



Do the species with *facies reclinobunoides* make up a clade?—A new *Lomanius* (Opiliones, Podoctidae) from Vietnam and a discussion on its relationships

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Abstract

Lomanius annae **sp. nov.** is described from southern Vietnam. The species is characterized by the greatly developed dorso-basal process on cheliceral hand of males and by the partial effacement of all mesotergal grooves. The genus *Lomanius* contains four generic synonyms and currently comprises eight valid species distributed in China, Java, peninsular Malaysia, the Philippines, and Taiwan. The new species displays a general morphology similar to the former genus *Paralomanius*, with a combination of sexually dimorphic interocular mound (which is very large and strongly leaned back in males) and pedipalpus (which is extremely elongate in males). This morphological suite of features is herein called *facies reclinobunoides*. The replacement name *Metibalonius triceratops* **nom. nov.** is proposed for *Trispinibunus abnormis* Roewer, 1915, which is a junior secondary homonym of *Ibalonius abnormis* Strand, 1911. Finally, **numerous** morphological structures found in Podoctidae are recognized and named: (1) the cheliceral comb, present on cheliceral fingers, (2) the chained tubercular ridges, present on dorsal scutum **and (3) several others related to the ocular region**. The distribution of these two structures among podoctid species is not fully known, but both are absent in the former Ibaloniinae. We suggest that both structures may be useful to define supra-generic groups in the clade composed of the former Podoctinae and Erecananiinae.

Key words: Arachnida; harvestmen; Erecananiinae; Indochina; Indo-Malaya; Philippines; cheliceral comb; chained tubercular ridges

Introduction

Podoctidae is a Palearctic family of Grassatores with nearly 130 species organized in 54 genera (Kury 2013). The family has been traditionally divided into three subfamilies, Ibaloniinae, Podoctinae, and Erecananiinae (Mello-Leitão 1938; Kury 2007). In a recent phylogenetic molecular treatment, Sharma *et al.* (2017) tested for the first time the monophyly of these subfamilies and defined generic relationships within the family. Their results showed that the subfamily Ibaloniinae can only be regarded as a monophyletic group if we exclude *Sitalcicus gardineri* (Hirst, 1911) and *Ibalonius inscriptus* Loman, 1902, both from the Seychelles. The subfamily Podoctinae is a paraphyletic group that includes the Erecananiinae, the only subfamily retrieved as monophyletic in the phylogeny. Two of the four genera belonging to the Erecananiinae were included in the analyses (namely *Lomanius* Roewer, 1923, and *Paralomanius* Goodnight & Goodnight, 1948), and both were synonymized under *Lomanius*. Although the Sharma *et al.* (2017) phylogeny represents an important first step towards the systematics of Podoctidae, the taxonomy of the family is still in an unsatisfactory state, and clear definitions of genera and subfamilies are needed.

The general morphology of podoctids is incredibly diverse, with great variation in size, leg length and armature, shape of the interocular mound, and forms of sexual dimorphism (Kury 2007). Some species, for instance, have a marked sexually dimorphic interocular mound, which is strongly spiked and reclined backwards in males (Fig. 1): *Lomanius longipalpus* (Goodnight & Goodnight, 1948), *L. mindanaoensis* Suzuki, 1977, *Metibalonius biantipalpis* (Roewer, 1915), *M. esakii* Suzuki, 1941, *M. longipalpis* Roewer, 1915. Some these

species also have a sexually dimorphic pedipalpus, which is much more elongate in males. We informally call this set of features related to the shape of interocular mound *facies reclinobunoides* and regard them as primary homologies *sensu de Pinna* (1991). This term is based on the generic name *Reclinobunus* (currently under the synonymy of *Metibalonius*), which comes from Latin verb *rēclīno* (to bend back, lean back) + Greek βουνός (mound). However, in the phylogeny by Sharma *et al.* (2017), *Metibalonius* is included in “Ibaloniinae”, while *Lomanius* in “Erecananinae”, thus not retrieving the species showing *facies reclinobunoides* as a clade (Fig. 1).

Here we describe a new podoctid from southern Vietnam that we recognize as a member of the genus *Lomanius sensu Sharma et al.* (2017). This new species shows marked sexual dimorphism in both the size and shape of the interocular mound and length of pedipalpus. Thus, we use the description to formally define components of the *facies reclinobunoides* and to discuss the putative homology of the components of this morphological syndrome shared by some species of *Metibalonius* and *Lomanius* (Fig. 1). Moreover, we describe for the first time an appendicular structure, the cheliceral comb, which is a row of lamellae located on the postero-mesal surface of the fixed cheliceral finger. This structure occurs in the new species but it is also found in other species of Podoctidae, although its distribution within the family is unknown (see “Discussion” for more details). Finally, we integrate our results and the internal topology of podoctids provided by Sharma *et al.* (2017) to briefly discuss the biogeography of the genera *Metibalonius* and *Lomanius*.

Material and methods

Terminology and abbreviations. Dorsal scutum outline terminology in Laniatores follows Kury & Medrano (2016). Cheliceral dentition terminology in Podoctidae follows Kury & Machado (2009). Rows of megaspines of pedipalpus are described by the formula $n + n + n$, where the plus signs represent gaps (diastemata) between spines or groups of spines (n). Tarsal formula refers to the numbers of tarsomeres in tarsus of legs I to IV. When an individual count is given, order is from left to right side (figures in parentheses denote number of tarsomeres only in the distitarsus I–II). Descriptions of colors follow Kury & Orrico (2006). As the traditional Podoctidae subfamilies were not recovered as monophyletic in the phylogenetic analysis by Sharma *et al.* (2017), they are used between quotation marks along the text.

Abbreviations of the repositories cited are: AMNH (American Museum of Natural History—Entomology, New York, USA), FMNH (Field Museum of Natural History, Chicago, USA), HCMUS (University of Science, Vietnam National University, Ho Chi Minh City), MNHN (Muséum National d’Histoire Naturelle, Paris, France), MNRJ (Museu Nacional, Rio de Janeiro, Brazil), SIE-VAST (Southern Institute of Ecology, Vietnam Academy of Science and Technology, Ho Chi Minh City, Vietnam). Other abbreviations used here are: CL = carapace length, CW = carapace width, ID = interocular distance, AL = abdominal scutum length, AW = maximum abdominal scutum width, Cx = coxa, Tr = trochanter, Fe = femur, Pa = patella, Ti = tibia, Mt = metatarsus, Ta = tarsus, A1 = distal pair(s) of antlers, A2 = proximal pair(s) of antlers, CTB = cervical tubercular bridge(s), DPS = dorsal process of the spear, IMs = interocular mound: spear, IMt = interocular mound: tower, LTB = lacrimal tubercular bridge, SS = superciliary spine, and ZTB = zygomatic tubercular bridge. All geographic coordinates have been converted to decimal.

Images and measurements. Scanning electron microscopy (SEM) was mostly carried out with a JEOL JSM-6390LV at the Center for Scanning Electron Microscopy of Museu Nacional, UFRJ. The preparation of structures for SEM comprised dissection, dehydration in increasing concentrations of ethanol with subsequent air drying, and mounting on a fold of tape onto an aluminum 3/8” cylindrical stub. The preparation of penis for drawing consisted of dissection, clarification with lactophenol, staining with acid fuchsin, and mounting on a concave slide with a circular cover glass so that the piece could be rolled into standard positions. Maps have been created with ESRI ArcGIS 10.1, and biogeographical units are from the WWF Terrestrial Eco-regions of the World (Olson *et al.* 2001). All measurements presented in this paper are in mm or μm .

Material examined. Specimens relative to the new species described here come from a recent expedition of Louis Deharveng and Anne Bedos (MNHN) in South-eastern Asia. Besides these, specimens of the following species showing *facies reclinobunoides* have been examined for comparative purposes:

- *Lomanius longipalpus* (Goodnight & Goodnight, 1948): 2 ♂ 6 ♀ (AMNH AK 175), PALAU (Micronesia), E Ngatpang, 65 m, Babelthuap, 7.xii.1952.

- *Lomanus mindanaoensis* Suzuki, 1977: 1 ♀ (FMNH AK 200), PHILIPPINES, Mindanao, Davao Prov., East slope Mt McKinley, tree in mossy forest, 6500 feet moss 35'30" above ground lot # 2/4, 8.ix.1946, H. Hoogstraal leg.
- *Lomanus minimus* Roewer, 1926: 2 ♂ 3 ♀ (AMNH AK 279), PHILIPPINES, Luzón, Mt. Makiling, Lagunas, rainforest, xi.1968, R. A. Morse leg.
- *Metibalonius esakii* Suzuki, 1941: 9 ♂ 23 ♀ 2 juv. (AMNH AK 179), FEDERATED STATES OF MICRONESIA, Ponape Isl., Nanpil, Nett District, Pacific Science Board, Ent. Survey of Micronesia, 27.ii.1948, Henry S. Dybas leg.; 11 ex. (AMNH AK 174), Micronesia, Ponape Isl., Mt. Kupwuriso, summit, 2000 ft, beating vegetation, 10.iii.1948, Henry S. Dybas leg.

We have also included in our study some species not showing *facies reclinobunoides*:

- *Baramia longipes* Banks, 1930: 1 ♂ 1 ♀ (MNRJ 8024), MALAYSIA, Lundu, Taman Negara Gunug Gading (1.6907°, 109.846067°, alt. 35 m), 21.xii.2012, A.B. & I.S. Kury leg.; 1 ♂ 1 ♀ (MNRJ 8025), MALAYSIA, Sarawak, Gunung Santubong, (1.729517°, 110.317417°, alt. 95 m), 18.xii.2012, A.B. & I.S. Kury leg.
- *Bonea scopulata* Roewer 1949: 1 ♂ (MNRJ 9260), SINGAPORE, Upper Pierce Reservoir Park (1.37369°, 103.81152°, alt. 47 m), nocturnal, on trees, 15.vii.2016 A. Giupponi & A. Kury leg.
- *Dongmoa* sp.: 1 ♂ 1 ♀ (AMNH AK 128), VIETNAM, Nghe An, Khe Choang ca 5 km from Khe Bu forest (19.010556°, 104.735556°), 1.v.1998, Minh & Kha leg.
- *Hoplodino continentalis* Roewer, 1915: 7 ♂ 29 ♀ (MNRJ 9257) SINGAPORE, Upper Pierce Reservoir Park (1.37369°, 103.81152°, alt. 47 m), on tree trunks at night, 15.vii.2016, A. Giupponi & A. Kury leg.
- *Santobius annulipes* (Sørensen, 1886): 1 ♂, 2 ♀ (AMNH AK 280) FIJI, Viti Levu, Nadarivatu, c. 870 m, 9 Jan. 1987 N. I. Platnick leg.; 1 ♀ (AMNH AK 305) Fiji, Viti Levu, Nausori highlands, 10 Jan. 1987 N. I. Platnick leg.

