SOIL ORGANISMS **85** (1) · April 2013 pp. 11–22

New Data on thysanurans preserved in Burmese amber (Microcoryphia and Zygentoma Insecta)

Luis F. Mendes[1,*] **and Jörg Wunderlich**[2]

[1] Instituto de Investigação Científica Tropical (IICT), Jardim Botânico Tropical / Zoologia. R. da Junqueira, 14, 1300-343 Lisboa, Portugal
[2] Oberer Häuselbergweg 24, 69493 Hirschberg, Germany
* Corresponding author, e-mail: luis.mendes@iict.pt

Received 22 November 2012 | Accepted 12 April 2013

Abstract

One undeterminable Microcoryphia specimen preserved in burmite, almost certainly belonging to the genus *Macropsontus*, is reported. One new Lepismatidae (Zygentoma), *Cretolepisma kachinicum* gen. n. sp. n., preserved in the same ca. 100 MY old Albian-Cenomanian amber from Myanmar, is described based upon one female. It is compared with the recent genera in the nominate subfamily as well as with *Burmalepisma cretacicum* Mendes & Poinar, 2008, the only other species of Zygentoma known to date from the same deposits. Some paleogeographical and phylogenetic data are discussed and one new combination is proposed.

Keywords New taxon | Fossil | Burmite | Cretaceous | Myanmar

1. Introduction

Fossil apterygotes are usually scarce and those of Protura are unknown. Concerning the 'thysanurans', fossil representatives of Microcoryphia (= Archaeognatha) belong to Monura and to both families with living species: Machilidae and Meinertellidae. Monura (Dasyleptidae species) are known from the Carboniferous to the Triassic (Bitsch & Nel 1999, Bechly & Stockar 2011). The Triassomachilidae were until recently understood to be a valid family (Sturm & Machida 2001) and believed to be the only representatives of Triassomachiloidea (Sturm & Bach 1993) – a superfamily not recognized, however, by Bitsch & Nel (1999) who placed them as true Machiloidea. They were definitely considered by Sinitshenkova (2000) to be a *Mesoneta* mayfly nymph, what was later accepted by Bechly & Stockar (2011). They were indeed previously suggested by other authors as Ephemeroptera nymphs, though without any consistent argument.

One 'Machilidae' plus five undetermined specimens of this 'group' preserved in Myanmar amber (burmite) were reported with no details by Grimaldi et al. (2002) from the Natural History Museum in London (NHM) and from the American Museum of Natural History (AMNH) in New York. We never saw these samples and their family-level identification, although eventually possible, remains unknown. One other non-identified (non-identifiable?), slightly younger fossil in the AMNH collection was detected in the New Jersey amber (Sturm & Machida 2001). Much more recent amber fossils include (Tab. 1) Machilidae from the Baltic (all in need of revision) and Meinertellidae from the New World (Dominican Republic and Mexico). An even younger specimen of Meinertellidae was described from the Venezuelan copal (Mendes 1997a). Only the Dominican *Neomachilellus (Praeneomachilellus) dominicanus* (Sturm & Poinar 1997 – Meinertellidae) seems to be abundant, and it is known from adult and immature specimens.

Fossil representatives of Zygentoma belong to the families Lepidotrichidae, Lepismatidae and Nicoletiidae. The Upper Aptian Brazilian 'Lepismatidae g. sp. from Araripe' (Sturm 1998) is the most ancient known fossil and was described from sandstone deposits; its detailed identification remains impossible due to the condition of

ISSN 1864-6417

the two only known specimens, although the described features suggest representatives of Lepismatinae. Four further somewhat younger Cretaceous lepismatids (no details published, not studied by us) were assigned by Grimaldi et al. (2002) as being deposited in the NHM Burma amber collection. *Burmalepisma cretacicum* (Lepismatidae – Lepismatinae) from the Myanmar amber was also recently described (Mendes & Poinar 2008).

Lepidotrix pilifera (Menge in Koch & Berendt, 1854) (Lepidotrichidae) and *Allacrotelsa dubia* (Koch & Berendt, 1854) (Lepismatidae) from the Eocene Baltic amber (see Silvestri 1912a, Paclt 1967 and Zuccon 2011) were the first fossil species described in the order. Later, some Nicoletiidae (Mendes 1997b, Mendes 1998, Sturm & Mendes 1998, Mendes & Poinar Jr. 2004) plus one Lepismatidae (Mendes 1998), all preserved in Oligocene Dominican amber, were also described.

Onychomachilis fischeri Pierce, 1951, preserved in the Cenozoic Arizona hydrothermal onyx-marble deposits and assigned as a 'machilid', is almost certainly neither a Microcoryphia as described (Pierce 1951) nor a Diplura as later suggested by Kukalová-Peck (1987). In fact, it may concern a Nicoletiidae (Zygentoma) due to the body shape, the lack of scales, the at least apparent

Table 1. Previously known fossil records of Microcoryphia and Zygentoma, their approximate age and type of fossilization. Lepm: Lepismatidae, Lepd: Lepidotrichidae, Mach: Machilidae, Mein: Meinertellidae, Nicl: Nicoletiidae, Tria: Triassomachilidae. Probable ages corrected based on more recent data: Cen: Cenozoic, Cre: Cretaceous, Eoc: Eocene, Mes: Mesozoic, Mio: Miocene, Oli: Oligocene, Tri: Triassic.

Order/family/species	Age (in MY)	Origin	Fossil in:	Author
Microcoryphia(♦)				
Tria: *Triassomachilis uralensis* (◘)	Mes: Tri: 200-235	Russia, S. Urals	?	Sharov 1948
Mein: *Cretaceomachilis libanensis*	Mes: Cre: 120-130	Lebanon	Amber	Sturm & Poinar 1998
1 "Machilid" + 5 non-identified specimens (*)	Mes: Cre: 120-130	Myanmar	Amber	Grimaldi et al. 2002
Mein: Non-identified (*)	Mes: Cre: 95	USA: New Jersey	Amber	Sturm & Machida 2001
Mach: 8 spp. (*)	Cen: Eoc: 38-50	Baltic	Amber	Revised or described by Silvestri 1912a
Mein: *Neomachilellus* sp	Cen: Mio: 22-26	Mexico: Chiapas	Amber	Wygodzinsky 1971
Mein: *Neomachilellus (P.) dominicanus*	Cen: Mio: ca. 25	Dominican	Amber	Sturm & Poinar 1997
Mein: *Meinertellus* sp.	Recent	Venezuela	Copal	Mendes 1997a
Zygentoma(●)				
Lepm: "gen. sp. from Araripe"	Mes: Tri: 110	Brazil –Santana formation	Sand-stone	Sturm 1998
Lepm: *Burmalepisma cretacicum*	Mes: Cre: 100-110	Myanmar	Amber	Mendes & Poinar 2008
Lepm. 4 non-identified specimens (*)	Mes: Cre: 100-110	Myanmar	Amber	Grimaldi et al. 2002
Lepd: *Lepidothrix pilifera*	Cen: Eoc: 38-50	Baltic	Amber	Revised by Silvestri 1912
Lepm: *Allacrotelsa dubia*	Cen: Eoc: 38-50	Baltic	Amber	Revised by Silvestri 1912
Nicl (?): *Onychomachilis fischeri* (*)	Cen: Oli (?)	USA: Arizona	Onyx-marble	Pierce 1951
Lepm: *Ctenolepisma electrans*	Cen: Oli: 25-34	Dominican	Amber	Mendes 1998
Nicl: *Archeatelura sturmi*	Cen: Oli: 25-34	Dominican	Amber	Mendes 1997b
Nicl: *Trinemurodes antiquus*	Cen: Oli: 25-34	Dominican	Amber	Sturm & Mendes 1998
Nicl: *Trinemurodes miocenicus*	Cen: Oli: 25-34	Dominican	Amber	Sturm & Mendes 1998
Nicl: *Hemitrinemura exstincta*	Cen: Oli: 15-45	Dominican	Amber	Mendes & Poinar 2004

