

Spiders of the Oriental-Australian region. II. Nesticidae

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A preliminary worldwide revision of nesticid genera is presented and taxonomic criteria for all nesticid taxa are discussed. Genital organs of the type-species of the family, *Nesticus cellulanus* (Clerck, 1757), are analysed.

Ten nesticid genera are accepted. They are classified into four groups: the tribes Nesticini and Nesticellini, and the genera *Gaucelmus* and *Eidmannella*. Tribe Nesticini consists of *Tuganobia* Chamberlin, 1933, *Nesticus* Thorell, 1869, *Carpathonesticus* gen. n. (type-species *Nesticus fodinarum* Kulczynski, 1894), *Ivesia* Petrunkevitch, 1925 (= *Yvesella* Arndt, 1928), *Cyclocarcina* Komatsu, 1942 (= *Sunitorypha* Komatsu, 1960 syn. n.), and *Typhlonesticus* Kulczynski, 1914 (corrected type designation: *T. speluncarum* Kulczynski, 1914 = *Nesticus absoloni* Kratochvil, 1933). *Gaucelmus* Keyserling, 1884 (= *Theridionex* Petrunkevitch, 1910, syn. n.) and *Eidmannella* Rower, 1935 (= *Gondwanonesticus* Dumitrescu, 1973) are both isolated genera.

All indigenous Oriental-Australian Nesticidae belong to the tribe Nesticellini, consisting mainly of species living in litter of tropical forests. This tribe comprises two new genera, *Howaia* (type-species *Nesticus mogera* Yaginuma, 1972) and *Nesticella* (type-species *Nesticus nepalensis* Hubert, 1973).

Howaia buiconghieni (♂♀ Vietnam), *H. inthanoni* (♀ Thailand), *H. prozyskii* (♀ Java), *Nesticella taurama* (♂ New Guinea), *N. robinsoni* (♂ New Guinea), and *N. sozi* (♀ New Guinea) are described and more than 30 new combinations are listed. New records of *Eidmannella pallida* (Emerton, 1875), *E. suggerens* (Chamberlin, 1924), and *Howaia mogera* (Yaginuma, 1972) are listed from the Pacific Islands and additional Nepalese records of *Nesticella nepalensis*.

Schenkeliella spinosa (O. Pickard-Cambridge, 1870), *Nesticus alteratus* Chamberlin, 1924, and *N. carteri* Emerton, 1875 are removed from Nesticidae.

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1. Introduction

The material of Nesticidae collected during the Oriental and Pacific expeditions of the Zoological Museum of Turku University includes seven species, five of them previously undescribed. All this material was collected from litter or grass in forests, bush, or savanna. Unpublished nesticid material from various sources was also checked for this revision.

The whole family Nesticidae has traditionally been regarded as more or less troglomorphic (Fage 1931, Kratochvil 1933, Caporiacco 1934, Yaginuma 1962, Brignoli 1971b, 1972a, Gertsch 1971, 1973), and this seems to be true of the Holarctic species and genera.

Towards the tropics, however, the habitat preference of Nesticidae covers a wider range. Yaginuma (1970, 1972a) and Gertsch (1971) listed several nesticid species from Southern

Japan and Mexico found both in caves and in forest litter, and Hubert (1970, 1971, 1973, 1977) described several Old World nesticid species from tropical and subtropical areas, all living in forest litter. Yaginuma (1977a) suggests that Nesticidae have become adapted to life in caves as a result of microclimatic similarities to the microhabitats of the forest floor.

The traditional generic concept in Nesticidae has been very wide. Dresco (1966) and Brignoli (1972a) were still convinced that there should be only one genus, *Nesticus*. During the last 15 years, only *Gaucelmus* and *Eidmannella* have sometimes been accepted (Gertsch 1971, 1977). This is clearly the result of basing supraspecific taxa in Nesticidae upon non-genital characters alone (Kratochvil 1933, Brignoli 1971b, 1972a, etc.). Genital characters as generic criteria have been mentioned only by Gertsch (1971, 1977).

Correct placing of our Oriental-Australian nesticid species would not have been possible without a generic revision of world Nesticidae. The weighing of characters has been carried out according to the general principles summarized by Lehtinen (1978) and discussed by Saaristo (1971). Analytical figures of the type-species of *Nesticus* are presented here to facilitate the homologizing of different parts of the genital organs in Nesticidae. For this revision, we have personally analysed representatives of all nesticid genera except *Tuganobia*.

2. Nesticidae Dahl, 1926

A detailed description of the family Nesticidae has been presented by Kratochvil (1933:60—61), but without an analysis of either male or female genital organs. Providing that Nesticidae is delimited as in this paper and in all previous papers dealing with Nesticidae, we mostly agree with Kratochvil (1933) in regard to non-genital characters. A few other tropical species (»*Theridion*» *citrinum* Taczanowski, 1874 from Guayana and an undescribed cave species from Vietnam, at least) may belong to Nesticidae. If so, a wider variation must be accepted for the shape and colour pattern of the abdomen, and especially for the cheliceral armature. No males of the above-mentioned possible nesticids are known, but the female genital organs are also rather aberrant, although not referable to any other described group of Araneoidea. For the nesticid species treated in this paper the following characters are diagnostic.

Carapace short, pear-shaped; fovea represented by a wide depression. Eight eyes in two rows, as in most groups of Araneoidea, but all of them may be strongly reduced or totally lacking in troglobionts. Chelicerae with 2—3 strong teeth on the anterior margin. Behind these teeth an irregular group of numerous small denticles, occupying not only the posterior margin of the cheliceral groove, but also the intervening area.

Abdomen more or less globular and without modifications; abdominal pattern of pale symmetrical spots or stripes on a darker ground, sometimes also with blackish stripes, but white guanine and silvery pigments lacking. Colulus well developed, widely triangular or sometimes almost fingerlike. Spinnerets and tracheal stigma unmodified, as in most Araneoidea.

Legs without strong spines, but long dorsal bristles present on tibiae and patellae. Three claws pectinate in one row; female palpal claw exceptionally long, pectinate. Trichobothrial pattern (shared with Theridiidae, Linyphiidae, Erigonidae, most Araneidae, etc.) two rows on tibiae, a single one on metatarsi. Serrate bristles present on tarsi IV, and erect sensory hairs on all tarsi and metatarsi.

Ultrastructure: skin smooth or covered with low papillae (Figs. 22, 28, 30); trichobothrial plate high, semi-globular, without falciform strengthening, pit very large, oblique in profile (Fig. 28); tarsal organ large, semi-globular; normal hairs (Figs. 22—24) serrate, with fine pattern of longitudinal furrows. Serrate bristles on tarsi IV strongly developed (Figs. 26—27).

Male palpal cymbium with more or less complicated basal process, usually fixed, but in the genus *Nesticella* movable. This process is usually called the paracymbium, but its homology with the paracymbium in Linyphiidae and Erigonidae is uncertain. Palpal tibia without apophyses and never significantly modified. Apex of cymbium with 0—2 short, strong spines.

Bulbus with semicircular embolus, which is modified subapically in many species of Nesticini. Conductor always present but very variable in structure, often with backwardly directed guide for embolus. Most species with an additional sclerite, the "terminal apophysis", close to or fused with base of conductor. Tegulum usually with a well-developed, projecting apophysis, but this is strongly reduced or absent in many genera and doubled in the genus *Nesticus*.

Female epigyne rather variable externally, with or without simple scape. Copulatory pockets usually complex in structure. One pair of seminal receptacula. Receptacular gland variable in structure and position, multiple in some *Cyclocarcina*, not separate from base of receptacula in Nesticellini.

Web three-dimensional, but not as regular as in Theridiidae. Cocoon globular, attached to the web or carried by the chelicerae. For details of ethology, see Kirchner & Kullmann (1972).

The majority of nesticidae in temperate areas (Nesticini) are more or less restricted to caves or microcaverns, but the majority of tropical species (Nesticellini & *Eidmannella*) live in litter or grass.

Distribution: representatives of Nesticidae are known from all zoogeographical regions except most parts of the Neotropical region. In remote archipelagoes of the Pacific and Atlantic Oceans only one species (or species group — *Howaia mogera*) is known, and it may have been dispersed mainly by man.

The known nesticid species are grouped here into more or less well-defined tribes, Nesticini and Nesticellini, while the genera *Gaucelmus* and *Eidmannella* each represent a group of their own. Six genera are listed here in Nesticini and two in Nesticellini, but within each genus there are more natural groups and a complete revision of Holarctic species of Nesticidae will probably lead to the creation of additional genera or subgenera. For differential diagnosis of the main nesticid groups, see Table 1.

Tribe Nesticini

Most Holarctic nesticids belong to this large tribe, which is very uniform in taxonomically

Table 1. Comparison of nesticid groups.

| | Nesticini | Nesticellini | <i>Gaucelmus</i> | <i>Eidmannella</i> |
|-------------------------|---|--|---|---|
| size | 3—7 mm | 2—3.5 mm | 3—5 mm | 2.5—3.5 mm |
| colour pattern | distinct — absent | distinct — absent | unicolorous | unicolorous |
| chelicerae | normal | normal | male fang with boss, denticles on hump | normal |
| position of Tmt I | 0.5—0.9 | 0.4—0.5 | 0.6—0.7 | 0.7 |
| male palpal tibia | longer than wide | as long as wide | longer than wide | longer than wide |
| paracymbium | prominent, three zones of modification | compact, two main branches | short and simple, directed backwards | small, modified distally, parallel to cymbium |
| conductor | tri- or bipartite distal part + embolic guide | simple, tapering distally + long embolic guide | flat with folded margins, complex parts | simple, tapering distally + short embolic guide |
| female copulat. pockets | lateral slits (-posterior) | posterior | posterior | posterior |
| vulval gland | separate | within thickened stalk of receptaculum | ? | separate |
| type of epigynal plate | variable (complicated) | protruding plate — scape | no ventral plate | with anterior pitted knob |
| seminal receptacula | variable | subglobular | subglobular | long and narrow |
| main habitat | caves | litter of forests | caves | under stones and in caves |
| distribution | Holarctic | Old World tropical | Mexico — West Indies | ? cosmopolitan |

significant non-genital characters. As a result, nesticid species with extremely variable genital organs have been listed under a single genus, *Nesticus*. It is quite obvious that only a minor part of Nesticini have been described as yet, because in large areas of the Holarctic the cave fauna is very imperfectly known. In such circumstances, a total specific revision would be premature, and in all probability a number of the aberrant species mentioned here in fact belong to undescribed genera or subgenera.