Systematic background

In 1905, the Dutch arachnologist Jan Loman described the species *Podoctis tridens* Loman, 1905, from Java, Indonesia. This species was later transferred to the new genus *Lomanus* erected by Roewer (1923: 187) and included in the subfamily Erecananinae (Phalangodidae). According to the original definition by Roewer (1912), the Erecananinae includes any phalangodid with five scutal grooves, Fe I armed with rows of spines, distitarsus I bearing two segments, and no scopula (Roewer, 1912). Subsequently, other five species have been added to the genus: *L. formosae* (Roewer, 1912) from Taiwan; *L. minimus* (Roewer, 1926) and *L. rectipes* (Roewer, 1963), both from Luzón, Philippines; *L. carinatus* Suzuki, 1976, from Kuala Pilah, Malaysia; and *L. bulbosus* Zhang, Kury & Zhang, 2013, from Yunnan Province, China.

Goodnight & Goodnight (1948: 9) described in Erecananinae the new genus *Paralomanus* Goodnight & Goodnight, 1948, along with two new sympatric species: *Paralomanus longipalpus* Goodnight & Goodnight, 1948, and *Paralomanus brevipalpus* Goodnight & Goodnight, 1948, from Palau, the first consisting only of males and the second only of females. They provided limited drawings of their habitus in lateral view, making it difficult to recognize both species based on their descriptions.

Having received paratypes of both species from the Goodnights, Roewer (1949) took the approach of the original authors one step further and described the new monotypic genus *Eulomanus* Roewer, 1949, for *Paralomanus brevipalpus*, leaving *Paralomanus* also monotypic. He also provided cursory figures of the species, marginally better than the original ones.

Some years later, Goodnight & Goodnight (1957: 75) synonymized several genera with *Lomanus* Roewer, 1923, including *Paralomanus* and *Eulomanus*. They belatedly recognized that both their alleged species *Paralomanus longipalpus* and *P. brevipalpus* were males and females of a single species and also proposed the latter to be a junior synonym.

Twenty years later, Suzuki (1977: 22) described the new subspecies *Lomanus longipalpus mindanaoensis* Suzuki, 1977, from the Philippines. In his figure 8C, Suzuki represented a “female” with variant development of the interocular mound, and which we strongly suspect to be a beta (or minor) male (see “Discussion” for more details).

More recently, Zhang *et al.* (2013) treated *Paralomanus*, revalidating the genus and providing an emended diagnosis. Sharma *et al.* (2017) again synonymized *Paralomanus* with *Lomanus* due to the nested placement of *Paralomanus* in a molecular phylogeny of Podoctidae.

Definition of morphological terms

Based on extensive examination of the external morphology of several species, as well as on the taxonomic literature of Podoctidae, we propose here names and formal definitions for some structures related to the ocular region, which are typical of this family. Some of these structures seem to be exclusive to species of *Lomanius* and *Metibalonius* exhibiting *facies reclinobunoides*.

Interocular mound (IM; Kury, 2007): a promontory located medio-anteriorly on the carapace (Kury & Machado 2009), most often composed of a *tower* and a *spear* (see below). The IM differs from the eye mound (ocularium), widespread in many other Phalangida, because: (1) the eyes in the ocularium are always imbedded into the mound, but this is not the case of the IM, in which the eyes are ancestrally separated from the mound, and imbeds into the IM only in some genera, such as *Dongmoa* and *Bonea* (Fig. 1); (2) the ocularium is a half-ellipsoid, wider than long, and usually as high as long, while the IM is a cone or a frustum (somewhat flattened anteriorly), usually higher than long (Fig. 1).

Tower: a granulose mound, usually with a blunt conical shape and somewhat flattened anteriorly. The tower can be relatively low, as in *Santobius* spp. and *Lomanius minimus* (Kury & Machado 2009; Fig. 1), or very high, as in *Baramia* spp., *Bonea* spp., and *Dongmoa* spp. (Fig. 1). In the species showing *facies reclinobunoides*, the tower of males is bent backwards in different degrees, ranging from slightly leaned back, as in *Metibalonius esakii*, to entirely prostrated on the dorsal scutum, as in *Lomanius annae*, *L. longipalpus*, and *L. mindanaoensis* (Fig. 1).

Spear: a spike with smooth tegument arising from the top of the tower (Fig. 1). Although the spear occurs in many species of podoctids, it is possible to recognize two main configurations: (1) a straight spear clearly distinct from the tower, usually bent forward, such as in *Baramia* spp., *Bonea* spp., and *Dongmoa* spp. (Fig. 1); (2) a curved spear streamlined to the point to which the distinction between it and the tower is not so clear, such as in all species of *Lomanius* and *Metibalonius* depicted in Fig. 1 (except *Lomanius minimus*).

Antlers: robust, paired spiniform processes arising from the laterals of the IM tower (Fig. 1). In many species it is possible to recognize a proximal (usually shorter) and a distal (usually longer) pair of antlers (Fig. 1). However, there are species with additional pairs of antlers and the homology of the supernumerary antlers with the proximal and distal antlers is still not established. Antlers are restricted to some species of *Lomanius* and *Metibalonius*, forming a necessary but not sufficient condition for the *facies reclinobunoides* (Fig. 1).

Dorsal process of the spear (DPS): a short, blunt projection arising from the dorsum of the spear forming an acute angle (Fig. 1). The DPS is a component of the *facies reclinobunoides*, and most species of *Lomanius* and *Metibalonius* depicted in Fig. 1 (except *L. minimus* and *M. triceratops*) have this structure. In species belonging to other genera, such as *Baramia*, *Bonea*, and *Dongmoa*, there are one or two spines reminiscent to the DPS, but they clearly emerge from the tower, instead of from the spear (Fig. 1). Moreover, these spines are usually longer and more acuminate than the DPS (Fig. 1).

Eye lumps: two widely separated small mounds, each one containing one eye. In some cases, the eye lumps may be close to the IM tower, but not imbedded into it, as in *Santobius* spp. (Kury & Machado 2009) and all species of *Lomanius* and *Metibalonius* depicted in Fig. 1. In other cases, the eye lumps may be completely imbedded into the IM tower, as in *Baramia* spp., *Bonea* spp., and *Dongmoa* spp. (Fig. 1). We introduce here the term eye lump, which bears one eye each side, to distinguish it from an eye mound (= **ocularium**), which bears two eyes (as in most Opiliones).

Superciliary spine (SS): small to large-sized acuminate tubercle emerging from the antero-dorsal region of the rim of the eye lump (Fig. 1). The SS is absent in all species of "Ibaloniinae" (except *Metibalonius* spp.) and in all species in which the eye lumps are completely imbedded into the IM tower (see above).

Ocular tubercular bridges: opposing pairs of tubercles, one arising from the eye lump and the other arising either from the anterior margin of the dorsal scutum or the post-ocular surface of the carapace. The tips of the paired tubercles touch each other forming a structure that resembles a tegumentary bridge (Fig. 1). We propose the names *lacrimal tubercular bridge* (LTB) for the anterior pair of tubercles (Fig. 1), which is likely to be a synapomorphy of Podoctidae (Kury 2007), and *zygomatic tubercular bridge* (ZTB) for the posterior pair, which is restricted to some species of *Lomanius* and *Metibalonius* and is a component of the *facies reclinobunoides* (Fig. 1).

