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Revisited phylogeny of Scleroderminae (Hymenoptera: Bethylidae) reveals a plastic evolutionary history

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Abstract. The first comprehensive phylogenetic study of Scleroderminae with all 30 valid genera is presented. It is based on 138 morphological characters. Phylogenetic analyses support the monophyly of the subfamily Scleroderminae. All genus-level clades are monophyletic, except *Cephalonomia*. The extensive homoplasy across the topology is regarded as evidence of the high morphological diversity in the subfamily. *Thlastepyris marquisensis* stat. et comb.n. are transferred from the bethyline subspecies *Sierola depressa marquisensis* with species status. The traditional characters historically used in the taxonomy of Scleroderminae were mapped onto the new topology, such as body flatness, number of flagellomeres, size shape of wings and the length of 2r-rs&Rs vein of the forewing, and were shown to be highly homoplastic. Five new genera and their respective type-species are proposed, described, and illustrated as follows: *Decemnoxus infrequens* gen. et sp.n., *Longinoxus inusitatus* gen. et sp.n., *Madanoxus patulus* gen. et sp.n., *Mutatio mutata* gen. et sp.n., and *Pilocutis mollis* gen. et sp.n., the former four from Madagascar and the latter from Thailand. Madagascar plays an important role in the evolutionary history of Scleroderminae by having several odd morphological pattern and endemic fauna.

Key words. Host inference, Madagascar, New genera, Polymorphism, Sexual dimorphism, Synapomorphy-less genera.

1. Introduction

Bethylidae belong to Chrysidoidea (Hymenoptera) and have been shown to be a monophyletic taxon and sister-group of Chrysididae (Brothers & Carpenter 1993; Ronquist 1999; Ronquist et al. 1999; Carr et al. 2010). Bethylidae are known to be parasitoids and external gregarian parasitoids of larval stage of Coleoptera and Lepidoptera (Evans 1964; Gauld & Bolton 1988; Gordh & Móczár 1990; Azevedo et al. 2018), but there is one record of them attacking Hymenoptera (Melo & Evans 1993) and one attacking Diptera (Turner & Waterston 1916) The family has about 2,920 species, arranged in 96 genera (Azevedo et al. 2018), which are currently divided into four extinct subfamilies: †Elektroepyrinae, †Holopsenellinae, †Lancepyrinae and †Protopristocerinae, and five living extant subfamilies: Bethylinae, Epyrinae, Mesitiinae, Pristocerinae and Scleroderminae. The latter is the subject of this present study.

Scleroderminae are a result of the more specialized stock of species inside the old Epyrinae and grouped in the tribes Sclerodermini and Cephalonomiini Evans (1964). These latter two tribes were fused into a single one after a cladistic treatment by Lanes & Azevedo (2008) and later it was restated to the status of subfamily by Alencar & Azevedo (2013).

Scleroderminae comprise hitherto 222 species in 25 genera (Azevedo et al. 2018; Colombo & Azevedo 2019, 2020; Falières & Nel 2019): *Acephalonomia* Strejček, 1990, *Allobethylus* Kieffer, 1905, *Alloplastanoxus* Terayama, 2006, *Alongatepyris* Azevedo, 1992, †*Archaeonoxus* Colombo & Azevedo, 2019, *Bethylopsis* Fouts, 1935, †*Celonophamia* Evans, 1973, *Cephalonomia* Westwood, 1833, *Chilepyris* Evans, 1964, *Discleroderma* Kieffer, 1904, *Galodoxa* Nagy, 1974, *Glenosema* Kieffer, 1905, *Israelius* Richards, 1952, *Megaprosternum* Azevedo,

2006, *Nothepyris* Evans, 1973, *Pararhabdepyris* Gorbatovsky, 1995, †*Paleoscleroderma* Falières & Nel, 2019, *Plastanoxus* Kieffer, 1904, *Platepyris* Lanes & Azevedo, 2008, *Proplastanoxus* Terayama, 2005, *Prorops* Waterston, 1923, *Sclerodermus* Latreille, 1809, *Solepyris* Azevedo, 2006, *Thlastepyris* Evans, 1973, and *Tuberepyris* Lanes & Azevedo, 2008. The wasps of this subfamily are characterized by having the body length between 0.7–6 mm, the forewing venation reduced and the cuticle widely polished, with the parasitoidism mainly on larvae of Coleoptera in protected or cryptic conditions. Some species are being used as bio-control agents against insect pests (ABRAHAM et al. 1990). More recently, AMANTE et al. (2017) provided a complete list of bio-control or pest-control based on bethylid wasps. Several groups exhibit strong sexual dimorphism, and some have the body very flattened, as seen in *Megaprosternum*, for example (GUPTA et al. 2017).

TERAYAMA (1995) made the first phylogenetic analysis of Sclerodermini sensu Evans (1964) based on nine genera and 27 morphological characters. He concluded that the reduced venation in addition to the body sculpture simplification supported the specialization tendency. However, he found several homoplasies and suggested that more characters would be necessary. Later, TERAYAMA (2006) proposed a hypothetical arrangement of relationships between Sclerodermini and five genera of Cephalonomiini, based on an unpublished data matrix.

That proposal recovered as monophyletic the tribes defined by EVANS (1964) and proposed (Sclerodermini + Cephalonomiini) as sister-group to Epyrini. LANES & AZEVEDO (2008), considered the scarcity of apomorphic characters and the low resolution of anterior analyses to distinguish the two tribes, suggesting that they would comprise a single clade and that one of them would be a paraphyletic group. The analysis was based on 72 morphological characters from 124 specimens of 35 species in 13 genera. As a result, several genera were reorganized and two genera of Cephalonomiini were consistently found nested within Sclerodermini. In this work, they synonymized the two tribes and pointed out that KIEFFER's (1914) classification was the most similar to their analysis and conclusions; additionally, a high level of incongruence was found among characters, with low resolution inside several clades defined by autapomorphies. The genera of Cephalonomiini were only represented by two of the seven genera described at that time.

CARR et al. (2010) used 28S and 16S rRNA genes from seven genera (three from Cephalonomiini and two from Sclerodermini) and recovered Sclerodermini as a sister group of Cephalonomiini and closely related to Mesitiinae, suggesting the polyphyly of Epyrinae and the monophyly of Cephalonomiini.

ALENCAR & AZEVEDO (2013) studied the phylogeny of Epyrini through 391 morphological characters, representing Sclerodermini sensu LANES & AZEVEDO (2008) with four genera. The definitions of the limits of old tribe Epyrini were analyzed; in addition, they confirmed several suggestions made by CARR et al. (2010), eliminated all tribal definitions inside Epyrinae and gave to Sclerodermini sensu LANES & AZEVEDO (2008) and Epyrini sensu EVANS (1964) subfamily status.

Between 2005 and 2020, two new extinct and six new extant genera with tents of new species have been added to Scleroderminae (AZEVEDO et al. 2018; COLOMBO & AZEVEDO 2019, 2020; FALIÈRES & NEL 2019), reducing the number of monotypic genera. Because of these additions, several questions have been raised regarding character congruence, internal phylogenetic relationships, and the group delimitation considering several taxa that were never phylogenetically accessed. Therefore, the present work provides an updated phylogenetic hypothesis to the subfamily, based on parsimony and using morphological characters.

2. Materials and methods

2.1. Taxon sampling

The examined material came from all of the zoogeographic regions. For most taxa, we coded females, the sex that has been used more frequently to characterize the Scleroderminae; however, the male was coded in the case of *Sierola depressa marquisensis* Fullaway.

The specimens came from the following collections, as follows: AEIC – American Entomological Institute, Gainesville, USA, now incorporated into Utah State University; ANIC – Australian National Insect Collection, Canberra, Australia; BMNH – The Natural History Museum, London, United Kingdom; BPBM – Bernice Pauahi Bishop Museum, Honolulu, USA; CASC – California Academy of Sciences, San Francisco, USA; CFRB – Chinese Academy of Forestry, Beijing, China; CNCI – Canadian National Collection of Insects, Ottawa, Canada; CZMA – Coleção Zoológica da Universidade Estadual do Maranhão, Caxias, Brazil; DCBU – Universidade Federal de São Carlos, São Carlos, Brazil; IAVH – Instituto Alexander von Humboldt, Villa de Leyva, Colombia; IBGE – Instituto Brasileiro de Geografia e Estatística, Brasília, Brazil; ISAM – Iziko South African Museum, Cape Town, South Africa; MCSN – Museo Civico di Storia Naturale "Giacomo Doria", Genova, Italy; MCZH – Museum of Comparative Zoology, Cambridge, U.S.A.; MPEG – Museu Paraense Emílio Goeldi, Belém, Brazil; MNHN – Muséum National d'Histoire Naturelle, Paris, France; MNNC – Museo Nacional de Historia Natural, Santiago, Chile; NHRS – Naturhistoriska Riksmuseet, Stockholm, Sweden; NZAC – New Zealand Arthropod Collection, Auckland, New Zealand; PAH/PIN Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; PMAE – Royal Alberta Museum, Edmonton, Canada; QSBG – Queen Sirikit Botanical Garden, Chaing Mai, Thailand; RMNH – National Naturhistorisch Museum, Leiden, The Netherlands; UFES – Universidade Federal do Espírito Santo, Vitória, Brazil; and, Uni-

Table 1. List of species examined in this study. Acronym of museum consult Material and Methods.