Nesticini includes no Oriental-Australian species, but a generic revision of Nesticellini cannot be presented without analysis of homologies of male and female genital organs in all nesticid groups. Such an analysis has resulted in the creation of supraspecific standards for Nesticidae, according to the general principles presented by Lehtinen (1978).

Although we have examined large amounts of type and other material of Nesticini for this study, analytical figures are presented only for *Nesticus cellulanus* (Clerck, 1757), the type-species of the type-genus of the family Nesticidae. Diagnostic characters of the genera of Nesticini are briefly summarized in Table 2, which also lists references to the most useful figures of previous authors.

Under each revised genus of Nesticini is a brief discussion of the range of variation of the most

important characters and the delimitation of the genus.

The most aberrant genus of Nesticini in regard to both female and male genital organs is *Typhlonesticus*, and its relationships to other genera remain obscure. *Cyclocarcina* and *Ivesia* are both widespread and rich in species, but they seem to be most closely related to each other, although they show very different trends in the evolution of their complex genital organs. *Carpathonesticus* is a compact group of Southeast-European species that seems to be related to *Ivesia* and *Cyclocarcina*. Its ejaculatory duct is the shortest among the Nesticini, and therefore it could be regarded as the most primitive of these three genera.

Nesticus and *Tuganobia* share the general shape of the terminal apophysis, the long, thin embolus, and the rather simple type of paracymbium. However, these two small genera differ greatly in several other genital characters, and they are probably not close relatives. The details of the vulva of *Tuganobia* are not known to us, because no material has been available, but the figures of Chamberlin (1933) and Gertsch (1971) suggest that the receptacula of *Tuganobia* are rounded, while *Nesticus* shares the branched type with *Ivesia*. However, the vulvae in these two latter genera represent two different types, and most

Table 2. Comparison of the genera of Nesticini.

| | <i>Tuganobia</i> | <i>Nesticus</i> | <i>Carpathonesticus</i> | <i>Inesia</i> | <i>Cyclocarcina</i> | <i>Typhlonesticus</i> |
|-----------------------|---------------------------------|-----------------------------|--|---|---|-----------------------|
| paracymbium | | | | | | |
| — basal modifications | rounded, marginal | rounded, marginal | rounded, marginal | rounded, marginal | complex, toothed | unmodified |
| — modified margin | lateral | mesial (-lateral) | lateral | lateral | both | none |
| — central modificat. | insignificant | insignificant | barbed or teeth | none or teeth | teeth | teeth |
| — apex | rugose | simple (wide) | simple (pointed) | simple (rounded) | pointed | simple |
| regular apophysis | small knob | 2 apophyses | small hook | strong hook | basal process | ? small knob |
| conductor | | | | | | |
| — distal part | ?bipartite | tripartite | bipartite | tripartite | tripartite | bipartite (pointed) |
| — embolic guide | ? | short, concave | short, concave | short, concave | short, concave | very long |
| terminal apophysis | long, tapering | long, tapering | compact, small | very complicated | 2-horned | bulbous |
| embolus | | | | | | |
| — type | long, thin | long, thin | short, thick | short, thick | long, thick | very long, thin |
| — apex | simple, thin | modified | simple, thick | simple, thick | modified (-simple) | simple |
| ejectulatory duct | ? (slightly curved) | slightly curved | straight (-curved) | variable | double coiled | ? (straight) |
| epigyne | | | | | | |
| — copulatory pockets | posterior margin | lateral slits | lateral pockets | lateral slits | under scape | behind epigyne |
| — epigynal plate | wide | posteriorly wide | anteriorly wide | with 2 depressions | scape | swollen |
| — type of gland | large, anterior | submedian (long) | short, lateral | variable (submedian) | short (-multiple) | very long, coiled |
| — receptacula | large, subglobular | large, branched | subglobular | branched | subglobular | small, globular |
| distribution | S Nearctic-Mexico | Holarctic | Palearctic (mainly E. Medit.) | Holarctic | E Palearctic | E Mediterranean |
| Figures | Chamberlin 1933 Gertsch 1971 | Figs. 1-6 (Gertsch 1971) | Kratochvil 1933 Wiehle 1963 Brignoli 1972a | Kratochvil 1933 Petrunkevitch 1925 Brignoli 1971b | Komatsu 1942, 1960 Yaginuma 1972a, c, 1976, 1977a, b Paik. et al. 1969 | Kratochvil 1933, 1939 |

details of the male genital organs are also different. Thus the only possible synapomorphy between *Ivesia* and *Nesticus* is the branched receptaculum, *Nesticus* having separated early from a common stock.

Tuganobia Chamberlin, 1933

Tuganobia Chamberlin, 1933. Pan-Pacif. Entomol. 9:122. Type-species by monotypy *T. potteria* Chamberlin, 1933 from California. Originally described in Linyphiidae and always listed there; transferred here to Nesticidae (see Table 2).

Nesticus nahuanæ Gertsch, 1971 (♂♀ Mexico) = *Tuganobia nahuanæ* comb. n.

Nesticus Thorell, 1869 (Figs. 1—6)

Nesticus Thorell, 1869. N. Acta reg. Soc. Sci. Upsala, Ser. 3(7):76. Type-species by monotypy, *Araneus cellulanus* Clerck, 1757, from Sweden. See Table 2 for differential diagnosis. As *Nesticus* is the type-genus for Nesticidae, a revised description is also given below.

Large to medium-sized nesticid spiders (4—7 mm) with distinct dark and light pattern on grey ground in populations not fully adapted to caves. No sexual dimorphism of carapace or chelicerae, but legs slightly longer in males (tibial index 2—2.5 in males, 1.2—1.4 in females). Position of metatarsal trichobothrium 0.54—0.70.

Male paracymbium distally entire, basally with insignificant modifications. Tegular apophyses two, the bigger very strongly developed; ejaculatory duct in ventral part of tegulum with one coil or slightly curved. Conductor consisting of several distal branches, but basal guide of embolus vestigial; terminal apophysis basally fused to base of conductor, distally simple, tapering. Female epigyne posteriorly wide; copulatory pockets lateral to the median plate in oblique slit. Seminal receptaculum bladderlike and with mesial appendix. Vulval gland with gland duct; apex of gland not reaching anterior to receptaculum, and situated close to anterior margin of copulatory slit.

Nesticus affinis Kulczynski, 1894 (♀ Hungary — holotype in IZPAN, Warsaw, examined) is a close relative of *N. cellulanus* or even a subspecies of it (cf. Kratochvil 1933). We regard the holotype as an exceptionally small specimen, and suppose that many populations outside caves in Southeast Europe should also be placed in this taxon.

N. hoffmanni Gertsch, 1971 (♂♀ Mexico — AMNH) is a rather close relative of *N. cellulanus*, and probably must be retained in *Nesticus* s. str. Thus the genus *Nesticus* is Holarctic.

Carpathonesticus gen. n.

Type-species *Nesticus fodinarum* Kulczynski, 1894 (♂♀ Romania — syntypes in IZPAN, Warsaw, examined). See Table 2.

C. fodinarum group

All known species live in caves of Southeast Europe. They are all rather closely related, and some of them may represent only subspecies. The following new combi-

nations are listed (all originally described under *Nesticus*):

C. puteorum (Kulczynski, 1894) (♂♀ Romania — syntype in IZPAN, Warsaw, examined).

C. hungaricus (Chyzer, 1894) (♂♀ Romania).

C. biroii (Kulczynski, 1895) (♂♀ Romania — syntype in IZPAN, Warsaw, examined).

C. spelaeus (Szombathy, 1917) (♂♀ Romania).

C. simoni (Fage, 1931) (♂♀ Romania).

C. borutzkyi group

Three well-defined species originally listed under *Nesticus* or *Typhlonesticus*. Paracymbium with simple apex and basal hook or hooks, but without barbed part. Copulatory openings of female at margin of epigyne.

C. borutzkyi (Reimoser, 1930) (♀ Caucasus; Wiehle 1963: ♀ Turkey), comb. n.

C. parvus (Kulczynski, 1914) (Yugoslavia; Brignoli 1971a ♂♀), comb. n.

C. menozzii (Caporiacco, 1934) (♂♀ Italy), comb. n.

Ivesia Petrunkevitch, 1925

Ivesia Petrunkevitch, 1925. Ann. Ent. Soc. Amer. 18:321. Type-species by original designation and monotypy: *Ivesia tennesseensis* Petrunkevitch, 1925 from Tennessee.

Yvesella Arndt, 1928. Described as a *nomen novum* for *Ivesia* Petrunkevitch, 1925, which was thought by Arndt (1928) to be a junior homonym of *Ivesia* Topsent, 1890. Unjustified *nomen novum*, according to ICZN (1964 § 56a), and consequently a junior objective synonym of *Ivesia* (see Table 2).

I. tennesseensis group

I. sp. (♀ North Carolina, material in AMNH & MCZ examined):

I. eremita (Simon, 1879) (♂♀ France — MNHN; material from different parts of Southern Europe examined in IZPAN, MNHN, AMNH & coll. C. Deltchev). Comb. n.

I. arenstorffi group

Male paracymbium with double central process; area of epigynal foveae wide. All species previously listed in *Nesticus*, and listed here as new combinations.

I. arenstorffi (Kulczynski, 1914) (♂♀ Yugoslavia).

I. fagei (Kratochvil, 1933) (♂♀ Yugoslavia).

I. beroni (Deltchev, 1977) (♀ Bulgaria — paratype ♀ in coll. Deltchev examined).

In addition to these groups, the following species should probably be included in *Ivesia*:

I. vazquezae (Gertsch, 1971) (♀ Mexico), comb. n.

I. speluncarum (Pavesi, 1873) (♂♀ Italy), comb. n.

I. lusitanica (Fage, 1931) (♀ Portugal), comb. n.

Cyclocarcina Komatsu, 1942

Cyclocarcina Komatsu, 1942. Acta Arachnol. 7:60. Type-species by monotypy *Cyclocarcina floronoides* Kishida (manuscript name) from Japan. According to ICZN (1964 §§ 8, 11, 12), both the genus *Cyclocarcina* and its type-species were first made available by Komatsu (1942). Originally described in Linyphiidae (compared with

Tapinopa and *Floronia*), but listed in *Nesticus* since Yaginuma (1962).

Sunitorypha Komatsu, 1960. Acta Arachnol. 17:9. Type-species by original designation and monotypy: *S. linyphoides* Komatsu, 1960 from Japan. Described in Theridiidae, but listed in Nesticidae since Yaginuma (1962), syn. n.

Cyclocarcina is the dominant nesticid genus in East Asian caves, and its species have been known as "long-legged *Nesticus*" (Yaginuma 1970 and later).