(♦) Monura (= Dasyleptidae), all fossil, known from the Permian to Triassic, not listed (see Bechly & Stockar 2011). (*) Samples in need of revision. (◘) Confirmed as a larval mayfly (Sinitshenkova 2000), accepted by Bechly &Stockar (2011). (●) For the fossil *Carbotriplura*, *Ramsdelepidion* and other dubious forms, see discussion in Bitsch & Nel (1999).

anophthalmy and the clear ectotrophy (a conspicuously articled maxillary palp was represented) among other features, but we never studied this material. *Onycholepisma arizonae* Pierce, 1951, from the same deposits, is too poorly described (or preserved) to allow its credible inclusion even in the Zygentoma.

The taxonomic position of the 'gigantic' *Ramsdelepidion schusteri* from the Illinois (USA) Carboniferous (Kukalová-Peck 1987) remains uncertain, as noted by Bitsch & Nel (1999) and Sturm & Machida (2001), although it hardly must be considered to be part of the 'thysanurans'. The same must be stated about the '*Dasytleptus'* described by Kukalová-Peck (1987), as was recently commented on by Bechly & Stockar (2011).

In the present paper, two fossil specimens preserved in the Myanmar burmite will be studied. This amber, formerly dated as being from the late Cenozoic (v. g. Poinar Jr. 1993, Arillo 1996 – ca. 40 MY old), was recently recognized as being Cretaceous (Grimaldi et al. 2002, Cruickshank & Ko 2003), dating from the Upper Albian to Lower Cenomanian (palynomorph analysis indicates in being ca. 100 MY old). The studied samples concern one eventually immature (and/or female) bristletail almost certainly of the genus *Macropsontus* Silvestri, 1912 (Meinertellidae: Microcoryphia) and one female Lepismatidae, which will be described as a new genus and species. Their descriptions are presented here, taking into account the difficulties inherent to the study of amber-preserved material. The precise location of the original amber mine is not known, but Myanmar's burmite mines are located in the Kachin State, close to the Hukawng valley in the northern country, not far from the eastern border of the Arunachal Pradesh and Nagaland Indian states (map of the area in Grimaldi et al. 2002). The amber is noted (Cruickshank & Ko 2003) as eventually originating from Araucariaceae (genus *Agathis*) or Taxodiaceae.

2. Material and methods

The studied samples (Figs 1–3) were reshaped and polished by the second co-author, allowing their more detailed study. The piece including the bristletail (F2280/BU/CJW) is irregularly ovoid, 30 mm × 18 mm × 12 mm, and weighs 4.1 g. Besides the studied specimen, it includes a few acarids (Acarina), one collembolan, a head and thorax of a cockroach (Dictyoptera, Blattaria), one gnat (Diptera, Nematocera), plus some insect fragments and (plant?) debris, which partially hinders the study of some taxonomically important structures. The specimen is distorted into itself, so the presented dimensions may be subject to a certain error and some morphological details remain impossible to analyse.

The piece with the silverfish (F2329/BU/CJW) is half-elliptical, with its upper surface somewhat convex. It is 29 mm × 26 mm × 6.5 mm and weighs 2.73 g. Minute granular undeterminable particles are densely included, which together with a few plant debris, minute fissures and air bubbles prevent a clear observation of some body parts, mainly on its dorsal area – the ventral surface is closer to the amber surface.

Figure 1. Studied samples. Left: sample F2280/BU/CJW, including the specimen of (?) *Macropsontus* sp. (Meinertellidae: Microcoryphia); right: sample F2329/BU/CJW, including the *Cretalepisma kachinicum* gen. n. sp. n. holotype (Zygentoma: Lepismatidae). Photo: A. Bivar-de-Sousa.

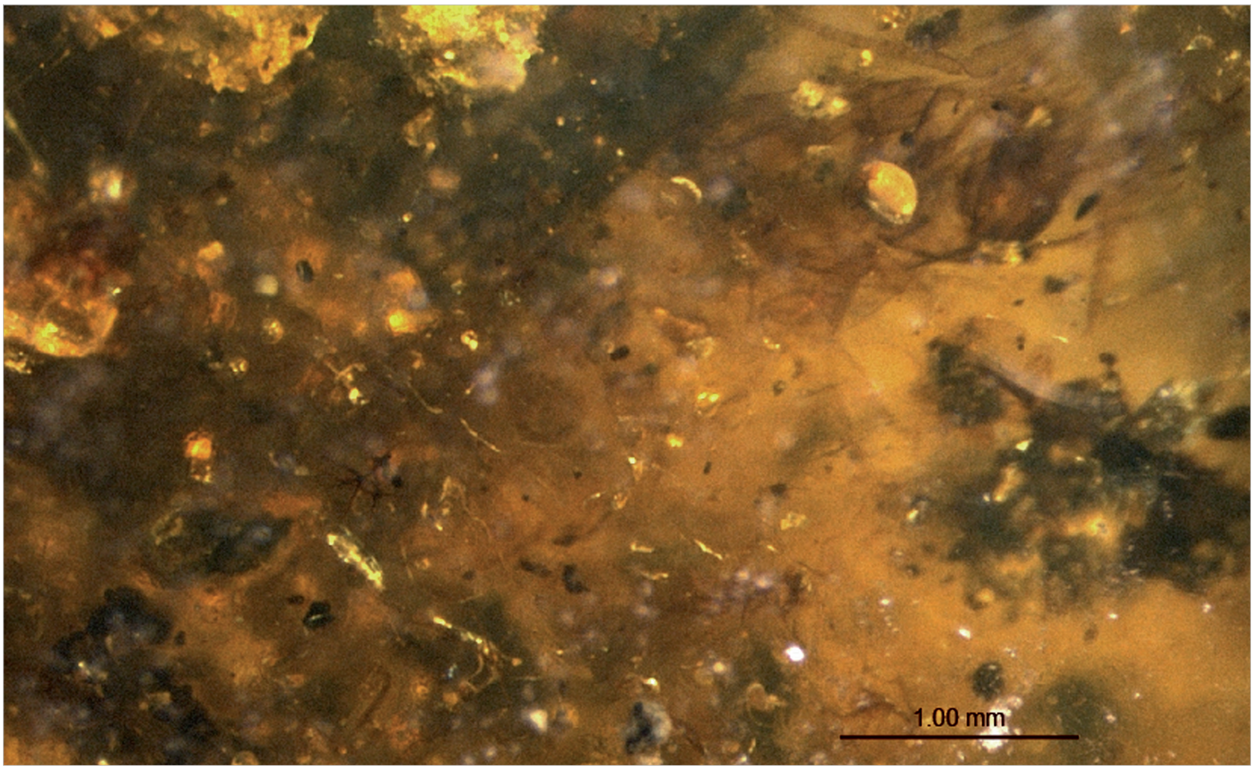


Figure 2. (?) *Macropsontus* sp. (Meinertellidae: Microcoryphia) specimen of sample F2280/BU/CJW; head in the upper right side; antenna separated from the body and above it, oriented from right to left. Photo: F. Rosa and A. Bivar-de-Sousa.

