaeola, Selimus* and *Steatoda*), paper no. 3 within this volume.
Most recent authors regard the subgenera of *Walckenaeria* BLACKWALL (Linyphiidae) sensu WUNDERLICH (1972) as species-groups. *Trichoncus* SIMON 1884 has turned out to be a polyphyletic genus, see below; the present author is preparing a revision.

(*) Due to the fossils – my personal findings – *Lepthyphantes* s. l. is a young genus in the geological sense, unknown from the Eocene European amber forests and the Oligocene Dominican amber forest as well, and apparently not older than the Miocene.

(**) Due to their genital organs I prefer to regard *Rhabdoria* HULL 1909 as a genus separate from *Centromerus* DAHL 1912 but *Neriene* BLACKWALL 1833 as only a subgenus of *Linyphia* LATREILLE 1804 (Linyphiidae).

In spiders, e. g., COKENDOLPHER (2004) used subgenera in the North American species of *Cicurina* MENGE (Dictynidae). Subgenera were furthermore already used in the Clubionidae by MIKHAILOV – but here I prefer genera of their own like in the Philodromidae, too -, in the Oonopidae: Orchestininae (*Orchestina*) (this volume), in the Salticidae, e. g. within *Heliophanus*, *Neon*, and *Sitticus* (this volume), in the Zoridae s. l. (this volume), in the Tetragnathidae (*Meta* s. l.) (this volume, paper no. 2), in the Theridiidae (e. g. *Argyrodes* s. l., *Lasaeola* s. l., and *Steatoda* s. l; paper no. 3 of this volume). On the other hand I regard the splitting of *Theridion* s. l. as justified – if it is compared with *Lepthyphantes* s. l. -; genera like *Neottiura, Paidiscura* and *Simitidion* were already split off from *Theridion*; further genera: See paper no.3 in this volume. A similar case is in my opinion the genus *Philodromus* s. l.: In the Holarctic I would like to split this genus into four genera at least: *Philodromus* s. str. (the *Philodromus aureolus*-group), *Horodromoides (?= Artanes)*, *Rhysodromus*, and *Tibellomimus*, see SCHICK (1965). The splitting of *Xyticus* s. l. (Thomisidae) – see SIMON (1932), Arachn. de France, 6 (4), WUNDERLICH (1995: 749-774) – is still in progress (LEHTINEN, in prep.), a splitting of *Scytodes* (Scytodidae) and of *Oecobius* (Oecobiidae) is also justified in my opinion. A splitting of the diverse genus *Pardosa* (Lycosidae) into subgenera – and partly into genera of their own – is a very difficult problem for revisions in the future. The recent splitting of *Hahnia* C. L. KOCH s. l.: See WUNDERLICH (2004: 1415-1428).

(5) Superspecies, species, subspecies, intraspecific variability ("varieties", morphs), and teratological structures (malformations)

I will focus here on some questions regarding subspecies and on the intraspecific variability.
A century ago no stringent term of "subspecies" existed, and under this term we find e.g. coloured forms, forms of different size and different shape. Most of these "forms" were recognized in the meantime as examples of intraspecific variability, but others were recognized as species of their own, e.g. as "sibling species", see below (B, C, D).
Regarding subspecies there is a general question: Why do so few – according to the titel of a paper of KRAUS (2002) even "no" – subspecies in spiders exist, in contrast to (e.g.) Coleoptera and other insects? KRAUS (2002) discussed this – apparently provocative – question, but he did not deal with or even mention taxa which have been described as subspecies, see, e.g., THALER (1978), WUNDERLICH (1979 and 1986), and below (B, C, D).
What are the "criteria of subspecies" and where may we expect subspecies? As defined by MAYR (1963) "subspecies form an 'aggregate of local populations of a species inhabiting a geographic subdivision of the range of the species and differing taxonomically from other populations of the species.' " (KRAUS (2000: 304)). – Genital structures may vary intraspecifically – see e. g. KRAUS (2000: Figs. 9 -10) -, but if there are constant differences in the structures of their genital organs, the taxa are – in almost all cases – species of their own. If only differences in (e.g.) the colour, the hairs, proportions and shape of the prosoma exist, AND furthermore their distribution/ecology are not identical, they MAY be only subspecies. Only few observations exist on natural interbreeding: In *Pardosa agrestis* and *purbeckensis* apparently natural interbreedings happen but the (in)fertility of the offsprings is unknown to me. See KRONESTEDT (1979). See also below (D): *Textrix intermedia* n. sp., and (A) (d).
New subspecies and species evolved on numerous archipelagos, see below: (E), and during glaciations. Populations which are isolated on younger islands or in caves or are separated by mountains are the best objects for investigations in this respect.

In the following I will discuss the VARIABILITY as well as possible cases of SPECIATION in selected extant "island species" and "cave species" of the Macaronesian Islands (Canary Islands and Azores) (I), as well as in extinct "chrono-taxa" of the Eocene Baltic amber forest (II).

(I.) EXTANT TAXA

"Aberrant"/teratological copulatory organs (malformations): I found the right bulbus of a male of *Silometopus interjectus* sensu TULLGREN 1955 (fig. 71d) (Linyphiidae) being teratological in contrast to the normal left bulbus. This specimen is really a member of *Silometopus reussi* (THORELL 1871).

A malformation of the ♂-prosoma of *Wubanoides uralensis lithodytes* SCHIKORA 2004 (Linyphiidae) was reported by SCHIKORA (2004: 332, fig. 11).

"Aberrant"/teratological structures of the copulatory organs may be the result of parasites, e.g. of Nematoda within the spiders lungs. An example of a paratized synonymous species is *Lepthyphantes beckeri* WUNDERLICH 1973 (Linyphiidae) which most probably is a junior synonym of *L. flavipes* or *mengei*; both species were captured together with the single known specimen of *beckeri*.

Pardosa barndti WUNDERLICH 1969 was based on a single male which is in my opinion most probably conspecific with *P. lugubris* (WALCKENAER 1802) (malformations of the pedipalpal structures).

The description of *Walckenaeria quarta* (WUNDERLICH 1972) (Linyphiidae) was based on a single female which was apparently freshly moulted. The species was synonymized – in a "hidden way" – with *W. antica* (WIDER 1834) already by PLATEN & WUNDERLICH (1990: 129).

Putative hybridizations in spiders were occasionally reported, e. g. in species of *Textrix*, see the description of *T. intermedia* n. sp. (Agelenidae) below (D), and within *Eresus* (Eresidae), see REZAC et al. (2008).

Most of the spider taxa which formerly have been described as subspecies from Europe are regarded in this paper (or were recognized during the second half of the 20th century):

(A) as INTRASPECIFIC VARIABILITY:

(a) Species of the Linyphiidae: Erigoninae in which the ♂-prosoma has two or more different shapes (lobes) and/or hairy areas, e.g. in *Oedothorax gibbosus (= tuberosus)*, see WIEHLE (1960: 454-458); due to my observations the thoracal part of the ♂-prosoma is rather variable in *tuberosus* and may be distinctly higher than shown in the fig. 838 which was given by WIEHLE (1960: 454). In *Pelecopsis elongata* two extreme shapes of the ♂-prosoma exist (figs. 11-12) (reported already by SIMON 1884), and intermediates are reported. *Metopobactrus prominulus* (= *M. schenkeli*) and *Pelecopsis radicicola*: See MUFF et al. (2007). A variability ("forms") is furthermore known within *Pelecopsis parallela* as well as *P. mengei* (person. observ.) in both species, already reported by HOLM), from *Parapelecopsis nemoraloides* (= *locketi*), see WUNDERLICH (1985), from *Diplocephalus latifrons* (= *Lophocarenum fallaciosum*), person. observ., see WIEHLE (1960: 514), as well as from *Troxochrus scabriculus (= cirrifrons)*, person. observ., see WIEHLE (1960: 465-466). The difficult/cryptic *Diplocephalus cristatus*-group: See below (C).

(b) Differing hairs of the anterior ♂-legs: *Dicymbium nigrum/brevisetosum* (Linyphiidae): Both have differing hairs of their anterior ♂-tibia, and occur occasionally syntopic. ROBERTS (1993: 38, fig. 10d (two figs.!)) reported intermediate ♂-tibiae of specimens of both nominal taxa, and therefore regarded them as "forms" of *D. nigrum*. See below (B): *Pardosa agrestis* and *purbeckensis*.

(c) Slightly differing structures of the copulatory organs: See the paper on the family Zoridae (*Liocranum variabile* n. sp.) in this volume, the variability of the tibial apophyses of the ♂-pedipalpus in *Parapelecopsis nemoraoides*, see WUNDERLICH (1985), the variability of the lamella characteristica in *Agyneta (Meinoneta) alpica*, the variabil-

ity of the pedipalpal tibia in *Zornella cultrigera*, see TANASEVITCH (2007) as well as in a member of the family Eresidae, see KRAUS (2000: figs. 9-10). The differences in the structures of the bulbus – if present – are weak and intermediates exist.
The European spider species *Centromerus ensifer* (SIMON 1884) and *C. unidentatus* MILLER 1958 (Araneidae: Linyphiidae) are regarded here as junior synonyms of *C. arcanus* (O. PICKARD-CAMBRIDGE 1873) (**n. syn**.). Numerous specimens were studied and are deposited in the CJW, the SMF and and the MNHP *(C. ensifer*). The bulbi of these nominal taxa are identical, the differences of their paracymbia are regarded as intraspecific variability. *Centromerus arcanus* (figs. 16-23) is related to *C. subalpinus* LESSERT 1907 (figs. 13-15) in which the paracymbium has a distinct ventral outgrowth (O in figs. 13-14) in contrast to *arcanus*. In both species the paracymbium bears a larger and strongly sclerotized tooth **OF VARIOUS SHAPE AND SIZE**, as well as a small and tooth-like structure in a more dorsal position (see the figs.), but the structures of their bulbi – especially of the terminal apophysis – are quite different, see figs. 15 and 21. The paracymbium of *C. arcanus* shows intraspecific variability (see figs. 16-20) but the structures of their bulbi vary only very slightly in the shape of the terminal apophysis, also within the same population, see figs. 21-23. The genital structures of the female are apparently identical, and therefore I regard *C. ensifer* (SIMON 1884), and *C. unidentatus* MILLER 1958 as junior synonyms of *C. arcanus* (O. PICKARD-CAMBRIDGE 1873) (**n. syn**.). According to the intrapopular variability and the distribution of the three taxa I see no evidence for a status as subspecies.