Subfamily	Species	Country	Museum
Bethylinae	*Eupsenella diemenensis*	Australia, New South Wales	ANIC
Bethylinae	*Bethylus cephalotes*	England	UFES
Mesitiinae	*Incertosulcus capensis*	South Africa	UFES
Mesitiinae	*Pilomesitius madagascarensis*	Madagascar	UFES
Epyrinae	*Bakeriella incompleta*	Brazil, São Paulo	UFES
Epyrinae	*Holepyris micidus*	U.S.A., Florida	UFES
Scleroderminae	*Acephalonomia micronesica*	Tinian Islands	BPBM
Scleroderminae	*Allobethylus floridanus*	U.S.A., Florida	UFES
Scleroderminae	*Allobethylus* sp. 1	Vanuatu	BPBM
Scleroderminae	*Alloplastanoxus unexpectatus*	Thailand	QSBG
Scleroderminae	*Alloplastanoxus* sp. 1	Madagascar	CASC
Scleroderminae	*Alongatepyris platunissimus*	Brazil, São Paulo (from Vargas & Azevedo 2008)	DCBU
Scleroderminae	*Alongatepyris ingens*	Colombia (from Vargas & Azevedo 2008)	IAVH
Scleroderminae	*Archaeonoxus scintillatus*	Russia, Baltic amber	PAH, PIN
Scleroderminae	*Bethylopsis fullawayi*	Marquesas Islands	BPBM
Scleroderminae	*Bethylopsis carinatus*	Chile (from Azevedo 1999)	MNCN
Scleroderminae	*Celonophamia granama*	Canada, Campanian amber (from McKellar & Engel 2014)	CNCI
Scleroderminae	*Celonophamia taimyria*	Russia, Taimyr amber (from Evans 1973)	PAH/PIN
Scleroderminae	*Cephalonomia brevipennis*	England	UFES
Scleroderminae	*Cephalonomia formiciformis*	Argentina, Buenos Aires	UFES
Scleroderminae	*Cephalonomia hyalinipennis*	U.S.A., Florida	UFES
Scleroderminae	*Cephalonomia gallicola*	U.S.A., New York	UFES
Scleroderminae	*Cephalonomia stephanoderis*	Brazil, São Paulo	UFES
Scleroderminae	*Chilepyris herbsti*	Chile (from Evans 1964)	MCZH
Scleroderminae	*Chilepyris platyhelis*	New Zealand	NZAC
Scleroderminae	*Discleroderma gundari*	Japan	UFES
Scleroderminae	*Discleroderma yemenensis*	Yemen	CNCI
Scleroderminae	*Discleroderma dolium*	Indonesia	RMNH
Scleroderminae	*Discleroderma concursum*	Thailand	QSBG
Scleroderminae	*Discleroderma tuberculatum*	Thailand	QSBG
Scleroderminae	*Galodoxa torquata*	Papua New Guinea	MNHN
Scleroderminae	*Glenosema crandali*	U.S.A., California	UFES
Scleroderminae	*Glenosema dentata*	Madagascar	UFES
Scleroderminae	*Glenosema elevata*	Madagascar	CASC
Scleroderminae	*Israelius amputatus*	United Arab Emirates	UFES
Scleroderminae	*Israelius carthami*	Palestine	BMNH
Scleroderminae	*Israelius* sp. 1	United Arab Emirates	UFES
Scleroderminae	*Megaprosternum longiceps*	Fiji	BPBM
Scleroderminae	*Megaprosternum pentagonal*	Australia, Queensland	ANIC
Scleroderminae	*Megaprosternum* sp. 1	U.S.A., Tinian Islands	BPBM
Scleroderminae	*Nothepyris brasiliensis*	Brazil, Espírito Santo	UFES
Scleroderminae	*Nothepyris sulcatus*	Brazil, Pará	MPEG
Scleroderminae	*Nothepyris* sp. 1	Brazil, Maranhão	CZMA
Scleroderminae	*Nothepyris* sp. 2	Dominican Rep.	CNCI
Scleroderminae	*Paleoscleroderma lamarrei*	France amber (from Falières & Nel 2019)	MNHN
Scleroderminae	*Pararhabdepyris lophos*	Thailand	UFES
Scleroderminae	*Pararhabdepyris ngangu*	Central Africa Republic	ISAM
Scleroderminae	*Pararhabdepyris balios*	Australia, Queensland	ANIC
Scleroderminae	*Plastanoxus chittendeni*	U.S.A., California	UFES
Scleroderminae	*Plastanoxus incompletus*	U.S.A., California	UFES
Scleroderminae	*Plastanoxus westwoodi*	Brazil, Rio Grande do Sul	UFES
Scleroderminae	*Platepyris sepalus*	South Africa (from Lanes & Azevedo 2008)	BMNH
Scleroderminae	*Proplastanoxus elegans*	Thailand	QSBG
Scleroderminae	*Prorops nasuta*	Brazil, São Paulo	UFES
Scleroderminae	*Prorops* sp. 1	Thailand	QSBG
Scleroderminae	*Prorops* sp. 2	Vietnam	RMNH
Scleroderminae	*Sclerodermus domesticus*	Turkey	UFES
Scleroderminae	*Sclerodermus macrogaster*	U.S.A., Florida	UCFC
Scleroderminae	*Sclerodermus pupariae*	China, Tianjin (from Yang et al. 2012)	CFRB
Scleroderminae	*Solepyris montuosus*	Brazil, Espírito Santo	UFES
Scleroderminae	*Solepyris unicus*	Brazil, Minas Gerais	UFES

Table 1 continued.

Subfamily	Species	Country	Museum
Scleroderminae	*Thlastepyris pertenuis*	Brazil, Santa Catarina (from Evans, 1973)	MCZH
Scleroderminae	*Tuberepyris basibrevis*	Tanzania (from Lanes & Azevedo, 2008)	CASC
Scleroderminae	*Tuberepyris hamus*	Central African Republic (from Azevedo & Mugrabi, 2014)	ISAM
Scleroderminae	*Piloceps mollis* **sp.n.**	Thailand	QSBG
Scleroderminae	*Decemnoxus infrequens* **sp.n.**	Madagascar	CASC
Scleroderminae	*Decemnoxus* sp. 1	Madagascar	CASC
Scleroderminae	*Decemnoxus* sp. 2	Madagascar	CASC
Scleroderminae	*Decemnoxus* sp. 3	Madagascar	CASC
Scleroderminae	*Longinoxus inusitatus* **sp.n.**	Madagascar	CASC
Scleroderminae	*Madanoxus patulus* **sp.n.**	Madagascar	CASC
Scleroderminae	*Mutatio mutata* **sp.n.**	Madagascar	CASC
Scleroderminae	*Thlastepyris marquisensis* **comb.n.**	Marquesas Island	BPBM

versity of Central Florida, Orlando, USA; UQIC – University of Queensland, Brisbane, Australia.

2.2. Morphological terminology

Morphological terms generally follow LANES et al. (2020); the sculptural nomenclature follows HARRIS (1979). Taxonomic abbreviations include LH (length of head in dorsal view); WH (maximum width of head including eyes in dorsal view); WF (minimum width of front in dorsal view); HE (height of eye in dorsal view); WOT (width of ocellar triangle in dorsal view); VOL (vertex-ocular line in dorsal view), LFW (length of forewing).

2.3. Outgroup and ingroup selection

In order to evaluate hypothetical homologous characters that might indicate phylogenetic relationships, we took *Bethylus cephalotes* (Förster) and *Eupsenella diemenensis* Dodd, as representatives of Bethylinae, *Bakeriella incompleta* Azevedo and *Holepyris micidus* Evans, as representatives of Epyrinae, *Incertosulcus capensis* Kieffer and *Pilomesitius madagascarensis* Móczár, as representatives of Mesitiinae. The outgroup selection follows WILEY & LIEBERMAN (2011) (Table 1).

We included 58 terminals for all 25 previously described genera and nine more terminals for new taxa, which we described here as new genera (Table 1). Only the type species of each new genus will be described, by nomenclatural requirement.

2.4. Character codification

The characters were treated as hypotheses of primary homology following DE PINNA (1991). We worked on improving character-coding systems, avoiding continuous quantitative characters and intraspecific polymorphisms as much as possible. Several important characters have been proposed from the codification of new features of the forewing (especially associated with venation); several characters are used again or modified mostly from TERAYAMA (1995), LANES & AZEVEDO (2008) and ALENCAR & AZEVEDO (2013). A total of 138 morphological characters were analyzed: one from the general body, 44 characters from the head, 55 from the mesosoma, 29 characters from the wing, and nine from the metasoma (Electronic Supplement S2).

2.5. Phylogenetic analyses

The morphological dataset was analyzed using maximum parsimony. The characters were treated as unordered and non-polarized. Characters coded as inapplicable were treated as missing data (Electronic Supplement S2).

The searches for the most parsimonious (MP) trees were carried out with the software TNT version 1.1 (GOLOBOFF et al. 2008). Characters were treated under implied weights (GOLOBOFF 1993; GOLOBOFF et al. 2008). We increased all parameter sets indicated as default of the software in order to get a more elevated the number of analyzed rearrangements. So, we used the parameter sets as follows: space for 99999 trees in memory; Wagner trees random seed 0; 1000 replications; TBR algorithm; 10 trees saved per replication; other parameter as in default mode. The tree was rooted with *Eupsenella diemenensis*.

Heuristic searches (GOLOBOFF 2003; GOLOBOFF et al. 2008) were performed under New Technology methods using a *sectorial search*, *ratchet* weighting probability of 10% with 15000 iterations, *tree-drifting* of 15000 cycles and *tree-fusing* of five rounds. This parameters were used to get trees more robust. Implied weights analyses using a concavity function (K) that weights against homoplastic data (GOLOBOFF et al. 1993) were also conducted, using a TNT script (setk.run) written by Salvador Arias to calculate the appropriate value. A value of 11.4355 was returned and subsequently used in the implied weighting scheme.

The only cladogram recovered with the software TNT was manipulated with Winclada-ASADO version 1.61 (NIXON 2002) and further edited in Adobe Illustrator. For the results, characters were mapped onto the implied weighting tree using Winclada, and edited in Adobe Illustrator CS6 version 23.0.3.

2.6. Illustrations

The specimens were photographed under a Leica Z16 APO stereomicroscope with a camera adaptor coupled to a Leica DFC 295 video camera (Leica Microsystems, Switzerland). The software Leica Application Suite V3. version 6.0 and Microsystems by Leica (Switzerland) Limited (LAS) were used to capture individual focal planes. Helicon Focus (Helicon Soft version 4.2.9) software was used for stacking the layers into a single combined-focus image using the following parameters: method C pyramid and full 23 resolution.

3. Results

3.1. Analytical outputs

In TNT analyses, 29.044.349.423 rearrangements were examined, and retrieved one MP tree, with a best score of 31.04, Ci = 0.21, Ri = 0.63 and 822 steps (Fig. 1).