Both samples belong to the co-author's collection, now in the Laboratory of Arachnology of the second co-author, in Hirschberg, Germany. They will probably be deposited in the Senckenberg Museum and Research Institute, Frankfurt-am-Main, also in Germany (CJW – collection of J. Wunderlich).

The stereoscopic microscopes Wild M5A and Leica M165C, plus a light microscope Leitz SM-Lux were used, always combining illumination from above (optical tubes of a Hund-Wetzlar apparatus) and from below. For the figures, a camera lucida was used in association with the light microscope. The photos were taken with a Canon EOS-450D supported by a Macintosh iMac 27-inchLED16:9 widescreen computer and with a camera connected with the stereoscopic microscope Leica M165C associated with LAS-2008 software.

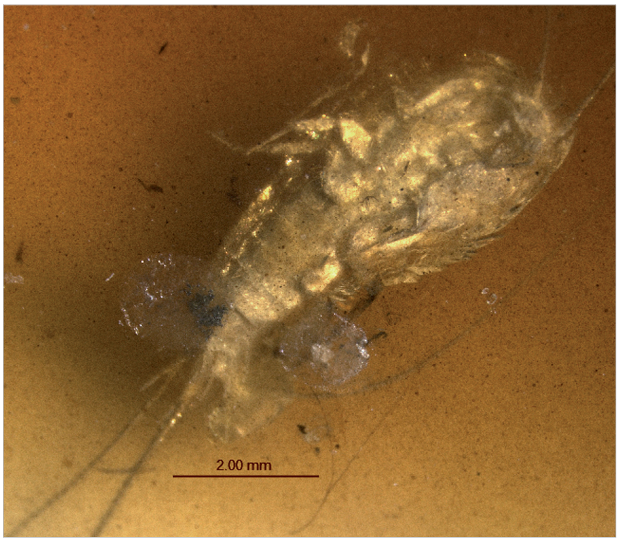


Figure 3. *Cretalepisma kachinicum* gen. n. sp. n., holotype, sample F2329/BU/CJW. Body general aspect (ventral). Photo: F. Rosa.

3. Results

3.1. Species descriptions

Order **Microcoryphia**

Gen. cf. *Macropsontus* Silvestri, 1911 (Figs 1, 2, 4–6)

Material examined. 1 (immature? female?) specimen in Myanmar amber, F2280/BU/CJW.

Description. Body length: 4.2 mm; antenna length: 4.1 mm, certainly longer, as several loose fragments of a flagellum are preserved close to the specimen; cerci length: 2.6 mm; total body length (body + paracercum): 8.3 mm; preserved scales dark, typical, present on the body only (lacking on all appendages).

Head damaged; compound eyes and ocelli impossible to see in detail. Preserved part of the antennae slightly shorter than the body (but in reality much longer than the body since the loose flagellum fragments almost certainly belong to the same specimen); scapus, pedicellus and flagellum completely devoid of scales, the scapus with several robust setae (Fig. 4). Mandibles typical, with four small apical teeth. Maxillary palp well developed, covered by thin small setae, its distal article conical, elongate and shorter than the preceding article; the second article cylindrical, devoid of apophysis and lacking modified chaetotaxy; the presence of a palp basal process not discernible (Fig. 5). Labium not observable; both labial palps lost.

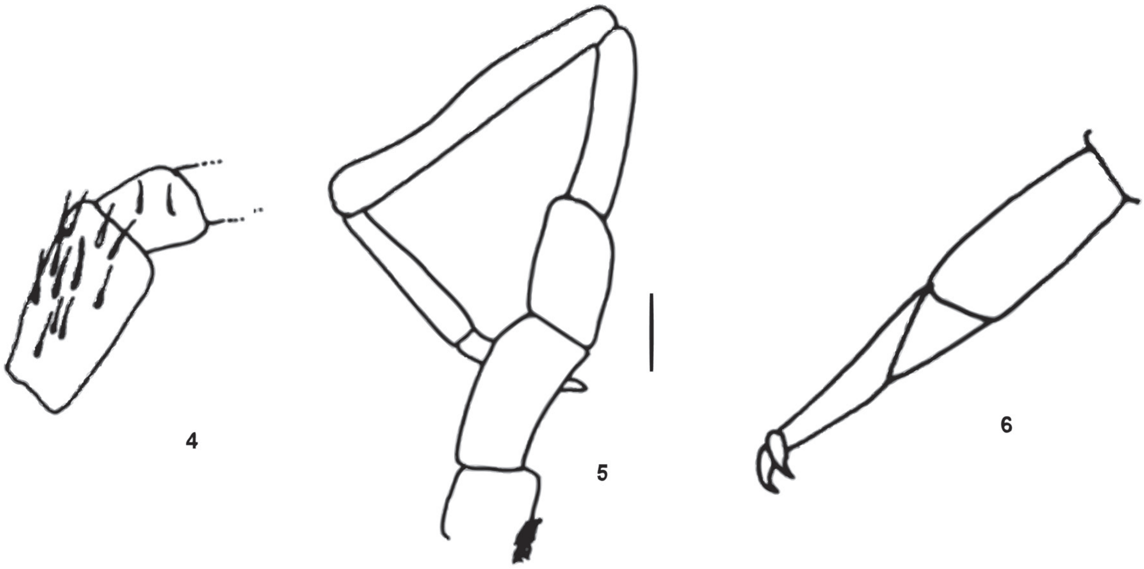
Thorax not very humped, the nota not particularly developed. All legs devoid of coxal stylets and without ventral spines. Tarsi simple, lacking scopula, clearly with only two articles (Fig. 6).

The abdominal coxites as well as the corresponding sternite development not observable; the abdominal vesicles and stylets as well as the genitalia not preserved. Cerci and paracercum almost non-divergent, scaly, delicate and with a few very strong setae.

Discussion. Extant Microcoryphia were indicated by Sturm & Bach (1993) and Sturm & Machida (2001) to integrate Machilidae and Meinertellidae plus a few *incerta sedis* genera, none of which are known to date as fossils, whose interrelationships with the two known families is generally not accepted. Koch (2003) considers that they must be regarded as true Machilidae, what could be true. They seem indeed to be clearly more related to the Machilidae (developed urosternites, male maxillary palp second article without apophysis, no basal process in this palp, paramera present), also under a geographical point of view, as they are all restricted to the Northern Hemisphere: *Mesomachilis* in North America and *Charimachlis* in the northern Mediterranean basin (the description of a closely related new genus and species from Turkey is in preparation by the Spanish team). *Ditrigoniophthalmus* Kaplin, 1979 was also considered to belong to this group but the recent data verifies its unique position in the family, as the only known representative of the Ditrigoniophthalminae.