(d) as intraspecific variability of the colour, the size, and other non-genitalic structures.
The colour of the body and legs is relatively constant in certain species and may be an important character for spiders identification, e. g. in the genus *Zora* (Zoridae), and it is also quite constant in *Hahnia*, (Hahniinae), especially on the dorsal side of the opisthosoma. In other taxa the colour of body and legs is quite variable within the same species, e. g. in *Pisaura mirabilis* (Pisauridae), in *Araneus diadematus* as well as in *Neoscona crucifera* (both Araneidae), see WUNDERLICH (1992: Figs. 369 a-h), and in numerous members of the Jumping Spiders (Salticidae), e. g in *Neon reticulatus*: A dark form in wet *Sphagnicola* – I found it in other habitats, too -, was called by DAHL (1926: 38) “variety *sphagnicola*”. In some species of the Salticidae two strongly differing “colour forms” without intermediates exist, e.g. in *Heliophanus tribulosus* (person. observ. in a single locality in SW-Germany), which reminds me of the conditions in a mammal, the black panther. See also WUNDERLICH (1987: 279).
The main opisthosomal colour forms of *Pisaura mirabilis* are shown in figs. 24a–e, see NITZSCHE (1999). The enormous variability in the colour of this species caused the erection of two “subspecies” of *mirabilis* – *albida* and *fusca* from Portugal – which were synonymized with *mirabilis* by BARRIENTOS (1979). Another former subspecies of *P. mirabilis* – *maderiana* – has been recognized as an independent endemic species, see WUNDERLICH (1987: 230).
Zodarion styliferum “forma” *extraneum* DENIS 1935: Although both taxa differ by the colour of body and legs as well the number of their chromosomes (!) they were regarded as “forms” – but not different species or subspecies – because PEKAR et al. did not find differences in the genital organs.
The body length: I found in spiders from the Canary Islands a variability of up to 300% (!) in *Zoropsis rufipes* (Zoropsidae), and a similar variability in other species, see WUNDERLICH (1987: 279).

The intraspecific variability of the size of the eye lenses may be enormous in cave spiders or in spiders which are inhabitants of ant nests: In *Mastigusa macrophthalma* (Dictynidae s. l.) which may be a free-living species, I found a low variability in the size of the eye lenses but in the related *M. arietina* – which lives in ant nests – I found a strong variability of this structure, see WUNDERLICH (1986: 70-71, figs. 70, 75-76, 88-94).
The intraspecific variability of the position of the metatarsal trichobothrium and of the tarsal organ in the genus *Walckenaeria* (Linyphiidae): See WUNDERLICH (1972: 414-416). There can be remarkable differences in the right/left position.

(B) as SPECIES IN THEIR THEIR OWN RIGHT (see also (C)):

E.g. *Meta mengei* and *segmentata* (Tetragnathidae) and *Achaearanea simulans* and *tepidariorum* (Theridiidae). – *Walckenaeria antica* (= *Wideria antica flavipes* SIMON) and *alticeps* (= *Wideria antica flavida* sensu BROEN & MORITZ 1963) (Linyphiidae), see WUNDERLICH (1972: 395-396): The determination of these similar and strongly related species caused some confusion: The males of both species are almost identical, in the structures of their pedipalpi, too (only the diameter of their emboli may be slightly different), but epigyne and vulva are quite distinct as their ecological claims are, too: *alticeps* is characterized as hygrobiont, and *antica* as photophilous-xerophilous, although both may exist in the same locality.
Dolomedes plantarius (Pisauridae) was formerly regarded as a subspecies of *D. fimbriatus*. – *Tegenaria gigantea* is apparently an independent species which is not a synonym of *duellica*.
The Scandinavian Zoridae *Zora nemoralis* and *palmgreni* are regarded as subspecies – see ALMQUIST (2006: 444-445) -, but according to the differences in their ♂♀ genital organs (pedipalpal tibial apophysis, structures of the bulbus, epigyne and vulva as well) I regard both taxa as distinct species (**n. stat**.). The next pair of species is a similar case:
The structures of the bulbus of *Ozyptila westringi* and *trux* (Thomisidae) possess several rather weak differences, but the structures of their vulva as well their habitats are distinct, *westringi* is apparently halophilous (see (C)). *Clubiona frisia* and *similis* (Clubionidae) is a taxonomically similar case, see WUNDERLICH & SCHUETT (1995); the habitat and the distribution of these species are distinct. – See also the species of the *Pardosa lugubris*-group (Lycosidae). Several "subspecies" of the *Philodromus aureolus*-group (Philodromidae) turned out to be distinct species during the last years thanks, e.g., to the work of C. MUSTER & THALER (2004). The existence of several species in the same locality and habitat (even on the same tree) caused irritations of numerous taxonomists, quite differing opinions, and a seemingly high variability in the copulatory organs of both sexes in apparently a single species.
According to REZAC et al. (2008) at least three species of the taxonomical difficult genus *Eresus* (Eresidae) exist in Europe. These authors reported no morphologically intermediate specimens, and found the species genetically complex, one species being paraphyletic. *Cheiracanthium* (Clubionidae): There seems to be an enormous intraspecific variability in colour, size and copulatory organs but the situation may be like in *Philodromus*. Due to the differing hairs of the anterior ♂-legs *Pardosa agrestis* and *purbeckensis* (Lycosidae) may be species in their own right (see above). SCHIKORA (1995) regarded intermediate characters of the copulatory organs of *Meioneta mos-*

sica and *saxatilis* as the result of “local interspecific hybridisation” of two different species. Are both taxa really independent species or subspecies or “varieties”? Further investigations are needed.

(C) QUESTIONABLE TAXA: SUBSPECIES AND/OR INDEPENDENT SPECIES are mainly taxa of the Alps, e. g. of the *Diplocephalus cristatus*-group (Linyphiidae), *Erigone arctica/maritima* (Linyphiidae), and of *Cryphoeca* (*lichenum lichenum* and *lichenum nigerrima*) (Dictynidae); see THALER (1978, 1986); at least in the last pair of taxa the criterium of vicariance is fulfilled. *Robertus arundineti* and *heydemanni* (Theridiidae) (the latter is apparently a halophil/-biont taxon) – see, e. g., WUNDERLICH (1973: 411–413, figs. 19-20) – are regarded as species of their own by recent authors but due to intermediates in the structures of the bulbus (person. observ.) I am not sure about the rank of these taxa. *Keijia nigropunctata* and *tincta* (= *Theridion*) (Theridiidae) may be independent species, see paper no. 3 within this volume. – See also above (B), e. g. *Meioneta mossica/saxatilis*.
Recently *Wubanoides uralensis lithodytes* (Linyphiidae) was described from Central Europe (Czech Republic and Germany) by SCHIKORA (2004) as a subspecies of *uralensis* from Siberia/North Asia. Both taxa – really subspecies? – possess numerous and more indistinct differences in their genital organs; their disjunct distribution pattern may indicate the existence of subspecies.
See also *Bathyphantes simillimus buchari* (Linyphiidae), and *Ozyptila trux* and *westringi* (Thomisidae) (above, B).

(D) ***Textrix intermedia* n. sp.** (raised from a putative hybridization) (figs.25a-b, 26b)

1986 *Textrix* sp.; regarded as possible intermediate/hybrid of *caudata* and *pinicola*.-- GALLARDO et al., Actas Jornadas Ent. Sevilla, 8: 60-63, fig. 4b.

Material: S-France, Provence, 10 km E Hyeres, close to the beach, under a stone, holotype ♂ JW leg. in VI 2003.

Diagnosis (♂; ♀ unknown): Prosomal length only 1.8 mm, pedipalpus (fig. 25a-b): Tibia with a large and pointed apophysis which stands out widely, cymbium (0.77 mm) and conductor (0.61 mm) fairly long, embolus of medium length.

Description (♂):
Measurements (in mm): Body length 3.7, prosoma: Length 1.8, width 1.15; leg I: Femur 1.3, patella 0.55, tibia 1.05, metatarsus 1.25, tarsus 0.82, tibia II 1.0, tibia III 0.9, tibia IV 1.3; diameter of a posterior median eye 0.175, length of an apical article of the posterior spinnerets 0.4.
Colour: Prosoma mainly medium brown, medially yellow, eye field black, sternum yellow brown, margin small black brown, legs annulated, opisthosoma ventrally yellow, laterally dark grey-brown, dorsally mainly dark brown; medially: anteriorly redbrown,

posteriorly light yellow.
Prosoma anteriorly abruptly narrow, posterior eye row strongly recurved, posterior median eyes very large, separated by less than their diameter. Basal cheliceral articles large, anterior margin of the cheliceral furrow with 3 teeth, posterior margin with 2. Fangs long, labium about 1/4 wider than long. – Legs fairly slender, order IV/I/II/III, covered with numerous bristles, femur I-II bear 3 dorsal bristles and an apical pair, tibia I bears ventrally 3 bristles, dorsally 2 and prolaterally 2, metatarsus I bears 2 ventral pairs and 3 apicals. – Opisthosoma 1.75 times longer than wide, with long posterior spinnerets. – Pedipalpus (figs. 25a-b; see above): Patella short, tibia short, bearing a large retrolateral apophysis and a short ventral outgrowth, cymbium slender.

Relationships: GALLARDO et al. (1986) regarded 6♂ (fig. 26b) as possible hybrids of *T. pinicola* SIMON 1875 (fig. 26a) and *T. caudata* L. KOCH 1872 (fig. 26c). According to the structures of the ♂-pedipalpus which differ strongly from both related species – with respect to the shape/length of the pedipalpal tibial apophysis, the cymbium, the conductor and the embolus – I regard *intermedia* without doubt as an independent species. In *pinicola* the pedipalpal tibial apophysis and the cymbium are shorter, in *caudata* body, cymbium, conductor and embolus are distinctly longer.

Distribution: S-France and Iberian Peninsula.

(E) QUESTIONABLE SUBSPECIES OF THE MACARONESIAN ISLANDS:

Especially on the Canary Islands an extraordinary radiation of certain genera – especially of *Dysdera, Pholcus, Spermophorides*, *Oecobius*, *Alopecosa*, *Hogna*, and *Psammitis/Proxysticus* – happened during the few last million years, see WUNDERLICH (1987: 281-283 and 1992), is apparently still continuing, and subspecies may be recognized in the future. In some species of the genus *Dysdera* LATREILLE 1804 (Dysderidae) the peculiar dorsal hairs of the opisthosoma and their vicariant distribution may indicate the existence of subspecies – see WUNDERLICH (1992) – although some species – according to their identical genital organs – were synonymized during the last years by Spanish authors.
In the following I will deal with two examples of possible "island species or subspecies" from the Canary Islands (1-2) and on a pair of epigean/cave-dwelling spiders from the Azores (3). Almost all of these taxa are not only known from single specimens but from populations.