3.2. List of characters and character states

1. **Head, texture**: (0) coriaceous; (1) polished; (2) foveolate.
2. **Head shape, dorsal view**: (0) quadrate or subquadrate (Azevedo et al. 2018: fig. 75B); (1) rectangular (Azevedo et al. 2018: fig. 80C); (2) triangular or subtriangular (Azevedo et al. 2018: fig. 82C). Adapted from Lanes & Azevedo (2008).
3. **Head, width**: (0) extremely wider than long (Azevedo et al. 2018: fig. 74C); (1) extremely longer than wide (Azevedo et al. 2018: fig. 66C); (2) almost as long as wide (Azevedo et al. 2018: fig. 81C).
4. **Head shape, profile**: (0) globoid, ventral margin very outcurved (Azevedo et al. 2018: fig. 75A); (1) subrectangular or rectangular (Azevedo et al. 2018: fig. 80A); (2) rounded (Azevedo et al. 2018: fig. 82A); (3) subtriangular (Azevedo et al. 2018: fig. 12B). Adapted from Lanes & Azevedo (2008).
5. **Vertex shape**: (0) incurved; (1) straight or nearly so; (2) outcurved. Adapted from Lanes & Azevedo (2008).
6. **Head setation**: (0) dense; (1) scarce or absent.
7. **Genal suture, presence**: (0) present; (1) absent. From Alencar & Azevedo (2013).
8. **Genal suture, visibility**: (0) conspicuous; (1) inconspicuous.
9. **Mandible surface**: (0) depressed (Lanes & Azevedo 2008: fig. 3B); (1) convex (Lanes & Azevedo 2008: fig. 3A).
10. **Relative width of mandibular apex**: (0) apex as wide or wider than base; (1) apex narrower than base. Adapted from Alencar & Azevedo (2013).
11. **Mandible teething**: (0) one to six teeth; (1) seven teeth. Adapted from Lanes & Azevedo (2008).
12. **Relative size of teeth**: (0) subequal; (1) distinctly different. Adapted from Alencar & Azevedo (2013).
13. **Shape of mandible**: (0) robust, as long as or shorter than wide; (1) slender, longer than wide. Adapted from Alencar & Azevedo (2013).
14. **Mandibular upper margin**: (0) smooth; (1) with one or two rounded large teeth; (2) with several sharpened small teeth.
15. **Occipital carina, presence**: (0) present; (1) absent. Adapted from Lanes & Azevedo (2008).
16. **Extension of occipital carina**: (0) complete; (1) incomplete. Adapted from Lanes & Azevedo (2008).
17. **Maxillary palpus**: (0) with six palpomeres; (1) with five or less palpomeres. Adapted from Lanes & Azevedo (2008).
18. **Labial palpus**: (0) with one palpomere; (1) with two or more palpomeres. Adapted from Lanes & Azevedo (2008).
19. **Hypostomal carina, shape**: (0) rounded; (1) angled; (2) straight; (3) arched.
20. **Median clypeal lobe, dorsal view**: (0) as long as or longer than lateral lobes; (1) shorter than lateral lobes; (2) ill-defined.
21. **Clypeus in frontal view**: (0) elevated (Lanes & Azevedo 2008: fig. 3E); (1) not elevated (Lanes & Azevedo, 2008: fig. 3F). Adapted from Lanes & Azevedo (2008).
22. **Transverse U-shaped clypeal elevation**: (0) present (Azevedo et al. 2018: fig. 74C); (1) absent.
23. **Median clypeal carina**: (0) present; (1) absent. Adapted from Alencar & Azevedo (2013).
24. **Height of median clypeal carina**: (0) low, lower than frons; (1) high, higher than frons. Adapted from Lanes & Azevedo (2008).
25. **Posterior extension of clypeus**: (0) reaching margin of torulus (Lanes & Azevedo 2008: fig. 2D); (1) reaching posterior margin of torulus (Lanes & Azevedo 2008: fig. 2E). Adapted from Lanes & Azevedo (2008).
26. **Frontal process**: (0) absent; (1) present (Azevedo et al. 2018: fig. 86B).
27. **Frontal process, development**: (0) overlapping clypeus (Azevedo et al. 2018: fig. 86B); (1) not overlapping clypeus.
28. **Antennal insertion**: (0) dorsal to clypeus (Lanes & Azevedo 2008: fig. 3A); (1) at same level of clypeus (Lanes & Azevedo 2008: fig. 3B). Adapted from Lanes & Azevedo (2008).
29. **Number of antennomeres**: (0) thirteen; (1) twelve; (2) ten; (3) nine. Adapted from Lanes & Azevedo (2008).
30. **Pedicel shape**: (0) rectangular; (1) caliciform; (2) barrel-shaped. Adapted from Alencar & Azevedo (2013).
31. **Pedicel length**: (0) longer than flagellomere I; (1) shorter than or as long as flagellomere I.
32. **Pedicel pubescence**: (0) appressed; (1) suberect or erect. Adapted from Alencar & Azevedo (2013).
33. **Flagellomere I, length**: (0) shorter than flagellomere II; (1) longer or as long as flagellomere II.

34. **Frontal line, presence**: (0) absent; (1) present. Adapted from Alencar & Azevedo (2013).
35. **Extension of frontal line**: (0) long, touching anterior ocelli (Lanes & Azevedo 2008: fig. 2F); (1) short, not touching anterior ocelli. Adapted from Lanes & Azevedo (2008).
36. **Size of eye**: (0) large and prominent; (1) small, but distinct.
37. **Eye setation**: (0) dense; (1) scarce or absent.
38. **Transverse location of eye, dorsal view**: (0) lateral, when gena not visible (Azevedo et al. 2018: fig. 83C); (1) sublateral, when gena visible (Azevedo et al. 2018: fig. 69A). Adapted from Lanes & Azevedo (2008).
39. **Eye, shape**: (0) circular; (1) elongated. Adapted from Lanes & Azevedo (2008).
40. **Longitudinal location of eye, lateral view**: (0) anterior, adjacent or next to mandibular base; (1) median, eye apart from mandibular base. Adapted from Alencar & Azevedo (2013).
41. **Eye counter**: (0) flat; (1) protruding. Adapted from Lanes & Azevedo (2008).
42. **Ocelli, presence**: (0) present; (1) absent. Adapted from Lanes & Azevedo (2008).
43. **Anterior ocelli**: (0) posterior to supra-ocular line; (1) crossing supra-ocular line; (2) anterior to supra-ocular line.
44. **Distance of posterior ocelli to vertex crest**: (0) shorter than diameter of posterior ocelli; (1) shorter than triangle ocellar, but longer than diameter of posterior; (2) longer than triangle ocellar.
45. **Posterior margin of pronotum**: (0) nearly straight; (1) incurved; (2) outcurved. Adapted from Lanes & Azevedo (2008).
46. **Anterior corner of propleuron, in dorsal view**: (0) protuberant; (1) not protuberant. Adapted from Lanes & Azevedo (2008).
47. **Shape of anterior corner**: (0) rounded (Azevedo et al. 2018: fig. 91D); (1) angulated (Azevedo et al. 2018: fig. 90D).
48. **Ventral propleural area**: (0) rectangular, parallel margins; (1) bottle-shaped, anteriorly constrict.
49. **Length of pronotal collar, dorsal view**: (0) not visible, when pronotal disc overlapping or very diminutive, indistinct; (1) short, less than 0.14×, but distinct; (2) long, more than 0.16×, but not as long as the pronotal disc; (3) very long, almost longer as pronotal disc.
50. **Lateral margin of pronotum**: (0) straight or nearly so; (1) strongly incurved; (1) incurved.
51. **Transverse pronotal carina, presence**: (0) present; (1) absent.
52. **Posterior pronotal sulcus, presence**: (0) present; (0) absent.
53. **Median pronotal line in dorsal pronotal area, presence**: (0) present; (1) absent.
54. **Size of prosternum**: (0) smaller than area of procoxa; (1) larger than area of procoxa (Azevedo et al. 2018: fig. 80F).
55. **Shape of prosternum**: (0) diamond-shape; (1) pentagonal (Azevedo et al. 2018: fig. 80F); (2) kite-shaped (Azevedo et al. 2018: fig. 89D); (3) triangular.
56. **Protrochanter length**: (0) smaller than procoxa; (1) longer than or as long as procoxa.
57. **Width of profemur**: (0) slender, longer than wide; (1) robust, wider or wide as long.
58. **Tarsal claws**: (0) simple; (1) bifid; (2) trifid.
59. **Mesonotum area**: (0) divided in mesoscutum and mesoscutellum in all forms; (1) not divided in mesoscutum and mesoscutellum in apterous forms (Azevedo et al. 2018: fig. 87C).
60. **Mesoscutellum**: (0) flattened and poorly differentiated; (1) posterodorsally swollen and protuberant; (1) posterodorsally produced and overlapping metanotum.
61. **Notaulus**: (0) present, well or ill impressed; (1) fully absent. Adapted from Alencar & Azevedo (2013).
62. **Notaulus, shape**: (0) straight; (1) irregular.
63. **Extension of notaulus**: (0) complete; (1) incomplete. Adapted from Alencar & Azevedo (2013).
64. **Parapsidal signum**: (0) present; (1) absent. Adapted from Alencar & Azevedo (2013).
65. **Mesoscutum-mesoscutellar suture**: (0) present; (1) absent.
66. **Mesoscutum-mesoscutellar sulcus**: (0) present; (1) absent.
67. **Mesoscutum-mesoscutellar sulcus**: (0) as narrow as suture; (1) wide.
68. **Mesoscutum-mesoscutellar fovea**: (0) distinct of mesoscutum-mesoscutellar sulcus; (1) indistinct of mesoscutum-mesoscutellar sulcus.
69. **Shape of mesoscutum-mesoscutellar fovea**: (0) circular; (1) oval; (2) rectangular. Adapted from Alencar & Azevedo (2013).
70. **Subalar impression of mesopleuron**: (0) present; (1) absent. Adapted from Lanes & Azevedo (2008).
71. **Mesopleural surface** (median area): (0) flattened, hardly seen in dorsal view; (1) convex, visible in dorsal view.
72. **Mesopleural suture, presence**: (0) present; (1) absent.
73. **Transepisternal line of mesopleuron, presence**: (0) absent; (1) present. Adapted from Lanes & Azevedo (2008).
74. **Extension of transepisternal line of mesopleuron**: (0) complete, crossing all ventral; (0) incomplete, present only on anteriorly. Adapted from Lanes & Azevedo (2008).
75. **Texture of transepisternal line of mesopleuron**: (0) smooth; (1) trabeculate. Adapted from Lanes & Azevedo (2008).
76. **Mesopleural pit, presence**: (0) present; (1) absent.
77. **Mesopleural pit, depth**: (0) shallow; (1) deep.
78. **Metanotum, dorsal view**: (0) absent; (1) present. Adapted from Lanes & Azevedo (2008).
79. **Metapectal-propodeal disc, width**: (0) wider than long; (1) longer or long as wide.