The accurate description of the reported Myanmar fossil species remains impossible because of the bad condition of the single specimen and due to the air bubbles and opaque debris present in the amber piece. Taking into consideration its measured body length (4.2 mm), there is a certain chance of the specimen being immature, though the *Cretaceomachilis libanensis* Sturm & Poinar, 1998 holotype only measures 4.5 mm. Despite the loss genitalia, the non-modified maxillary palp suggests it to be a female.

Sturm & Machida (2001) point out that the completely non-scaled antennae (scapus, pedicellus and flagellum) is exclusively known, apart from Meinertellidae, only in the Machilidae (Petrobiellinae) (genus *Petrobiellus*, known in the Japanese Honshu island and in the Kuril Simushir island), leaving the problem of *Ditrigoniophthalmus* suspended. In his first attempt of a Microcoryphia phylogeny, Kaplin (1985) considered, indeed, its (then) only species, *D. oreophilus*, to be part of the Petrobiellinae. However, the Ditriginiophthalminae were later recognized by himself (Kaplin 2000, today a few species from the Asian part of Russia: Outer Manchuria to the Altai) to lack also scales all along the antennae,



Figures 4–6. (?) *Macropsontus* sp. (**4**) Antennal scapus and pedicellus, (**5**) Maxillary palp, (**6**) Median leg, tibia and tarsus. Scale bar = 0.1 mm.

although they are well isolated inside the order due to the abdominal stylets on urosternites I–IX. Indeed, the real presence of stylets on urosternite I was rejected by Sturm & Machida (2001) among others, who consider that the genus should be regarded as *incerta sedis*. All those known Machilidae genera have, however, coxal stylets at least on the posterior legs (i.e., on P II and P III or at least on P III) and in all the known cases their tarsi are, as usual in the order, typically trimerous.

Indeed, only three Microcoryphia genera are known with dimerous tarsi and all of them are extant Meinertellidae (Sturm & Machida 2001: 33): *Hypermeinertellus* Paclt, 1969 from Melanesia has a conspicuous tarsal scopula, which – among further dissimilarities – allows its immediate distinction relative to the Myanmar specimen. It must be noted that, in this proposal of a phylogenetic tree for the genera, characters 14 and 17 are mistaken in the fifth and sixth 'branches': as character 17 – dimerous tarsi – is considered to be typical of *Nesomeinertellus* and character 14 – a special type of gonapophyses – as characteristic for *Hypermeinertellus*, whereby the opposite is actually true: they must be reversed. *Machilontus* and *Macropsontus*, both Oriental, are part of the same genus-group and are mutually distinguished by their coxal stylets. These stylets are completely lacking in the second genus, as is true in the amber specimen. The knowledge of the adult male, the precise morphology and development of the compound eyes, of the ocelli and of the labial palp distal article in the fossil specimen should help to confirm its generic position in this group, but they are not well preserved (eyes) or are lost (palps) as mentioned above. The known ranges of these two genera and of each of their described species, discussed below in the section Paleogeographical and Phylogenetic Notes, however, strongly reinforce the integration of the present specimen in *Macropsontus*.

Order **Zygentoma**

Family **Lepismatidae**

***Cretalepisma* gen. n.**

Diagnosis. The genus can be identified by the following combination of characters: medium-large specimens; thorax wider than the abdomen, tapering to its distal area; macrochaetae smooth, the cephalic ones lacking on the clypeus and labrum; distal article of labial palp elongated and club-shaped; anterior setal collar of the pronotum absent; more than 1+1 setal combs on the metasternum; pretarsus simple and complete; urotergite X not triangular; urosternites without median setal combs; three pairs of stylets.

Description. Female: Thorax wider than long, ca. half of the abdomenal length and clearly detached from its base. Macrochaetae smooth, pointed or slightly bifid apically. Scales round, with numerous thin longitudinal rays not surpassing their free border.

Head wider than long, with dense frontal macrochaetae, which are completely missing on the clypeus and labrum. Compound eyes as usual, with few large ommatidia. Antennae long, without special features, the morphology of the specialized sensilla impossible to observe. Visible part of the mandibles and maxillae as usual, the labium typically shaped: maxillary palp without special features, 5-articled; specialized bifid sensilla existence on the distal article apex not visible. Distal article of the labial palp ovoid, much longer than wide, the number and arrangement of papillae not perceivable.

Posterior border of the nota progressively more concave, the pronotum devoid of an anterior setal collar. Dorsal posterior macrochaetae, dorsal-lateral setation and trichobothrial areas impossible to see in detail, but no notal combs present (neither lateral, nor posterior). Thoracic sternites semi-elliptical and, as usual, covering the base of the coxae. Prosternum smaller than the remaining sterna, though not reduced, the metasternum with more than 1+1 apical combs. Legs without special features, the praetarsus simple and complete; empodium claw-like and short; no pulvilli present.

Urotergal setation not observable, the urotergite X shorter than wide and not triangular (trapezoidal?), its posterior border straight or slightly depressed. Urosternites I–II without setae, III–VI (VII?) with 1+1 lateral combs. Three pairs of stylets (VII-IX) are present, those of IX longer and more robust than the remaining ones. Ovipositor without special features, only with thin short setae. Paracercus and cerci, thin, long, hairy and clearly divergent.

Male unknown.

Etymology. From the Latin *Creta* (chalk), in the root of the name of the Cretaceous Period, alluding to the amber age, and *Lepisma*, the nominate genus of the family; gender neuter.

Type-species. C. *kachinicum* sp. n.; monotypical genus.

Discussion. *Cretalepisma* gen. n. agrees with the likewise Burmese amber *Burmalepisma* (Mendes & Poinar 2008) concerning the type of macrochaetae (smooth, larger ones apically bifid) and the absence of a pronotal setal collar, which strongly indicates its inclusion in the nominate subfamily, the Lepismatinae (Mendes 1991). Besides, both genera lack median combs on the urosternites. Despite the lack of details of some features in these two genera, it may be stated that 1) their body shape is quite distinct, as in *Cretalepisma* the thorax is much wider and clearly detached from the abdomen base, which tapers visibly to the distal area, while in *Burmalepisma* it is more or less parallel-sided. 2) The distal labial palp article is elongate and club-shaped in the new genus, although it is much shorter and rounder in *Burmalepisma*. 3) There are three conspicuous pairs of abdominal stylets, on urosternite VII and on coxites VIII–IX, the last ones being much longer and more robust than the preceding, versus one pair only in *Burmalepisma*. 4) The only studied *Cretalepisma* specimen is clearly larger than the two known *Burmalepisma,* attaining almost twice their body length. 5) The preserved part of the antennae is much longer in the new genus, each one of the distal subarticles being thinner and longer, mainly the second and the fourth unities of each article.

Relative to the extant genera, *Cretalepisma* gen. n. approaches those of the nominate subfamily, and, among them, those of the *Lepisma* s. l. complex (see Mendes 1988 for the generic revision) all have 1 or 2 pairs of abdominal stylets and all with submedian setal comb on at least some urosternites. Excluding the type of antennal specialized sensilla, unknown in *Cretalepisma* gen. n., and despite the difficulties concerning the detailed observation of the dorsal surface of the only known specimen, it differs from *Lepitrochisma* Mendes, 1988 by the simple praetarsus, without pulvilli, as well as by several chaetotaxic features, and from *Lepisma* Linnaeus, 1758, *Afrolepisma* Mendes, 1981, *Neoasterolepisma* Mendes, 1988, *Tricholepisma* Paclt, 1967 and *Xenolepisma* Mendes, 1981, all with 1+1 combs only on the metasternum as well as by the absence of median urosternal comb. The same must be considered concerning *Allacrotelsa* Silvestri, 1935. *Anallacrotelsa* Mendes, 1996, more recently described, is like the new genus devoid of urosternal submedian combs, but presents (as *Allacrotelsa*) a triangular, posteriorly acute urotergite X. *Heterolepisma* Escherich, 1905, the only known representative of the subfamily Heterolepismatinae (*Anisolepisma* Paclt, 1967 is now under revision and belongs to a quite distinct group – G. Smith pers. com.) presents a distinct body shape and an anterior pronotal collar of macrochaetae, among several other dissimilarities.