Twenty nesticid taxa described from Japan and Korea belong to *Cyclocarcina*, but in addition to them 6 undescribed males have been figured by Yaginuma (1977b). The following new combinations are listed here, but no attempt is made to revise the rank of these taxa.

C. a. akiyoshiensis (Uyemura, 1941) (♂♀ AMNH, examined).

C. a. ofuku (Yaginuma, 1977).

C. linyphoides (Komatsu, 1960).

C. koreana (Paik & Namkung, 1969) in Paik, Yaginuma & Namkung (1969).

C. l. latiscapus (Yaginuma, 1972).

C. l. kosodensis (Yaginuma, 1972).

C. kuriko, (Yaginuma, 1976).

C. anagamianus (Yaginuma, 1976).

C. l. longiscapus (Yaginuma, 1976).

C. l. draco (Yaginuma, 1978).

C. l. kiuchii (Yaginuma, 1978).

C. l. awa (Yaginuma, 1978).

C. rakanus (Yaginuma, 1976).

C. t. tosa (Yaginuma, 1976).

C. t. iwaya (Yaginuma, 1976).

C. t. niyodo (Yaginuma, 1976).

C. higoensis (Yaginuma, 1977).

C. flavidus (Paik, 1978).

C. zenjoensis (Yaginuma, 1978).

"*Nesticus*" *uenoi* Yaginuma, 1972 (♂♀ Japan) and "*Nesticus*" *idriacus* Roewer, 1931 (♀ Italy) cannot be placed exactly, but they are certainly members of Nesticini, although not of *Typhlonesticus*.

Typhlonesticus Kulczynski, 1914

Typhlonesticus Kulczynski, 1914. Bull. Ac. Sci. Cracov. 1914:380. Kratochvil (1933) designated *T. parvus* Kulczynski, 1914 as the type-species, but this designation is invalid, according to ICZN (1964, § 67h). *T. parvus* was originally listed as a questionable representative of *Typhlonesticus* (Kulczynski 1914), and through this revision it is provisionally listed in the new genus *Carpathonesticus*. *Typhlonesticus speluncarum* Kulczynski, 1914 from Yugoslavia, is here designated as the type-species of *Typhlonesticus*.

Kratochvil (1933) transferred *T. speluncarum* to *Nesticus*, and it then became a junior secondary homonym of *N. speluncarum* Pavesi, 1873. Therefore the former species was renamed *N. absoloni* Kratochvil, 1933. *T. speluncarum* Kulczynski, 1914 and *N. speluncarum* Pavesi, 1873 are not considered congeneric here, and neither of them is any longer listed under *Nesticus*, but the former must be called *Typhlonesticus absoloni* (Kratochvil, 1933). comb. n., as the homonymy was established before 1960 (ICZN 1964, § 59).

For description and differential diagnosis, see Table 2.

Nesticus vejdotskyi Kratochvil, 1939 = *T. vejdotskyi* comb. n., is a close relative of *T. absoloni* or even conspecific with

it. In species with strongly coiled vulval ducts two specimens even from a single population are seldom identical in vulval structure, and normally the ducts of the right and left halves are not identical with each other. We have confirmed this phenomenon in several cases, e.g. in *Tuberta arietina* (Thorell, 1870). Only additional material of *Typhlonesticus* from Yugoslavia can settle the status of *T. vejdotskyi*.

Gaucelmus Keyserling, 1884

Gaucelmus Keyserling, 1884. Die Spinnen Americas II. Theridiidae, 99. Type-species by monotypy *Gaucelmus augustinus* Keyserling, 1884, from Florida.

Theridionexus Petrunkevitch, 1910. Ann. New York Acad. Sci. 19:209. Type-species, by original designation and monotypy, *Theridionexus cavernicolus* Petrunkevitch, 1910, from Jamaica. Syn. n.

Our study of *Gaucelmus* is based on type and/or additional material of *G. augustinus* Keyserling, 1884, *G. calidus* Gertsch, 1971, and "*Theridion*" *eigenmanni* Banks, 1902 in AMNH. Much of the American material of Nesticidae has been on loan to another specialist, and no attempt is made here to present a specific revision of *Gaucelmus*, which seems to be a strictly American genus.

Although the vulval structure of *Gaucelmus* spp. was not studied by us from mounted vulvae, it is evident that *Gaucelmus* is an aberrant nesticid genus in regard to both genital and non-genital characters. For differential diagnosis, see Table 1.

The male cheliceral fang has a strong basal boss and the cheliceral denticles are situated on a raised knob, while the female chelicerae strongly resemble those of other nesticid species. The legs are extremely long in the males and in the females are also relatively longer than in other nesticid females. The colulus is very wide. There is no well-defined abdominal pattern apart from a faint lanceolate lighter area centrally.

The male genital organs lack both tegular apophyses and a terminal apophysis. The conductor is a complicated plate with central and marginal folds and the embolus is short and simple. The ductus ejaculatorius is straight. The paracymbium is directed backwards — in contrast to that of all other nesticids — and is structurally simple, suggesting a primarily simple, plesiomorphic type within Nesticidae. Detailed figures of *Gaucelmus calidus* have been presented by Gertsch (1971).

Eidmannella Roewer, 1935

Eidmannella Roewer, 1935. Veröff. Kolon.-Übersee-Museum 1:195. Type-species by original designation and monotypy: *Eidmannella atae* Roewer, 1935, from Brazil (SMF — Frankfurt — not examined). Originally described as a representative of Theridiidae: Pholcomminae, but listed in Nesticidae by Millidge & Locket (1955). *E. atae* is usually regarded as a junior synonym of *Nesticus pallidus* Emerton, 1875 (♂♀ Virginia, USA — topotypical material examined in AMNH), but this synonymy must be checked.

Gondwanonesticus Dumitrescu, 1973. Result. Exp. Biospeol. Cuban-Roum. Cuba 1:295, as a subgenus of *Nesticus*. Type-species by original designation and

monotypy: *Nesticus (Gondwanonesticus) dragani* Dumitrescu, 1973, from Cuba = *Nesticus suggerens* Chamberlin, 1924 from Louisiana, USA (♂♀ paratypes MCZ, examined). This synonymy was first published by Gertsch (1977).

Small, pale, unicolorous nesticids with very insignificant fovea and erect hairs in ocular area. Position of metatarsal trichobothrium I 0.60—0.70. Male paracymbium small, closely parallel to cymbium, distally dentate. Tegular apophysis small, distally obtuse. Conductor simple, distally pointed; terminal apophysis totally lacking. Female epigyne anteriorly with a chitinous knob with lateral depressions; copulatory openings at posterior margin of the epigynal plate. Receptacula long and narrow; vulval glands distinctly separate from receptacula.

The genus *Eidmannella* consists of several widespread, closely related species that probably all tend to be spread by man. The whole list of synonyms of *Eidmannella pallida* by previous authors (Millidge & Lockett 1955; Levi 1957, Bonnet 1958) must be revised. We have checked only the records from the Oriental-Australian region.

Gertsch (1971) listed several records of *Eidmannella pallida* (Emerton, 1875) from Hawaii. 1 ♂ 3 ♀ from Kauai, Koloa Cave, 24. VI 1972, leg. F. G. Howarth & W. C. Gagné (BBM, Honolulu, examined) belong to *E. suggerens* (Chamberlin, 1924).

One female from Fiji, Waiyanitu, leg. W. H. Mann (MCZ, examined) belongs to *E. pallida*. Thus both species are present in the Pacific area.

Nesticus maculatus Bryant, 1948 (♂♀ from the Dominican Republic) must be removed from *Nesticus*. The type material (MCZ) has been on extended loan to another scientist, and this species cannot be placed on the basis of generalized figures alone. It is probably related to *Eidmannella* but may represent an undescribed genus. The elongated and truncate abdomen is unique among nesticids.

Tribe Nesticellini

No generic names have ever been suggested for tropical nesticids of the Old World living outside caves, mainly in litter and forests, although many such species have recently been described by Hubert (1970, 1971, 1973, 1977). Their partly cave-dwelling relatives in Japan have recently been referred to as "short-legged *Nesticus*" by Yaginuma (1970 and later), and only one true cave species is known from this group (Brignoli 1972b), regarded here as tribe Nesticellini.

Females of this tribe are very easily separated from all other nesticid groups by the vulval structure, which shines through the integument. There is no separate vulval gland, but the secretory functions are taken over by the thickened walls of the duct leading from the posterior copulatory pockets to the simple receptaculum.

The male paracymbium is much more compact in structure than in Nesticini, but the details are rather variable in the different groups of

Nesticellini. There is no tegular apophysis and the terminal apophysis can only partly be homologized with the similarly named sclerite in Nesticini. It is a rather simple extension of the tegulum at the base of the conductor, but not fused with the latter, and never with complex processes. The conductor, too, is simple, and the embolic guide is always long.

In Nesticellini, in contrast to all other nesticid groups, the metatarsal trichobothrium is situated in the basal half (0.4—0.5). A comparison of diagnostic characters of Nesticellini with other groups of Nesticidae is presented in Table 1.

It is highly probable that the majority of Nesticellini are still undescribed, and the generic limitations suggested here must also be regarded as provisional. All species with a fixed paracymbium are listed here under a single genus, *Howaia*.

Howaia gen. n.

Type-species *Nesticus mogera* Yaginuma, 1972. Bull. Nat. Sci. Mus. Tokyo 15:621, from Japan.

Small nesticids (2—3.5 mm). Eyes usually well developed, but may be totally absent in cave populations; AME distinctly the smallest eyes. Abdomen unicolorous or with distinct light pattern; colulus long and narrow, with two setae; metatarsal trichobothrium on all legs in positions 0.40—0.44, tarsal organ in position 0.5.

Paracymbium totally fixed to cymbium, usually without prominent, complex branches; conductor distally simple; terminal apophysis represented by triangular lobe of tegulum below apex of conductor.

Female epigyne with a short scape, thin or thick, but posterior margin of epigyne (including base of scape) always without a thick, sclerotized plate. Vulval structure similar in most respects to *Nesticella*.

Species of *Howaia* are found in all tropical areas of the Old World, and in East Asia they extend into the Holarctic region. The concept of species within *Howaia* is not yet established, and many deviating populations of described species probably represent new species.

H. mogera group

Male paracymbium not branched at all, terminal apophysis distally simple, conductor distally pointed. Female epigynal scape thin. Abdomen unicolorous.

Only one named species known, but variation of local populations suggests that it should be divided into several taxa. The paucity of the material available to us now makes it impossible to decide whether this variation is subspecific, locally adaptive or taxonomically insignificant.