80. Shape of first abdominal spiracle: (0) circular; (1) curved; (2) oval; (3) elongated. Adapted from Lanes & Azevedo (2008).
81. Position of first abdominal spiracle: (0) on lateral surface of metapectal-propodeal complex; (1) on dorsal surface of metapectal-propodeal complex. Adapted from Lanes & Azevedo (2008).
82. Anterior transverse carina of metapectal-propodeal disc: (0) present; (1) absent.
83. Metapostnotal median carina, presence: (0) absent; (1) present. Adapted from Lanes & Azevedo (2008).
84. Extension of metapostnotal median carina: (0) complete, reaching transverse posterior carina; (1) incomplete, not reaching transverse posterior carina.
85. First pair of metapostnotal carina: (0) present; (1) absent. Adapted from Lanes & Azevedo (2008).
86. Extension of first pair of metapostnotal carina: (0) complete, reaching posterior transverse carina; (1) incomplete, not reaching posterior transverse carina.
87. Second pair of metapostnotal carina: (0) present; (1) absent.
88. Extension of second pair of metapostnotal carina: (0) complete, reaching posterior transverse carina; (1) incomplete, not reaching posterior transverse carina.
89. Third pair of metapostnotal carina: (0) present; (1) absent.
90. Extension of third pair of metapostnotal carina: (0) complete, reaching posterior transverse carina; (1) incomplete, not reaching posterior transverse carina.
91. Metapostnotal-propodeal suture: (0) present; (1) absent. Adapted from Lanes & Azevedo (2008).
92. Extension of metapostnotal-propodeal suture: (0) complete, reaching posterior transverse carina; (1) incomplete, not reaching posterior transverse carina.
93. Lateral carina of metapectal-propodeal disc: (0) present; (1) absent. Adapted from Lanes & Azevedo (2008).
94. Paraspicular carina, presence: (0) present; (1) absent. Adapted from Lanes & Azevedo (2008).
95. Transverse posterior carina of metapectal-propodeal disc: (0) present; (1) absent. Adapted from Lanes & Azevedo (2008).
96. Posterior corner with spine-shaped projection: (0) absent; (1) present (Azevedo et al. 2018: fig. 61F).
97. Median carina of propodeal disc: (0) present; (1) absent. Adapted from Lanes & Azevedo (2008).
98. Ventral area of mesopectus: (0) coriaceous punctured; (1) polished punctured; (2) foveolate.
99. Metasternum: (0) coriaceous punctured; (1) polished punctured; (2) foveolate.
100. Aptery: (0) absent; (1) present.
101. Microptery (wing almost fully covered by tegula): (0) absent; (1) present.
102. Brachyptery (wing reaching propodeum to metasomal segment I): (0) absent; (1) present.
103. Macroptery (wing fully developed): (0) absent; (1) present.
104. Wings, color: (0) hyaline; (1) yellowish or colorful.
105. Forewing setation: (0) dense; (1) scarce.
106. Fringe setation of forewing: (0) smaller than regular setation; (1) as long as regular setation; (2) longer than regular setation.
107. First cubital cell of forewing, length: (0) less than half radial cell (Azevedo et al. 2018: fig. 76E); (1) more than half radial cell (Azevedo et al. 2018: fig. 66F).
108. First cubital cell of forewing, when less than half radial cell length: (0) Cu-a vein rounded (Azevedo et al. 2018: fig. 68D); (1) Cu-a vein straight (Azevedo et al. 2018: fig. 76E).
109. Length of anal (A) vein of forewing: (0) short as stub; (1) long, at least one third of median+cubital (M+Cu) vein; (2) very long, longer than median+cubital (M+Cu) vein; (3) equal to median+cubital (M+Cu) vein.
110. Anal (A) vein of forewing, opacity: (0) spectral; (1) tubular.
111. Median+cubital (M+cu) vein, opacity: (0) spectral; (1) tubular.
112. Subcostal + Radial (Sc+R) vein of forewing, opacity: (0) spectral; (1) tubular.
113. Cubital (Cu) vein of forewing as stub, presence: (0) absent; (1) present.
114. Radial sector (Rs) of Rs&M vein of forewing: (0) present; (1) absent.
115. Radial sector (Rs) of Rs&M vein of forewing: (0) linear; (1) enlarged.
116. Prestigmal abscissa of radial 1 (R1) vein of forewing: (0) present; (1) absent.
117. Prestigmal abscissa of radial 1 (R1) vein of forewing: (0) linear; (1) enlarged.
118. Pterostigma of forewing, presence: (0) present; (1) absent.
119. Size of pterostigma of forewing: (0) large and prominent; (1) medium to small but distinct; (2) very small and not distinct.
120. Shape of pterostigma of forewing: (0) circular; (1) elongated; (2) subtriangular; (3) quadrate.
121. Second radial cross & Radial sector (2r-rs&Rs) vein of forewing: (0) present; (2) absent.
122. Second radial cross & Radial sector (2r-rs&Rs) vein of forewing, direction: (0) angled anterad; (1) smoothly curved anterad.
123. Poststigmal abscissa of radial 1 (R1) vein of forewing: (0) present; (1) absent.
124. Distal flexion lines of forewing: (0) present; (1) absent.
125. Number of distal flexion lines of forewing: (0) one; (1) two or more.
126. Number of distal hamuli: (0) one; (1) two; (2) three; (3) four; (4) five. Adapted from Lanes & Azevedo (2008).

127. Distance among distal hamuli: (0) equally spaced; (1) irregularly spaced. Adapted from LANES & AZEVEDO (2008).
128. Jugal lobe of hind wing: (0) fused to hind wing; (1) distinct to hind wing. Adapted from LANES & AZEVEDO (2008).
129. Differentiation of petiolar root, ventral view: (0) petiolar body distinct of root; (1) root and petiolar body fused. Adapted from ALENCAR & AZEVEDO (2013).
130. Petiolar ventral carina: (0) present; (1) absent.
131. Metasomal apex orientation: (0) upward; (1) downward (AZEVEDO et al. 2018: fig. 75F); (2) straight.
132. Metasomal tergum I: (0) punctate; (1) polished; (2) coriaceous.
133. Posterior margin of metasomal sternum I: (0) simple; (1) divided in two sepal-shaped (AZEVEDO et al. 2018: fig. 84D).
134. Metasomal tergum II: (0) punctate; (1) polished; (2) coriaceous.
135. Length of metasomal tergum II: (0) longer than remaining segments; (1) shorter than two subsequent segments together.
136. Acute tubercles of metasomal tergum IV–VI: (0) present (AZEVEDO et al. 2018: fig. 75F); (1) absent. Adapted from LANES & AZEVEDO (2008).
137. Expansions of metasomal sternum IV: (0) present (AZEVEDO et al. 2018, fig. 76F); (1) absent.
138. General body, lateral view: (0) robust (AZEVEDO et al. 2018: fig. 74A); (1) strongly flat (AZEVEDO et al. 2018: fig. 80A).

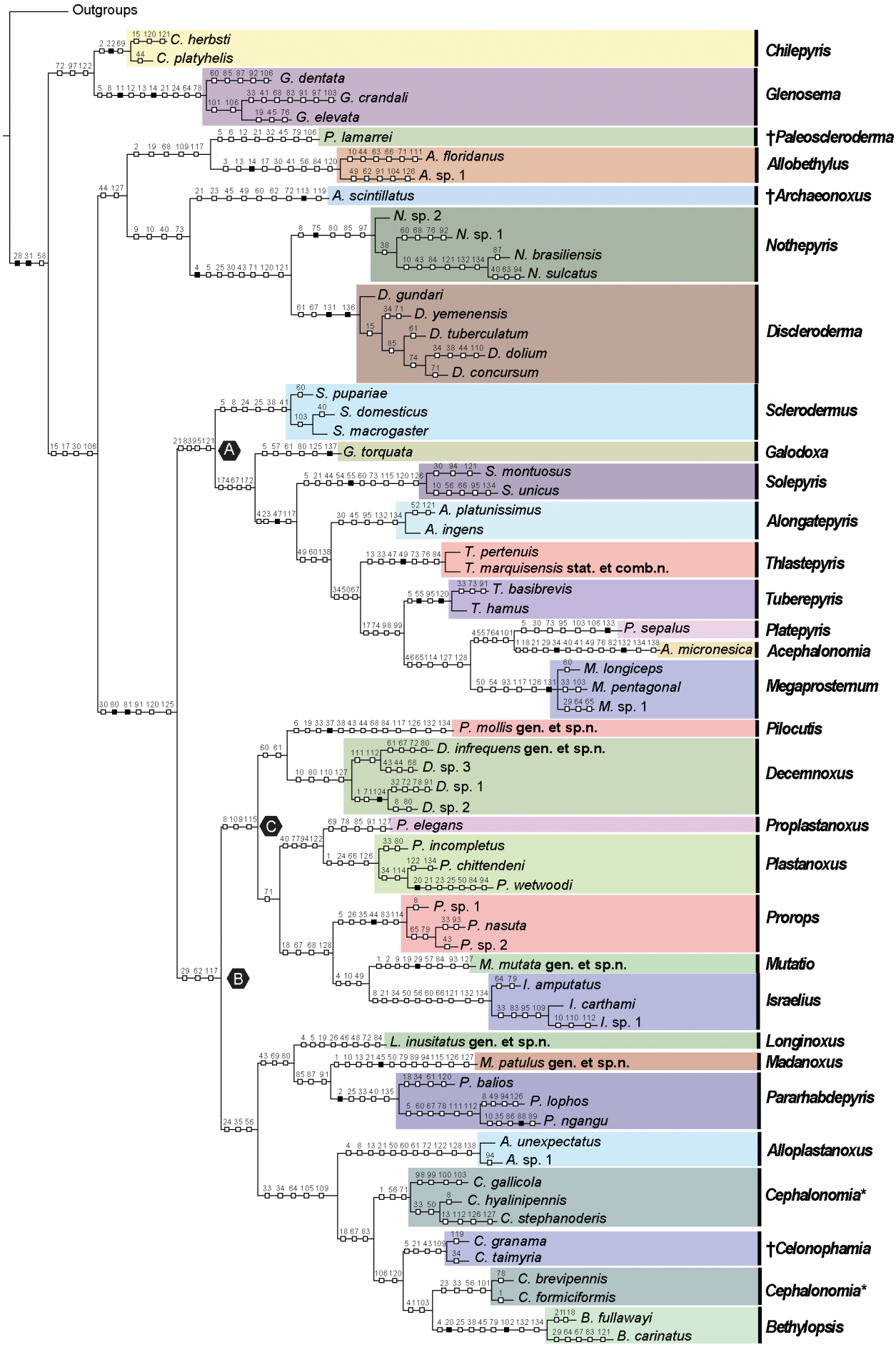
3.3. Subfamily topology

General. Scleroderminae were recovered as a monophyletic subfamily with two synapomorphies, viz antennal insertions parallel to clypeus (28:1) and pedicel longer than flagellomere I (31:0), and sister to Mesitiinae, supporting the molecular studies of CARR et al. (2010).

The results provided support to the monophyly of the subfamily and of all genera, except by *Cephalonomia*, which was recovered as a polyphyletic (Fig. 1). Some genera do not show synapomorphies, so that their monophyly is not truly demonstrated.