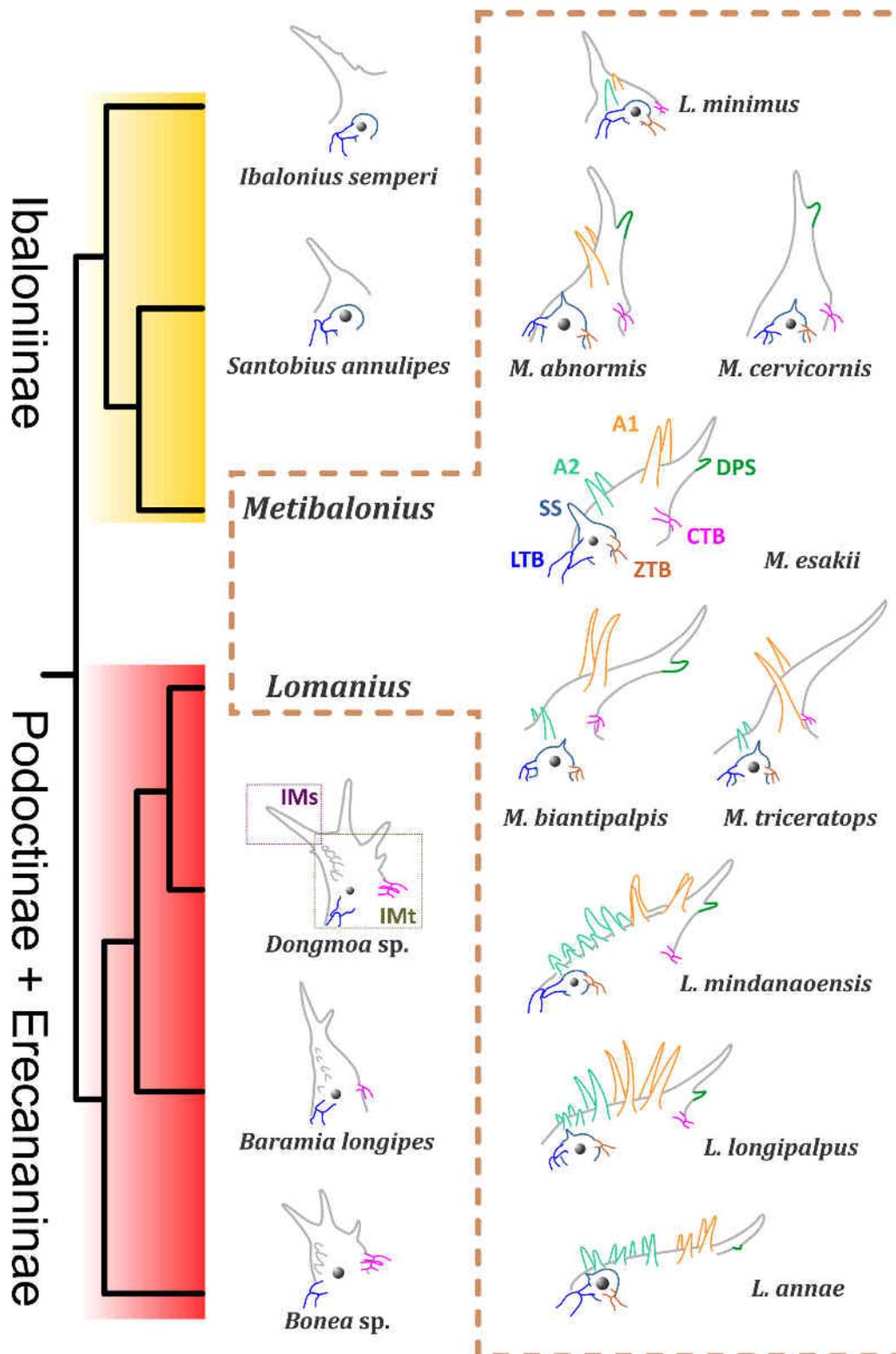


FIGURE 1. Features related to the interocular mound plotted on a simplified topology of the podocetid phylogeny (modified from Sharma *et al.* 2017). The yellow shaded background represents the “Ibaloniinae” and red shaded background represents the clade “Podocetinae + Erecananinae”. The dashed area to the right side includes species of *Lomanius* and *Metibalonius* showing different degrees of *facies reclinobunoides*. All species depicted here show putatively homologous structures on the interocular mound (grey line). Abbreviations and their respective color codes are: A1 = distal pair(s) of antlers (orange); A2 = proximal pair(s) of antlers (light-green); CTB = cervical tubercular bridge(s) (pink); DPS = dorsal process of the spear (dark-green); IMs = interocular mound: spear; IMt = interocular mound: tower; LTB = lacrimal tubercular bridge (blue); SS = superciliary spine (navy blue); ZTB = zygomatic tubercular bridge (brown). *Bonea* is represented here by the type species *Bonea sarasinorum* Roewer, 1913.

Cervical tubercular bridges (CTB): opposing pairs of tubercles, one arising from the posterior margin of the IM tower and the other arising from the middle surface of the carapace (Fig. 1). In some species there are multiple pairs CTBs in the posterior margin of the IM tower, as in *Baramia* spp., *Bonea* spp., and *Dongmoa* spp. (Fig. 1).

Systematic accounts

Lomanius Roewer, 1923

Lomanius Roewer 1923: 187 [type species: *Podoctis tridens* Loman, 1905, by subsequent designation of Roewer (1949: 283)].

Paralomanius Goodnight & Goodnight 1948: 9; Roewer 1949: 286 (diagn.); Zhang *et al.* 2013: 216 (revalidated; diagn.) [junior subjective synonym of *Lomanius* Roewer, 1923, by Goodnight & Goodnight (1957: 75); synonymy disclaimed by Zhang *et al.* (2013: 216); synonymy reaffirmed by Sharma *et al.* (2017: 171); type species: *Paralomanius longipalpus* Goodnight & Goodnight, 1948, by original designation].

Thaipea Roewer 1949: 284 [junior subjective synonym of *Lomanius* Roewer, 1923, by Goodnight & Goodnight (1957); type species: *Erecanana formosae* Roewer, 1912, by original designation].

Maquilingius Roewer 1949: 284 [junior subjective synonym of *Lomanius* Roewer, 1923, by Goodnight & Goodnight (1957); type species: *Lomanius minimus* Roewer, 1926, by original designation].

Eulomanius Roewer 1949: 286 [junior subjective synonym of *Lomanius* Roewer, 1923, by Goodnight & Goodnight (1957: 75); type species: *Paralomanius brevipalpus* Goodnight & Goodnight, 1948, by original designation].

Orthossus Roewer 1963: 225 [junior subjective synonym of *Lomanius* Roewer, 1923, by Suzuki (1977: 22); type species: *Orthossus rectipes* Roewer, 1963, by original designation].

Etymology. *Lomanius* honors Dutch arachnologist Jan Cornelis Christiaan Loman (1856–1929). Gender masculine.

Placement. *Lomanius* has been originally placed in Phalangodidae, Erecananinae. The subfamily was transferred to Podoctidae by Mello-Leitão (1938), which was never accepted by Roewer. Therefore, Podoctidae Erecananinae of Mello-Leitão (and as used today) is equivalent to Phalangodidae Erecananinae of Roewer.

Included species. *Lomanius annae* sp. nov., *Lomanius bulbosus* Zhang, Kury & Zhang, 2013, *Lomanius carinatus* Suzuki, 1976, *Lomanius formosae* (Roewer, 1912), *Lomanius longipalpus* (Goodnight & Goodnight, 1948), *Lomanius mindanaoensis* Suzuki, 1977, *Lomanius minimus* Roewer, 1926, *Lomanius rectipes* (Roewer, 1963), *Lomanius tridens* (Loman, 1905).

Diagnosis. See Suzuki (1977: 22) and “Discussion” below.

Distribution. Micronesia, Philippines, and Indochina.

Lomanius annae sp. nov.

(Figs 2–7)

Type data. 1 ♂ holotype (HCMUS Vn06-267) Vietnam: Dong Nai: Tan Phu: forest nature reserve, 17/12/06, secondary forest, litter, Berlese (11.138756°, 107.376677°, alt. 120 m), Louis Deharveng & Anne Bedos leg. ♂ paratype, mounted for SEM (MNHN VIET-746), Vietnam, Tây Ninh province, Tây Ninh, Nui Ba Den, 06/01/2000, secondary forest, litter, Berlese (11.379271°, 106.173827°, alt. 600 m), Louis Deharveng & Anne Bedos leg. 1 ♀ paratype (MNHN Vn 05-110), Vietnam, Kiên Giang Province, Ha Tien, Nui Da Dung, 05/12/05, litter, Berlese (10.4288°, 104.477°), Louis Deharveng & Anne Bedos leg. 3 ♂ 1 ♀ 1 juv. paratypes (MNHN Vn 05-116), Vietnam, Kiên Giang Province, Ha Tien, Nui Da Dung, 05/12/05, litter, Berlese after sifting (10.4288°, 104.477°), Louis Deharveng & Anne Bedos leg. 1 ♀ paratype (SIE-VAST Vn06-210) Vietnam: Binh Thuan: Ta Kou: au sommet, 13/12/06, Rainforest, litter, Berlese (10.814757°, 107.900135°, alt. 695 m), Louis Deharveng & Anne Bedos leg. 2 ♂ 1 ♀ paratypes (MNRJ 9461 Vn06-258) Vietnam: Dong Nai: Tan Phu: forest nature reserve, 17/12/06, Secondary forest, litter, sifting & Berlese (11.138756°, 107.376677°, alt. 120 m), Juliette Arabi leg.

Distribution. The new species is known only from Vietnam (Fig. 8A), occurring in the following eco-regions: Tonle Sap-Mekong peat swamp forests (IM0165), Southeastern Indochina dry evergreen forests (IM0210), and Southern Vietnam lowland dry forests (IM0211).

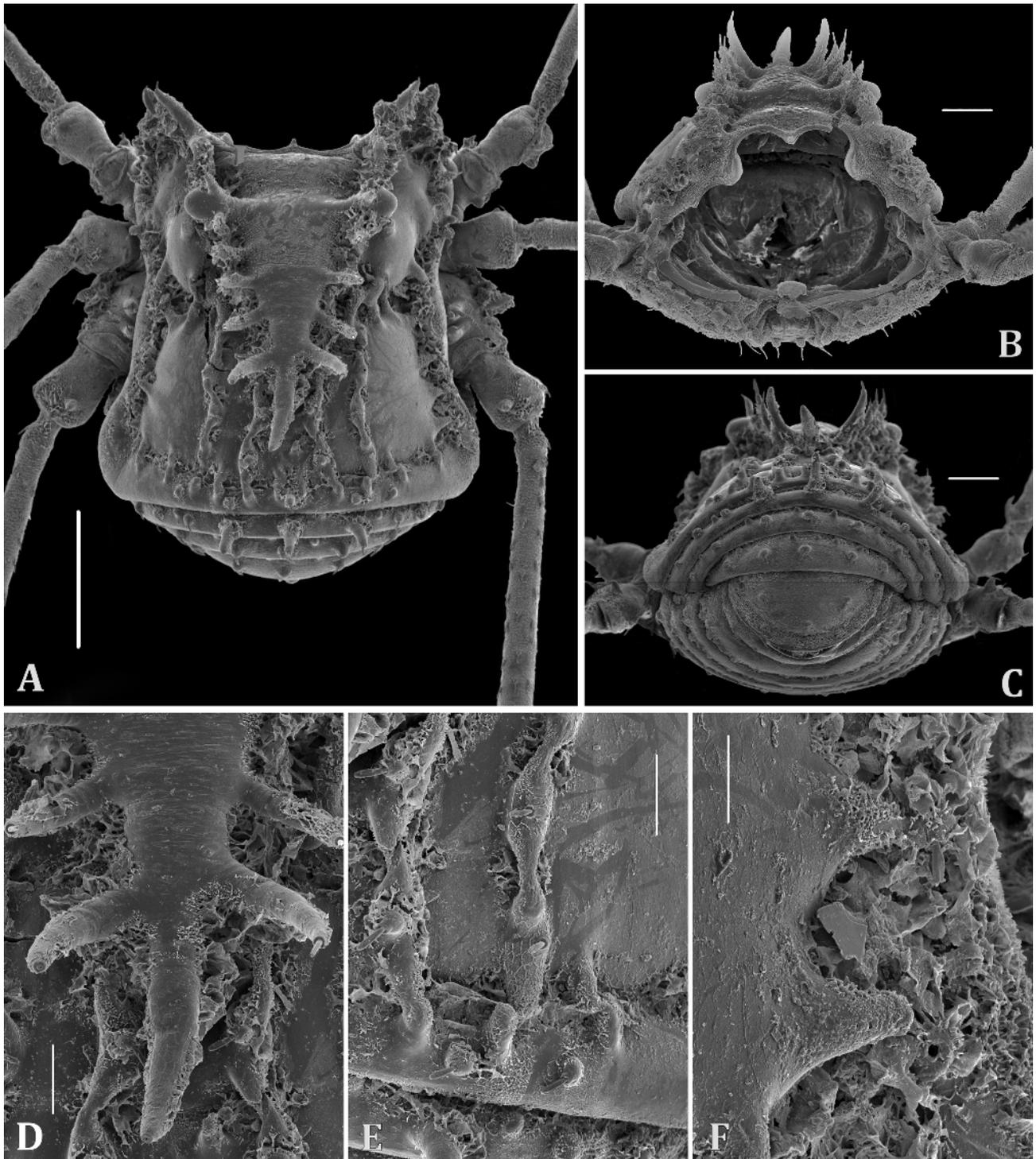


FIGURE 2. *Lomanius annae* sp. nov., male paratype (MNHN VIET-746): A. Habitus, dorsal view. B. Same, frontal view. C. Same, posterior view. D. Reclined interocular mound, distal portion, dorsal view. E. Scutal areas III to V, detail of chained tubercular ridges, dorsal view. F. Boundary groove between mesotergum and lateral margin of scutum, showing tubercular bridges. Scale bars: 500 μ m (A), 200 μ m (B, C), 100 μ m (D, E), 50 μ m (F).