(1) *Minicia* THORELL 1875 (Linyphiidae): *M. gomerae* (SCHMIDT 1975) from the Canary Islands (figs. 1-6), see WUNDERLICH (1979).
Two subspecies have been described:
- *M. gomerae gomerae* (SCHMIDT 1975) from the westernmost Canary Islands La Gomera and La Palma, and
- *M. gomerae teneriffensis* WUNDERLICH 1979 from Tenerife.

M. g. gomerae possesses a small dorsal outgrowth of the ♂-prosoma (figs. 1-3); in *M. g. teneriffensis* the outgrowth is much larger and a hairy fold between this outgrowth and a clypeus outgrowth exists (figs. 4-5). The genital structures of the ♀ and of the ♂-pedipalpus (fig. 6) are identical in both taxa; the colour of the opisthosoma is fairly different. Due to the absence of genital-morphological differences and the geographical separation it seems likely to me that both are subspecies of *M. gomerae* although I formerly regarded both as independent species, see WUNDERLICH (1987: 174). Interbreeding experiments and molecular studies are needed to be more sure about the status of these taxa.

(2) Micaria WESTRING 1851 (Gnaphosidae): *M. gomerae* STRAND 1911 from the Canary Islands; see WUNDERLICH (1979: 297-304, figs. 63a-g, 64-65) and (1987: 247). Three taxa have been described as subspecies (and furthermore a questionable subspecies):
M. gomerae gomerae STRAND 1911 from Tenerife, La Gomera and La Palma,
M. gomerae grancanariensis WUNDERLICH 1979 from Gran Canaria,
M. gomerae hierro SCHMIDT 1977 from El Hierro,
as well as an unnamed, questionable subspecies from Gran Canaria.
In 1987: 247, 280 I regarded the subspecies as populations or „ecological morphs“ of a single species, *M. gomerae,* which is known from five Canary Islands. Today the status of the taxa in question appears doubtful to me, again. Their ♀♂ genital structures show no differences, but – with respect mainly to the different spination of the ♂-tibiae I-II, the size/shape and the coloration of body and legs as well as the probably linked co-existence/co-evolution with different species of ants – a status of at least two subspecies (*gomerae* and *grancanariensis*) seems likely to me. Field and laboratory investigations are needed in this highly interesting case!

(3) Rugathodes ARCHER 1950 (Theridiidae): *R. acoreensis* WUNDERLICH 1992 and *R. pico* (MERRETT & ASHMOLE 1989) from the Azores (figs. 7-9), see WUNDERLICH (1992).
R. acoreensis (fig. 7) is an epigean taxon which is widely spread on the Azorean islands; it is well pigmented, has large eyes and relatively short legs (fig. 7). Members of *R. pico* are a true cave-dwelling spiders from the young islands Fajal and Pico (their age may be only about one million years or less) which are only weakly pigmented, have tiny eyes and long/slender legs (fig. 8). The genital structures of both taxa are identical (♂-pedipalpus see fig. 9), and therefore I do not want to exclude that both are subspecies of a single species, *R. pico*. Breeding experiments and molecular studies are needed to be more sure about the status of these taxa.

(II.) FOSSIL TAXA

The situation in fossils is still more complicated than in extant taxa: The use of molecular genetical studies is impossible, sexual behaviour and the exact palaeo-distribution are unknown in the spiders of the Baltic amber forest, and even the exact age of the suggested chrono-taxa/chrono-subspecies are unknown. The reasons are: Material of different strata is mixed in various secondary or tertiary deposits of the amber, and a direct dating of the amber pieces is impossible. Furthermore in amber fossils it is impossible to study populations and their variability (only rarely more than a single specimen of a species is preserved in the same piece of amber, and specimens which – apparently – are conspecific may originate from quite different populations in space and time).

Spiders from the Eocene European amber forests: The Baltic amber forest – as the largest part of them – probably existed for more than 10 million years, and therefore "chrono-taxa" can be expected; a few probable subspecies of the genus *Eopopino* (Nesticidae) were discussed by WUNDERLICH (1986: 53-61). Weak differences in the structures of the ♂-pedipalpus may or may not indicate the existence of subspecies in these fossils; weak differences in the genital-morphology per se can never allow sure conclusions in this respect.

Of great interest in this matter are those species and groups of strongly related species which (a) are available in a high number of specimens, and which (b) possess complicated structures of the male pedipalpus as well. (Fossils of *Orchestina* (Oonopidae) are frequent in Baltic amber, but they possess only simple structures of the ♂-pedipalpus; see the paper on the subfamily Orchestininae in this volume). Weak differences in the structures of their embolus may indicate the existence of subspecies or they are nothing more than an intraspecific variability. The genus *Acrometa* (Synotaxidae; numerous indet. ♂ are kept in the CJW) has to be revised more closely in the future.

In the numerous fossil members of the genus *Clya* KOCH & BERENT 1854 (Theridiidae) in Baltic amber the structures of their ♂-pedipalpi (fig. 10) are not so simple, their emboli build loops of various length, their embolic peaks have various positions, and the spiders are well studied, see the paper on the family Theridiidae in this volume (no. 3) which includes numerous drawings and photos. These spiders are excellent candidates for such an investigation.

My recent findings:

- In the males of this genus the emboli differ greatly in their length; they build 1 1/4 up to 4 1/4 loops (fig. 10) (*);
- there are overlappings but no gaps (!) within the "descriptive row" of the embolic lengths, and regarding the outgrowths of the embolic base (the peak) as well;
- the shape of the loop(s) shifts from oval (the first drawing in fig. 10) to circular;
- non-genitalic characters which may be linked with the embolic length are unknown.

Discussion: There are much more questions than answers: How many species of *Clya* inhabited the Baltic amber forest? We know nothing about the definitive number of species – and/or subspecies – which are described in my paper on the Theridiidae. Which characters allow us to recognize/diagnose different (sub)species? The length of their embolus – the number of loops – and the position of the outgrowth of the embolic base (the peak) may indicate the number of morphospecies.

The ancestral species of *Clya* is unknown (if there actually was only a single one of a single group of taxa). Did the hypothetical ancestral species possess the shortest or a longer embolus? Have there been branchings in the fossil populations which gave rise to subspecies or even species – or are all populations members of a single and very long-living "chrono-superspecies" (**) which lived for several million years? Have there been reversals in the lengthening/shortening of the embolus? Did different species exist which had the same number of embolic loops? What is the range of the intra(sub)specific variability of the embolic length?

A hint to the answer to the last question may come from the conditions in the genus *Latrodectus* of the same family (Theridiidae), and from genera of the family Sparassidae in which coiled emboli also exist (P. JÄGER (2006, 2007)): The intraspecific variability of the embolic loops is usually less than 10%, rarely slightly more. Thus one may conclude that there were members of far more than a single morpho-species (if we compare extant taxa) of the genus *Clya* in the Baltic amber forest. (In other genera of the Baltic amber forest – e. g. *Acrometa* PETRUNKEVITCH (Synotaxidae) or *Kochiuridion* n. gen. (Theridiidae, this volume, paper no. 3) – I did not find a great variability in the length of the embolus).

For "practical reasons" I chose the following PROVISIONAL proceeding: As a "fixed point" I started with the description of the peculiar species which has the shortest embolus – *Clya lugubris* (the first drawing in fig. 10), which may be related to the ancestral species -, and went on in a more or less arbitrary way with the designation of those taxa which possess more and more embolic loops, see e. g. the remaining drawings in fig. 10. (The) branchings within this "descriptive genital-morphological row of questionable descendents" are unknown. Most probably there are at least three or four (I suggest more) hypothetical palaeotaxa which may be species or subspecies – or are all members of a single "chrono-superspecies"? (**); see the paper on the family Theridiidae in this volume (no. 3).

Regarding the problem of fossil subtaxa and chrono-taxa: After the separation of populations exist – of course – subtaxa at different levels during a speciation. The different "forms" of the male copulatory organ – the pedipalpus in *Clya* (fig. 10) – may reflect the results of microevolutions. In this respect fossils may possess a unique importance, because we never can observe the effect of microevolution in extant animals in the fourth dimension. The sequence of peculiar fossils over time may – as chronotaxa – preserve a "FROZEN MICROEVOLUTION" which is totally different from findings in intraspecific subtaxa of extant animals.

(*) As can be concluded from the different position of the pointed basal embolic outgrowth, the embolic loops increased during the evolution by turning the embolic base.

(**) (a) The term "chrono-superspecies" is the counterpart to the term "geo-superspecies" which refers to extant taxa; see the concept of the "superspecies" sensu KRAUS (2002). A "chrono-superspecies" has characters of more than a single palaeo(morpho)species. According to WILLMANN (1985: 96) SYLVESTER-BRADLEY (1951: 98 and 1954) introduced the term "chronological superspecies" which is composed of several chronospecies. The concept of chronospecies is a typological one, but basicly there are – limited – possibilities to conclude from a morphospecies to the existence of a biospecies with the help of selected characters; e. g., strongly differing stridulatory organs may indicate a different courtship behaviour, and strongly differing particular structures of the ♂-pedipalpus – e. g. of the embolus – may indicate incompatible copulatory organs of both sexes.

(b) We do not know the different geological strata in which the fossil spiders of the genus *Clya* were deposited, and we also do not know the time span of the existence of certain (sub)species; therefore the term "chrono(super)species" can be used here only in a restricted and hypothetical sense. Indeed, the Baltic amber forest existed most probably for several million years, and therefore the existence of "chrono(super)species" in this genus seems likely to me.

REFENCES, cited

ALMQUIST, S. (2006): Swedish Araneae, part 2 – families Dictynidae to Salticidae. – Insects Systematics & Evolution, supplement no. 63: 283–601.

BERTKAU, P. (1882): Über das Cribellum und Calamistrum. – Arch. Naturgesch., 48: 316–362.

COKENDOLPHER; J. C. (2004): *Cicurina* spiders from caves in Bexar County, Texas (Araneae: Dictynidae). -- Texas Mem. Mus., Speleol. monographs, 6: 13–58.

DAHL, F. (1926): Spinnentiere oder Arachnoidea. I: Springspinnen (Salticidae). -- In DAHL, F. (ed.): Die Tierwelt Deutschlands, 3: 1–55.

GRISWOLD, C. E. at al. (1999): Towards a phylogeny of entelegyne spiders (Araneae, Araneomorphae, Entelegynae). -- J. Arachnol., 27: 53–63.