***Cretalepisma kachinicum* sp. n.** (Figs 1, 3, 7–13)

Holotype and only known material. Myanmar amber, 1 female, F2329/BU/CJW.

Diagnosis. See the diagnosis of the genus.

Description. Female: Body length: 6.9 mm; antennae length (damaged): 5.5 mm, cerci length: 4.1 mm (preserved portion); total body length (body + paracercum): 9.7 mm (terminal filament apically damaged).

Body as in the genus description and in Figs 1 and 3. Dorsal scales light brownish (golden?), the ventral ones silvery grayish. Antennae long and thin; scapus more or less cylindrical, ca. three times longer than wide, the pedicellus as long as wide (Fig. 7); flagellum thin, the distal articles composed of 4 unities, the basal and third one more or less as long as wide, the second and fourth ca. twice longer than wide, their detailed chaetotaxy impossible to see and thus the specialized sensilla, if present, of unknown type (Fig. 8); at least on the second and fourth unities there is a crown of subdistal thin cilia, longer than the correspondent unity. The maxillary palp delicate and long, covered with thin short setae, the two apical articles more or less equally elongated, the apical one ca. 12 times longer than wider (Fig. 9). Labial palp apical article elongated, club-shaped and much longer than wider, the papillae type and arrangement not discernible (Fig. 10).

Nota almost completely impossible to see clearly, but neither lateral nor posterior setation exists; they are progressively more concave at their posterior border and the pronotum lacks a anterior setal collar. Notal trichobothrial areas not discernible. Pro-, meso- and metasternum partially covering each other, the last one posteriorly truncate and with 2 or 3 pairs of setal combs, the distal pair widely separated, the combs' distance at least three times their width. Legs as in the genus description; median claw unguiform, quite short and delicate. Tibia of P I (foreleg) ca. 1/5 shorter than that of P II (median leg); tibia of P III (posterior leg) longer and thinner, ca. 1/3 longer than that of P I (Figs 11–13).

Urotergites impossible to see in detail, but X short and wide, apparently trapezoidal – not distinctly visible, though definitely not triangular. Urosternites as in the generic description, the setal combs with only 3-5 setae. No abdominal vesicles, the stylets on the VII-IX, without special characteristics, the last one clearly longer and stronger than the remaining. Ovipositor robust, with thin short setae, not attaining the stylets IX posterior limit, although surpassing the level of coxites IX inner process.

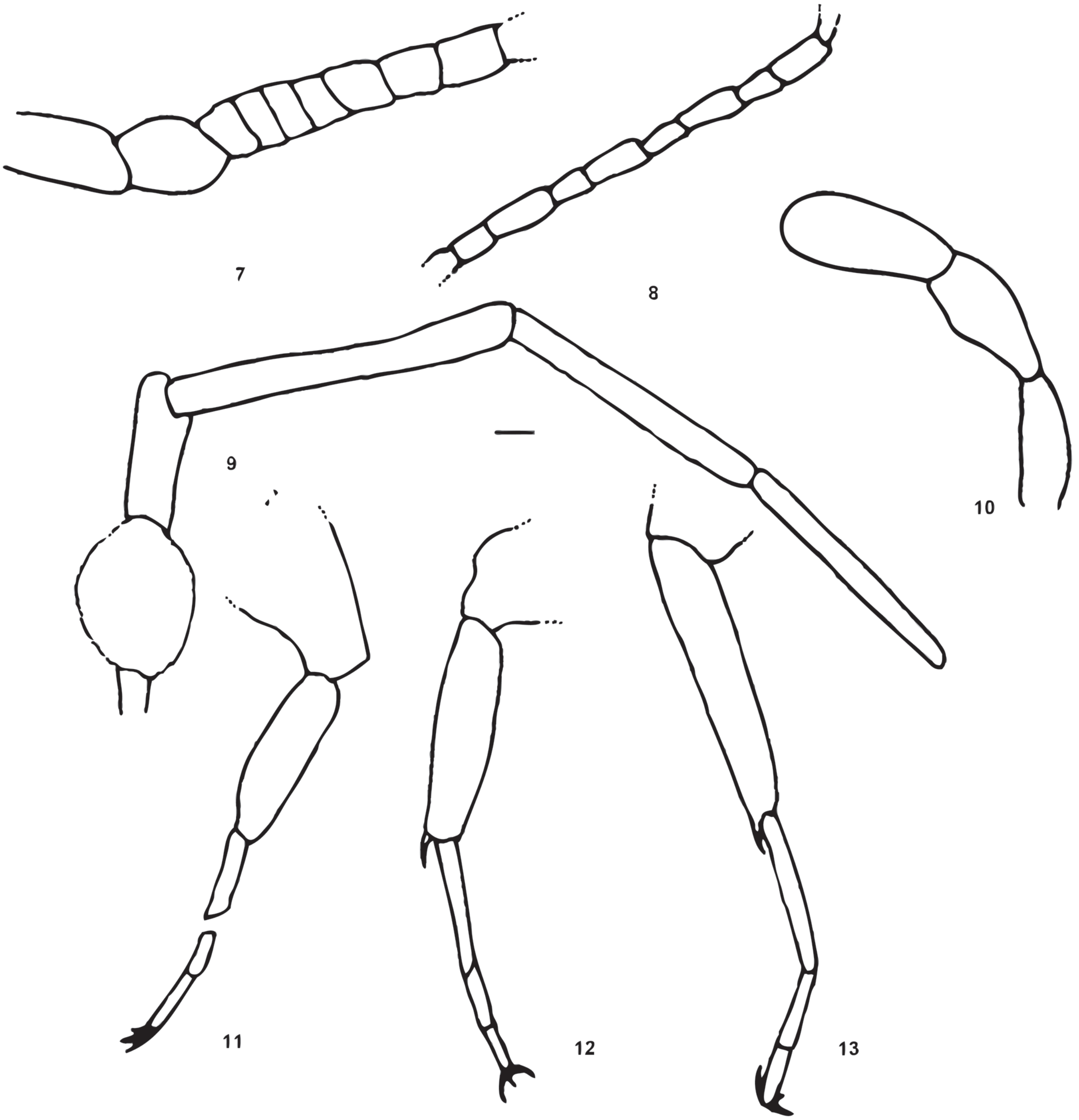
Etymology. From Kachin, the Myanmar north-westernmost State, in regard to the 'burmite' mines geographical occurrence.