Howaia mogera (Yaginuma, 1972) comb. n. Figs. 7—9.

? *Nesticus helenensis* Hubert, 1970. Rev. Zool. Bot. Afr. 81:368, *nomen nudum*, (? syn. n., cf. below *N. helenensis* Hubert, 1970). Hubert (1970) stated that *N. benoiti* is a

close relative of *N. helenensis*, but no characters were described or compared.

N. terrestris, Yaginuma, 1970. Bull. Nat. Sci. Mus. Tokyo 13:390, fig 7 only (allotype ♂), not holotype ♀.

N. mogera Yaginuma, 1972. Bull. Nat. Sci. Mus. Tokyo 15:621.

? *N. helenensis* Hubert, 1977. Ann. Mus. R. Afr. Centr., Sci. Zool. 220:153, figs 67 a-h, syn. n. The figures fit well to *N. mogera*, but no material from St. Helena has been examined by us. If dispersal occurs with the aid of man the synonymy is probable.

Holotype ♂ (= alloparatype ♂ of *Nesticus terrestris* Yaginuma, 1970) from Japan, Tokyo, Tamagawa 3. XI. 1969, leg. H. Kobayashi (NSMT, Tokyo).

Yaginuma (1972b:619, 621) erroneously writes that he is giving a new name to the allotype of *Nesticus terrestris*, and this is later cited as a true *nomen novum* by Gertsch (1973:168).

Hubert (1970, 1977) has repeatedly emphasized the existence of an old description of a tropical nesticid species, *N. inconcinus* Simon, 1907 from São Thome, Atlantic Ocean, close to West Africa. The type material of this species has not been available to nesticid specialists of recent times, and there is nothing in the original description that would exclude the conspecificity of this species with *H. mogera*.

Even if there should be several different species among published records of *H. mogera*, it is evident that our material from Fiji is conspecific with the type material, and it seems probable that *H. mogera* is well adapted to habitats strongly influenced by human activities, and has partly been dispersed with the aid of man.

Material from Fiji. Viti Levu: Lautoka district. Ellington, in bush between cultivated field and coastal mangrove swamp 3.II.—26.III. 1974, 2♂ 3♀ (PTL). — Nadroga district, Nakolo, in jungle litter 31.I.1974 3♀ 5 juv. (PTL). — Nadroga district, Nalimbali, in jungle litter 31.I.1974, 1♀ (PTL).

Male: carapace 0.9—1.0 x 0.8—0.9 mm, abdomen 1.0 mm, total length 2 mm; leg I 1.4 mm (rest broken), leg IV 1.24+0.37+1.02+1.00+0.56 mm; tibial index (IV) 1.09.

Abdomen greenish grey, with indistinctly limited lighter transverse bars; legs whitish or light greenish grey, with distinct dark apical rings on femora and tibiae: femora also with dark longitudinal markings. Tarsi and distal part of metatarsi yellowish brown. Clypeus and ocular area with a few short hairs. Palpal paracymbium with distal margin darkened, ventral margin with an inwardly directed hook.

Female: carapace 1.0 x 0.8 mm, abdomen 1.2 mm, total length 2.2 mm; leg I 1.24+0.41+1.14+1.00+0.63 mm, IV 1.22+0.41+0.98+0.84+0.51 mm; tibial index 1.14.

Carapace and abdomen as in male, legs throughout yellowish grey, annulations absent or less distinct than in males. Epigyne with long, protruding, trapezoidal scape.

Gertsch (1973) recorded *N. mogera* from Hawaii. One of his specimens from Kazumura Cave (♀) has been checked and measured by us (BBM, Honolulu): carapace 1.25+1.04 mm, abdomen 1.5 mm, total length 2.7 mm; leg I 1.55+0.49+1.46+1.40+0.70 mm, tibial index 1.16; position of metatarsal trichobothrium 0.47. In addition to its much larger size, the Hawaiian female differs from all Fijian females in its yellowish brown coloration, and exceptionally unicolorous legs (only a dark spot is visible

apically on the ventral side of femur IV and a very faint spot on tibia IV). According to the figure of Gertsch (1973, fig. 5) the Hawaiian male has a distally wider conductor than the Japanese holotype or our Fijian males. The epigyne of the Hawaiian female is presented in Fig. 9.

The dimensions of the male holotype from Tamagawa, Tokyo (Yaginuma 1970:391) agree with those of our Fijian males, but the dimensions of the alloparatype female from Tenryū-shi, Shizuoka Pref., are only slightly smaller than those of the big Hawaiian female (cf. Yaginuma 1972b:621).

The eyeless cave population from Ryu-kyu Islands described by Shimojana (1977:354, fig. 6) has a much narrower male cymbium, while details of the paracymbium, terminal apophysis, and conductor seem also to be slightly different from the type.

It is evident that the taxonomic status of the various populations of the *H. mogera* group from Japan and the Pacific Islands cannot be finally revised on the basis of the material available to us, but it seems quite probable that our Fijian populations agree in all respects with the holotype.

H. brevipes group

Male paracymbium with distal and subdistal branches, at least partly homologous with branches of the paracymbium in *Nesticella*. Terminal apophysis with double apex, conductor distally rounded or at least not simply pointed. Female epigynal scape thick, well sclerotized. Abdomen with very distinct pattern to totally unicolorous. Probably true forest species, not distributed with the aid of man. *H. brevipes* is ecologically exceptional, living in caves also.

New species have only been described here for material examined by us, and at least the populations listed under *Nesticus brevipes* by Yaginuma (1972b) represent more than one taxon.

Howaia brevipes (Yaginuma, 1970) comb. n.

Theridion pilula, Komatsu, 1940. Acta Arachnol. 5:186, fig. 5, not *T. pilula* Karsch, 1879 (misidentification).

Nesticus brevipes Yaginuma, 1970. Bull. Nat. Sci. Mus. Tokyo 13:386, figs. 1—2 (most probably not figs. 8—10, as suggested by Yaginuma 1972b:622) from caves in Japan.

N. terrestris Yaginuma, 1970. Bull. Nat. Sci. Mus. Tokyo 13:390, figs. 3—6 (not fig. 7), only ♀ holotype. Primary homonym of *Theridion terrestre* Emerton, 1875, which is a junior subjective synonym of *Nesticus cellulamus* Clerck, 1757. Synonymized by Yaginuma (1972b).

Howaia quelpartensis (Paik & Namkung, 1969) comb. n.

Nesticus quelpartensis Paik & Namkung, 1969 (in Paik, Yaginuma & Namkung 1969:812, figs. 37—42) from Korea.

Howaia buiconghieni sp. n. Figs. 10—12.

Holotype ♂ from Vietnam, Vinh Phu, Tam Dao (1450 m), on stony jungle slope with leaf litter 19.X.1978, P. T. Lehtinen, preserved in MZT, Turku. Alloparatype ♀

(1420 m) in litter of bamboo forest mixed with pines 20.X. 1978 and 1 paratype ♀ (1400 m) in moist stone bed of jungle slope 20.X.1978, both PTL.

Male: carapace 1.2 x 1.0 mm, abdomen 1.4 mm, total length 2.6 mm; leg I 1.81+0.49+1.63+1.56+0.69 mm, tibial index 1.35; position of Tmt I 0.39.

Thoracic area of carapace rounded, cephalic area short and narrow in comparison to female. Eyes well developed, AME distinctly the smallest. Carapace with very dark margins and a triangular mark projecting backwards from the cephalic area also dark. Abdomen with very distinct pattern (Fig. 10). Legs brownish yellow, very distinctly annulated with wide dark annuli (base and apex of femora and tibiae, apex of metatarsi, and whole patellae). Male palp Fig. 11.

Female: carapace 1.2 x 1.0 mm, abdomen 1.4 mm, total length 2.6 mm; leg I 1.65+0.49+1.44+1.26+0.64 mm, tibial index 1.19; position of Tmt I 0.44.

Carapace of normal pear shape; coloration as in male. Abdominal pattern very distinct, light areas slightly larger relatively than in male; legs annulated, but annuli slightly less distinct than in male. Epigyne Fig. 12.

Separated from *H. brevipes* and *H. quelpartensis* by much more complex inner teeth of male paracymbium and by details of vulva. Separated from geographically close and superficially very similar *H. inthanoni* by much narrower epigynal scape, and from *H. prozyskii* by different colour pattern and shape of epigynal scape.

Howaia inthanoni sp. n. Fig. 13.

Holotype ♀ from Thailand, Lampang Province, Doi Inthanon National Park, cloud forest at 2000 m in pitfall traps 15.XI. — 27.XII.1976, P. T. Lehtinen & Raoul Laine, in MZT, Turku.

Female: carapace 1.15×0.95 mm, abdomen 1.6 mm, total length 2.65 mm; leg I 1.59 (+ rest broken), leg IV 1.33+0.45+1.08+0.88+0.56 mm; tibial index (IV) 0.93.

Shape of carapace as in female *H. buiconghieni*, yellowish brown; ocular area with short hairs; abdominal pattern as in *H. buiconghieni*, but contrast between light and dark less distinct. Annulation of legs very dark; pattern as in *H. buiconghieni*, but femora less distinctly annulated. Epigyne Fig. 13.

Male unknown.

Howaia prozyskii sp. n.

Holotype ♀ from Indonesia, Java, Tjibulan close to Bogor, 9.IV.1959 (in sample consisting only of spiders and insects living in vegetation and probably collected with a sweep net) J. Prószyński & B. Pisarski, in IZPAN, Warsaw.

Female: carapace 1.33×1.11 mm, abdomen 1.7 mm, total length 3.0 mm; leg I 1.88+0.52+1.65+1.61+0.76 mm, tibial index 1.24; position of Tmt I 0.48.

Shape of carapace as in *H. buiconghieni*, coloration greenish grey. Abdomen greenish grey, except for long oval whitish spot dorsal to spinnerets. Legs I—II practically unicolorous, III—IV with faint distal annulations on femora and tibiae. Epigyne Fig. 14; epigynal scape centrally high, in profile very distinctly raised from the flat anterior part.

Male unknown.

H. inthanoni and *H. prozyskii* are clearly referable to the *H. brevipes* group, although the males are unknown. On the other hand, the following species from the Ethiopian region cannot be placed in the species groups discussed here, although the generic affiliation to *Howaia* is indisputable.

Howaia machadoi (Hubert, 1971) comb. n.

Nesticus machadoi Hubert, 1971, Publ. Cult. Comp. Diam. Angola 84:75, figs. 1—5. from Angola.

The male palpal paracymbium seems to be distally slightly lobate, and the female epigyne has an exceptionally wide central plate, which is virtually without a true scape.