GALLARDO, L. et al. (1986): Aspectos taxonomicos de los especies del genero *Textrix: T. Caudata* L. KOCH y *T. pinicola* E. SIMON (Araneae; Agelenidae). – Actas de las Jornadas Ent. Sevilla, 8: 54–64.

HORMIGA, G. et al. (2005): *Nanoa*, an enigmatic new genus of pimoid spiders from western North America (Pimoidae, Araneae). -- Zool. J. Linn. Soc., 145: 249–262.

JÄGER, P. (2006): Lengthening of embolus and copulatory duct: a review of an evolutionary trend in the spider family Sparassidae (Araneae). -- Acta zoologica bulgarica, Suppl. No. 1: 49–62.

-- (2007): Evolution von Kopulationsorganen bei Spinnen/Evolution of copulatory organs in spiders. -- Evolution von Kopulationsorganen bei Spinnen: 16–17. -- In Jäger, P. et al. (ed.): Senckenberg 2005–2006. Frankfurt am Main, Senckenbergische Naturforschende Gesellschaft, 96pp.

JOCQUE, R. & DIPPENAAR-SCHOEMAN, A. S. (2006): Spider Families of the World. 336pp. – Second edition 2007.

KRAUS, O. (2002): Why no subspecies in spiders? -- European Arachnology 2000: 303–314.

KRONESTEDT, T. (1979): Ecologiska karaktärer vid taxonomiska studier av vargspindlar. – Ent. Tidskr., 100: 194–199.

LEHTINEN, P. T. (1967): Classification of the Cribellate spiders and some allied families, with notes on the evolution of the suborder Araneomorpha. -- Ann. Zool.Fennici, 4: 199–468.

MUFF, P. et al. (2007): Spider (Arachnida: Araneae) distribution across the timberline in the Swiss Central Alps (Alp Flix, Grisons) and thre morphologically remarkable species. – Arachnol. Mit., 34: 16–24.

MUSTER, C. & THALER, K. (2004): New species and records of Mediterranean Philodromidae (Arachnida: Araneae): I. *Philodromus aureolus* group. – Denisia (N. S.) 12: 305–326.

NITZSCHE, R. (1999): Das Brautgeschenk der Spinne. 254 pp.

PEKAR, S., CARDOSO, P. & MEIEROSE, C. (2003): Additions to the knowledge of Portuguese zodariid spiders (Araneae: Zodariidae). – Bull. Br. arachnol. Soc., 12 (9): 385–395.

PLATEN, R. & WUNDERLICH, J. (1990): Die Spinnenfauna des Naturschutzgebietes Pfaueninsel in Berlin. -- Zool. Beitr. (N. F.), 33 (1): 125–160.

RAMIREZ, M. J. et al. (1997): Revision del genero *Macerio* y commentarios sobre la ubicacion de *Cheiracanthium*, *Tecution* y *Helebiona* (Araneae, Miturgidae, Eutichurinae). – Iheringia (Zool.), 82: 43–66.

REZAC, M, PEKAR, S. & JOHANNESEN, J. (2008): Taxonomic review and phylogenetic analysis of central European *Eresus* species (Araneae: Eresidae). – Zoologica Scripta, 37 (3): 263–287.

ROBERTS, M. J. (1993): The Spiders of Great Britain and Ireland, 1 (2).

SAARISTO, M. I. (2007): A new subfamily of linyphiid spiders based on a new genus created for the *keyserlingi*-group of the genus *Lepthyphantes* (Aranei: Linyphiidae. – Arthropoda Selecta, 16 (1): 33–42.

SAUPE, E.E. & SELDEN, P. A. (2008?, in prep.): First fossil Mecysmaucheniidae (Arthropoda: Chelicerata: Araneae) from Lower Cretaceous (Upper Albian) amber of Charente-Maritime, France.

SCHICK, R. X. (1965): The Crab Spiders of California (Araneida, Thomisidae). – Bull. Amer. Mus. Nat. Hist., 129 (1): 1–180.

SCHIKORA, H.-B. (1995): Intraspecific variation in taxonomic characters, and notes on distribution and habitats of *Meioneta mossica* SCHIKORA and *M. saxatilis* (BLACKWALL), two closely related spiders from northern and central Europe (Araneae: Linyphiidae). -- Bull. Br. arachnol. Soc., 10 (2): 65–74.

-- (2004): *Wubanoides uralensis* (PAKHORUKOV 1981) – Geographic variation, mating behaviour, postembryonic development and description of a new subspecies (Araneae, Linyphiidae). -- In: Diversität und Biologie von Webspinnen, Skorpionen und anderen Spinnentieren. Ed.: Biologiezentrum/Oberösterreichisches Landesmuseum (Land Österreich). Denisia (N. S.) 12: 327–341.

SCHÜTT, K. (2000): The limits of the Araneoidea (Arachnida: Araneae). -- Australian J. Zool., 48: 135–153.

SIMON, E. (1932): Les Arachnides de France, 6 (4): 773–978.

SPAGNA, J. C. & GILLESPIE, R. G. (2007): More data, fewer shifts: Molecular insights into the evolution of the spinning apparatus in non-orb-viewing spiders. -- Molecular Phylogenetics and Evolution, 46: 347–368.

TANASEVITCH, A. V. (2007): New records of linyphiid spiders from Russia, with taxonomic and nomenclatural notes (Aranei: Linypgiidae). – Arthropoda Selecta, 16 (2): 115–135.

THALER, K. (1978): Die Gattung *Cryphoeca* in den Alpen (Arachnida, Aranei, Agelenidae). -- Zool. Anz., 200: 334–346.

-- (1986): Über wenig bekannte Zwergspinnen aus den Alpen – VII (Arachnida: Aranei, Linyphiidae: Erigoninae). – Mitt. schweiz. ent. Ges., 59: 487–498.

WIEHLE, H. (1960): Micryphantidae – Zwergspinnen. -- In DAHL (ed.): Die Tierwelt Deutschlands, 47: 1–620.

WILLMANN, R. (1985): Die Art in Raum und Zeit. 207pp.

WUNDERLICH, J. (1972): Zur Kenntnis der Gattung *Walckenaeria* BLACKWALL 1833 unter besonderer Berücksichtigung der europäischen Subgenera und Arten (Arachnida: Araneae: Linyphiidae). -- Zool. Beitr. (N. F.), 18 (3): 371–427.

-- (1973): Zur Spinnenfauna Deutschlands, XV. Weitere seltene und bisher unbekannte Arten sowie Anmerkungen zur Taxonomie und Synonymie.-- Senckenbergiana biol., 54 (4/6): 405.428.

-- (1979): Revision der europäischen Arten der Gattung *Micaria* WESTRING 851, mit Anmerkungen zu den übrigen paläarktischen Arten (Arachnida: Araneida: Gnaphosidae). -- Zool. Beitr. (N. F.), 25: 233–341.

-- (1979): Drei Beispiele für Artbildung (Speziation) bei Spinnen von den Kanarischen Inseln (Arachnida: Araneida: Linyphiidae, Oecobiidae, Gnaphophosidae). -- Zool. Beitr. (N. F.), 25: 415–426.

-- (1985): Zur Synonymie einiger europäischer Arten der Gattung *Pelecopsis* SIMON 1864 (Arachnida: Araneae: Linyphiidae). -- Senckenbergiana biol.,66 (1/3): 111–114.

-- (1986): Spinnenfauna gestern und heute. Fossile Spinnen und ihre heute lebenden Verwandten. 283pp.

-- (1987): Die Spinnen der Kanarischen Inseln und Madeiras. 435pp.

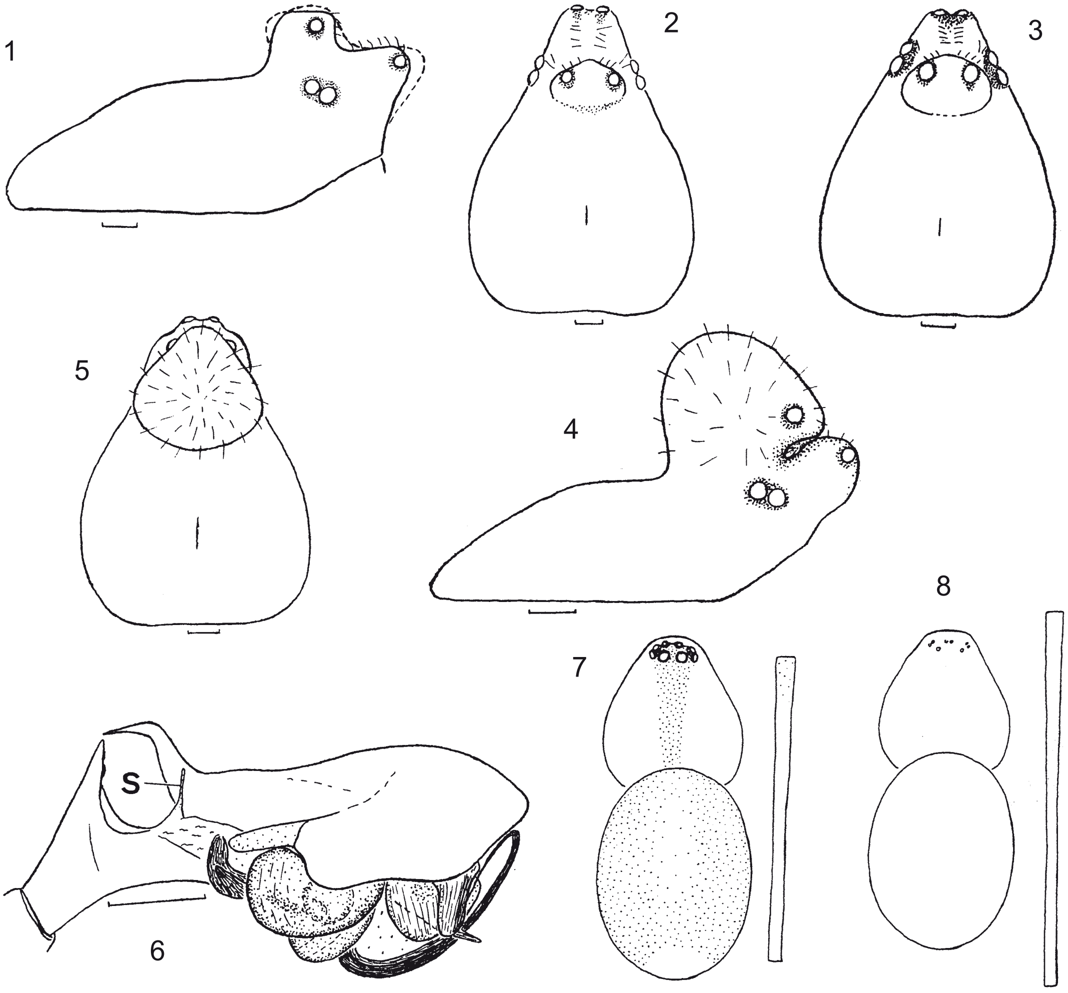
-- (1992): Die Spinnen-Fauna der Makaronesischen Inseln. -- Beitr. Araneol., 1: 1–619.