4. Discussion

4.1. Extant fauna of Myanmar

The recent Microcoryphia fauna of Myanmar remains poorly studied and only three recognisable species have been described (Silvestri 1912b): *Machilis gravis*, *Megalopsobius convergens* and *Machilontus gravely*. They were all collected near Myawadi, in the south-eastern former Amherst District, now Kyaikkami, close to the Thai border (ca. 16º42'N, 98º30'E). The two last species are typical Meinertellidae, now considered to be con-generics as *Machilontus (Megalopsobius) convergens* and *Machilontus* (*M.*) *gravely*. This at least apparently orophylous genus is known today by species from India (Meghalaya), Nepal and Tibet, south-eastwards to the Indonesian Wallacia (Flores Island) (see map in Song et al. 2011). Undetermined species (females and juveniles) were furthermore reported from northern Thailand (Mendes 1981), India (Assam) and western Malaysia (Bach 1981), while data (in press) show it also occurs in northern Vietnam. Material from the Sulawesi (Bach 1981, as Indonesia: Celebes: N slope of Klabat) doubtfully concerns Meinertellidae as was then discussed.

Machilis gravis, known only by its 14 mm holotype female, is with no doubt a representative of the Machilidae (large, triangular urosternites were described



Figures 7–13. *Cretalepisma kachinicum* gen. n. sp. n., holotype. (**7**) Scapus and pedicellus of antenna, (**8**) Two most distal preserved chains of flagellum, (**9**) Maxillary palp – 2nd to 5th articles, the second one with a superposed air bubble, (**10**) Labial palp, (**11**) P I (anterior leg), (**12**) P II (median leg), (**13**) P III (hind leg). Scale bar = 0.1 mm.

and figured). Its type was deposited in Portici (Viggiani 1973), which we could not verify, but it is certainly not a *Machilis*, a genus restricted to the Western Palearctic, whose easternmost known species was described from Cappadocia. The shoe-shaped paired ocelli, simple tarsi (no scopula), 2+2 abdominal vesicles on the segments II–V (with wide sternites) and the unscaled antennal flagellum (scales are reported exclusively to 'articulus 1–2'), allow the conclusion that it is a taxon of the Petrobiinae and, taking into account the number of paired coxal vesicles, certainly belongs to *Pedetontus (Verhoeffilis)* Paclt, 1972. Otherwise, its description under *Machilis* allows to state (not originally explicit in either the text or the figures) that coxal stylets exist on the median (P II) and posterior legs (P III). The species thus corresponds to a southern recent extension of a typically Laurasian amphi-Pacific subgenus (scarcely extending nowadays to tropical Asia) and must be named *Pedetontus (Verhoeffilis) gravis* (Silvestri, 1912) n. comb. Described Asian species of the subgenus are exclusively known from Eastern Russia, China, Taiwan, Vietnam and Japan. Non-identifiable females reveal its presence also in Luzon, Philippines. Furthermore, non-mature specimens collected in Macau, on the border between Palaearctic and Oriental regions, during 1989, then a territory under Portuguese administration, confirm the occurrence of *Pedetontus (Verhoeffilis)* in the Chinese province of Guangdong.

Extant Zygentoma known from Burma (Myanmar) are even rarer and remain known by *Ctenolepisma burmanica* (Ctenolepismatinae), possibly endemic, described from Palon (17º41'N, 97º31'E – Parona 1892, Escherich 1905), and by the pan-tropical *Acrotelsa collaris* (Acrotelsatinae) collected near Rangoon (Paclt 1966). Both belong to two more specialized subfamilies, while the two known fossil Lepismatidae both integrate the subfamily Lepismatinae. Parona (1892) reports, further, three undetermined '*Machilis*' also collected in Palon and one '*Lepisma*' from Toungoo (18º57'N, 96º26'E), all nowadays impossible to identify, but certainly not part of those genera. The only reference of *C. burmanica* outside of Burma is that of Wygodzinskky (1952: Pernambuco, Eastern Brazil), who recognised its possible inaccuracy.

4.2. Phylogenetic and paleogeographical notes

Microcoryphia and Zygentoma reported from the Cretaceous burmite raise problems on taxonomical grounds, though these problems will become even more interesting if it is possible to fit them into the Myanmar complex paleogeography.

Despite the immense lack of knowledge on the Burmese bristletails, as it happens with most of the southern Asian Microcoryphia fauna, *Pedetontus gravis* n. comb. is, for now and as noted above, the only Machilidae known from the country. It almost certainly corresponds to a northern colonizer, according to that genus' amphi-Atlantic recent distribution, whose highest diversity is known in eastern Palearctic Asia.

Indeed, Machilidae, probably the most primitive family, and Meinertellidae present distinct geographical patterns, the first being today predominantly distributed along the northern hemisphere, while the second occurs mostly along the southern hemisphere (e.g. Wygodzinsky 1967, Sturm 1984, Mendes 1990, Sturm & Machida 2001). Sturm & Poinar (1998) and Sturm & Machida (2001) maintain that the split of the two families should have occurred '...in the northern hemisphere, perhaps at the beginning of Mesozoic…', although in total absence of paleontological proof. The oldest named fossil Microcoryphia was described from the Lebanese Lower Cretaceous (120–130 MY) and, like the studied Myanmar bristletail, is a representative of the Meinertellidae. The male of *Cretaceomachilis libanensis* (Sturm & Poinar, 1998) is better preserved, despite its urosternites dilapidation. It was reported as being strictly related to *Machiloides* Silvestri, 1905 and was considered to be the most primitive recent genus in the family, as both share a non-protruding frons, not very enlarged compound eyes, shoe-shaped paired ocelli, coxal stylets on the median and hind legs as well as no tarsal scopula. In the male, the hook-shaped dorsal apical apophysis of the maxillary palp second article lacks specialized setation and the labial palp is not modified. The non-reduced excertile vesicles, penis with unspecialized setation and ovipositor of the tertiary type, which remain unknown in *Cretaceomachilis* whose male is the only known sex, are also recognized as being typical of this group of genera – see also Sturm & Machida (2001, Fig. 4.5), although *Allomachilis* Silvestri, 1906 and *Kuschelochilis* Wygodzinsky, 1951 were recently synonymised (Mendes et al. 2009). Very close to *Machiloides*, *Cretaceomachilis libanensis* was characterized by '…a small, oval sensory (?) field with fine characteristic parallel stripes…' at the base of the second maxillary palp distal dorsal hook, a feature we wonder if is sufficient by itself to separate this 120-135 MY old species from those today considered under *Machiloides*. Indeed, several male Meinertellidae have thick groups of spines that, when lost, leave their contiguous insertions as an irregular area of the integument.

Regarding the studied Myanmar specimen and the known recent ranges of the only three genera with dimerous tarsi, *Hypermeinertellus* Paclt, 1969, known from New Britain / Melanesian off eastern New Guinea

– see note above – is the only one with scopulated tarsi, which justifies its integration in a distinct evolutionary line. Indeed, it is the only genus with a reduced number of tarsal articles, which seems linked to the Australian Region. Sturm & Machida (2001) consider it to belong to the *Meinertellus*-group, whose known genera are all provided with tarsal scopula.

Machilontus and *Macropsontus* show a clear Oriental range, although the first slightly enters the Australian Region (one species in the Flores Island). If Sturm & Machida (2001) are correct, then these two genera plus the trimerous tarsi *Machilellus* Silvestri, 1911 are exclusively south-eastern Asian. They were considered to be phylogenetically related to the mainly Mexican *Hypermeinertellus*-group, one more reason to accept the northern origin of the group.