Nesticella gen. n.

Type-species *Nesticus nepalensis* Hubert 1973, Senckenb. Biol. 54:167 from Nepal.

Small nesticids (2—3.5 mm). Eyes well developed, AME distinctly the smallest. Abdomen unicolorous greyish or with longitudinal rows of ill-defined patches. Legs unicolorous in males, but may be annulated in females. Colulus large, long triangular, with many hairs. Metatarsal trichobothria in positions 0.40—0.46.

Male palpal paracymbium connected with cymbium by movable joint (in contrast to all other nesticid genera), compact, and consisting of ventral and lateral branches, both modified distally. Conductor simple, but its posterior embolic guide with basal modifications; terminal apophysis pointed and protruding as in *Nesticus*, basally thickened or with separate knob; tegular lacking or at least strongly reduced; embolus thin, semicircular.

Female epigyne covered posteriorly with thin, rounded plate (which is lacking in all species of *Howaia*); posterior margin of epigyne variably rounded, but scape small or lacking. Vulval structure very similar to *Howaia*.

Most known species of *Nesticella* live in litter of tropical forests and only one species, *N. aelleni*, has been reported from tropical caves.

Distribution: Old World tropics, but so far not recorded from the Pacific Islands (east of New Guinea) or Madagascar.

The Oriental-Australian species of *Nesticella* are all rather closely related and constitute a single species group, in which should probably also be placed the African species, which are not treated in detail here, but only listed as a new combinations. The only possible exception is *Nesticella sogi*, of which no males are known.

Nesticella nepalensis Hubert, 1973) comb. n.

Nesticus nepalensis Hubert, 1973. Senckenb. Biol. 54:167, Figs. 2—5. Holotype ♂ and numerous paratypes (♂♂♀♀ juv.) from Nepal, Myangdi Khola, Rhododendron forest at 2100 m, in litter and under stones III. — IV.1970, J. Martens, (SMF - Frankfurt), paratypes 1 ♂ 1♀ (MNHN - Paris, examined).

Distribution in Nepal listed by Hubert (1973). New material from Nepal, Bagmati, Katmandu District: Gokarna, Gokarnaban wildlife reserve, in litter or big-leaved jungle, 13.V.1979, P. T. Lehtinen: 1 ♂ 1♀ 2 juv.

— Godavari (1540 m), in small-leaved jungle litter, 12.V.1979, P. T. Lehtinen: 1♀9 juv. — Phulchoki (1800 m), in litter of dry bush slope, 12.V.1979, P. T. Lehtinen: 1 juv.

Male 2.0—2.8 mm (maximum according to Hubert 1973). Carapace 1.03×0.95, index 1.08, abdomen 1.1 mm, Leg I 1.64+0.45+1.47+1.50+0.67, tibial index 1.43. Male metatarsi slightly swollen, except at both ends.

Female 2.1—3.8 mm (maximum according to Hubert 1973). Carapace 1.09—1.17×0.95—1.03, index 1.14, abdomen 1.1—1.7. Leg I (small specimen) 1.50+0.46+1.31+1.18+0.64, tibial index 1.21; (large specimen) 1.35+0.48+1.22+1.12+0.54, tibial index 1.04.

Both sexes were described in detail by Hubert (1973), but his information about the carapace index (1.00 in both sexes) is probable erroneous (paratype specimens were not measured by us). On the other hand, the details he gives for both male and female genital organs correspond exactly to those in our material.

N. nepalensis is separated from *N. aelleni* by the distinctly bifurcate apex of the conductor, the narrower basal tooth of the terminal apophysis and the longer and more strongly curved inner lobe of the paracymbium. The female epigynal plate of *N. nepalensis* is narrow, angular and with a distinct central pit, while that of *N. aelleni* seems to be more rounded and without a pit. *N. nepalensis* is also bigger and the carapace is relatively wider. *N. nepalensis* is separated from *N. taurama* by the shape of the paracymbium, but also by the much smaller basal tooth of the terminal apophysis. The relative length of the legs as well as of their individual segments differs greatly in our two female specimens, although the epigyna are identical. The variation in size and intensity of colour pattern seems to be large within a small area.

Nesticella aelleni (Brignoli, 1972)

Nesticus aelleni Brignoli, 1972. Rev. Suisse Zool. 79:917, Figs. 17—23. Holotype ♂ + 3 ♀♀ 3 juv. paratypes from Sri Lanka, Kuruwita, Stripura Cave 22.I.1970, V. Aellen & P. Strinati (MHNG - Geneva, not examined).

Male 2.2 mm, female 2.5 mm, described in detail by Brignoli (1972). Separated from *N. nepalensis* only by minor details of genital organs (see above), but seems to be ecologically very different. These two species might be regarded as subspecies of an ecologically adaptable and widespread species. However, the absence of *Nesticella* from our recent collections from the Darjeeling and Shillong areas shows that *N. nepalensis* is not common in the intervening mountain areas of India.

Nesticella sechellana (Simon, 1897) comb. n.

Nesticus sechellanus Simon, 1897. Ann. Soc. Ent. France 66:378.

N. sechellanus, Hubert, 1970. Rev. Zool. Bot. Afr. 81:367, figs. 9—10.

Holotype ♀ from Seychelles, Mahé (ZMH - Hamburg, examined). Although the type material of spiders in ZMH was catalogued by Rack (1961), Hubert and his colleagues believed that this holotype was lost, and Hubert (1970:367) designated a neotype ♀ from Mahé (MRAC - Tervuren, not examined). This designation is here declared invalid.

Female 2.7 mm, more or less unicolorous. Described in detail by Hubert (1970). The vulva of *N. sechellana* is coiled and resembles *Hovaia buiconghieni* more than any species of *Nesticella*. It is listed here under *Nesticella* mainly because of the well-developed covering plate of the epigyne, but its final generic affiliation can be confirmed only through a study of the male genital organs.

Nesticella taurama sp. n. Figs. 15—18

Holotype ♂ (with paratypes 1 ♂ 1 juv.) from Papua New Guinea, Central district, Port Moresby, Taurama, in litter of gallery forest 25.II.1974, P. T. Lehtinen, in MZT, Turku.

Male: carapace 1.05—1.25 × 0.95—1.1 mm, abdomen 1.2—1.35 mm, total length 2.0—2.3 mm; leg I 1.69 + 0.48 + 1.57 + 1.65 + 0.73 mm; tibial index 1.25.

Carapace slightly longer than wide, index 1.11—1.14. Other non-genital characters mostly as in *N. nepalensis*, but abdomen dorsally without a true pattern, having only a lighter anterior triangle.

Male palp close to that of *N. nepalensis*, but outer part of lateral branch of paracymbium much narrower; terminal apophysis basally wider, and associated tegular knob less prominent.

Female unknown.

Nesticella robinsoni sp. n. Figs. 19—20.

Holotype ♂ from Papua New Guinea, Morobe district, Wau (1400 m), fern bush bordering yard of guesthouse of Wau Ecology Institute, 8.III.—2:IV.1974 with pitfall traps, P. T. Lehtinen & J. L. Gressitt, in MZT, Turku. Paratypes 1 ♂ 7 juv. from Wau, in litter of *Piper* bush 6—8.III. 1974, P. T. Lehtinen.

Male: carapace 1.2 × 0.9 mm, abdomen 1.2 mm, total length 2.4 mm; leg I 1.66 + 0.49 + 1.53 + 1.60 + 0.72 mm, leg IV 1.57 + 0.45 + 1.20 + 1.35 + 0.62 mm; tibial index 1.28, carapace index 1.33.

Chelicerae anteriorly with 3 long teeth and abdomen unicolorous grey. Other non-genital characters as in *N. nepalensis*.

Male palp close to *N. africana*, but distal parts of both paracymbial branches different and basal modifications of terminal apophysis very different; metatarsi thickest centrally, tapering slightly towards both ends, probably representing a secondary sexual character. Without doubt closer to *N. africana* than to any Oriental species of *Nesticella*.

Female unknown.

Nesticella africana (Hubert, 1970) comb. n.

Nesticus africanus Hubert, 1970. Rev. Zool. Bot. Afr. 81:361, figs. 1—4 from Congo.

Nesticella benoitii (Hubert, 1970) comb. n.

Nesticus benoitii Hubert, 1970. Rev. Zool. Bot. Afr. 81:364, figs. 5—8, from Rhodesia.

Hubert (1970:364) erroneously listed “♀ holotype, ♀ allotype, ♀ paratype” The only ♂ from the original material is herewith selected as the holotype, as obviously intended by the original author.

This species is easily separated in the male sex from other species of *Nesticella* by the bipartite knob at the base of the terminal apophysis, but in the structural details of the palpus and vulva it is nearer to the Oriental species than to *N. africana*.

Nesticella sogi sp. n. Fig. 21.

Holotype ♀ from Papua New Guinea, Central district, Goilala subdistrict, Woitape, kunaigrass meadow at 1450 m, 17.II.1974, P. T. Lehtinen, in MZT, Turku. Paratype ♀ also Goilala subdistrict, Mt Albert Edward, Avios (2600 m), in *Sphagnum* of cloud forest, 20.II.1974, H. Hippa.

Female: carapace 1.35 × 1.1 mm, abdomen 1.55 mm, total length 2.9 mm; leg I 1.53 + 0.49 + 1.27 + 1.16 + 0.65; tibial index 0.94, carapace index 1.23.

Carapace and abdomen unicolorous greyish yellow; legs yellowish, femora and tibiae distally distinctly annulated with black.

Epigyne strongly sclerotized, especially the semicircular cover plate typical of *Nesticella*. Seminal receptacula exceptionally large, ducts short.

N. sogi differs from all other Oriental species of *Nesticella* in the different relative lengths of the leg segments as well as in the type of vulva. Therefore it can hardly be the female of *N. robinsoni*, another mountain species from New Guinea.

3. Evolution and relationships of Nesticidae

In the known nesticid spiders, analysis of the evolution of the various genital characters both in males and in females seems to indicate several incompatible patterns, and for several characters the polarity of evolution remains uncertain.

Vulva. A typical nesticid vulva consists of a pair of seminal receptacula with separate vulval glands. This pattern has been figured in detail by most modern specialists on Nesticidae, although the functions of the different parts have been mentioned only by Paik et al. (1969). Gertsch (1971) did not use vulval characters at all in his descriptions of American nesticids, and the vulval structure of *Gaucelmus* has never been figured. One of us (Lehtinen) has made a superficial study of the epigynes of *G. augustinus* and *G. calidus*. The seminal receptacula are large and regularly subglobular as in *Cyclocarcina* and in the tribe Nesticellini, but the glands if any could not be seen through the integument.