-- (1992): The Macaronesian cave-dwelling spider fauna (Arachnida: Araneae). -- Memoirs Queensland Mus., 33 (2): 681–686.

-- (1995): *Ozyptila westringi* (THORELL 1873), eine in Deutschland seltene Krabbenspinnenart (Arachnida: Araneae: Thomisidae). -- Beitr. Araneol., 4 (1995): 329–333.

-- (2004): Fossil spiders in amber and copal. -- Beitr. Araneol., 3 (A, B). 1908pp. Publishing House J. Wunderlich, D-69493 Hirschberg.

WUNDERLICH, J. & SCHUETT, K. (1995): Beschreibung der bisher verkannten Sackspinnen-Art *Clubiona frisia* n. sp. aus Europa (Arachnida: Araneae: Clubionidae). -- Entomol. Z., 105 (1/2): 10–17. (As well as a correction: Entom. Z., 105 (5): 10–17).



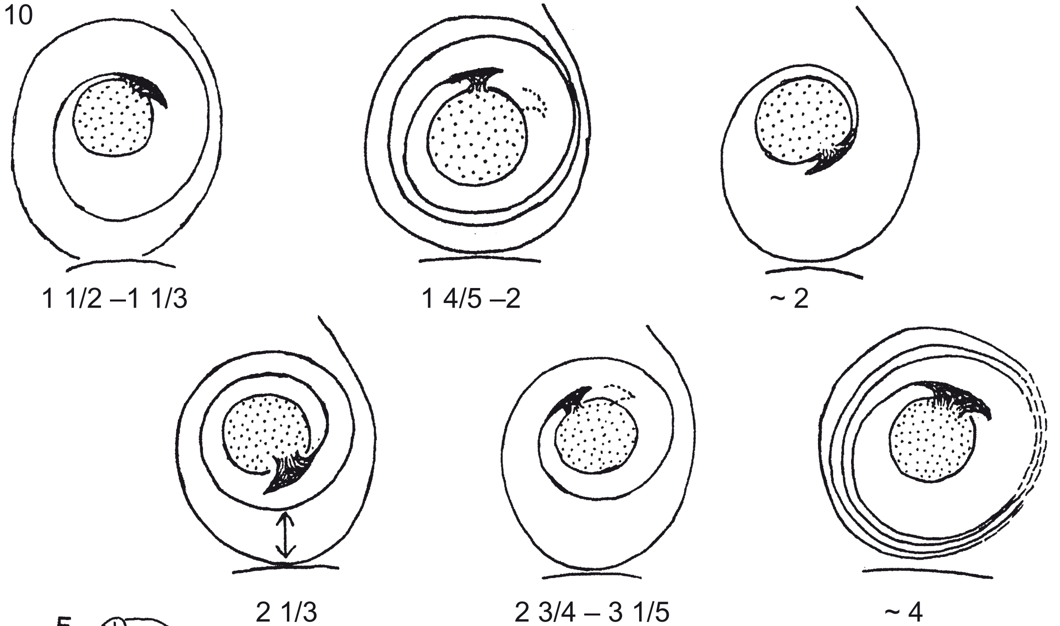
Figs. 1–3: *Minicia gomerae gomerae* (SCHMIDT 1975) (Linyphiidae), extant ♂ from the Canary Island La Gomera; lateral (1) and dorsal (2–3) aspects of the prosoma, variable shape;

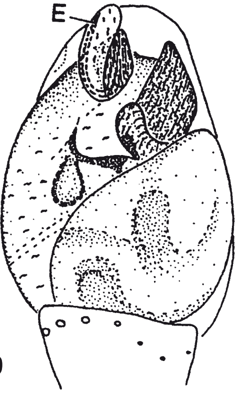
figs. 4–5: *Minicia gomerae teneriffensis* WUNDERLICH 1979 (Linyphiidae), extant ♂ from the Canary Island Tenerife, lateral and dorsal aspect of the prosoma;

fig. 6) retrolateral aspect of the right ♂-pedipalpus of *M. gomerae gomerae* and *M. gomerae teneriffensis*; the structures of both pedipalpi are identical;

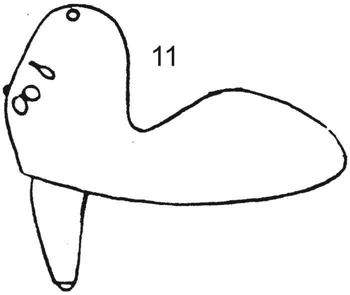
fig. 7) *Rugathodes acoreensis* WUNDERLICH 1992 (Theridiidae), extant epigean ♂ from the Azores, dorsal aspect of the prosoma and an anterior tibia;

fig. 8) *Rugathodes pico* (MERRETT & ASHMOLE 1989) (Theridiidae), extant cave-dwelling ♂ from the Azores, dorsal aspect of the prosoma and an anterior tibia. Note the reduced eye lenses and the long slender tibia;





9


11

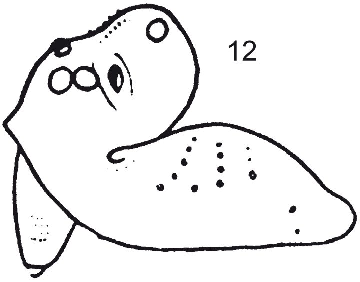
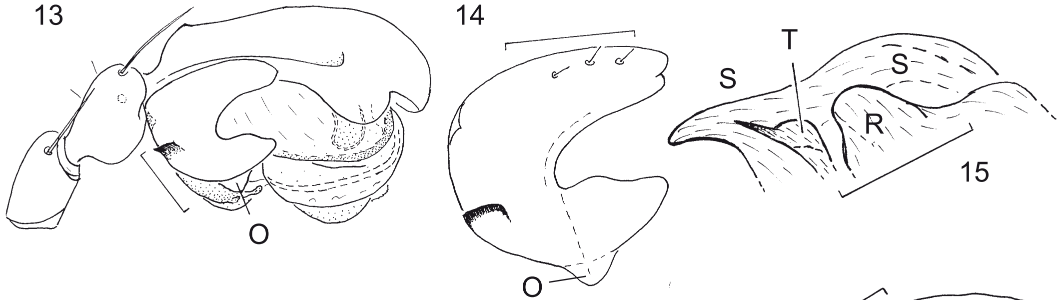
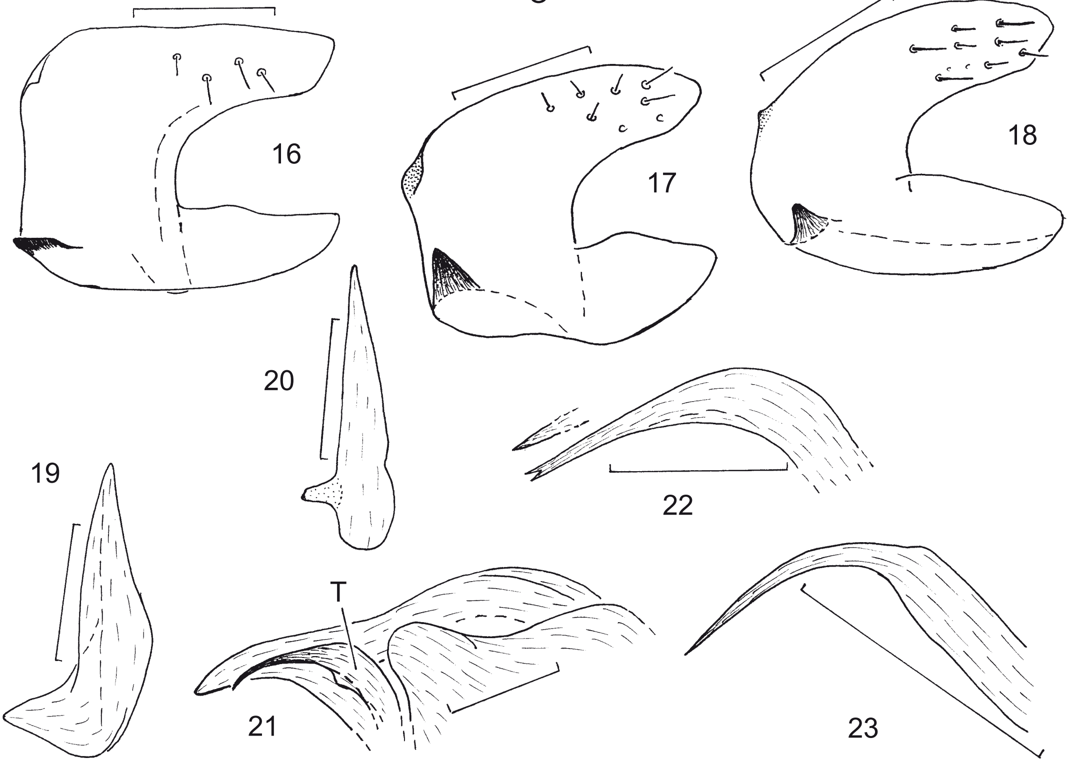

12

fig. 9) ventral aspect of the right ♂-pedipalpus of *Rugathodes acoreensis* and *R. pico*; the structures of both pedipalpi are identical;

fig. 10) Ventral aspects of the right bulbi with emboli and basal embolic outgrowths of six palaeotaxa of the Eocene genus *Clya* KOCH & BERENDT 1854 (Theridiidae) in Eocene Baltic amber. This is basically a “descriptive genital-morphological row of questionable descendents”. The emboli describe 1 1/4 up to 4 1/4 loops. There are no gaps in the increasing embolic length between these hypothetical “palaeotaxa” which may represent subspecies or species or even a single “chrono-superspecies”, and reflect the evolutionary result of an unknown span of time, most probably of several (more than ten) million years;