1. *Acephalonomia* is supported by two apomorphies 'ten antennomeres' (29:2), 'anterior transverse carina of metapectal-propodeal disc absent' (82:1) and retrieved 11 homoplasies as follow: 138:0; 1:1; 18:0; 21:0; 34:1; 40:1; 41:0; 49:2; 76:1; 132:1; 134:1;
2. *Allobethylus* is supported by one synapomorphy 'upper margin of mandible with one or two rounded large teeth' (14:1) and retrieved eight homoplasies as follow: 3:1; 13:1; 17:0; 30:0; 41:0; 56:1; 84:1; 120:3;
3. *Alloplastanoxus* is not supported by homologies, but retrieved eleven homoplasies as follow: 138:1; 4:1; 8:1; 13:1; 21:1; 50:2; 60:0; 61:0; 61:0; 72:0; 122:0; 128:0;
4. *Alongatepyris* is not supported by homologies, but retrieved five homoplasies as follow: 30:0; 45:1; 95:0; 132:1; 134:1;
5. †*Archaeonoxus* is supported by one apomorphy 'Cu vein as stub' (113:1) and retrieved eight homoplasies as follow: 21:1; 23:1; 45:1; 49:1; 60:0; 62:1; 72:0; 119:0;
6. *Bethylopsis* is supported by two synapomorphies 'median clypeal lobe shorter than lateral lobes, in dorsal view' (20:1) and ‚brachyptery present' (102:1), and retrieved seven homoplasies as follow: 4:1; 25:0; 38:1; 45:1; 79:0; 132:2; 134:2;
7. †*Celonophamia* is not supported by homologies, but retrieved four homoplasies as follow: 5:2; 21:1; 43:2; 109:3;
8. *Cephalonomia* was not retrieved as monophyletic genus, and formed two distinct clades.
9. *Chilepyris* is supported by one synapomorphy, 'presence of a transverse U-shaped clypeal elevation' (22:0), and retrieved two homoplasies as follow: 2:1; 69:0;
10. *Decemnoxus* gen. n. is not supported by homologies, but retrieved four homoplasies as follow: 10:1; 80:1; 110:0; 127:1;
11. *Discleroderma* is supported by two synapomorphies, 'metasomal apex orientation upward' (131:0) and 'presence of metasomal modifications in dorsal position' (136:0) and retrieved two homoplasies as follow: 61:1; 67:0;
12. *Galodoxa* is supported by one apomorphy, 'presence of expansions of metasomal sternum' (137:0) and retrieved five homoplasies (5:0; 57:1; 61:0; 80:3; 125:1).
13. *Glenosema* is supported by two synapomorphies, ‚mandible with seven teeth' (11:1), and 'upper margin of mandible with several sharpened small teeth' (14:2), and retrieved eight homoplasies as follow: 5:2; 8:1; 12:0; 13:1; 21:1; 24:0; 64:1; 78:0;
14. *Israelius* is not supported by homologies, but retrieved ten homoplasies as follow: 8:0; 21:1; 34:0; 50:2; 56:1; 60:0; 66:1; 121:1; 132:2; 134:2;
15. *Longinoxus* gen. n. is not supported by homologies, but retrieved eight homoplasies as follow: 4:1; 5:2; 19:2; 26:1; 46:0; 48:0; 72:0; 84:1;
16. *Madanoxus* gen. n. is supported by one apomorphy 'posterior margin of dorsal pronotal area outcurved' (45:2), and retrieved eleven homoplasies as follow: 1:1; 10:1; 13:1; 21:1; 50:2; 79:0; 89:0; 94:0; 115:1; 126:3; 127:1;
17. *Megaprosternum* is supported by one synapomorphy 'metasomal apex orientation straight' (131:2), and retrieved five homoplasies as follow: 50:1; 54:1; 93:1; 117:0; 126:3;
18. *Mutatio* gen. n. is supported by one apomorphy 'nine antennomeres' (29:3), and retrieved eight homoplasies

→ **Fig. 1.** Maximum parsimony morphological tree of Scleroderminae. Synapomorphies in black squares and homoplasies in white squares indicated above the branches.


Outgroups
C. herbsti
C. platyhelis
Chilepyris
G. dentata
G. crandali
G. elevata
Glenosema
P. lamarrei
†Paleoscleroderma
A. floridanus
A. sp. 1
Allobethylus
A. scintillatus
†Archaeonoxus
N. sp. 2
N. sp. 1
N. brasiliensis
N. sulcatus
Nothepyris
D. gundari
D. yemenensis
D. tuberculatum
D. dolium
D. concursum
Discleroderma
S. pupariae
S. domesticus
S. macrogaster
Sclerodermus
G. torquata
Galodoxa
S. montuosus
S. unicus
Solepyris
A. platunissimus
A. ingens
Alongatepyris
T. pertenuis
T. marquisensis stat. et comb.n.
Thlastepyris
T. basibrevis
T. hamus
Tuberepyris
P. sepalus
Platepyris
A. micronesica
Acephalonomia
M. longiceps
M. pentagonal
M. sp. 1
Megaprosternum
P. mollis gen. et sp.n.
Pilocutis
D. infrequens gen. et sp.n.
D. sp. 3
D. sp. 1
D. sp. 2
Decemnoxus
P. elegans
Proplastanoxus
P. incompletus
P. chittendeni
P. wetwoodi
Plastanoxus
P. sp. 1
P. nasuta
P. sp. 2
Prorops
M. mutata gen. et sp.n.
Mutatio
I. amputatus
I. carthami
I. sp. 1
Israelius
L. inusitatus gen. et sp.n.
Longinoxus
M. patulus gen. et sp.n.
Madanoxus
P. balios
P. lophos
P. ngangu
Pararhabdepyris
A. unexpectatus
A. sp. 1
Alloplastanoxus
C. gallicola
C. hyalinipennis
C. stephanoderis
Cephalonomia*
C. granama
C. taimyria
†Celonophamia
C. brevipennis
C. formiciformis
Cephalonomia*
B. fullawayi
B. carinatus
Bethylopsis
A
B
C

as follow: 1:1; 2:1; 9:0; 19:0; 49:1; 57:1; 84:1; 93:1; 127:1;
19. *Nothepyris* is supported by one synapomorphy 'transepisternal line of mesopleura smooth' (75:0), and retrieved four homoplasies as follow: 8:1; 80:1; 85:0; 97:0;
20. †*Paleoscleroderma* is not supported by homologies, but retrieved eight homoplasies as follow: 5:0; 6:0; 12:0; 21:1; 32:0; 45:1; 79:0; 106:1;
21. *Pararhabdepyris* is supported by one synapomorphy 'head triangular or subtriangular in dorsal view' (2:2), and retrieved four homoplasies as follow: 25:0; 33:1; 40:1; 135:0;
22. *Pilocutis* gen.n. is supported by one apomorphy 'eye with dense setation' (37:0), and retrieved eleven homoplasies as follow: 6:0; 19:0; 33:1; 38:1; 43:1; 44:2; 68:1; 84:1; 117:0; 126:1; 132:2; 134:2;
23. *Plastanoxus* is not supported by homologies, but retrieved four homoplasies as follow: 1:1; 24:0; 66:1; 126:1;
24. *Platepyris* is supported by one apomorphy 'posterior margin of first sternum divided in two sepal-shaped segments' (133:1), and retrieved six homoplasies as follow: 5:2; 30:0; 73:1; 95:0; 103:0; 106:0;
25. *Proplastanoxus* is not supported by homologies, but retrieved five homoplasies as follow: 69:0; 78:1; 85:0; 91:0; 127:1;
26. *Prorops* is supported by one synapomorphy 'posterior ocelli touching the vertex' (44:0), and retrieved five homoplasies as follow: 5:0; 26:0; 35:0; 83:0; 114:1;
27. *Sclerodermus* is not supported by homologies, but retrieved six homoplasies as follow: 5:2; 8:1; 24:0; 25:0; 38:1; 41:0;
28. *Solepyris* is supported by one synapomorphy 'prosternum kite-shaped' (55:2), and retrieved nine homoplasies as follow: 5:2; 21:0; 44:2; 54:1; 60:2; 73:1; 115:1; 120:3; 126:4;
29. *Thlastepyris* is supported by one synapomorphy 'pronotal collar not visible, when pronotal disc overlapping or very diminutive, indistinct' (49:0), and retrieved six homoplasies as follow: 13:1; 33:1; 47:1; 73:1; 76:1; 84:1; and,
30. *Tuberepyris* is supported by two synapomorphies 'prosternum triangular' (55:3) and 'pterostigma subtriangular' (120:2), and retrieved two homoplasies as follow: 5:0; 95:0.

3.4. Taxonomic accounts

Four of the five new genera that are described below are from Madagascar. They represent very distinctive morphological patterns in Scleroderminae. Madagascar plays an important role in the evolutionary history of Scleroderminae by having several odd morphological pattern and endemic fauna. This island has high levels of endemism for many biological groups (MYERS et al. 2000), and bethylids are not different.

3.4.1. *Decemnoxus* gen.n.

Fig. 2.A–D

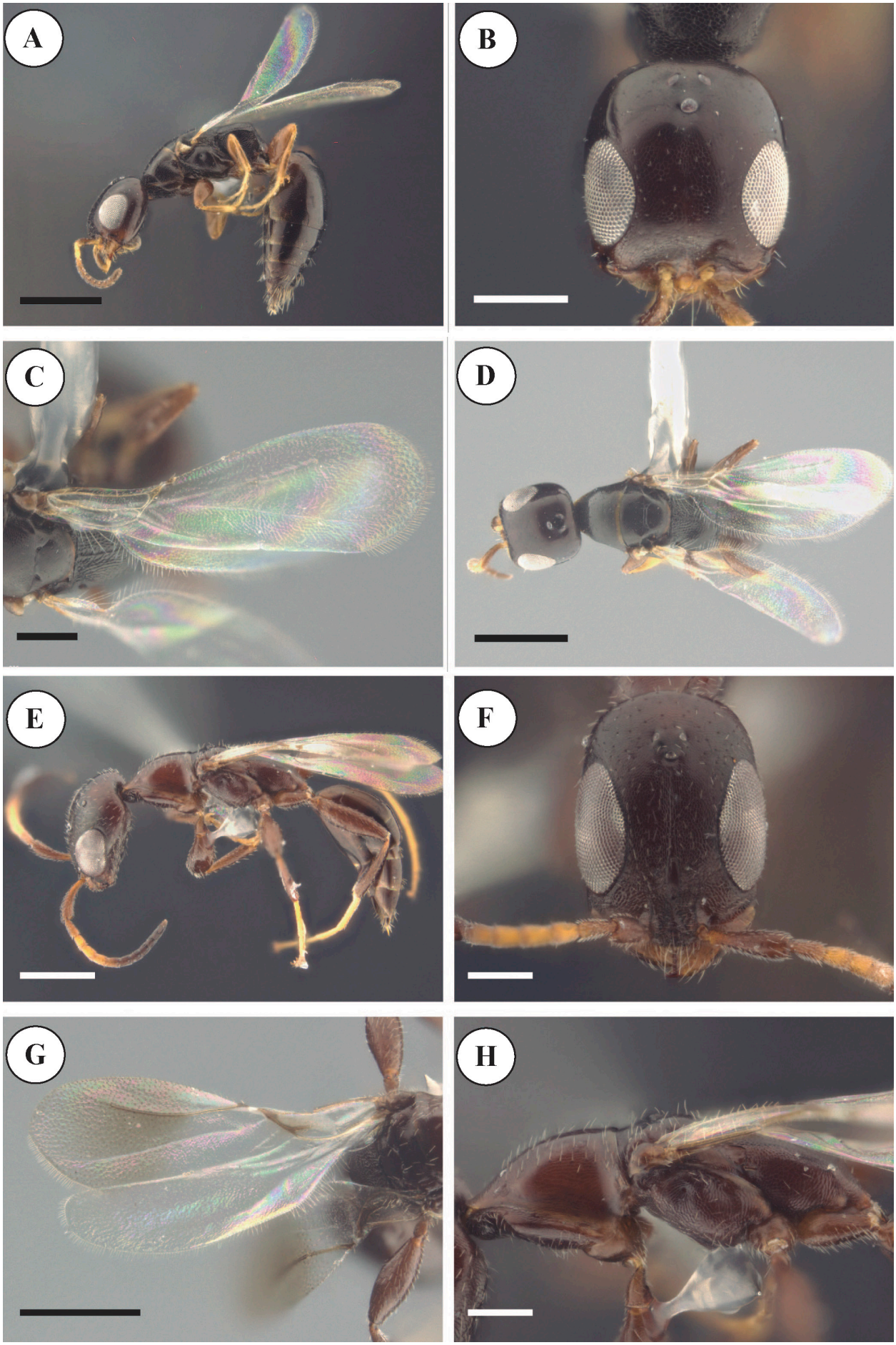
Type species. *Decemnoxus infrequens* sp.n. by monotypy and present designation.