The original description of *Cyclocarcina latiscapus kosodoensis* (Yaginuma, 1972) very distinctly figures a nesticid vulva of multiglandular type, and it remains uncertain whether the vulvae of any other species of *Cyclocarcina* are of this type.

In Nesticellini the vulva is always without a separate vulval gland, but the secretory functions certainly persist. The duct leading from the

copulatory openings to the receptaculum is strongly thickened, and the lumen is not simple. Vulval glands of a similar type are found, for example, in the cribellate families Dictynidae and Titanoecidae (Lehtinen 1967:451, 459).

The most apomorphic vulvae are found in Nesticini, especially in *Ivesia*, but a separate gland may be plesiomorphic within the family Nesticidae.

Paracymbium. The homology of the traditional paracymbium within Araneoida is not indisputable, and a movable paracymbium has probably originated from a fixed type more than once during the evolution of Araneoida. In our opinion, evolution may also have been in the opposite direction, as a paracymbium has an important function to perform in copulation, and changes of functional type in the copulatory organs have been very common in the evolution of Araneoida, even within a single family.

The movable paracymbium of *Nesticella* is probably apomorphic. The paracymbium of the *Hovaia brevipes* group is homologous with that of *Nesticella* even in minor details, and the development of a movable paracymbium within this line of evolution may be rather recent.

The paracymbium of Nesticidae cannot easily be homologized as a whole with the paracymbium of Linyphiidae, Erigonidae, or Mysmenidae, and only with some hesitation with that of Metidae or Araneidae. On the other hand, the paracymbium of Mimetidae consists of two separate outgrowths of the cymbium, and the lateral part may be homologous with the paracymbium of Nesticidae.

Within the Nesticidae, the paracymbium in small, isolated populations in caves has frequently evolved morphologically into easily recognizable types. Yaginuma (1977a:307) has suggested genetic drift as the main reason for this variability. If a parallel concept of species (as by him for *Cyclocarcina higoensis*) is applied to cave spiders in general, the number of species will be greatly reduced — and this may be a sound solution for the taxonomic treatment of cave species.

Male palpal bulb. The homology of bulbal sclerites within the Araneomorpha can be established only partly. The embolus, conductor, and terminal apophysis of all typical Araneoida (Araneidae, Linyphiidae, Erigonidae) are united basally with the tegulum by a common sclerite, the suprategulum (= median apophysis auct.), but in Nesticidae, Mimetidae, and Cyatholipidae as well as in more distantly related Theridiidae, Hadratarsidae, and Anapidae the embolus proper originates from the tegulum separately

from the other bulbal organs, and in most cases these sites of origin are on opposite sides of the tegulum. In Metidae and Tetragnathidae the topography of the bulbal organs is intermediate: the embolus and conductor are contiguous at their bases, but these sclerites originate separately from the tegular surface.

Thus, the polarity of evolution of the "terminal apophysis" within the Nesticidae remains obscure. Although there is a general trend towards simplification of complex structures in many lines of spider evolution, it seems probable that the simple nesticid palpi of *Gaucelmus* and *Eidmannella* in fact represent plesiomorphic types in regard to lack of a "terminal apophysis" and the simple structure of the conductor.

Tegular apophyses occur scattered throughout all lines of spider evolution, and so are of little taxonomic value for analysis of the relationships of Nesticidae. However, within the Nesticidae the evolution of tegular apophyses has probably tended towards large, well-developed apophyses.

Non-genital characters. The relationships of nesticids have traditionally been discussed only on the basis of non-genital macromorphological characters. Therefore these species were listed mainly in Theridiidae or Linyphiidae by the older authors. The placing in Theridiidae was also supported by the three-dimensional type of nesticid web.

Simon (1895) was the first to emphasize the differences in structure of the gnathocoxae, chelicerae and male palpi, erecting a group, Nesticidae, in his Argiopidae: Tetragnathinae. Dahl (1926) was the first to treat the Nesticidae as an independent family related to Theridiidae, but this was done in a handbook for identification without any discussion of argumentation.

Kratochvil (1933) finally defined the Nesticidae. He mentioned the typical auxiliary claws on the tarsi, the shape of the gnathocoxae and labium, and a few other less significant non-genital characters, but also the presence of a well-developed paracymbium. He also figured and discussed the peculiar cheliceral armature of all Nesticidae. This curious pattern of small denticles connected with lack of true teeth on the posterior margin of the cheliceral groove is shared only with Mysmenidae. However, complicated patterns of cheliceral armature are also known from Anapidae as well as some unplaced species of Araneomorpha, known only as females (see p. 48). The genital organs of Nesticidae and Mysmenidae are very difficult to homologize in the males, while the vulva of *Mysmena* does not deviate greatly from that typical of Nesticellini. We do not

suggest synapomorphy of cheliceral armature between Mysmenidae and Nesticidae, but there remains a slight possibility of it. The cheliceral armature of Mimetidae does not resemble that of Nesticidae, but in this character both families deviate strongly from typical Araneoidea.

Ultrastructure. The ultrastructure of Araneoidea is surprisingly uniform as compared with that of most other groups of spiders (Lehtinen 1975a), and therefore the differences in ultrastructure between Nesticidae and the Araneoidea (see p. 48) appear to be taxonomically significant. The curious type of basal trichobothrial plate is unique, while the smooth skin is shared within Araneomorpha only by some species of Cyatholipidae. The skin in *Nesticus* and *Nesticella* is not actually smooth, as in *Howaia*, but covered throughout with low papillae.

A final classification of Araneomorpha (sensu Lehtinen 1978) is not yet possible, although there are at least three main lines of evolution: Araneoidea, Theridioidea, and Nesticoida, but the delimitation of Nesticoida will only be possible when all the minor groups of Araneomorpha have been analysed by similar methods.

Probably the closest relatives of Nesticidae are Mimetidae and Cyatholipidae. For the latter family, familial status is first suggested here, although Todd-Davies (1978) has used the family name Teemenaariidae for some species included by us in Cyatholipidae. Wunderlich (1978) placed Cyantholipinae with hesitation in the Tetragnathidae. The grouping of Nesticidae, Mimetidae, and Cyatholipidae is here based mainly on the homologous structure of male genital organs, but all three families differ from the Araneoidea in regard to many other, non-genital, characters. The genital organs of both males and females of Theridiidae (Theridioidea is probably a monotypic superfamily) are very different, and the similarities between Nesticidae and Theridiidae (serrate bristles on tarsi IV, threedimensional web) are purely adaptive.

4. Misplaced species

Nesticus alteratus Chamberlin, 1924 from China is, according to the detailed description and accompanying figure, a typical representative of Linyphiidae: Linyphiinae. It belongs to *Neriene* in the revised sense of Helsingin (1969), but specific revision can only be done through analysis of the type material.

Nesticus carteri Emerton, 1875 from Indiana, USA (♀ MCZ), has normal Araneoidean teeth on both margins of the cheliceral groove and a narrow scape protruding from the anterior part of the epigyne. It must be removed from

Nesticidae, although its position in Araneoidea remains uncertain.

Since the catalogues of Roewer (1942) and Bonnet (1958), some species have been removed from Nesticidae. *Schenkeliella spinosa* (O. Pickard-Cambridge, 1870) from Sri Lanka, originally selected as the type-species of *Oeta* O. Pickard-Cambridge, 1870, was still catalogued in Nesticidae by Roewer (1942), but in Linyphiidae by Bonnet (1958). The original generic name of this Oriental species is a junior homonym of *Oeta* Grote, 1865. Brignoli (1972b) doubted the placing of *Schenkeliella* in Nesticidae. In our opinion, *S. spinosa* is a typical representative of Leucauginae (Metidae sensu Lehtinen 1975b or Tetragnathidae sensu Lockett, Millidge & Merret 1974) and congeneric with or closely related to *Opadometa grata* (Guérin, 1838).

Nesticus cericeus Saito, 1934 was first included in *Menosira* (Leucauginae) by Yaginuma (1960), but later he (Yaginuma 1977c) regarded this as an error due to misidentification, and transferred *N. cericeus* to *Lepthyphantes* (Linyphiidae).

N. oculiprominentis Saito, 1939, *N. obcaecatus* Simon, 1907, and *N. ambiguus* Denis, 1949 have been regarded as doubtful representatives of Nesticidae by Yaginuma (1962), Fage (1931), and Hubert (1971), respectively.

N. mayanus Chamberlin & Ivie, 1938 was probably included in *Nesticus* because of cheliceral armature. It was transferred to the genus *Maymena* by Gertsch (1960). He listed it in Symphytognathidae, but in our opinion this genus belongs to Mysmenidae.

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Dr. Wojciech Starega, IZPAN, Warsaw, Dr. Norman Platnick, AMNH, New York, Dr. Herbert W. Levi,