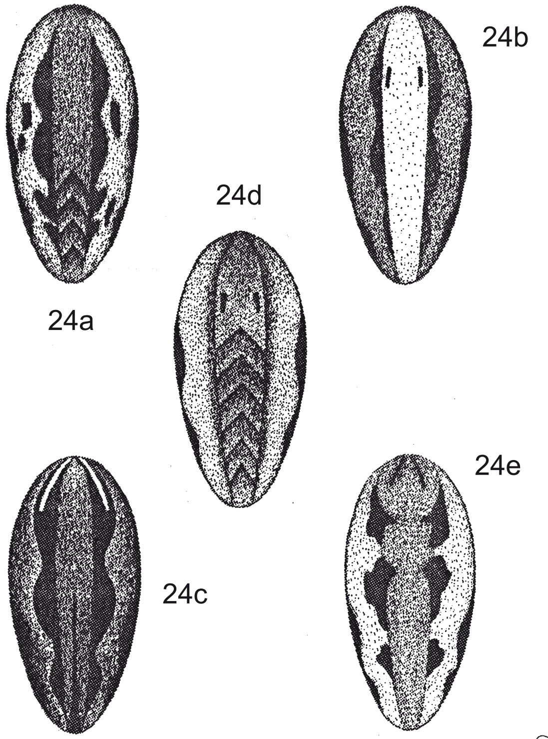
figs. 11–12: Two forms of the ♂-prosoma of *Pelecopsis elongata* (WIDER 1834) (Linyphiidae: Erigoninae), lateral aspects; fig. 11) shows the frequent form, fig. 12: A rare form; intermediates exist. Taken from MILLER (1971: T. 51, figs. 7–8);

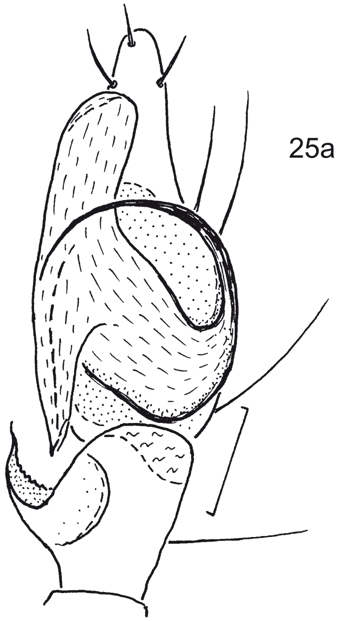


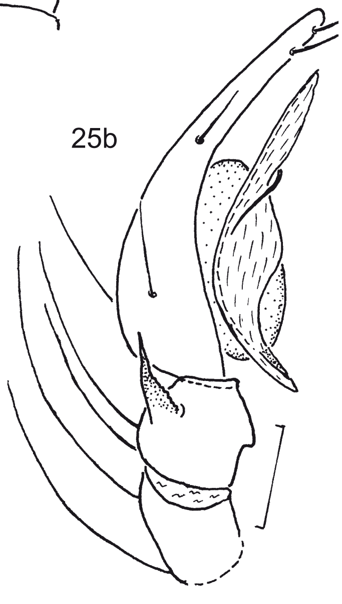


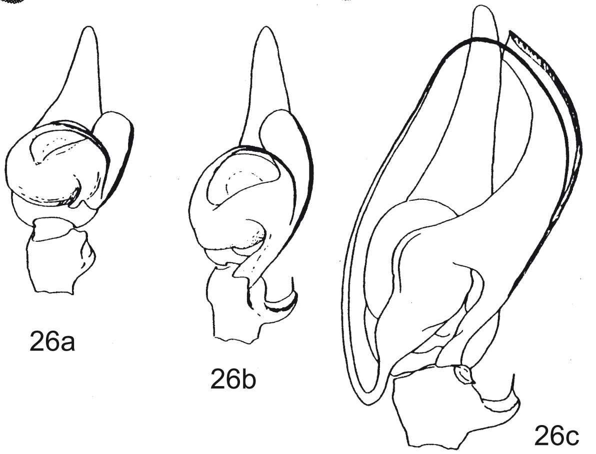
figs. 13–15: *Centromerus subalpinus* LESSERT 1907, ♂; 13) retrolateral aspect of the r. pedipalpus (bulbus slightly expanded); 14) exact retrolateral position of the r. paracymbium; 15) proventral aspect of selected structures of the r. bulbus; O = ventral outgrowth of the paracymbium, R = radix, S = subtegulum, T = terminal apophysis; scale bars = 0.1 mm;

figs. 16–23: <u>*Centromerus arcanus*</u> (O. PICKARD-CAMBRIDGE 1873) (Linyphiidae), ♂; 16) r. paracymbium in an exact retrolateral position; 17) exact retrolateral position of the r. paracymbium of the "forma" *ensifer*; 18) exact retrolateral position of the r. paracymbium of the “forma” *unidentatus*; 19–20) ventral aspect of the r. paracymbium of the “forma” *ensifer* and the “forma” *unidentatus*; 21) proventral aspect of selected structures of the r. bulbus (T = terminal apophysis); 22) “forma” *ensifer* (France), proventral aspect of the r. terminal apophysis, variability; 23) “forma” *unidentatus* (Black Forest), proventral aspect of the r. terminal apophysis; scale bars = 0.1 mm;









figs. 24a–d: Variable dorsal pattern of the opisthosoma of Pisaura mirabilis (CLERCK 1757) (Pisauridae). Taken from Nitzsche (1999: Fig. 9b, from PERICAUD (1979));

figs. 25a–b: *Textrix intermedia* n. sp. (Agelenidae), ♂, ventral and retrolateral aspect of the r. pedipalpus; scale bars = 0.2 mm;

figs. 26a–c: Ventral aspect of the ♂-pedipalpus of three species of the genus *Textrix* (Agelenidae); a) *T. pinicola* SIMON 1875; b) *T. intermedia* n. sp. (an "intermediate form" of *caudata* and *pinicola* according to GALLIARDO et al.); c) *T. caudata* L. KOCH 1872; taken from GALLIARDO et al. (1986: Figs. 4a–c).

BEITR. ARANEOL., 5 (2008)

PROOFS OF CAMOUFLAGE (MIMICRY, MIMESIS) IN FOSSIL SPIDERS (ARANEAE) / NACHWEISE VON SCHUTZANPASSUNG (TARNUNG) BEI FOSSILEN SPINNEN

JOERG WUNDERLICH, Oberer Häuselbergweg 24, D-69493 Hirschberg.

Abstract: Proofs of camouflage (Batesian mimicry, mimesis) are reported from some fossil spiders.

The „normal“ body of a Garden orb web spider will be known to the reader: an eight-legged animal with a two-partite body as well as a rounded opisthosoma, bearing the spinnerets at its end and separated from the front part by a short and thin stalk. Similar spiders have been described excellently preserved with hundreds of species from millions of years old amber and from young copal, see WUNDERLICH (2004). (Copal can be ten thousands of years old or just few years; it is found in great quantities e.g. on Madagascar).

Sometimes fossil spiders are found whose bodies have a totally unusual or even bizarr shape, see fig. 2 and the photos 56–83 in the book of WUNDERLICH (2004) WHICH ARE REFERED HERE. These exotic shapes make one think and speculate about their biological implications (which the reader is asked to do, too); Do they exist merely by chance or do they have a special function, which should be found out and prooved?

OPELL & WARE (1987) discussed specimens of the Uloboridae which resembles thorns, bud or broken twigs; see the paper no. 6 in this volume (the genus *Hyptiotes*), photo 383. Representatives of this family already existed in the Cretaceous, see paper no. 5 in this volume.

The four spider species, dealt with in this report in more detail, belong to the family Archaeidae, which are known as fossils from Burmese and Baltic amber as well as from young copal and extant in Madagascar. In Baltic amber they were quite diverse in the Tertiary, ca. 40–50 million years ago, see WUNDERLICH (2004: 768–805). Nowadays they have become extinct not only in Europe but in the whole Northern Hemisphere; they have survived only as relicts in the tropical and subtropical regions of South Africa, Madagascar and Australia. These spiders move slowly, don’t build capture webs

and feed almost entirely on spiders of other families, which they lie in wait for hanging upside down and often totally still in higher vegetation. The most conspicuous characteristics of these long-legged spiders are their enormous and extremely long chelicerae which are standing apart – most strongly developed and best recognizable in fig. 2 and photo 58 –; the longitudinal furrows of their opisthosoma as well as the unusual shape of their bodies compared to other spiders: The prosoma is higher in the anterior part and can even bear a marked headlike part (fig. 2), which bears the eyes.
The shape of the spiders dealt with here is not only totally unusual, but also very diverse; therefore they can be regarded as a challenge to different interpretations in which the species however, must be dealt with separately:

(1) *Baltarchaea conica* (fig. 1, photo 56). This specimen is 3 1/2 mm long and preserved in Baltic amber. Its body is compact, prosoma and opisthosoma almost making up a unity, their chelicerae and their legs are – compared to their relatives – unusually short, the furrows of their opisthosoma, however, are very well developed. Could that be the mimesis of parts of plants (phytomimesis)? The shape of these spiders reminds me somewhat of wart-, knot- or budlike structures on twigs but also of rotting or drying or shrinking parts of plants; the folded opisthosoma also implies these parts of plants. Representatives of a small extant tropical species of Orb Weavers imitate the knot of a twig. – I suppose that kinds of mimesis in theridiid spiders of the genera *Phoroncidia* and *Ulesanis*, see WUNDERLICH (2004: Photo 434), and the revision of fossil Cobweb Spiders in this volume, paper no. 3; see also p. 481 and photo 380.

(2) *Myrmecarchaea petiolus* (photos 76–77). The body length of this spider is 2.1 mm, it is also preserved in Balic amber. The legs, body and especially the stalk between prosoma and opisthosoma (petiolus) are extremely long. The channels for blood vessels, the digestive system and the nerves are all pressed into this thin and long petiolus. A similarly long stark exists with some Corinnidae and Salticidae, which are similar to ants. The long opisthosoma bears a weak saddle-shaped constriction in the middle. According to the physical characteristics of the spider a similarity with certain graceful and defensive Hymenoptera could be present here, e.g. with ants – or even more probably – with Shecidae. The usually two-partite spider body approaches the three-partite insect body with this spider; it is far from the normal spider shape which seems to be dissolved; for us human beings this spider does not conform to the normal image of a spider. This spider genus might have exchanged its spider shape for a warning disguise as a wasp using mimicry, thus it could appear as a “sheep in wolfscin” (Batesian mimicry).