Description. **FEMALE**: Body with scattered short setae. Head elliptical in lateral view, subquadrate in dorsal view. Malar space mid-sized. Malar sulcus present. Mandible robust, dorsal margin not denticulate. Clypeus short, subvertical, median carina absent. Antenna with 10 flagellomeres. Eye scarcely setose. Gena hidden by eye in dorsal view. Dorsal pronotal area ecarinate, trapezoidal, only slightly depressed forward, cervical pronotal area short and subvertical. Notaulus absent. Parapsidal signum present. Mesoscutum-mesoscutellar sulcus complete. First abdominal spiracle located at lateral surface of metapectal-propodeal complex. Propleural corners not prominent in dorsal view. Prosternum small, smaller than ventral surface of procoxa. Macropterous. Forewing with anterior margin incurved, Radial (R) cell closed, First Cubital (1Cu) cell opened; costal vein absent; M+Cu vein present; Rs&M vein and prestigmal abscissa of R1 vein dilated; pterostigma short and subtriangular; 2r-rs&Rs vein fully absent; 1Cu cell subequal than R cell; cu-a vein arched; flexion line simple. Hind wing with three distal hamuli irregularly spaced. Mesopleuron with posterior projection. Femora with cross-section subcylindrical. Metasoma robust, cross-section subcylindrical, densely setose at posterior half, without tubercles; apical segments orientated downward. **MALE**: Unknown.

Etymology. The generic epithet *decem* refers to the antennae with ten antennomeres, and *noxus* is in allusion to *Plastanoxus*, a common genus of Scleroderminae. Gender masculine.

Remarks. The general body ground plan of *Decemnoxus* is similar to those of *Plastanoxus* and *Cephalonomia*. The genus runs to the couplet 23 in the key by AZEVEDO et al. (2019), however it failed to runs to *Israelius* or *Cephalonomia*. The main difference with *Israelius* is that the forewings of *Decemnoxus* has the 2r-rs&Rs vein fully absent, whereas the forewings of *Israelius* has the 2r-rs&Rs vein short. The main difference with *Cephalonomia* is that the forewings of *Decemnoxus* has the First Cubital cell clearly closed, whereas the forewings of *Cephalonomia* has the First Cubital cell opened, because of absence of A and cu-a veins.

→ **Fig. 2. A–D**: *Decemnoxus infrequens*, gen. et sp.n.: ♀. **A**: Habitus, lateral; **B**: Head, dorsal view; **C**: Wings, dorsal view; **D**: Head and mesosoma, dorsal view; **E–H**: *Longinoxus inusitatus*, gen. et sp.n., ♀. **E**: Habitus, lateral; **F**: Head, dorsal view; **G**: Wings, dorsal view; **H**: Head and mesosoma, dorsal view. — ***Scale bars***: B, C, F, H – 200 µm; A, D, E, G – 500 µm.


A
B
C
D
E
F
G
H

We have seen more species from Madagascar, with some conspicuous differences, which were grouped under the same clade in our analysis (Fig. 1). The forewings can have only one closed cell (Radial) or can have 2r-rs&Rs vein. That makes the genus with a high degree of variation as many others, viz. *Solepyris*, *Alongatepyris* and *Plastanoxus*, just to cite few examples. This genus deserves to be revised under alpha taxonomic approach in next future.

3.4.2. *Decemnoxus infrequens* sp.n.

Description. **FEMALE**: ***Measures***: Body 2.25 mm long. Forewing 1.33 mm long. LH 0.49 mm. WH 0.45 mm. WF 0.23 mm. HE 0.23 mm. WOT 0.09 mm. OOL 0.17 mm. ***Color***: Body dark castaneous, clypeus medially, mandible and antenna castaneous, palpi pale castaneous, legs with coxae dark castaneous, femora and tibiae castaneous, trochanters and tarsi pale castaneous; wings hyaline, veins light castaneous. ***Head***: Sides badly outcurved when seen in dorsal view. Mandible with at least two large distal teeth, lower tooth larger. Clypeus wholly projected forward, very broadly trapezoidal, median and lateral lobes not outlined. Toruli not covering anterior clypeal margin in dorsal view. Inter-torular space slightly more than torular diameter. Pedicel about 2.6 × flagellomere I, flagellomeral pubescence short and appressed, with some setae erect and as long as one third of thickness of flagellomeres. Frontal line very inconspicuous. Frons weakly coriaceous, with very few minute punctures. Eye subtriangular, contour not protruding, setae about as long as ommatidium. WH 0.91 × LH. WF 0.52 × WH. WF 1.0 × HE. OOL 1.83 × WOT. Frontal angle of ocellar triangle acute. VOL shorter than HE. Anterior ocellus posterior to supra-ocellar line. ***Mesosoma***: Parapsidal signum inconspicuous, absent on posterior half of mesoscutum. Mesoscutum-mesoscutellar sulcus conspicuous, continuous, slightly wider and deeper at lateral ends. Metapectal-propodeal disc slightly wider than long, antero-central area areolate, otherwise coriaceous, metapostnotal median carina complete, transverse posterior and lateral carinae complete; first abdominal spiracle elliptical, located at lateral surface of metapectal-propodeal× complex. Propodeal declivity weakly coriaceous, without median carina. Mesotibia not spinose. Forewing with M+Cu vein tubular, complete, pterostigma short and subquadrate, 2r-rs&Rs vein absent; 1Cu cell narrower than R cell. Hind wing with three hamuli very closed one to another. Mesopleural pit conspicuous deep and sharp. ***Metasoma***: Sternites V and VI with paired calli.

Material examined. Holotype ♀, MADAGASCAR, Toliara Prov., Fiherenana, el. 100m, 23°10.37′S 43°57.39′E, 21–24 October 2002, colls: Frontier Wilderness Project, sifted litter (leaf, mold, rotten wood) gallery forest, MGF 040, CASENT 2083233 (CASC). – Paratype: 1 ♀, MADAGASCAR, Antsiranana, Forêt de Bekaraoka, 6.8km, 60°NE Daraina, elev. 150m, 7 December 2003, 13°10′00″S 49°42′36″E, collector: B.L. Fisher, general collection night spider, tropical dry forest, CASENT 2103988 (CASC).

Etymology. The specific epithet *infrequens* from Latin means infrequent, it refers to the scarce general body pubescence.

3.4.3. *Longinoxus* gen.n.

Figs. 2E–H, 3A–H

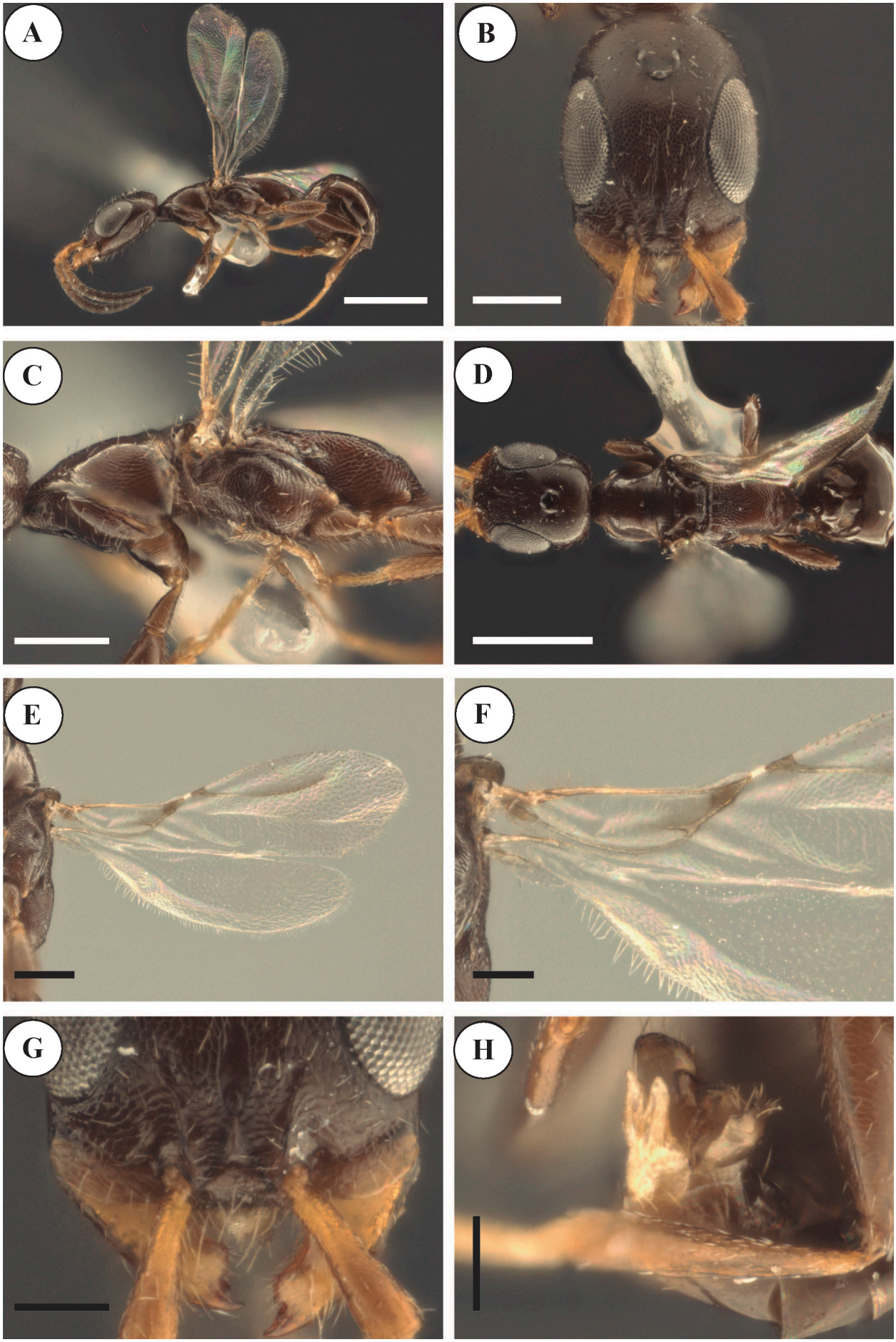
Type species. *Longinoxus inusitatus* sp.n. by monotypy and present designation.