Etymology. Specific name is a patronymic in honor to Anne Bedos (MNHN) for her relentless work on soil arthropods from Asia.

Diagnosis. *L. annae* sp. nov. shares with the former *Paralomanius* species (i.e., *L. longipalpus* and *L. mindanaoensis*) the IM reclined backwards (in males) and the pedipalpus sexually dimorphic in length (much elongate in males). Males of *L. annae* sp. nov. differ from both in having the IM tower very thin and strongly prostrate against dorsal scutum (Figs 3A, C). The dorso-basal projection of cheliceral hand (Figs 5A, B) is unique in Podoctidae.

Description. Male holotype (HCMUS Vn06-267): Measurements (in mm): CL = 0.6, CW = 1.1, ID = 0.6, AL = 0.8, AW = 1.4, Basichelecerite = 0.5, cheliceral hand without fingers = 0.8, cheliceral fingers = 0.3, Pedipalpal Fe = 2.0, Pedipalpal Pa = 1.8, Pedipalpal Ti = 0.7, Pedipalpal Ta = 1.0, Pedipalpal claw = 0.2, Fe I = 1.0, Pa I = 0.6, Ti I = 0.7, Mt I = 0.9, Fe II = 1.7, Ti II = 1.4, Mt II = 1.1, Fe III = 1.1, Ti III = 0.7, Mt III = 1.1, Fe IV = 1.5, Ti IV = 1.1, Mt IV = 1.7.

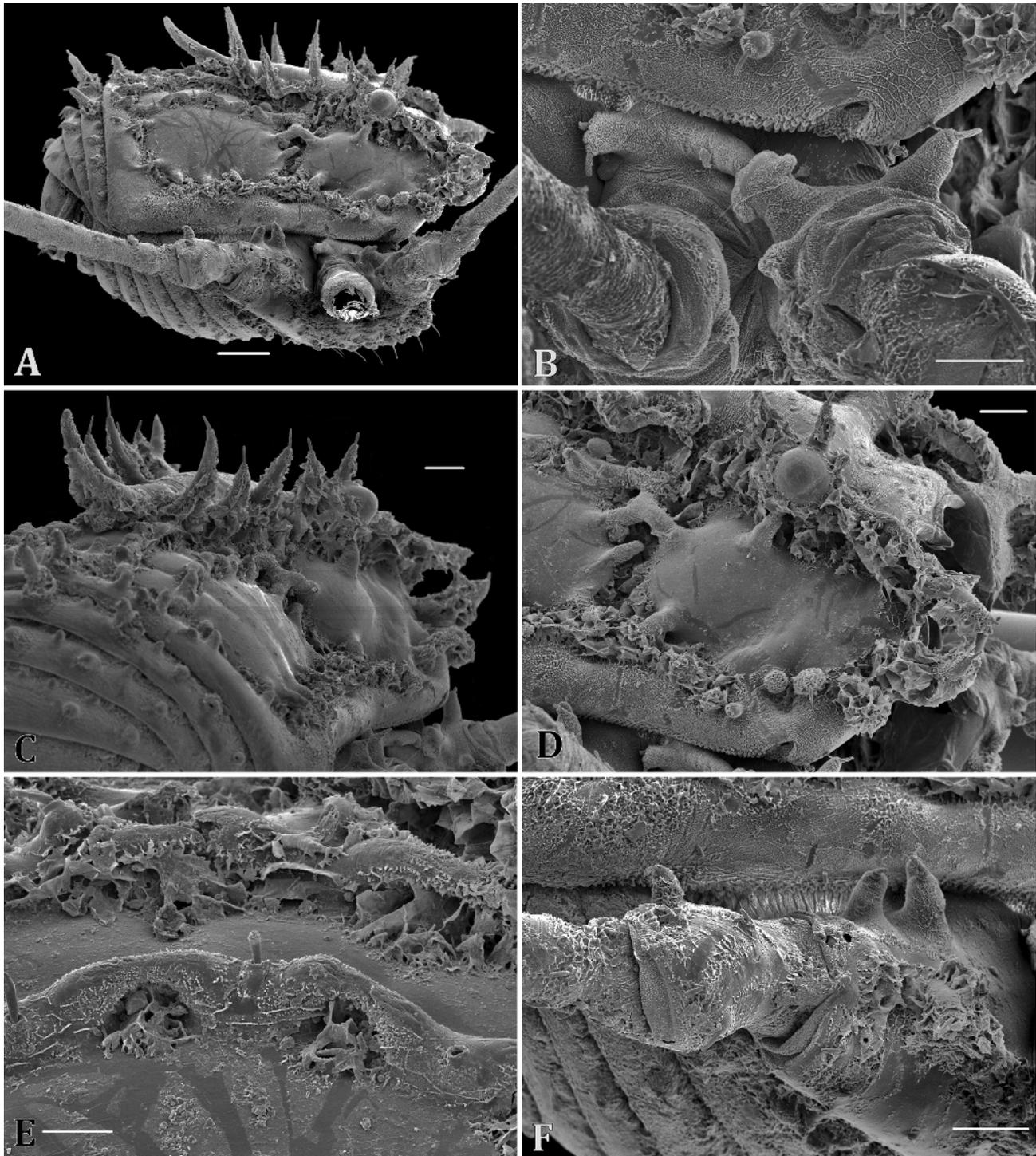


FIGURE 3. *Lomanius annae* sp. nov., male paratype (MNHN VIET-746): A. Habitus, right side, lateral view. B. Same, detail of ozopore region. C. Dorsal scutum, postero-lateral view. D. Carapace, latero-frontal view. E. Scutal area III, detail of tubercular bridges linking it to areas II and IV, latero-anterior view. F. Coxa and trochanter IV in situ, lateral view. Scale bars: 200 μ m (A), 100 μ m (B, C, D, F), 50 μ m (E).

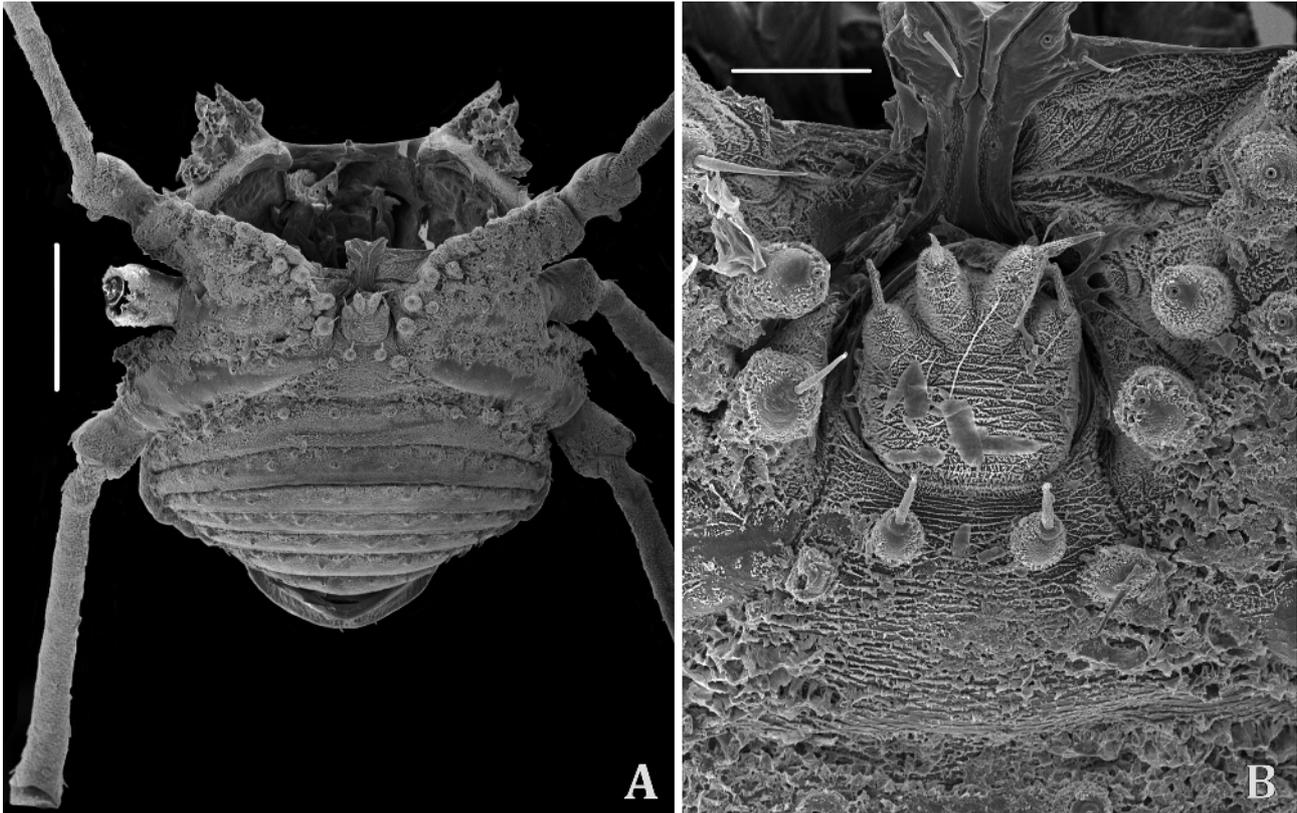


FIGURE 4. *Lomanius annae* sp. nov., male paratype (MNHN VIET-746): A. Coxa I to IV, stigmatic area, and free sternites, ventral view. B. Same, detail of genital operculum. Scale bars: 500 μ m (A), 100 μ m (B).