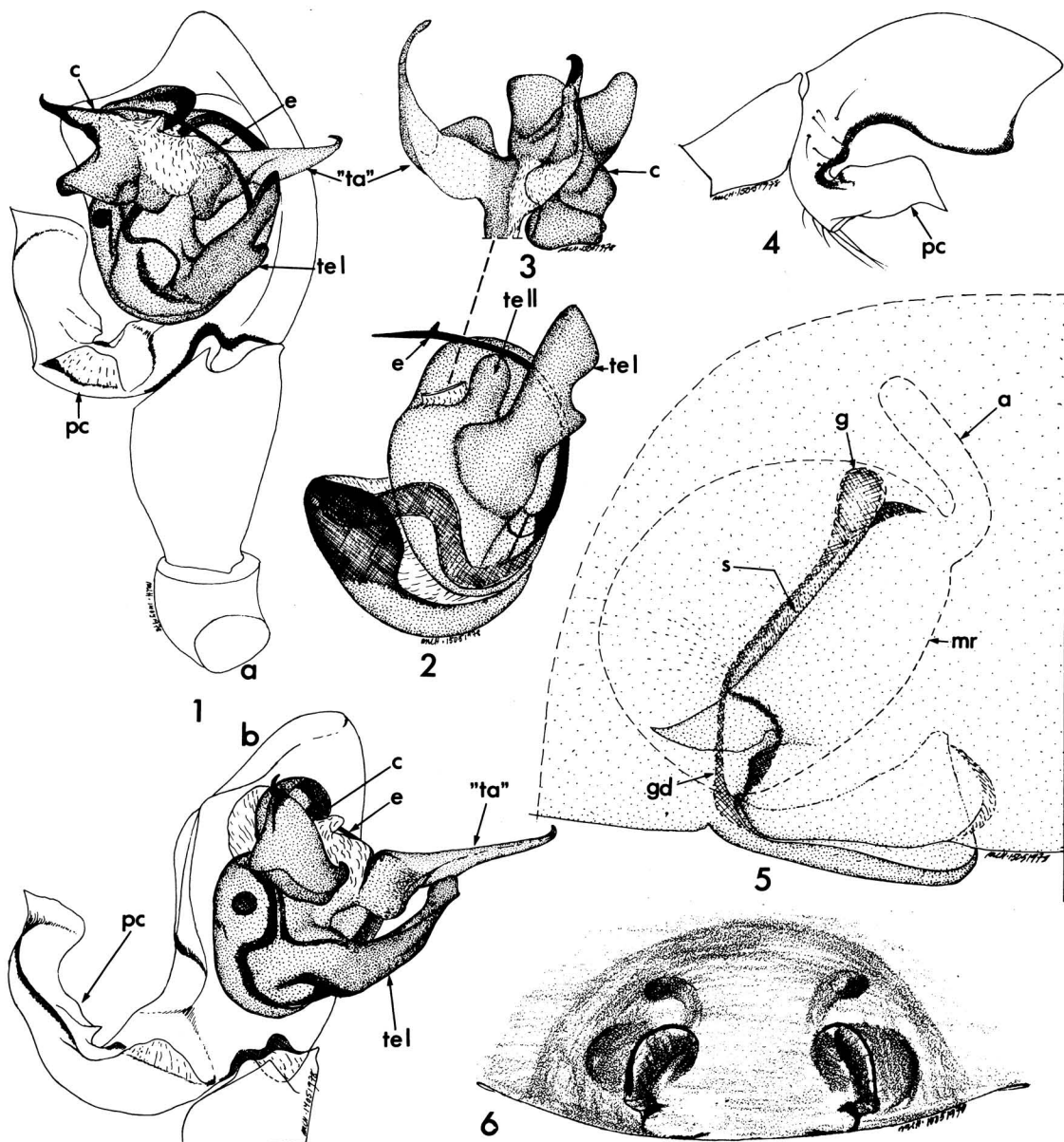
MCZ, Cambridge, Mass., Dr. Gisela Rack, ZMH, Hamburg, and Dr. Michel Hubert, MNHN, Paris, kindly allowed one of us (Lehtinen) to study nesticid type material preserved under their curatorship. Dr. JoAnn Tenorio, BBM, Honolulu, and Dr. Christo Deltchev kindly sent nesticid material for this study. The generosity of all these persons and institutions is gratefully acknowledged. Mrs. Jean Margaret Perttunen, B. Sc. kindly revised the English text.

Abbreviations of museums

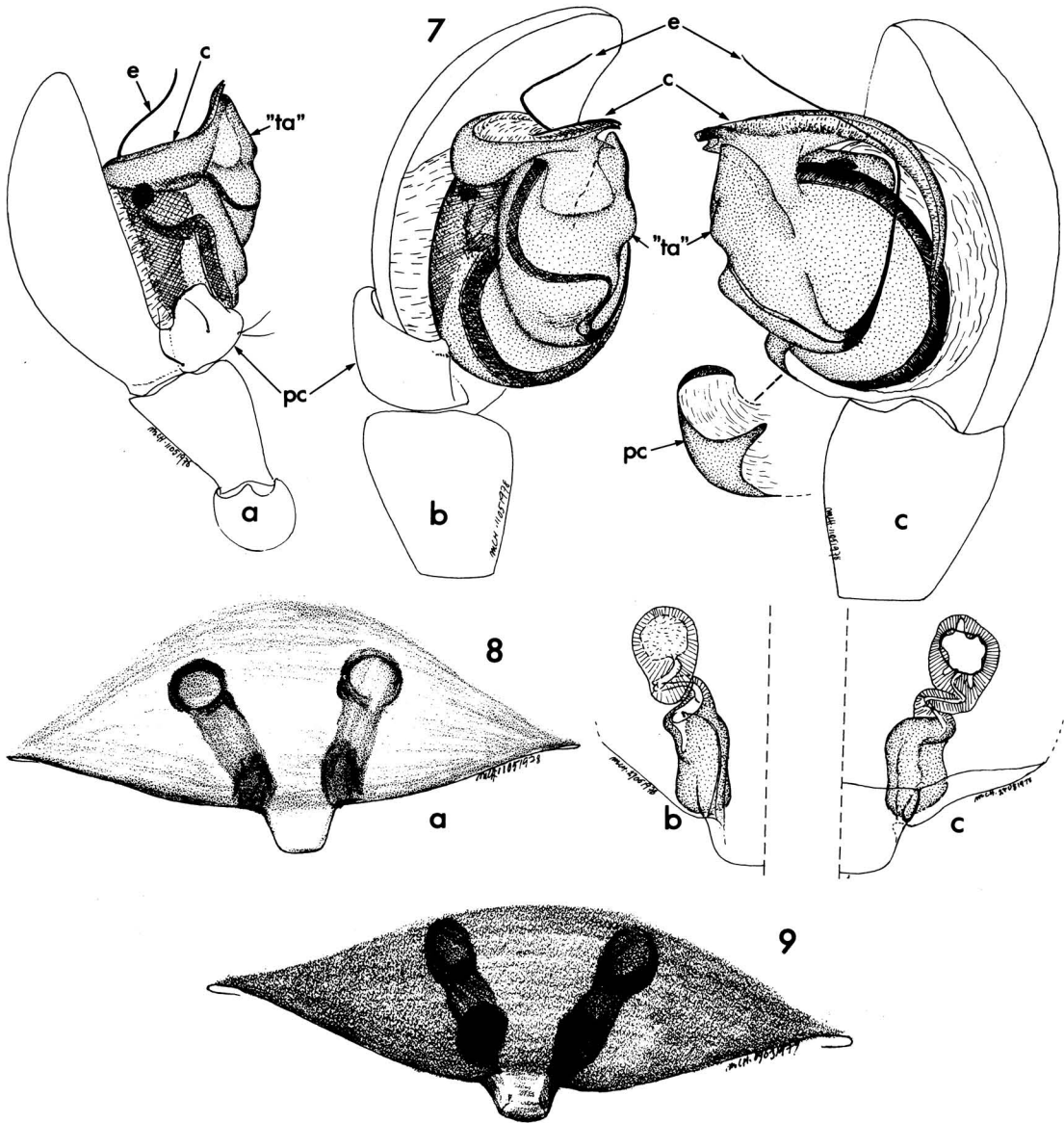
| | |
|-------|---|
| AMNH | = American Museum of Natural History, New York, N.Y. |
| BBM | = Bernice P. Bishop Museum, Honolulu, Hawaii |
| IZPAN | = Instytut Zoologiczny, Polska Akademia Nauk, Warsaw |
| MCZ | = Museum of Comparative Zoology at Harvard University, Cambridge, Mass. |
| MHNG | = Museum d'Histoire Naturelle, Geneva |
| MRAC | = Musée Royal d'Afrique Centrale, Tervuren |
| MZT | = Zoological Museum, University of Turku, Turku |
| NSMT | = National Science Museum, Tokyo |
| SMF | = Senckenberg-Museum, Frankfurt-am-Main |
| ZMH | = Zoologisches Museum der Universität Hamburg, Hamburg |

Note added in proof

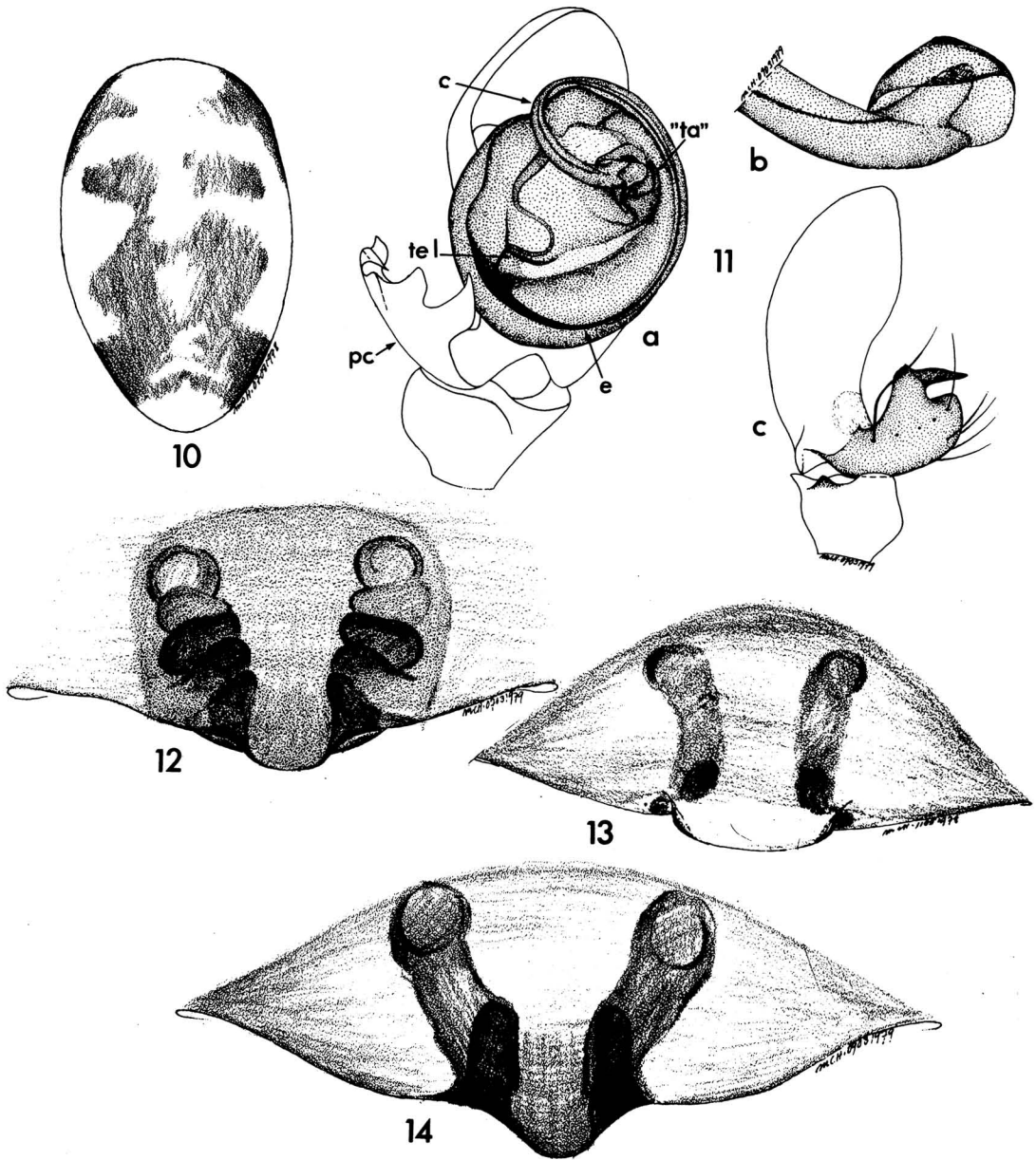
When this paper was already in press, a revision of Japanese nesticids was published by Yaginuma (1979: A study of Japanese species of nesticid spiders. — Fac. Let. Rev. Otemon Gakuin Univ., 13: 255—287), listing 47 taxa, all in *Nesticus*. According to generic criteria used in this paper, his new species will be placed in *Howaia* (*N. okinawaensis*) and *Cyclocarcina* (*N. yesoensis*, *N. breviscapus*, *N. kataokai*, *N. iwatensis*, *N. abukumanus*, *N. gondai*, *N. akamai*, *N. shinkaii*, *N. floronoides tatoro*, *N. f. notoi*, *N. f. komatsui*, *N. kaiensis*, *N. monticola*, *N. mikawanus*, *N. gujoensis*, *N. masudai*, *N. suzuka*, *N. yamato*, *N. tarumii*, *N. nishikawai*, *N. akiensis*, *N. furenensis*, *N. bungonus*, *N. iriei*, and *N. takachiho*). No attempt is made here to discuss the status of these taxa. The known spider fauna of Japan now includes 43 named taxa in *Cyclocarcina*, one Nesticini incertae sedis (*N. uenoi*), and three species of *Howaia*.