Description. **FEMALE**: Head long and rectangular in dorsal view, somewhat flat in lateral view. Malar space shorter than mandibular proximal width. Malar sulcus conspicuous. Mandible robust, with subhorizontal surface, dorsal margin not denticulate. Clypeus subvertical medially, median lobe outlined from lateral ones. Antenna with 10 flagellomeres. Eye little setose. Gena not seen in dorsal view. Dorsal pronotal area ecarinate, bell-shaped. Mesoscutum with subhorizontal surface Notaulus absent. Parapsidal signum present. Mesoscutum-mesoscutellar sulcus complete. First abdominal spiracle located at lateral surface of metapectal-propodeal complex far from lateral carina. Propleural corner prominent and angled in dorsal view. Prosternum small. Macropterous. Forewing with anterior margin incurved, with only Radial (R) and First Cubital (1Cu) cells closed; costal vein absent; M+Cu vein incomplete, present only on posterior fifth, so that R and 1Cu cells are mostly fused; prestigmal abscissa of 1R dilated; 2r-rs&Rs vein tubular and long; 1Cu narrower than R cell; cu-a vein tubular. Hind wing with three hamuli closed one to another. Metasomal cross-section elliptical. **MALE**: Very similar to female, except by having metasomal tergite II with pair of depressions with light castaneous spot inside. Genitalia with paramere simple, not divided into two arms.

Etymology. The generic epithet *longi* refers to the very elongate head, and *noxus* is in allusion to *Plastanoxus*, a common genus of Scleroderminae. Gender masculine.

Remarks. This genus has some bizarre characteristics, which make it unique among all Bethylidae. The head is long, as much as in *Megaprosternum* (AZEVEDO 2006), the propleural corners are very prominent; the dorsal pronotal area is bell-shaped, with lateral and anterior areas depressing smoothly; mesoscutum with surface subhorizontal. These three latter characteristics are unique in Bethylidae. The Radial and First Cubital cells are partial-

→ **Fig. 3.** *Longinoxus inusitatus*, gen. et sp.n.: ♂. **A**: Habitus, lateral; **B**: Head, dorsal view; **C**: Mesosoma, lateral view; **D**: Head and mesosoma, dorsal view; **E**–**F**: Wings, dorsal view; **G:** Anterior head, dorsal view; **H**: Genitalia, lateral view. ***Scale bars***: B, C, E – 200 µm; A, D – 500 µm; F–H – 100 µm.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ly fused because of reduction of M+Cu vein, resembling *Thlastepyris*. However, in *Longinoxus*, the First Cubital cell is long, whereas in *Thlastepyris*, this cell is much shorter than Radial cell. One additional observation that deserves to be highlighted, the sexual dimorphism is minimal; the only difference we were able to find is the presence of a pair of depressions on the metasomal tergite II, what is not frequent in Scleroderminae. This modification resembles the tergal process in *Dissomphalus*, a genus of Pristocerinae.

In the list of unique characteristics of this genus in comparison to other Scleroderminae, it is included frontal line very wide, depression-shaped; antennal scrobe strongly carinate; clypeus with quadrate median area flat, and lateral and median clypeal lobes about equally-sized. The genus runs to *Proplastanoxus* at the couplet 25 in the key by AZEVEDO et al. (2019), however the forewings of *Longinoxus* has Radial and First Cubital cells of partially fused because of reduction of M+Cu vein, whereas the forewings of *Proplastanoxus* has M+Cu vein fully developed and consequently the Radial and First Cubital cells are fully outlined.

3.4.4. *Longinoxus inusitatus* sp.n.

Description. FEMALE: ***Measures***: Body 2.82 mm long. Forewing 1.61 mm long. ***Color***: Body, clypeus, mandible, antenna, palpi and legs castaneous to dark castaneous; wings hyaline, with darker spot around 2r-rs&Rs vein, veins castaneous. ***Head***: Mandible with three distal teeth, lower tooth sharpened, two upper teeth truncate, upper one wider. Median clypeal lobe trapezoidal, without median carina, lateral lobe well projected forward. Frontal line present. Eye oval, very large, contour slightly protruding. Inter-torular space about 2 × torular diameter. Antennal scrobe strongly carinate. Pedicel about 1.4 × flagellomere I, flagellomeral pubescence short and subappressed. Frons coriaceous, with sparse mid-sized punctures. Frontal line polished, shallow, very wide, but narrowing posterad almost until anterior ocellus. WH 0.75 × LH. WF 0.47 × WH. WF 0.86 × HE. OOL 1.43 × WOT. VOL shorter than HE. Frontal angle of ocellar triangle acute. Anterior ocellus crossing supra-ocellar line. ***Mesosoma***: Parapsidal signum very inconspicuous, straight, narrow, almost parallel. Mesoscutum-mesoscutellar sulcus, arched, with lateral fovea wider and deeper than median sulcus. Metapectal-propodeal disc wholly strongly areolate, longer than wide, with transverse anterior, metapostnotal median and transverse posterior carinae; metapostnotal median carina incomplete absent on posterior half of disc; lateral margin absent. First abdominal spiracle narrowly elliptical. Propodeal declivity without median carina, lateral carina very incipient. **MALE**: Similar to female, except for: Body 2.14 mm long. Forewing 1.19 mm long. Ratio of first four antennomeres about 12:5:3:4, flagellomeral pubescence suberect, with some setae erect and as long as one third of thickness of flagellomeres. Frons with very few minute punctures. Frontal line narrower than in female. WH 0.84 × LH. WF 0.50 × WH. WF 0.79 × HE. OOL 1.10 × WOT. Frontal angle of ocellar triangle right. Genitalia with paramere simple, short with apical end somewhat truncate; aedeagus bottle-shaped, its apex anterior to paramere apex, deeply divided apically with paired lobes, cuspis wide with margin rounded, its apex anterior to digitus apex, posterior board of digitus sawed.

Etymology. The specific epithet *inusitatus* from Latin means unusual, it refers to the set of bizarre and unique characteristics when compared to other Scleroderminae and even to Bethylidae.

Remarks. Although the lateral carina of metapectal-propodeal complex is absent, the encounter of both dorsal and lateral surfaces of this complex are sharp, so leading us to believe that it is present.

Material examined. Holotype ♀, MADAGASCAR, Province Fianarantsoa, Parc National Ranomafana, radio tower at Forest edge, elev. 1130 m, 24 Dec. 2001-2 Jan. 2002, 21°15.05′S 47°24.43′E, Collector: R. Harin'Hala, Malaise, mixed tropical forest, MA-02-09B-09, CASENT 2063390 (CASC). – Allotype: ♂, MADAGASCAR, Toliara Prov., Parc Nat. d'Anfohahela, Forêt d'Ambohibory, 1.7 km 61° ENE Tsomelahy, 36.1 km 308° NW Tolagnaro, 16–20.2002, 24°55′48 ″S 46°38′44″E, coll: Fisher, Griswold et al. Malaise trap in tropical dry forest, elev. 300 m, BLF4917, CASENT 2086477 (CASC). – Paratype: 1 ♀, MADAGASCAR, Toliara Prov., Parc Nat. de Tsimanampetsotsa, Forêt de Bemanatiza, 20.7 km 81° E Efoetse, 23.0 km 131° SE Beheloka, 22–26 March 2002, 23°59′32″S 43°52′50″E, coll: Fisher, Griswold et al. Malaise trap in spiny forest thicket, elev. 90 m, CASENT 2111557 (CASC).

3.4.5. *Madanoxus* gen. n.

Fig. 4A–D

Type species. ***Madanoxus patulus*** sp.n. by monotypy and present designation.

Description. FEMALE: Body robust, scattered short setae. Head elliptical in lateral view, subquadrate in dorsal view. Malar space small. Malar sulcus present. Antenna with 10 flagellomeres. Mandible robust, dorsal margin not denticulate. Clypeus short, subvertical, median carina absent. Antenna with 10 flagellomeres. Eye scarcely setose. Gena hidden by eye in dorsal view. Dorsal pronotal area ecarinate, trapezoidal, only slightly depressed forward, cervical pronotal area short and subvertical. Notaulus absent. Parapsidal signum present. Mesoscutum-mesoscutellar sulcus complete. First abdominal spiracle located at dorsal surface of metapectal-propodeal disc. Propleural corners not prominent in dorsal view. Propleural corners not prominent in dorsal view. Prosternum small, smaller than ventral surface of procoxa. Macropterous. Forewing with anterior margin usually incurved, with Radial (R) and First Cubital (1Cu) cells closed; costal vein absent; M+Cu vein present; Rs&M vein and prestigmal abscissa of R1 vein dilated; pterostigma short and subtriangular; 2r-rs&Rs vein tubular and long; 1Cu cell subequal than

R cell; cu-a vein arched; flexion line simple. Hind wing with four distal hamuli irregularly spaced. Mesopleuron with posterior projection. Femora with cross-section subcylindrical. Metasoma robust, cross-section subcylindrical, densely setose at posterior half, without tubercles; apical segments orientated downward. **Male**: Unknown.

Etymology. The generic epithet is a combination of *Mada* in allusion to Madagascar and *noxus* in allusion to *Plastanoxus*. Gender masculine.

Remarks. This genus has an unusual combination of characters. The 10-flagellomered genera have the body and carinae delicate. However, *Madanoxus* has the body robust, head and mesosoma wide, carinae of the metapectal-propodeal complex strong and well defined. The dorsal pronotal area short and the forewing with conspicuous 2r-rs&Rs vein are also characters not frequent among the 10-flagellomered genera.