All spines of body and leg I with tegument entirely microtuberculate-rivulose-microgranulate (Fig. 4B). Main grooves of scutum covered by adhesive flakes (Figs 2F, 3D, E), which gather debris. Pedipalpus and chelicerae glossy (Figs 5A–D).

Dorsal scutum outline type eta, subrectangular, flaring posteriorly (Fig. 2A). Carapace with three pairs of antero-lateral spines (Figs 2A, B, 3A, D). IM tower strongly prostrate against dorsal scutum, covering most of mesotergum. It has the shape of a thin triangular tongue, bordered with 4 pairs of antlers and ending in a large apical spear bearing a dorsal process (Figs 2A–D, 3A, C). Eye lumps situated widely apart (Figs 2A, B), connected to scutum anteriorly and posteriorly by lacrimal and zygomatic tubercular bridges, respectively (Figs 3C, D). Ozopore well-marked, rivulose, clearly visible from lateral, but not from above (Fig. 2A), opening into a slanted frame opposite to Cx II (Figs 3A–C). Taenidium formed by large tubercles with rivulose-microgranulate sculpture (Fig. 3B). Cx I and II each with the usual pair of dorsal apophyses forming a wide angle with each other. Apophyses Cx II posterior + Cx III anterior connected to each other (Fig. 3B).

Mesotergum trapezoid, well-defined by a perimeter groove, but not clearly divided into areas (Figs 2A and 3A do not allow vision of grooves), except for faint grooves in the middle third that allow recognizing the general regions of the four typical areas (Fig. 3C), whereas both lateral thirds are unmarked. In the central portion of mesotergum each area I to IV possesses a transverse row of four anterior and four posterior stout tubercles that are strongly interlocked with their anterior and posterior counterparts forming tubercular bridges like chain links (Fig. 2A). These bridges are connected among them forming four strong longitudinal ridges (Figs 2E, 3E). Besides those ridges, mesotergum is further connected to carapace (Figs 3A, C, D), lateral margin of scutum (Fig. 2F), and area V (Fig. 2E) by larger tubercular bridges.

Dorsal scutum unarmed, except for area V with 1 median tubercle (Fig. 3A). Free tergite I with 3 conical tubercles, plus extra smaller setiferous tubercles. Free tergites II–III each with double transverse row of setiferous tubercles, but none of those standing out (Figs 2C, 3A, C). Anal operculum with an arch of three setiferous tubercles (Fig. 2C).

Cx I to III ventrally bordered by an inner series of large setiferous tubercles forming an arch. Processus

fulcrites numerous and obscured by flakes and pastes debris (Fig. 4A). Stigmatic area extremely short T-shaped, with a posterior transverse groove separating it from posterior margin (= opisthosomal sternite 2). Opisthosomal sternites 3 to 6 and 7/8 bearing each a transverse row of small setiferous tubercles (Fig. 4A). Stigmatic area and genital operculum with rivulose-microgranulate sculpture, the latter with 4 stout setiferous tubercles (Fig. 4B).

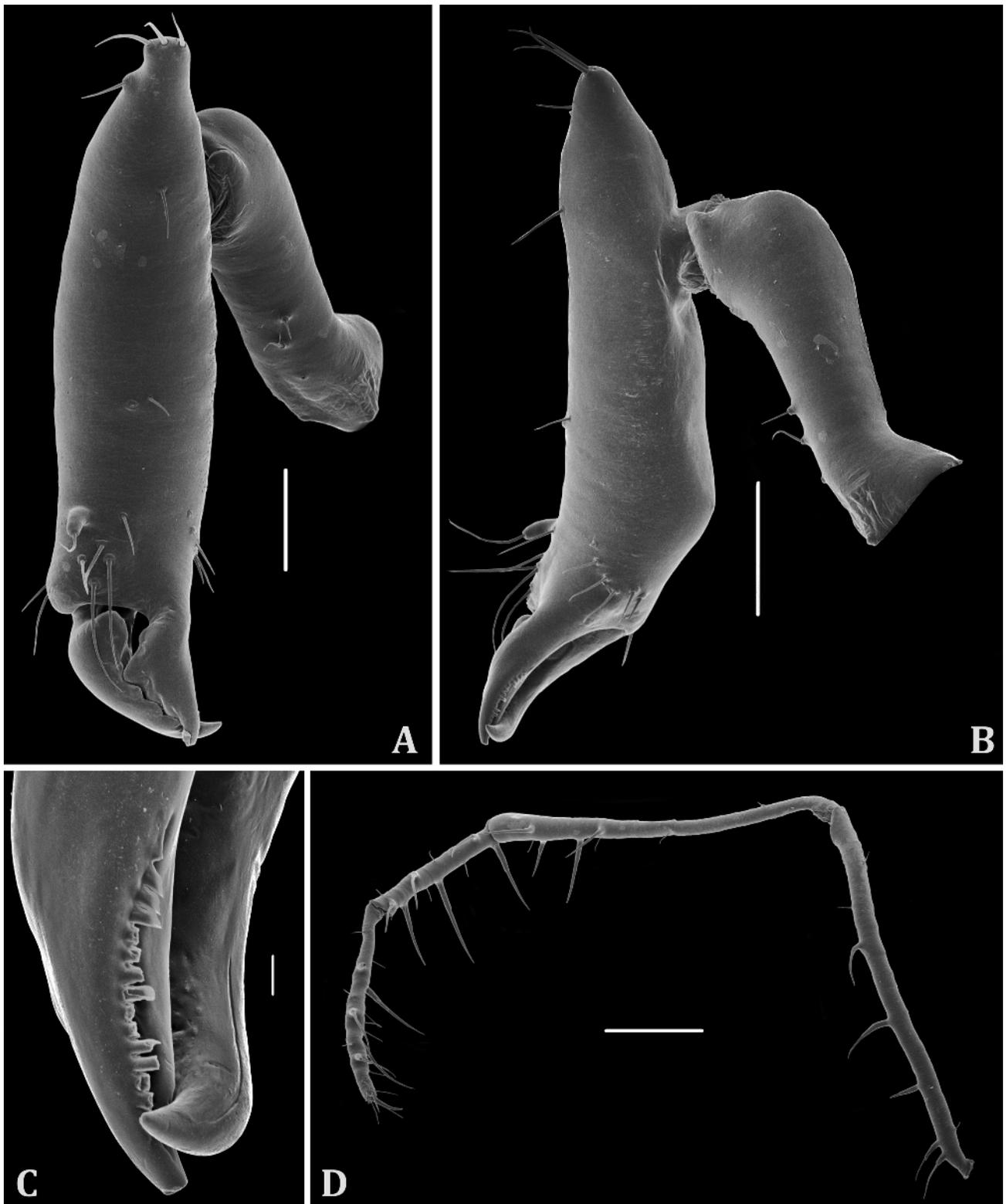


FIGURE 5. *Lomanius annae* sp. nov., male paratype (MNHN VIET-746), mouthparts: A. Right chelicera, frontal view. B. Same, mesal view. C. Same, detail of cheliceral comb on fixed finger, postero-mesal view. D. Right pedipalpus, mesal view. Scale bars: 500 μ m (D), 200 μ m (A, B), 20 μ m (C).