Annotations concerning wasp- and ant-mimicry in fossil representatives of other spider families in Baltic amber: (A) The shape of the body and light opisthosomal spots in fossil Corinnidae of the genus *Ablator* indicate a further kind of imitating Hymenoptera: the similarity with wing-less Mutillidae, see WUNDERLICH (2004: photos 368 and 386) and BRISTOWE (1941). – (B) Ant mimicry apparently existed in fossil Corinnidae of the genus *Eomazax* and in fossil Zodariidae, see WUNDERLICH (2004: e.g. photos 346, 376–377). In extant species of the genus *Steatoda* s.l. (Theridiidae: Asageninae) – which are distinctly spotted – probably also Batesian mimicry existed.

(3) Juvenile male of the genus *Eriauchenius* (Archaeidae) (photo 79) in copal from Madagascar, body length 3.3 mm. Its opisthosoma is high and almost globular, coni-

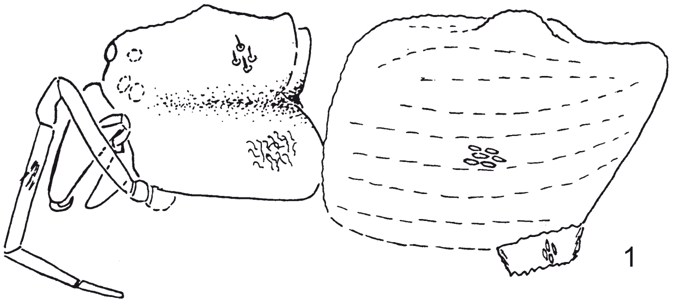
cally pointed anteriorly. – The spider's prosoma appears similar to the thorn of a plant. One may think of the real position of the spider, hanging upside-down on a twig. After turning the photo by 180° you will find it hard to identify this "thing" as a spider! As in the spiders (1) and (4) this may be a case of phytomimesis, too.

(4) Male archaeid spider of *Eriauchenius gracilicollis* (fig. 2; photos 81–83) in copal from Madagascar, body length 3 mm. The legs of this spider are very thin and possess a peculiar length, and the rounded-triangular opisthosoma (at the right side in the figure) is small; on top of an extremely long "neck" and an oval "head" sits which bears the eyes, and the extremely long and diverging chelicerae originate anteriorly. The opening of the mouth (arrow in fig. 2) is situated below (!) the "neck", and therefore a true head – which should bear a mouth – is absent in this spider. In any position this animal can easily be identified as a spider. The typical body of a spider is bipartite, a head and a neck are absent. The bizarr body of this spider appears tripartite, the long chelicerae and legs look like appendages of unknown structures. The prosoma and its long chelicerae may remind one of seed, fruit or the rotten part of a plant. Probably this is a further case of phytomimesis.

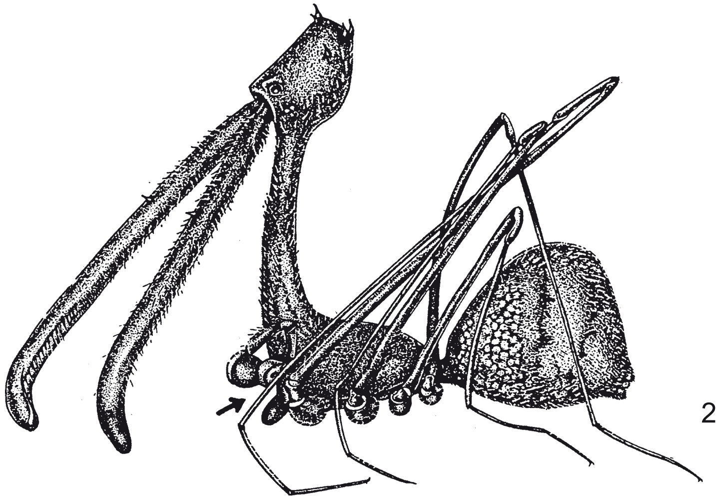
If one compares the four spider species dealt with above one character they have in common is striking: They have a shape that is totally untypical for spiders, at least one part of the body is changed considerably. A non-specialist cannot identify them easily as a spider and even arachnologists will have to think twice. Similarly the enemies of spiders that orientate themselves optically in searching for prey could be made uncertain: The members of various small bird species capture spiders in the vegetation being able to learn – as experiments have shown – to recognize a spider by its typical shape and to distinguish it for example from a "bad tasting", acid excreting ant or a wasp that could even be armed with a poisonous sting (see photo 76). Such birds are certain not to eat parts of a plant which are indigestible for them (figs. 1, 2, photos 56, 79, 81). These spiders which look similar to ants, certain wasps or parts of plants (imitating them) could therefore be protected almost totally or at least partly from spider-eating birds. Mimicry always serves to deceive a receiver of signals, in this case obviously a bird. – A selection advantage in this sense might have enforced for generations the evolution of these unusual shapes and structures as can be found with the fossil spiders dealt with here. A typical character of all fossil and extant representatives of the family Archaeidae – unless they are under suspicion of existing mimicry or mimesis – is the prosoma whose anterior part is heightened (*); this can supposedly be regarded as the physical disposition for the spider shapes described above, whose high-rising "head part" has developed in an unusual – and different way each. See also BRISTOWE (1939/1941) und FOELIX (1996: 253–256).

Astonishing examples of mimicry have been described in extant spiders: Especially some tropical spiders resemble leaves, twigs, buds, flowers, fruits, parts of bark – even birds shit – in an amazing way. Examples of protective adaptations – mimicry (fig. 2, photo 76) and mimesis (fig. 1, photo 56; see the papers no. 5 and 6 in this volume) – before the Eocene have hardly been documented in fossil spiders so far. The first proof for the development of mimesis in spiders can thus be dated back to the time about 50 million years ago.

(*) The high prosoma of these spiders leaves room for the extremely long chelicerae which are obviously connected to the capturing of prey (spiders).



1



2

Fig. 1) Fossil female of *Baltarchaea conica* (Archaeidae) in Baltic amber, body length 3 1/2 mm, lateral aspect; only one of its legs is drawn;
Abb. 1) Fossile Konische Urspinne (*Baltarchaea conica*) im Baltischen Bernstein, Weibchen, Körper-Länge 3 1/2 mm, Seitenansicht; es ist nur ein Bein gezeichnet;

fig. 2) Male „Long-necked spider“ of the genus *Eriauchenius* (family Archaeidae) in copal from Madagascar and extant, body length 3 mm, lateral asoect. Note the unusually long and thin legs, the extremely long chelicerae, the long „neck“, and the position of the opening of the mouth (arrow). Who recognizes this „object“ – hanging upside-down on a twig – as a spider? Will a bird accept it as a prey? – Taken from LEGENDRE (1970).
Abb. 2) „Langhals“-Urspinne (Gattung *Eriauchenius*) in Kopal aus Magagaskar und heute existierend, Männchen, Körper-Länge etwa 3 mm, Seitenansicht. Man beachte die ungewöhnlich langen und dünnen Beine, die extrem langen Kiefer, den langen „Hals“ und die Position der Mundöffnung (Pfeil). Wer denkt bei diesem kopfunter (!) an einem Zweig hängenden „Objekt“ an eine Spinne? Würde sie ein spinnenfressender Vogel als Beute akzeptieren?

Der “normale” Körper einer Spinne – etwa einer Kreuzspinne – ist dem Leser bekannt: Ein Achtbeiner mit zweiteiligem Körper sowie rundlichem Hinterkörper, der am Ende die Spinnwarzen trägt und der durch einen kurzen, dünnen Stiel vom Vorderkörper getrennt ist. Ähnliche Spinnen sind fossil mit Hunderten von Arten beschrieben worden, so auch in hervorragender Erhaltung in Millionen Jahre altem Bernstein und in jungem Kopal, siehe WUNDERLICH (2004). (Kopal kann Zehntausende oder auch nur wenige Jahre alt sein; er wird z. B. in großen Mengen auf Madagaskar gefunden).
Gelegentlich werden fossile Spinnen gefunden, deren Körper eine ganz ungewöhnliche oder sogar bizarre Gestalt besitzt, siehe Abb. 2 und die Farbfotos 56–83, die unten nach dem Buch von WUNDERLICH (2004) zitiert sind. Diese “exotischen” Körperformen regen zum Nachdenken und zum Spekulieren über ihre biologische Bedeutung an (wozu auch die Leser aufgefordert sind!): Existieren sie rein “zufällig” oder kommt ihnen eine besondere Bedeutung (Funktion) zu, die zu ergründen und zu belegen ist?
OPELL & WARE (1987) diskutieren Vertreter der Kräusel-Radnetzspinnen (Uloboridae), die Dornen, Knospen oder abgebrochenen Zweigen ähneln; siehe die Arbeit Nr. 6 in diesem Band (die Gattung *Hyptiotes*, Foto 383). Vertreter dieser Familie existierten bereits in der Kreidezeit, siehe die Arbeit Nr. 5 in diesem Band.
Die in dieser Arbeit eingehender behandelten vier Spinnenarten gehören zur Familie Urspinnen (Archaeidae), die fossil von Burmesischem und Baltischem Bernstein sowie in jungem Kopal und heute lebend von Madagaskar bekannt geworden sind. In Baltischem Bernstein (Tertiär, etwa 40–50 Millionen Jahre alt) waren sie recht divers, vgl. WUNDERLICH (2004: 768–805). Heute sind sie nicht nur in Europa, sondern in der gesamten nördlichen Hemisphäre ausgestorben; lediglich in tropischen und subtropischen Regionen Südafrikas, Madagaskars und Australiens haben sie als Relikte überlebt. Die Spinnen bewegen sich langsam, bauen keine Fangnetze und ernähren sich fast ausschließlich von Spinnen anderer Familien, denen sie auflauern, wobei sie bauchoben und oft bewegungslos in der höheren Vegetation hängen. Die auffälligsten Kennzeichen dieser meist sehr langbeinigen Spinnen sind die gewaltigen, extrem langen und auseinanderweichenden Kiefer – am stärksten entwickelt und am besten erkennbar sind sie in Abb. 2 und Foto 58 –, die Längsfurchen des Hinterkörpers sowie die für Spinnen ungewöhnliche Körperform: Der Vorderkörper ist vorn deutlich erhöht und kann sogar einen ausgeprägten „Kopfteil“ tragen (Abb. 2), auf dem die Augen sitzen.