The genus *Machilelloides* (Sturm & Smith 1993), assigned (Sturm & Machida 2001) as part of the same evolutionary line as *Machilontus* and *Macropsontus*, monotypical from Western Australia and devoid of coxal stylets, is very well separable from the previous taxa mainly by the lack of vesicles on urosternite I, modified male labial palp, and male and female genitalias indicating an older and eventually independent evolutionary line.

Regarding Zygentoma, none of the Lepismatidae genera with smooth macrochaetae is known exclusively from the Oriental or the Australian region. Indeed, *Heterolepisma* (Heterolepismatinae), with a pronotal anterior setal collar, is known along most of the tropical areas, and among the Lepismatinae genera, *Afrolepisma* extend to these two regions, with one species in Polynesia and one other in India (Orissa), while representatives of *Tricholepisma* and *Xenolepisma* known from the Oriental (no Australian similar taxon) were described respectively from West Bengal (Calcutta) and Kerala (Coimbatore) – see above for the generic comparison with *Cretalepisma* gen. n.. The highest diversity of the recent genera initially considered under *Lepisma* Lin., 1758 is known, however, from mainland Africa and the Mediterranean basin (Mendes 1988).

If we accept the proposal of Sturm & Machida (2001) for Meinertellidae phylogeny as a whole (some considered apomorphies concern, however, losses, not acquisitions, and they were partially faced as parallelisms), the analysis of one further point should be particularly interesting: the displacements and connections among the southern Asian tectonic plates and microplates from the Mesozoic. Indeed, these plates' relative positions along time were (and still are) discussed, and we believe that they may shed some light on the understanding of the known ranges of extant and fossil bristletails and silverfishes known from Myanmar, because Microcoryphia and Zygentoma are not flying insects and their dispersal capacity is per se reduced.

Cruickshank & Ko (2003) mentioned the geology and tectonics of the Hukawng valley area, and Pramumijoyo et al. (2010), suggest that the Burma Plate (associated with the Sunda plate and the Hukawng block) collided with the Eurasian Plate during the early Cretaceous, while the Indian Plate started to move north-westwardly and, after its voyage towards the northeast and corresponding rotation, collided with the southern Eurasian Plate much later, during the Eocene, i. e. ca. 100 MY later – both plates abut, indeed, along Myanmar. The fossiliferous deposits' biotope was reported as probably being a near-shore marine setting (bay, lagoon or estuary), but the adjacent land mass was assigned as either the Asian mainland or an island, and the climate was humid warm temperate.

Both studied fossils, when alive, were certainly part of the local fauna of the Hukawng Block. *Macropsontus*, known by species in Sri-Lanka, Sulawesi and Java, has its known range today clearly more restricted than that of *Machilontus* (Nepal and China south-eastwardly to Flores, though not in India). None of them shows any close relation to Australia – the same must be stated for *Machilellus* known from Vietnam and Java with three-articled tarsi. Their ranges indicate genera that reached the Oriental region from north, having never entered India but having extended south-eastwardly, reaching Australasia. They suggest further that the studied burmite fossil (almost certainly a *Machilontus*) was present in the Hukawng area already before the Indian plate collided with the southern Eurasian plate, but after the Hukawng block was in situ. *Cretamachilis kashinicum* gen. n. sp. n. is part of one of the eventually most primitive subfamily of Lepismatidae, whose recent distribution indicates an eventual Laurasian origin. As registered, no genus of Lepismatinae is known from the Nearctic, and the data reported from India and Polynesia are quite far from the areas where its genera diversity is higher.

5. Acknowledgements

We are deeply obliged to Prof. António Ribeiro, a retired although active geologist in the Museu Nacional de História Natural in Lisbon, Portugal, for the quite interesting discussions on the paleogeography of the recent Myanmar area, from the Gondwana breakup to the end of Cretaceous. We also thank the colleagues and friends Louis Deharveng from the Paris Natural History for the offered Luzon bristletails, Yuri Binev from the IICT for the translations of Kaplin's papers from the Russian, as well as Fernanda Rosa also from the IIC and A. Bivar de Sousa from the Sociedade Portuguesa de Entomologia, for their photographic assistance. We also wish to present our best thanks to the referees as their suggestions certainly contributed to increasing the quality of this contribution.

6. References

Arillo, A. (1996): Los insectos en ámbar. – Boletín de la Sociedad Entomológica Aragonesa **16:** 147–149.

Bach de Roca, C. (1981): Studies on a collection of Microcoryphia (Apterygota) from the World present in the British Museum (Natural History). – Oriental Insects **15** (3): 295–311.

Bechly, G. & R. Stockar (2011): The first Mesozoic record of the extinct apterygote insect genus *Dayleptus* (Insecta: Archaeognatha: Monura: Dasyleptidae) from the Triassic of Monte San Giorgio (Switzerland). – Palaeodiversity **4**: 23–37.

Bitsch, J. & A. Nel (1999): Morphology and classification of the extinct Archaeognatha and related taxa (Hexapoda). – Annales de la Société entomologique de France (N. S.) **35** (1): 17–29.

Cruickshank, R. D. & K. Ko (2003): Geology of an amber locality in the Hukawng valley, northern Myanmar. – Journal of Asian Earth Sciences **21**: 441–455.

Escherich, K. (1905): Das System der Lepismatiden. – Zoologica, Stuttgart **43** (18): 1–164.

Grimaldi, D. A., M. Engel & P. C. Nascimbene (2002): Fossiliferous Cretacean amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. – American Museum Novitates **3361**: 1–72.

Kaplin, V. G. (1985): On the classification and phylogeny of the fam. Machilidae (Thysanura, Microcoryphia). – Revue d'Entomologie de l'URSS **64** (2): 336–350 (in Russian).

Kaplin, V. G. (2000): The fauna of bristletails of the family Machilidae (Thysanura) from Altai. – Zoologicheskii Zhurnal **79** (9): 1053–1060 (in Russian).

Koch, M. (2003): Character evolution in the Archaeognatha: consensus and conflict. – In: Klass, K.-D. (ed.): Proceedings of the 1st Dresden Meeting on Insect Phylogeny: 'Phylogenetic Relationships within the Insect Orders' (Dresden, September 19–21, 2003). – Entomologische Abhandlungen **61** (2) 119–172.

Kukalová-Peck, J. (1987): New Carboniferous Diplura, Monura and Thysanura, the hexapod ground plan and the role of thoracic side lobes in the origin of wings (Insecta). – Canadian Journal of Zoology **65**: 2327–2345.

Mendes L. F. (1981): Note sur quelques Microcoryphia de l'Asie orientale. Notes et descriptions (Insecta: Apterygota). – Nouvelle Revue d'Entomologie **11** (1): 15–28.

Mendes, L. F. (1988): Revisão do género *Lepisma* Lin., 1758 *s. lat.* (Zygentoma, Lepismatidae). – Boletim da Sociedade portuguesa de Entomologia, supl. **2**: 1–236.

Mendes, L. F. (1990): An annotated list of generic and specific names of Machilidae (Microcoryphia) with identification keys for the genera and geographical notes. – Estudos, Ensaios e Documentos, IICT/Lisboa, **155**: 1–127.