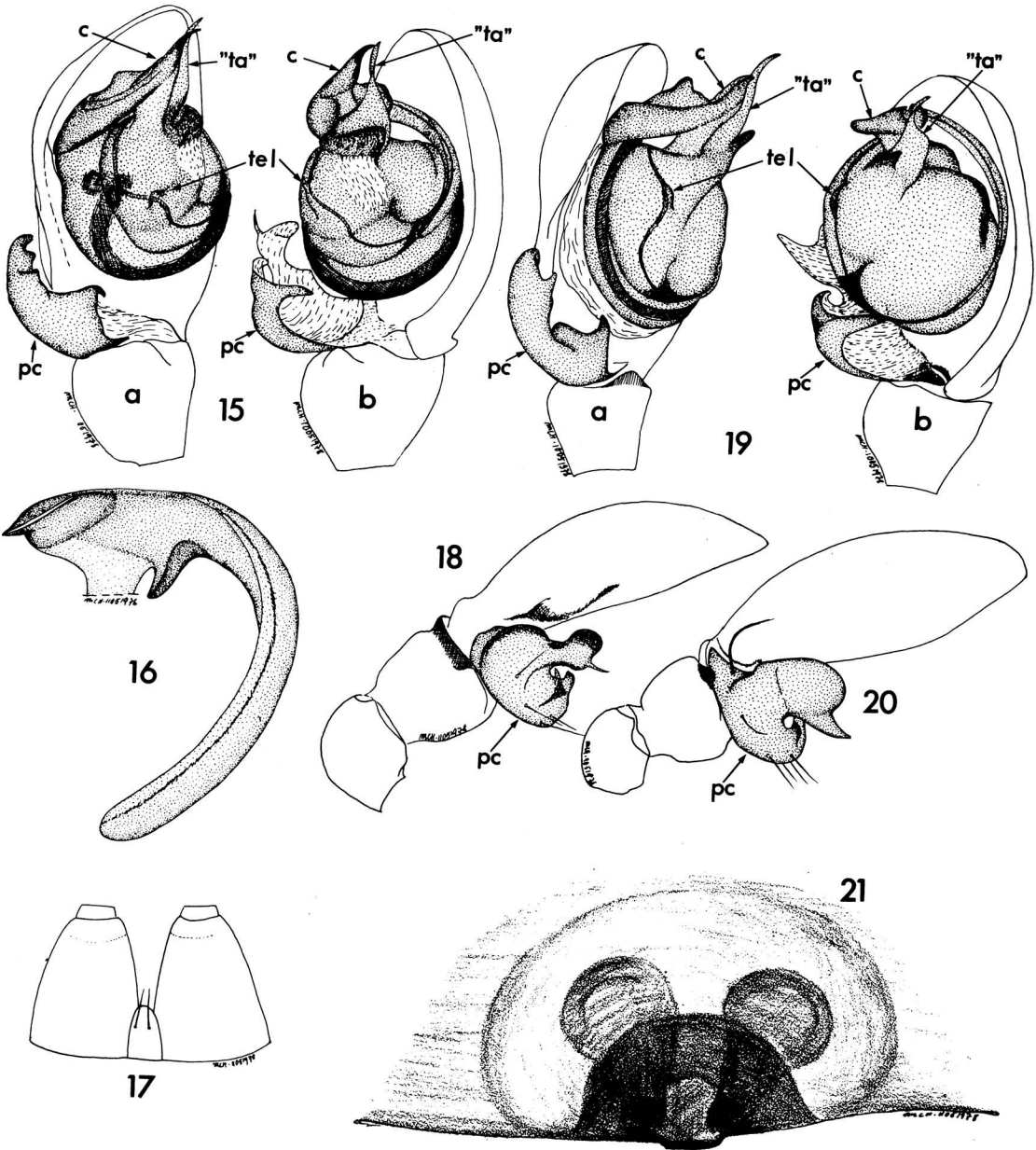
Figs. 1–6. *Nesticus cellulanus* (Clerck). — 1: male palp ventrally (a) and laterally (b). — 2: subtegulum and tegulum ventrally with conductor-tegular apophysis complex detached. — 3: conductor-tegular apophysis complex dorsally. — 4: tibia and cymbium dorsally. — 5: right half of vulva ventrally. — 6: epigyne ventrally. — Abbreviations: a = appendix, c = conductor, e = embolus, g = vulval gland, gd = gland duct, mr = main receptacula, pc = paracymbium, s = epigynal slit, st = subtegulum, t = tegulum, "ta" = "terminal apophysis", te I = tegular apophysis I, te II = tegular apophysis II.



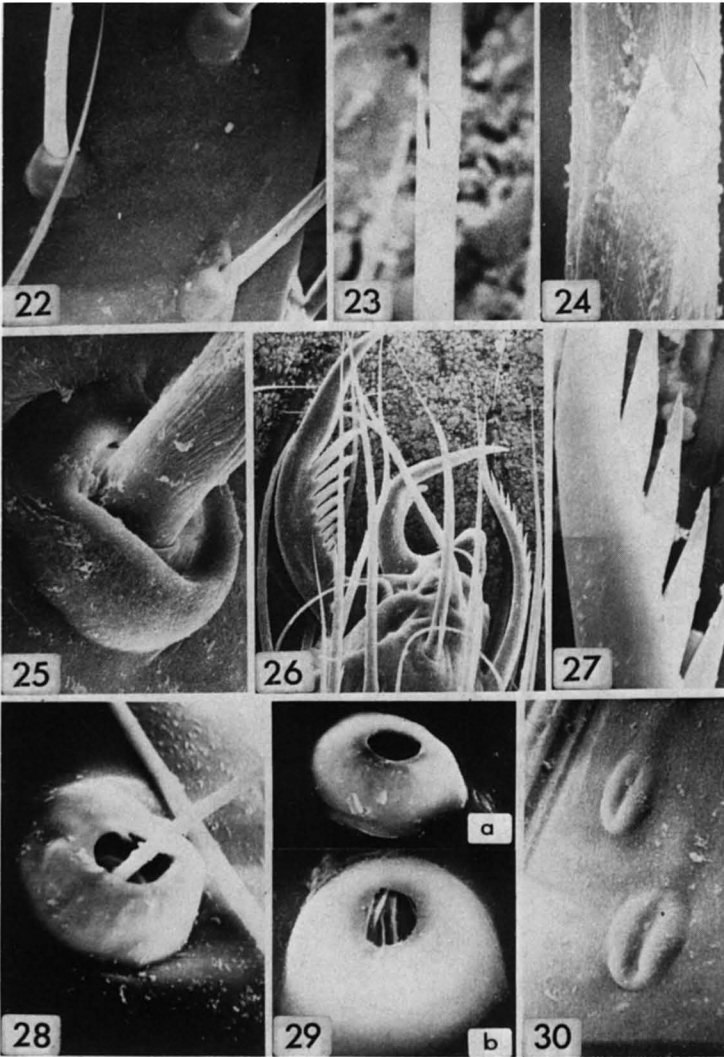
Figs. 7—9. *Howaia mogera* (Yaginuma). Figs. 7—8 Fiji; Fig. 9 Hawaii. — 7: male palp laterally (a) and right half of vulva ventrally (b) and dorsally (c). — 9: epigyne ventrally. — Abbreviations: see legend to Figs. 1—6.



Figs. 10—14. *Howaia buiconghieni* sp. n. (Figs. 10—12), *H. inthanoni* sp. n. (Fig. 13), and *H. proszynskii* sp. n. (Fig. 14). — 10: male abdomen dorsally. — 11: male palp ventrally (a), tip of conductor (b), and paracymbium laterally (c). — 12—14: epigynes ventrally. — Abbreviations: see legend to Figs. 1—6.



Figs. 15—21. *Nesticella taurama* sp. n. (Figs. 15—18), *N. robinsoni* sp. n. (Figs. 19—20), and *N. sogi* sp. n. (Fig. 21). — 15: male palp ventrally (a) and mesially (b). — 16: conductor mesially. — 17: cymbium, tibia, and patella dorsally. — 18: colulus and anterior spinnerets. — 19: male palp ventrally (a) and mesially (b). — 20: cymbium, tibia, and patella dorsally. — 21: epigyne ventrally. — Abbreviations: see legend to Figs. 1—6.



Figs. 22—30. *Howaia mogera* (Yaginuma) (Figs. 22—23, 29 b), *Nesticus cellulanus* (Clerck) (Figs. 26—27, 30), *Nesticella sogi* sp. n. (Figs. 28, 29 a). — 22: tarsal surface, 600x. — 23: tarsal hair, 1800x. — 24: erect tibial hair, 3600x. — 25: base of erect tibial hair, 3600x. — 26: tarsal tip, 360x. — 27: serrate bristle of tarsal tip, 3000x. — 28: base of metatarsal trichobothrium, 1800x. — 29: tarsal organ, 1800x. — 30: slit sense organs of tibial surface, 1200x.

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