Die Gestalt der hier behandelten Spinnen ist nicht nur ganz ungewöhnlich, sondern auch sehr verschiedenartig; daher sind unterschiedliche Deutungsversuche gefordert, und die einzelnen Spinnenarten müssen gesondert behandelt werden:

(1) Konische Urspinne (*Baltarchaea conica*) (Abb. 1, Foto 56). Das vorliegende Exemplar ist eine 3 1/2 mm lange Spinne, die in Baltischem Bernstein konserviert ist. Ihr Körper ist kompakt, Vorder- und Hinterkörper bilden nahezu eine Einheit, ihre Kiefer und ihre Beine sind – verglichen mit ihren Verwandten – ganz ungewöhnlich kurz, die Längsfurchen des Hinterkörpers sind dagegen besonders gut entwickelt. – Könnte hier die Nachahmung pflanzlicher Teile (Phytomimese) vorliegen? Mich erinnert die Körperform dieser Spinnen am ehesten an warzen-, knoten- oder knospenähnliche Strukturen an Zweigen, aber auch an verrottende oder vertrocknete und geschrumpfte pflanzliche Teile; auf derartige Pflanzenteile deutet wohl auch der faltige Hinterkörper der Spinne hin. Vertreter einer kleinen rezenten tropischen Art von Radnetzspinnen

(Araneidae) ahmen einen Astknoten nach. – Mimese liegt vermutlich auch bei Kugelspinnen der Gattungen *Phoroncidia* und *Ulesanis* vor, siehe WUNDERLICH (2004: Foto 434) und die Revision der fossilen Kugelspinnen (Theridiidae) in diesem Band (Nr. 3) sowie bei der Krabbenspinne *Tmarus piochardi* (Abb. in SAUER & WUNDERLICH S. 73). Siehe auch Foto 380 in diesem Band und S. 481.

(2) Die Ameisen-Urspinne *Myrmecarchaea petiolus* (Fotos 76–77). Die Körperlänge dieser Spinne beträgt 2.1 mm, sie ist ebenfalls in Baltischem Bernstein konserviert. Beine, Körper und – insbesondere – der Stiel zwischen Vorder- und Hinterkörper (Petiolus) sind extrem langgestreckt. Durch den langen und dünnen Petiolus „drängeln" sich die „Kanäle" für Blugefäße, Verdauungssystem und Nerven (!). Ein ähnlich langer Stiel existiert bei einigen Ameisen-Sackspinnen (Corinnidae) und einigen Springspinnen (Salticidae), die als ameisenähnlich gelten. Der langgestreckte Hinterkörper trägt in der Mitte eine schwache sattelförmige Einschnürung. – Nach den körperlichen Merkmalen der Spinne könnte hier eine Ähnlichkeit mit bestimmten grazilen – und wehrhaften! – Hautflüglern vorliegen, etwa mit Ameisen oder – wohl noch wahrscheinlicher – mit Grabwespen (Sphecidae). Der normalerweise zweiteilige Spinnenkörper nähert sich bei dieser Spinne dem dreiteiligen Insektenkörper an; von der üblichen Spinnengestalt ist er weit entfernt; sie erscheint „aufgelöst"; auch für uns Menschen fällt sie aus dem normalen „Suchbild für Spinnen" heraus. Diese Spinnenart könnte als „Tarnung" (Mimikry) ihre Spinnengestalt gegen eine „Warntracht" in Wespengestalt „eingetauscht" haben; damit erschiene sie als „Schaf im Wolfspelz" (Bates'sche Mimikry).

Anmerkungen zu Wespen- und Ameisenmimikry bei fossilen Vertretern anderer Spinnenfamilien im Baltischen Bernstein: (A) Die Körperform und helle Flecken auf dem Hinterkörper bei fossilen Ameisen-Sackspinnen (Corinnidae) der Gattung *Ablator* deuten auf eine weitere Wespen-Mimikry, nämlich auf die Ähnlichkeit mit wehrhaften flügellosen Ameisenwespen oder Bienenameisen (Mutillidae), siehe WUNDERLICH (2004: Fotos 368 und 386) und BRISTOWE (1941). – (B) Ameisenmimikry lag offenbar bei fossilen Ameisen-Sackspinnen der Gattung *Eomazax* und bei fossilen Ameisenjägern (Familie Zodariidae) vor, siehe WUNDERLICH (2004: z. B. Fotos 346, 376–377). Bates'sche Mimikry könnte weiterhin bei einigen heutigen Kugelspinnen der Unterfamilie Asageninae (= Latrodectinae) (Witwen-Verwandte) vorliegen, z. B. bei deutlich gefleckten Vertretern der Gattung *Steatoda* im weiten Sinne.

(3) Junges, nicht näher bestimmtes Urspinnen-Männchen der Gattung *Eriauchenius* (Foto 79) in Kopal aus Madagaskar, Körper-Länge 3.3 mm. Der Hinterkörper der Spinne ist der Kugelform angenähert, hoch aufragend, der Vorderkörper ist im vorderen Abschnitt stark konisch erhöht, spitz zulaufend. – Der Vorderkörper der Spinne scheint einem pflanzlichen Dorn zu ähneln. Man denke sich die tatsächliche Position der Spinne vertikal um 180° gedreht, also bauchoben an einem Zweig hängend (die Beinhaltung der lebenden Spinne ist mir nicht bekannt). Dreht man das Bild in diesem Sinne herum, dann ist ein Spinnenkörper nicht ohne weiteres zu identifizieren! Wie bei den Spinnen (1) und (4) möchte ich auch hier eine „Phytomimese" (Nachahmung pflanzlicher Teile) nicht ausschließen, sondern halte diese sogar für wahrscheinlich.

(4) Männliche Urspinne von *Eriauchenius gracilicollis* (Abb. 2; Fotos 81–83) in Kopal aus Madagaskar, Körperlänge 3 mm. Die Beine dieser Spinne sind besonders lang

und dünn; der dreieckig-runde Hinterkörper (rechts im Bild) ist klein, auf einem extrem langen „Hals“ sitzt ein rundlicher „Kopf“, der die Augen trägt, und davor entspringen die grazilen, extrem langen und auseinander weichenden Kiefer (Chelizeren). Von einem Hals und einem Kopf kann man eigentlich nicht sprechen, da die Mundöffnung (Pfeil in Abb. 2) sich unterhalb (!) des „Halses“ befindet. – Dieses Tierchen ist in keiner Position leicht als Spinne zu identifizieren, schon gar nicht, wenn es vertikal um 180° gedreht wird. Der typische Spinnenkörper ist zweiteilig und ihm fehlt ein halsähnlich abgesetzter Teil. Der bizarre Körper dieser Spinne erscheint dagegen dreiteilig, die langen Kiefer und Beine wirken wie Anhänge einer unbekannten Struktur; der Vorderkörper mit den langen Kiefern könnte einem Samen oder einer Frucht ähneln. Möglicherweise handelt es sich hier ebenfalls um „Phytomimese“; vielleicht um die Nachahmung beschädigter oder verrottender Pflanzenteile.

Vergleicht man die vier behandelten Spinnenarten, so fällt eine Gemeinsamkeit auf: Sie besitzen eine für Spinnen ganz untypische Gestalt, wenigstens ein Körperteil ist stark abgewandelt. Der Nicht-Spezialist kann sie nicht so leicht als Spinne identifizieren und selbst so mancher Kenner von Spinnen kommt ins Grübeln. Entsprechend verunsichert könnten Feinde von Spinnen sein, die sich bei ihrer Beutesuche optisch orientieren: Vertreter zahlreicher kleiner Vogelarten erbeuten Spinnen in der Vegetation, wobei sie – wie Experimente gezeigt haben – lernen können, eine Spinne an ihrer typischen Gestalt zu erkennen, und etwa von einer „schlecht schmeckenden“ – Ameisensäure ausscheidenden Ameise – oder mit einem Giftstachel bewehrten Wespe (vgl. Foto 76) zu unterscheiden. Solche Vögel werden sicher nicht nach pflanzlichen Teilen (Abb. 1, 2, Fotos 56, 79 und 81) picken, die für sie ungenießbar sind. Derartige Spinnen, die Ameisen, bestimmten Wespen oder pflanzlichen Strukturen ähneln (diese „nachahmen“), könnten daher vor spinnen-fressenden Vögeln weitgehend oder teilweise geschützt sein. Mimikry dient immer zur Täuschung eines „Signalempfängers“, in diesem Fall wohl eines Vogels. – Ein Auslesevorteil in diesem Sinne dürfte über viele Generationen hinweg die Entwicklung (Evolution) derartig ungewöhnlicher Körperformen und Strukturen verstärkt haben, wie wir sie bei den behandelten fossilen Spinnen vorfinden. Ein typisches Merkmal aller fossilen und heutigen Vertreter der Familie Urspinnen – auch sofern sie nicht im Verdacht existierender Mimikry oder Mimese stehen – ist der vorn erhöhte Teil des Vorderkörpers (*); dieser kann vermutlich als körperliche Voraussetzung (Disposition) für die oben beschriebenen Spinnengestalten (2)–(4) angesehen werden, deren hoch aufragender „Kopfteil“ in ungewöhnlicher – und jeweils unterschiedlicher – Weise „fortentwickelt“ worden ist. – Siehe auch BRISTOWE (1939/1941) und FOELIX (1996: 253–256).

Von heutigen Spinnen sind erstaunliche Beispiele von Tarnung beschrieben worden: Insbesondere manche tropische Spinnen ähneln Blättern, Zweigen, Knospen, Blüten, Früchten, Teilen von Baumrinde – ja sogar Vogelkot! – in verblüffender Weise. Beispiele von Schutzanpassungen – Mimikry (Abb. 2, Foto 76) und Mimese (Abb. 1, Foto 56; vgl. die Arbeiten Nr. 5 (Kreidezeit!) und Nr. 6 in diesem Band) – vor dem Eozän sind bisher für fossile Spinnen noch kaum belegt worden. Der späteste Zeitpunkt der Entstehung von Mimese bei Spinnen kann somit in die Zeit vor etwa 50 Millionen Jahren zurückdatiert werden.

(*) Der hohe Vorderkörper dieser Spinnen gibt Raum für die extrem langen Kiefer, die offenbar im Zusammenhang mit der Erbeutung von Spinnen stehen.

REFERENCES, cited / ZITIERTE SCHRIFTEN

BRISTOWE, W. S. (1939/1941): The comity of spiders. 2 vol., 560 pp, 22 plates.

FOELIX, R. F. (1996): Biology of spiders. 330 pp.

OPELL, P. D. & WARE, A. D. (1987): Changes in Visual Fields Associated With Web Reduction in the Spider Family Uloboridae. -- J. Morphology, 192: 87–100.

WUNDERLICH, J. (2004): Fossil spiders in amber and copal – Fossile Spinnen in Bernstein und Kopal. -- Beitr. Araneol., 3 (A, B): 1-1873. Joerg Wunderlich Verlag/ Publishing House Jörg Wunderlich, 69493 Hirschberg. (Orders direct to the author/ Bestellungen direkt an den Autor und Verlag).