Mendes, L. F. (1991): On the phylogeny of the genera of Lepismatidae (Insecta: Zygentoma). – In: Veeresh, G. K., J. Rajagopal & C. A. Viraktamath (eds): Advances in Management and Conservation of Soil Fauna. – Oxford & IBH Publications, Delhi, Bombay, Calcutta: 1–13.

Mendes, L. F. (1997a): On a new fossil Microcoryphia (Insecta: Apterygota) from South-American copal. – Boletim da Sociedade portuguesa de Entomologia **6** (18) (168): 245–250.

Mendes, L. F. (1997b): First contribution to the study of the Dominican amber Zygentoma (Insecta). Family Ateluridae. – Pedobiologia **41**: 40–43.

Mendes, L. F. (1998): Second contribution to the study of the Dominican amber Zygentoma (Insecta). Family Lepismatidae. – The Canadian Entomologist **130**: 899–904.

Mendes, L. F. & G. O. Poinar Jr. (2004): A new fossil Nicoletiidae (Zygentoma, 'Apterygota') in Dominican amber. – Proceedings of the Entomological Society of Washington **106** (1): 102–109.

Mendes, L. F. & G. O. Poinar (2008): A new fossil silverfish (Zygentoma: Insecta) in Mesozoic Burmese amber. – European Journal of Soil Zoology **44**: 491–494.

Mendes, L. F., M. Gaju-Ricart, R. Molero-Baltanás & C. Bach de Roca (2009): On the genera *Allomachilis* Silvestri, 1906, and *Kuschelochilis* Wygodzinsky, 1951 (Insecta: Microcoryphia). – Pesquisa agropecuária brasileira, Brasília **44** (8): 984–987.

Paclt, J. (1966): Neue Beiträge zur Ketnnis der Apterygoten-Sammlung des Zoologischen Statsinstitut und Zoologischen Museums Hamburg. II. Lepismatidae und Maindroniidae (Thysanura). – Entomologische Mitteilungen aus dem Zoologischen Staatsinstitut und Zoologischen Museums Hamburg **3** (57): 147–161.

Paclt, J. (1967): Thysanura. Fam. Lepidotrichidae, Maindroniidae, Lepismatidae. – Genera Insectorm, Creinhaim: 1–86.

Paclt, J. (1969): Neue Beiträge zur Kenntnis der Apterygoten-Sammlung des Zoologischen Staatsinstitut und Zoologischen Museums Hamburg. III. Meinertellidae und Machilidae. – Entomologische Mitteilungen aus dem Zoologischen Staatsinstitut und Zoologischen Museums Hamburg **3** (63): 1–24.

Parona, C. (1892): Di alcuni Tisanuri e Collembole della Birmania raccoleti da L. Fea. – Atti della Societá italiana di Scienze Naturale **34**: 123–135.

Pierce, W. D. (1951): Fossil arthropods from onyx-marble. 9. Fossil primitive insects from onyx-marble. – Bulletin of the Southern California Academy of Sciences **50** (1): 34–49.

Poinar Jr., G. O. (1993): Insects in amber. – Annual Review of Entomology **46**: 145–159.

Pramumijoyo, I. S., K. L. Zaw & K. Z. Lat (2010): Report on Regional Geology of Myanmar. – Dept. Geological Engineering, Faculty of Engineering, Gadjah Mada University: 20 pp.

Silvestri, F. (1912a): Die Thysanuren des baltischen Bernsteins. – Schriften der physikalische-ökonomische Gesellschaft zu Königsberg **54**: 42–66.

Silvestri, F. (1912b): Machilidarum (Thysanura) species nonnullae novae ex regione indo-malayana. – Zoologischer Anzeiger **40** (1): 1–8.

Sinitshenkova, N. D. (2000): A review of Triassic mayflies, with description of new species from Western Siberia and Ukraine (Ephemerida = Ephemeroptera). – Paleontological Journal **34** (suppl. **3**): 275–283.

Song, Z. S., F. S. Huang & A. P. Liang (2011): *Machilontus* (*s. str.*) *medogensis* Song & Huang, sp. nov. from Tibet, the northernmost record of the genus *Machilontus* Silvestri, 1912 and the first record of the family Meinertellidae (Insecta: Microcoryphia: Machiloidea) in China. – Zootaxa **2822**: 61–68.

Sturm, H. (1984): Zur Systematic, Biogeographie und Evolution der südamerikanischen Meinertellidae (Machiloidea, Archaeognatha, Insecta). – Zeitschrift für Zoologische Systematic und Evolutionforschung **22** (1): 27–44.

Sturm, H. (1998): Erstnachweis fischchenartiger Insekten (Zygentoma, Insecta) für das Mesozoikum (Untere Kreide, Brasilien). – Senckenbergiana lethaea **78** (1/2): 135–140.

Sturm, H. & C. Bach de Roca (1986): Nachbeschreibung der Gattung *Hypermeinertellus* Paclt, 1969 (Insecta, Archaeognatha, Meinertellidae). – Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg **8** (126): 165–170.

Sturm, H. & C. Bach de Roca (1993): On the systematics of the Archaeognatha (Insecta). – Entomologia Generalis **18** (1/2): 55–90.

Sturm, H. & G. B. Smith (1993): New bristle tails (Archaeognatha: Meinertellidae) from Australia. – Journal of the Australian entomological Society **32**: 233–240.

Sturm, H. & L. F. Mendes (1998): Two new species of Nicoletiidae (Zygentoma, 'Apterygota', Insecta) in Dominican amber. – American Museum Novitates **3226**: 1–11.

Sturm, H. & G. O. Poinar Jr. (1997): A new *Neomachilellus* species from Miocene amber of the Dominican Republic and its phylogenetic relationships (Archaeognatha: Meinertellidae). – Entomologia Generalis **22** (2): 157–170.

Sturm, H. & G. O. Poinar Jr. (1998): *Cretaceomachilis libanensis*, the oldest known bristle-tail on the family Meinertellidae (Machiloidea, Archaeognatha, Insecta) from the Lebanese amber. – Deutsches Etomologische Zeitscrift **45** (1): 43–48.

Sturm, H. & R. Machida (2001): Archaeognatha. – In: Kristensen, N. P. & R. G. Beutel (eds): Handbook of Zoology, 4 (37) Arthropoda: Insecta. – W. de Gruyter, Berlin, New York: 1–213.

Viggiani, G. (1973): Le specie descritte da Filippo Silvestri (1873–1949). – Bolletino del Laboratorio de Entomologia agraria 'Filippo Silvestri' **30**: 351–417.

Wygodzinsky, P. (1952): Apuntes sobre 'Thysanura' americanas (Apterygota, Insecta). – Acta zoologica Lilloana **11**: 435–458.

Wygodzinsky, P. (1967): On the geographical distribution of the South American Microcoryphia and Thysanura (Insecta). – In: Delamare-Deboutteville, C. & E. Rapoport (eds): Biologie de l'Amérique Australe, CNRS, Paris **3**: 505–524.

Wygodzinsky, P. (1971): A note on a fossil Machilid (Microcoryphia) from the amber of Chiapas, Mexico. – University of California Publications in Entomology **63**: 101–102.

Zuccon, D. (2011): The case of Lepidothrix, Lepidotrix and Neolepidothrix: the importance of the original literature in taxonomic decisions. – Zoosystematica and Evolution **87** (2): 379–382.