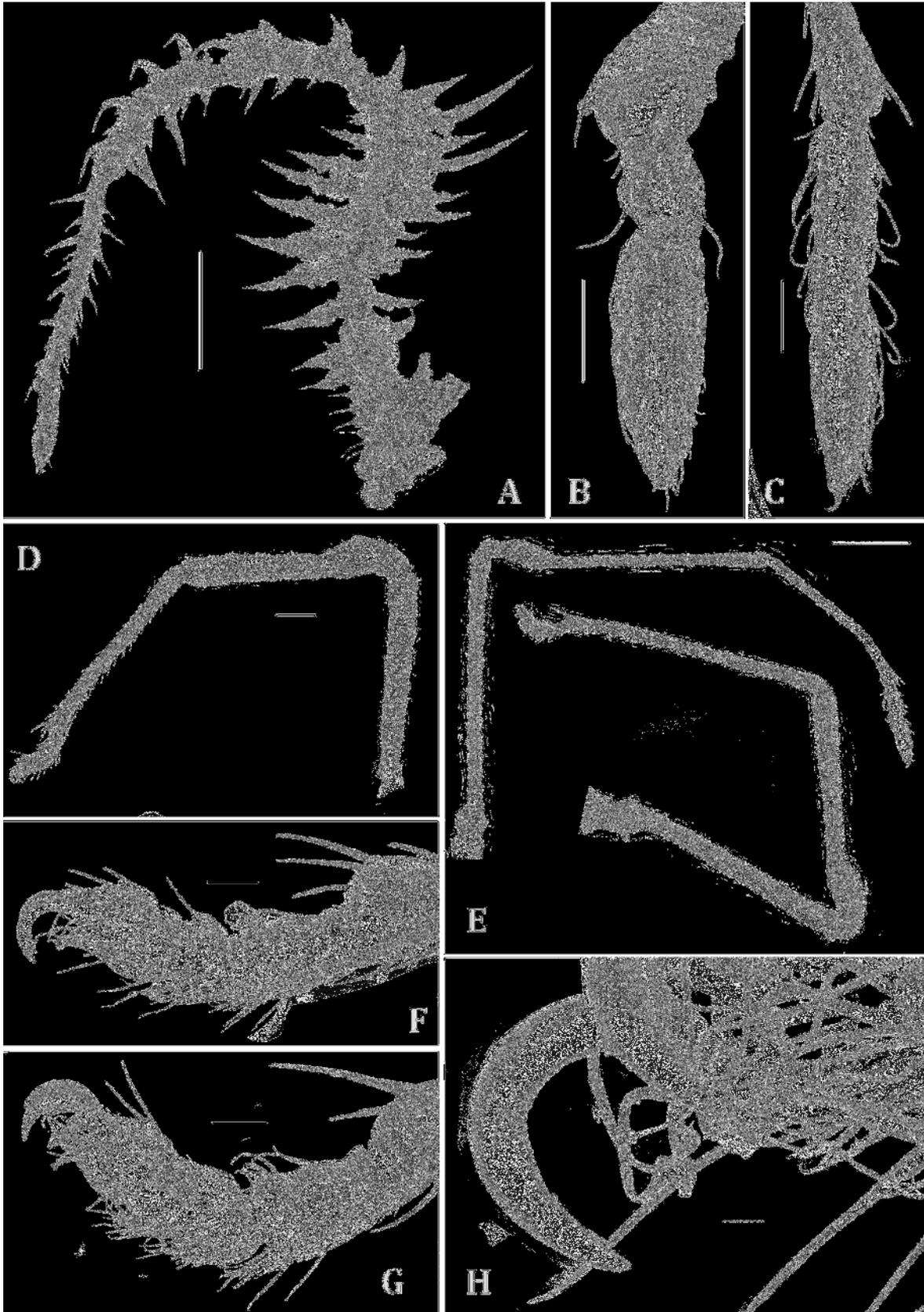


FIGURE 6. *Lomanius amae* sp. nov., male paratype (MNHN VIET-746): A. Right leg I, prolateral view. B. Left leg I, tarsus, retrolateral view. C. Right leg II, tarsus, prolateral view. D. Right leg III, prolateral view. E. Right legs II and IV, retro- and prolateral views. F. Right leg III, tarsus, prolateral view. G. Right leg IV, tarsus, prolateral view. H. Right leg III, tarsus, showing claws and incipient scopula, pro-ventro-apical view. Scale bars: 500 μ m (A, E), 200 μ m (D), 100 μ m (B, C), 50 μ m (F, G), 10 μ m (H).

Basichelicerite unarmed, except for two small ventral setiferous tubercles, elongate slender, thicker distally, but without well-defined bulla (Figs 5A, B). Cheliceral hand slender and elongate, with basal part greatly projected dorsally much beyond articulation with basichelicerite and tipped with 4 setae. Other scattered setae concentrated on distal part (Fig. 5A). Distal part of cheliceral hand along with cheliceral fingers sharply bent frontally (Fig. 5B). Fm1 as a low mound, Fc1 massive, determining the whole slope of cheliceral blade, Fi1–3 diminishing in size to distal. Mc1 huge, almost occluding with the notch formed by apical part of cheliceral hand. Mi1–3 small (Fig. 5A). Cheliceral comb present on the postero-mesal surface of the fixed cheliceral finger, and composed of 14 lamellae (Fig. 5C).

Pedipalpal Fe much longer and a bit slenderer than Fe I, only gently bent distally, unarmed, except for a ventral row of 2 + 1 + 1 + 1 megaspines and a few scattered much smaller setiferous tubercles. Pedipalpal Pa much elongate, as long as Fe, thicker on distal half, with 2 ventral and 2 mesal megaspines also on distal half. Pedipalpal Ti and Ta each with a mesal and an ectal row of 3 megaspines and smaller accessory spines. All segments cylindrical, but Ta with some clearly marked constrictions (Fig. 5D).

Leg I (Fig. 6A) heavily incrustated with dirt. Tr I with 1 dorsal, 2 ventral, and 3 ectal spines. Fe I with dorsal (13 spines) and ventral (8) rows of unequal powerful megaspines and 1 subdistal ectal megaspine. Pa to Mt I also heavy spined. Legs II to IV (Figs 6D, E) unarmed, without notable features. Tarsi I–IV inserted subdistally on Mt. Tarsi III–IV without thick scopula, although some modified setae can be seen (Fig. 6H). Tarsal claws unpectinated (Figs 6F–H). Tarsal counts: 2(1)-2(1)/2(1)-2(1)/5-5/5-5 (Figs 6B, C, F, G).

Male genitalia (Figs. 7A–C). Truncus a little thicker distally, apical border gently concave. Six pairs of short macrosetae: 3 on the lateral border of ventral plate, 2 ventro-distal, and 1 the shortest on the apical border of ventral plate. *Follis* as a lamellar sac typical of the family, situated distally, even surpassing distal border of ventral plate. A pair of flattened conductors, expanded apically. Stylus, long, sinuous, and flattened.

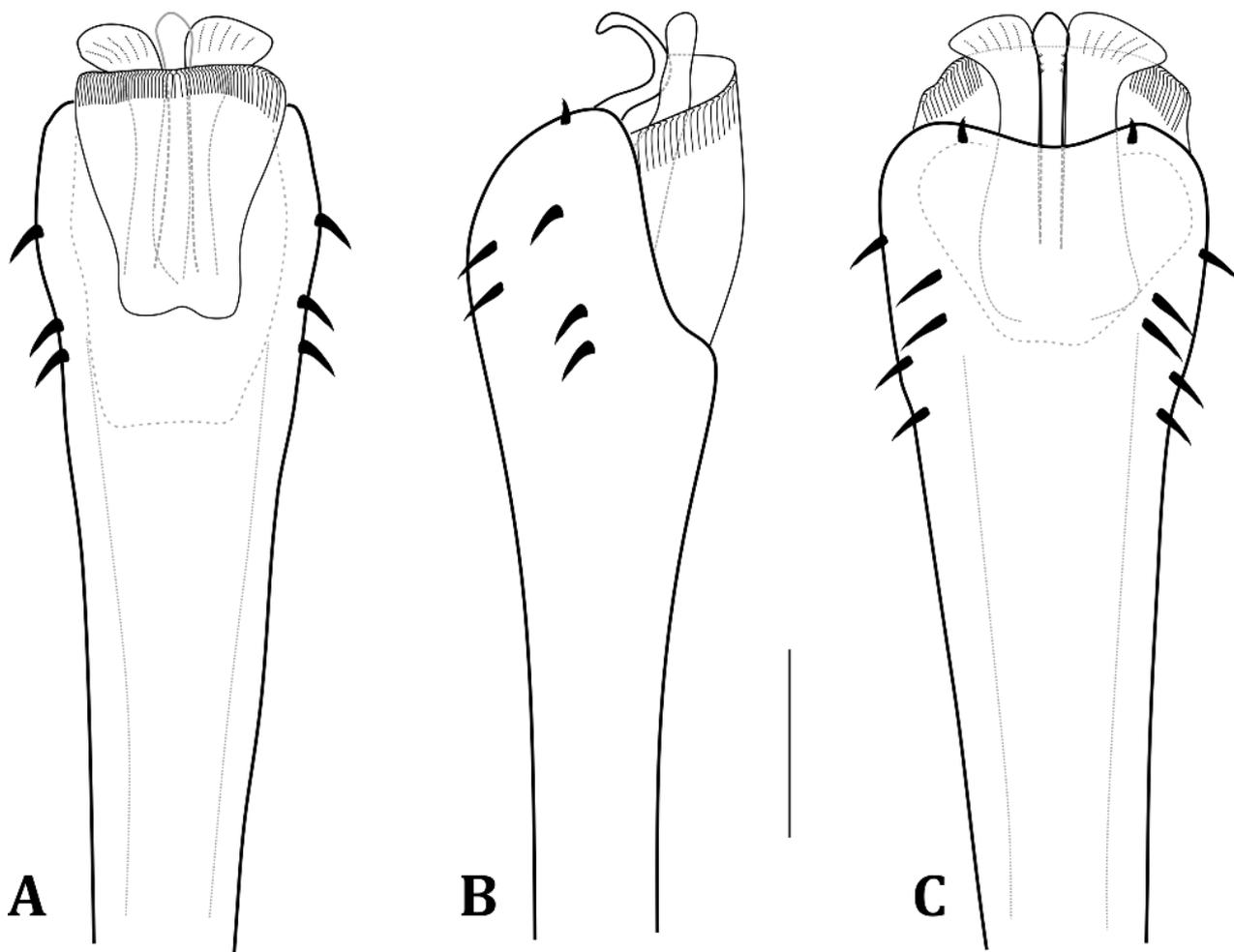


FIGURE 7. *Lomanius annae* sp. nov., male paratype (MNHN Vn-05-116), male genitalia, distal part: A. Dorsal view. B. Lateral view. C. Ventral view. Scale bar: 100 μ m.

Color (in alcohol) (Figs 8A–D). Body and appendages “moderate orange yellow” (71), densely reticulated in “deep brown” (56), especially on carapace, mesotergum and free tergites. Antlers, spear, and free tergite I lighter in the same way as the background.

Sexual dimorphism. Typical of species showing *facies reclinobunoides*, in that the IM tower of female is much smaller and not prostrate backward, and the pedipalpus not especially elongate, with patella, tibia and tarsus subequal in length (Figs 8C–D). Examples of this dimorphism in the literature are *L. longipalpus* (see Goodnight & Goodnight, 1957, figs 2–3) and *L. mindanaoensis* (see Suzuki, 1977, fig. 8). Furthermore, the female cheliceral hand lacks any dorsal projection and distal angle, and the basichelicerite is not elongate, with the bulla well-marked, contrasting with the attenuated bulla of male.



FIGURE 8. *Lomanius annae* sp. nov.: A. Male holotype (HCMUS Vn06-267), habitus, dorsal view. B. Same, lateral view. C. Female paratype (MNHN Vn 05-110), habitus, dorsal view. D. Same, lateral view. Scale bars: 1 mm.

***Metibalonius triceratops* nomen novum**

Trispinibunus abnormis Roewer 1915: 46; Roewer 1923: 171, fig. 190; Roewer 1949: 258, figs 30a–c.

Metibalonius abnormis; Goodnight & Goodnight, 1957, by **implication**. [junior secondary homonym of *Metibalonius abnormis* (Strand, 1911), first noted here]

Type data. ♂ holotype (SMF RI 1139), from PAPUA NEW GUINEA, “Friedrich-Wilhelmshafen”, [= Madang Province, Madang, -5.22°, 145.8°].

Remarks. When Goodnight & Goodnight (1957: 77) proposed the synonymy of *Trispinibunus* Roewer, 1915 with *Metibalonius* Roewer, 1915, they inadvertently created a secondary homonymy of *Trispinibunus abnormis* Roewer, 1915 with *Ibalonius abnormis* Strand, 1911, type species by monotypy of *Strandibalonius* Roewer 1912, also synonymized with *Metibalonius* by Goodnight & Goodnight (1957), but this homonymy has not been hitherto detected. Therefore, we here propose the **new replacement name** *Metibalonius triceratops* **nom. nov.** The new name refers to the three main prongs: two antlers in the IM tower and the apical spear (Fig. 1).

Discussion

Based on the information presented here, and also on the available literature on the family Podoctidae, we address six major questions in our discussion that are related to: (a) the putative existence of a clade composed of species showing *facies reclinobunoides* (question 1), (b) the evolution of some conspicuous morphological characters, such as male pedipalpus elongation, cheliceral comb, chained tubercular ridges, and some specific traits of male genitalia (questions 2 to 5), and (c) the biogeographic significance of a *Lomanius* species occurring in continental Asia (question 6).

(1) Do the species with *facies reclinobunoides* make up a clade?

It is difficult to compare our results in the light of the single published phylogenetic hypothesis for the Podoctidae (Sharma *et al.* 2017) because only eight of the 55 podoctid terminals therein could be identified to described species. Sharma *et al.* (2017) recovered *Metibalonius* sp. 1 to sp. 5 (all from Australia or Papua) as a clade in their paraphyletic “Ibaloniinae”, but we do not know if any of those morphotypes matches the *facies reclinobunoides*. Moreover, it should be noted that some of the formally described *Metibalonius* species are known only by females, such as *M. cervicornis* (Strand, 1911). Thus, their matching to the *facies reclinobunoides* cannot be evaluated.

In the phylogeny by Sharma *et al.* (2017), there is also a clade of *Lomanius* sp. 1 to sp. 6 (all also from Australia or Papua) nested in a clade that match with the former “Erecananinae”. This is the sister group to the other clade of “Erecananinae”, composed of *Paralomanius longipalpus longipalpus* (from Palau) plus *Lomanius* sp. 7 to sp. 11 (all from Luzón). Of these, *Lomanius* sp. 8 and sp. 10 are shown in the accompanying photographs. *Lomanius* sp. 8 is a typical *Lomanius sensu* Suzuki (1977), with short pedipalpus and a small, sprawled interocular mound (fig. 3, photo 8), while *Lomanius* sp. 10 displays a reclined interocular mound and a short pedipalpal femur (fig. 3, photo 7). This combination is equal to the one that appeared in figure 8C from Suzuki (1977), which was reported as a female, and which could be a beta (= minor) male. Intrasexual dimorphism in the length, thickness, or armature of the pedipalpus has already been reported in several species of the suborders Eupnoi and Laniatores (reviewed in Buzatto & Machado 2014), but there is no formal description of this phenomenon among podoctids.

The “Erecananinae” sampled in Sharma *et al.* (2017) correspond to the former *Paralomanius* (from the Philippines and Palau) plus the traditional *Lomanius sensu* Suzuki (1977) (from the Philippines) and a third group of *Lomanius* from Australia and Papua New Guinea (from which they were hitherto unreported, see Fig. 9B). Their *Metibalonius* are all from Australasia, which matches well the previous reported distribution of the genus (Fig. 9B). However, the 16 species currently placed in *Metibalonius* show great variation in external morphology, and almost certainly comprise a non-monophyletic group. It is necessary to check the morphology of the terminals used in Sharma *et al.* (2017) in order to know if some of those species show the *facies reclinobunoides* and to have an idea about the concept of *Metibalonius* that was tested in that study. Considering the lack of morphological information, there are two hypotheses that need to be tested in order to access the status of the *facies reclinobunoides* as a clade.

The first hypothesis is that the species showing *facies reclinobunoides* compose a monophyletic group. This hypothesis is based on two main assumptions: (1) The *Metibalonius* studied by Sharma *et al.* (2017) are not related to the *Metibalonius* depicted in Fig. 1, and thus they do not show sexual dimorphism in the shape and size of the interocular mound. This is the case of at least six nominal species in the genus, namely *M. femoralis* (Roewer, 1949), *M. gracilipes* Roewer, 1915, *M. obscurus* (Roewer, 1915), *M. oppositus* (Roewer, 1927), *M. scaber* (Roewer, 1915), and *M. spinatus* (Roewer, 1949); (2) The nominal *Metibalonius* species showing *facies reclinobunoides* (Fig. 1) are more closely-related to the clade composed of “*Paralomanius*” and *Lomanius* sp. 7 to sp. 11 of Sharma *et al.* (2017).

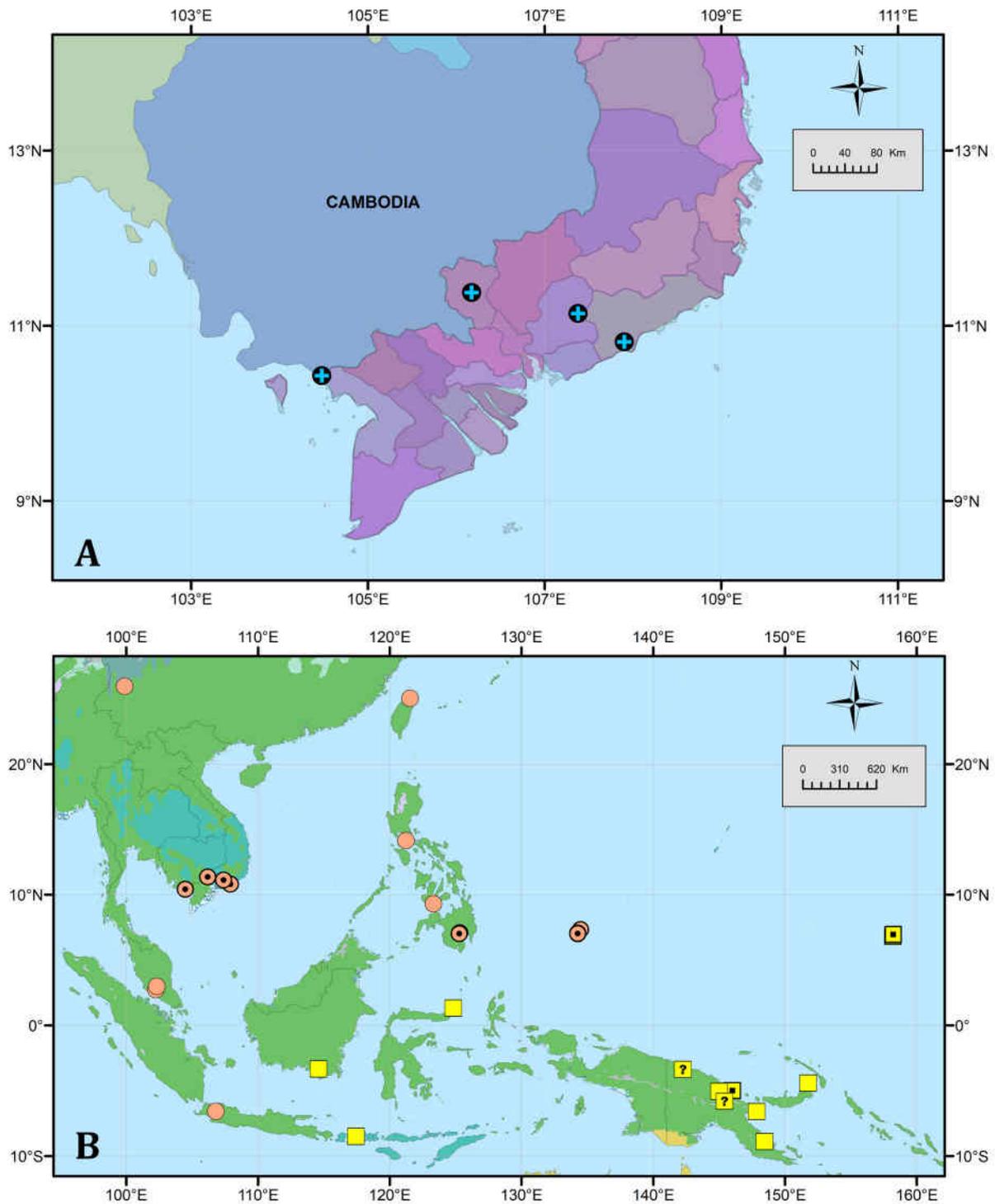


FIGURE 9. Maps of southeastern Asia and northwestern Australasia. A. Detail of southern Vietnam, showing distribution of *Lomanius annae*. Shaded areas in the background are Vietnamese provinces. B. Distribution of the known species of *Lomanius* (circles) and *Metibalonius* (squares). Species showing *facies reclinobunoides* are marked by a middle black dot within each symbol. Empty symbols denote species without reclinobunoid features. Symbols with a question mark indicate doubt about possession of *facies reclinobunoides* because only females have been described. Shaded areas in the background are WWF biomes.

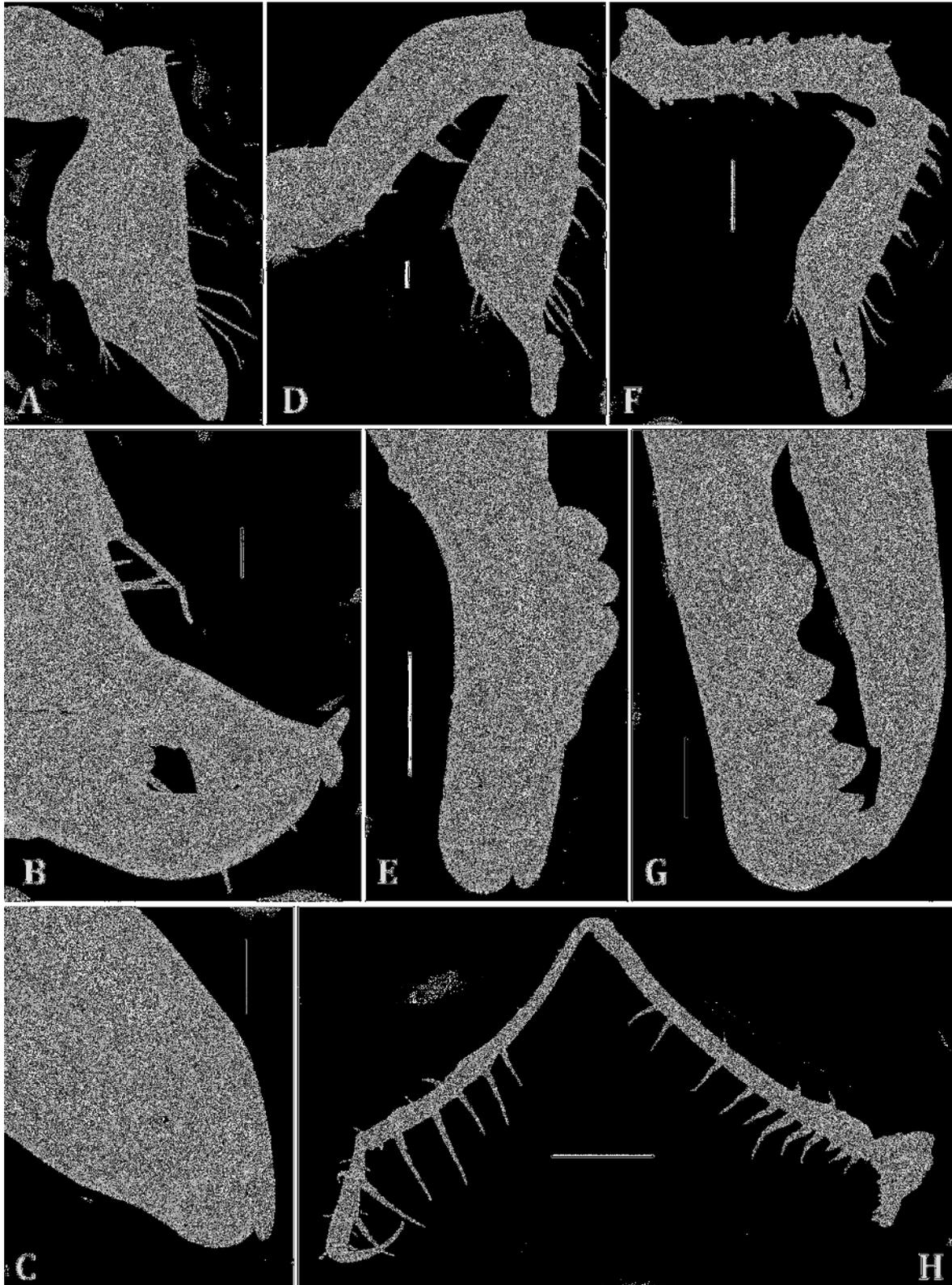


FIGURE 10. Morphology of chelicerae and pedipalpi in diverse species of Podoctidae. A–C: *Metibalonius esakii* Suzuki, 1941, female (MNRJ 5943) from Ponape, left chelicera. A. Hand, postero-mesal view. B. Fingers, ventro-posterior view. C. Same, detail, mesal more oblique to posterior view. D–E: *Lomanius longipalpus* (Goodnight & Goodnight, 1948), male (AMNH AK 175) from Palau, left chelicera. D. Whole chelicera, mesal view. E. Fingers, postero-mesal view. F–H: *Hoplodino continentalis* Roewer, 1915, male (MNRJ 9257) from Singapore, left chelicera and pedipalpus. F. Chelicera, mesal view. G. Cheliceral fingers, postero-mesal view. H. Left pedipalpus, whole, ectal view. Scale bars: 1 mm (H), 500 µm (F), 100 µm (A, D, G), 50 µm (B, C), 10 µm (E).

The second hypothesis is that species showing *facies reclinobunoides* compose a polyphyletic group. This hypothesis is also based on two main assumptions: (1) The *Metibalonius* studied by Sharma *et al.* (2017) show sexual dimorphism in the shape and size of the interocular mound, as the species depicted in Fig. 1. This is the case of at least five nominal species in the genus, namely *M. biantipalpis* Roewer, 1915, *M. esakii* Suzuki, 1941, *M. longipalpis* Roewer, 1915, *M. spinulatus* (Roewer, 1915), and *M. triceratops* **nom. nov.**; (2) The nominal *Metibalonius* species showing *facies reclinobunoides* (Fig. 1) are not related to the clade composed of “*Paralomanius*” and *Lomanius* sp. 7 to sp. 11 of Sharma *et al.* (2017), so that the morphological similarities in the structures associated to the interocular mound (Fig. 1) should be regarded as convergences.

With the information currently available in the literature, it is not possible to say which of the two hypotheses presented above is *a priori* more plausible. We stress, however, that there are other morphological characters not related to the interocular mound that are shared by *L. annae* **sp. nov.**, *L. longipalpus*, *L. mindanaoensis*, and at least one species of *Metibalonius* (*M. esakii*), all of them showing *facies reclinobunoides*. Among these characters, we may cite: (1) few pairs of X- or Y-shaped tubercular bridges over scutal groove connecting carapace to area I, which are absent in all “Ibaloniinae” (see fig. 8 in Suzuki 1977); (2) paramedian armature of scutal area V, and (3) macroseta C1 very short, apical, and located at the tip of each valve of ventral plate (see below). Thus, further phylogenetic analyses including a denser sample of nominal species of Podoctidae are necessary to test whether these characters represent synapomorphies of a putative clade composed of species showing *facies reclinobunoides*.

(2) Has the podoctid’s pedipalpus undergone a single event of elongation?

The elongate pedipalpus of podoctids not showing *facies reclinobunoides*, such as *Hoplodino continentalis* (Fig. 10H), is only superficially similar to those of *L. annae* **sp. nov.**, *L. longipalpus*, and *L. mindanaoensis* by having a ventro-basal cluster of megaspines on femur, patella not so extremely elongate, and shape of tibia entirely different, gradually growing thicker distally and without any constriction. Thus, it is likely that the elongation of the pedipalpus has evolved independently at least twice within podoctids. Considering that both in *Hoplodino continentalis* and in the *Lomanius* species mentioned above only males have elongate pedipalpus, the most obvious explanation is that this character has evolved independently in response to sexual selection. In several harvestman species belonging to the suborders Eupnoi and Laniatores males have either longer pedipalpus than females or structures, such as spurs and hooks, that are absent in females (examples in Buzatto & Machado 2014). In all harvestman species for which there is information on the mating behavior, males use the elongate or otherwise modified pedipalpus to grasp the female before and during intromission (Machado *et al.* 2015). However, considering that there is no behavioral study on podoctids, it is still not possible to understand the role of male pedipalpal elongation in the family and the convergent evolution of elongate pedipalpus needs to be tested in a phylogenetic framework.

(3) What is the distribution of the cheliceral comb in Podoctidae?

The cheliceral comb on the fixed finger, associated with a secondary distal groove on the cheliceral movable finger is a structure of unknown function, described here for the first time. This secondary groove on the movable finger in most species of Podoctidae does not bear a comb, although in some species it also has a comb smaller than the main one on the fixed finger. The cheliceral comb occurs in other species showing *facies reclinobunoides*, such as *M. esakii* and *L. longipalpis* (Figs 10A–E). Interestingly, the cheliceral comb is absent in *H. continentalis* (Figs 10F–G), which provides further support to our suggestion that this species is not closely-related to the species showing *facies reclinobunoides*. More information on the fine morphology and behavior of podoctids is necessary to understand the evolution of the cheliceral comb and its functional role, respectively.

(4) What are the chained tubercular ridges?

The bridges formed by facing slanted tubercles of adjacent areas of mesotergum occur in several species of podoctids, in varied conformations. In *Hoplodino* spp., for instance, the bridges occur as scattered pairs of wide ring arches (Roewer 1949, fig. 69), whereas in *Bonea cippata* Roewer, 1927, they occur as denser, but still isolated, rows (Roewer 1927, fig. 21; Suzuki 1977, figs 16A–B). In *Metapodoctis siamensis* Suzuki, 1985, the bridges become an extremely thick lattice, in which the bridges are additionally connected with neighbor bridges forming a continuous transverse suture over the mesotergal grooves (Suzuki 1985, figs 11A–B). However, the extra

longitudinal bridges merging of those tubercles with the matching tubercles in the same scutal area is of much more restrict occurrence within the family. These here called *chained tubercular ridges* were reported in *Lomanius carinatus* Suzuki, 1976 (Suzuki 1976, figs. 4A–B) and *Metibalonius yalomensis* Suzuki, 1982 (Suzuki 1982, fig. 74), but they also occur unreported in other already inadequately described species, such as *Lomanius longipalpus* (Goodnight & Goodnight, 1948). The phylogenetic distribution of those kinds of bridges is poorly known, especially because the iconography in the literature is many times tantalizingly inadequate for understanding morphological details. However, it is important to emphasize that the *chained tubercular ridges* are completely absent in the “Ibaloniinae” *sensu lato*, and occur only in some species of the “Podoctinae” and “Erecananinae”. Thus, we predict that a careful analysis of this character may reveal a useful source of phylogenetic information within the clade “Podoctinae+Erecananinae”.

(5) Are there special genital similarities between *Metibalonius* and *Lomanius*?

As opposed to the highly diverse genitalia of the “Ibaloniinae”, male genitalia in most species belonging to the “Podoctinae” + “Erecananinae” clade (Sharma *et al.* 2017) are rather uniform, with the *follis* not trespassing the ventral plate and situated dorsally, and extremely distal, even surpassing the truncus *in situ*. This is in stark contrast with the elongate structure of basal members of this clade, such as *Podoctis* spp. and *Bonea* spp., in which the truncus is deeply divided and the *follis* situated much more proximally (Kury & Machado unpublished data). The truncus may bear an apical parabolic cleft (as in *Bonea longipalpis* Suzuki, 1977, figs 18 J, M, also in *M. esakii*), but in *L. annae* **sp. nov.**, *L. longipalpus*, and *L. mindanaoensis* it is unleft (Suzuki, 1977; Kury & Machado unpublished data). Another unifying feature of most species belonging to the clade “Podoctinae + Erecananinae” is the very short macroseta C1 located at the tip of each valve of ventral plate. Thus, as occurs with other harvestman groups, male genital morphology is likely to provide important characters to support supra-generic clades within podoctids.

(6) What is the biogeographic significance of a *Lomanius* occurring in Vietnam?

Species formally placed in *Lomanius* have already been described from Indochina (Roewer 1912; Suzuki 1976; Zhang *et al.* 2013; Fig. 9B). Therefore, the discovery of a new species from Vietnam is not at odds with what we already know of the distribution of the genus. However, the occurrence of Australasian *Lomanius* (Sharma *et al.* 2017) offers a tempting hint that they might be somehow related to the Australasian *Metibalonius*, which show *facies reclinobunoides* (Fig. 9B).

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