The genus runs to *Proplastanoxus* at the couplet 25 in the key by Azevedo et al. (2019), however in *Madanoxus* the forewings do not have Costal vein, so that the Costal cell is opened, whereas in *Proplastanoxus* the forewings have Costal vein and consequently the Costal cell is closed.

3.4.6. *Madanoxus patulus* sp.n.

Description. Female: ***Measures***: Body length 3.85 mm. LFW 2.54 mm. LH 0.83 mm. WH 0.91 mm. WF 0.52 mm. HE 0.42 mm. WOT 0.20 mm. OOL 0.25 mm. ***Color***: head and mesosoma dark castaneous almost black, metasoma dark castaneous, clypeus, mandible, antenna and legs mostly somewhat dark castaneous, palpi pale castaneous; wings subhyaline, veins castaneous. ***Head***: Depressed anteriorly, lateral margin outcurved. Mandible with upper margin not denticulate, with three conspicuous distal teeth. Median clypeal lobe very short, as long as lateral ones, not separated by emargination from lateral lobes, surface almost vertical, median carina absent. Toruli not covering anterior clypeal margin in dorsal view. Intertorular space very wide, about 3 × torular diameter. Pedicel about 1.6 × flagellomere I, flagellomeral pubescence dense, mid-long and subappressed, without erect setae. Frontal line extending from clypeus to anterior ocellus as shallow sulcus. Frons coriaceous, with few minute punctures. Eye subtriangular, contour not protruding, setae slightly longer ommatidium. WH 1.09 × LH. WF 0.58 × WH. WF 1.24 × HE. OOL 1.23 × WOT. Frontal angle of ocellar triangle acute. VOL much shorter than HE. Anterior ocellus crossing supra-ocellar line. ***Mesosoma***: Parapsidal signum almost complete, somewhat inconspicuous, straight and parallel. Mesoscutum-mesoscutellar sulcus conspicuous, continuous, deep, slightly arched, wider and deeper at lateral ends. Metapectal-propodeal disc much wider than long, mostly strongly striate, otherwise coriaceous, metapostnotal median carina complete; paraspiracular carina complete, twisted; first abdominal spiracle elliptical. Propodeal declivity coriaceous, without median carina, and lateral surface of metapectal-propodeal complex coriaceous, Mesotibia not spinose. Mesopleuron with posterior tubercle. ***Metasoma***: Sternites without paired calli.

Etymology. The specific epithet *patulus* from Latin refers to the wide and robust body.

Material examined. Holotype ♀, MADAGASCAR, Toamasina, Montagne d'Anjanaharibe, 18.0 km, 21°NNE Ambinanitelo, elev. 470 m, 8–12 March 2003, 15°11′18″S 49°36′54″E, Coll: Fisher, Griswold et al. Malaise trap, in rainforest, CASENT 2087370 (CASC).

3.4.7. *Mutatio* gen. n.

Fig. 4E–H

Type species. ***Mutatio mutata*** sp.n. by monotypy and present designation.

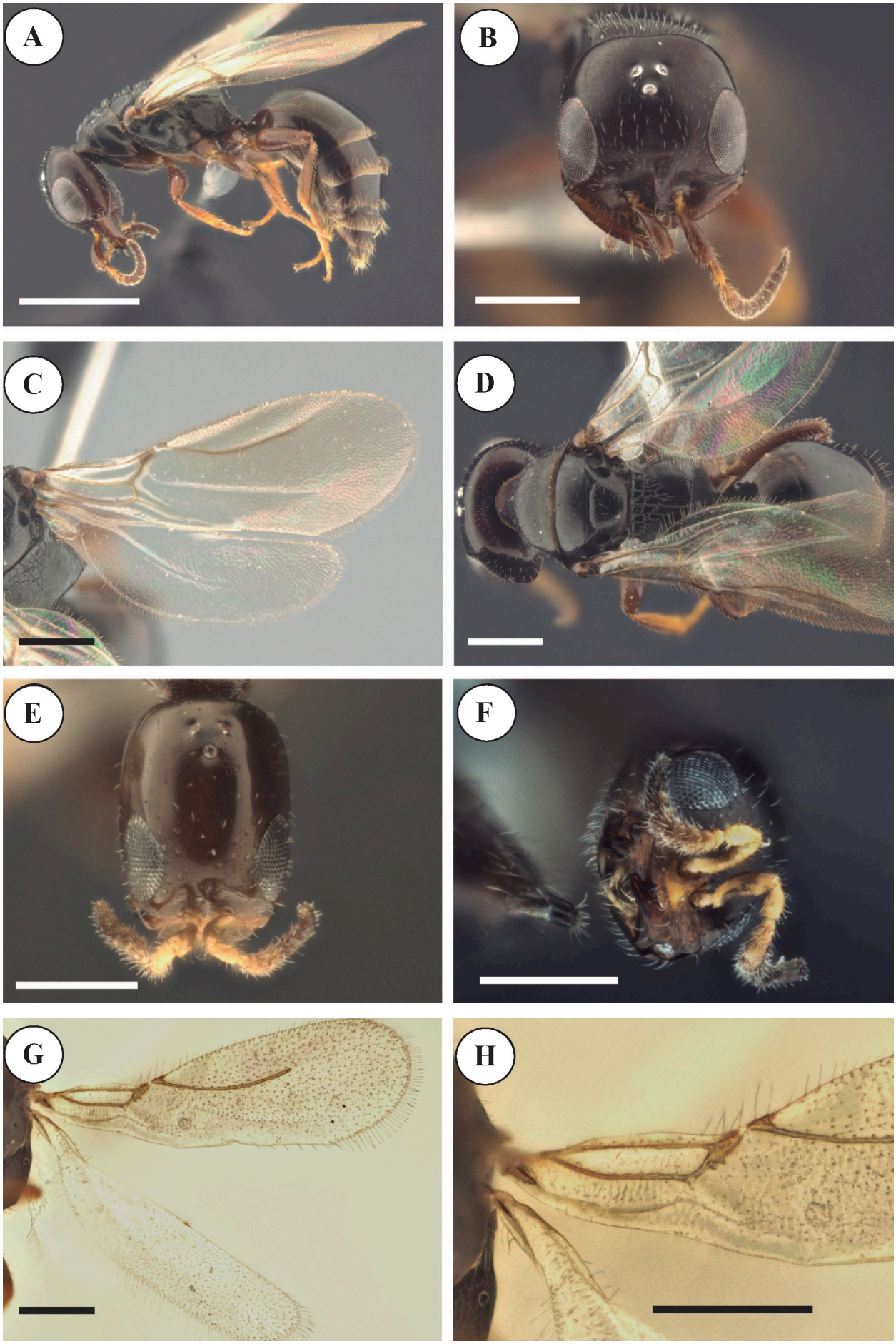
Description. Female: Body little setose. Head subgloboid in lateral view and subrectangular in dorsal view. Malar space shorter than mandibular proximal width. Malar sulcus present. Mandible robust, dorsal margin not denticulate. Clypeus well projected forward. Antenna with seven flagellomeres. Eye sparsely setose. Gena hardly visible lateral to eye in dorsal view. Pronotal flange conspicuous, dorsal pronotal area depressed forward. Dorsal pronotal area ecarinate, trapezoidal. Notaulus absent, parapsidal signum present. Mesoscutum-mesoscutellar sulcus complete. First abdominal spiracle located at lateral surface of metapectal-propodeal complex, touching lateral carina. Propleural corners not prominent, in dorsal view. Prosternum small, smaller than ventral surface of procoxa. Macropterous. Forewing with anterior margin incurved, with only Radial (R) cell closed; costal vein absent; M+Cu vein complete; prestigmal abscissa of R1 vein dilated, pterostigma subtriangular, 2r-rs&Rs vein present; A vein tubular as anterior stub, otherwise mostly spectral, and absent posteriorly; cu-a vein present as dorsal stub. Hind wing with 3 hamuli irregularly spaced. Femora with cross-section elliptical. Metasoma robust, cross-section elliptical, without tubercles; apical segments orientated downward. **Male**: Unknown.

Etymology. The generic epithet *Mutatio* from Latin means change, it refers to the big surprise to find the first Bethylidae ever with only seven flagellomeres. Gender feminine.

Remarks. This genus differs from all other genera of Bethylidae by having only seven flagellomeres. The genus stops at the couplet 18 in the key by Azevedo et al. (2019), because it does not have neither 11 nor eight or ten of flagellomeres.

3.4.8. *Mutatio mutata* sp.n.

Description. Female: ***Measures***: Body 1.99 mm long. Forewing 1.02 mm long. ***Color***: Body, clypeus, man-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dible, antenna, and legs castaneous to dark castaneous, median area of clypeus, venter of antenna and palpi light castaneous; wings hyaline, veins light castaneous. ***Head***: Sides of head parallel, vertex outcurved. Malar space inconspicuous. Malar sulcus narrow and inclined. Mandible with at least two large distal teeth, lower tooth larger. Clypeus trilobite, lobes outcurved, median lobe narrower than lateral ones, median carina apparently double and present only posteriorly. Inter-torular space about 0.5 × torular diameter. Pedicel about 3.0 × flagellomere I, flagellomeral pubescence short and subappressed, with some setae suberect and about as long as half of thickness of flagellomeres. Frontal line very inconspicuous, short. Frons weakly coriaceous, with very few minute punctures. Eyes elliptical in lateral view, contour not protruding. WH 0.89× LH. WF 0.42× WH. WF 1.11× HE. OOL 2.0× WOT. Frontal angle of ocellar triangle acute. VOL only slightly longer than HE. Anterior ocellus far posterior to supra-ocellar line. ***Mesosoma***: Dorsal pronotal area depressed forward. Parapsidal signum inconspicuous, very narrow and shallow, straight, parallel. Mesoscutum-mesoscutellar sulcus badly arched, evenly wide and deep, without lateral fovea. Metapectal-propodeal disc weakly areolate, except weakly coriaceous mid posteriorly, with transverse anterior, transverse posterior and lateral carina, metapostnotal median carina fully absent. First abdominal spiracle elliptical, located below lateral carina of metapectal-propodeal complex. Propodeal declivity weakly coriaceous, without median carina. Mesotibia not spinose. Forewing with 2r-rs&Rs vein long, 0.34 × as long as forewing. Mesopleural pit small and sharply outlined. **Male**: Unknown.

Etymology. The specific epithet *mutata* from Latin means modified, that is to emphasize how bizarre is to have seven flagellomeres.

Material examined. Holotype ♀, MADAGASCAR, Antsiranan, Rés. Analameranana, 28.4 km, 99° Anivorano-Nord, elev. 60 m, 5 December 2004, 12°44′48″S 49°29′41″E, Coll: B.L. Fisher, sifted litter (leaf, mold, rotten wood) tropical dry forest, CASENT 2089809 (CASC).

3.4.9. *Pilocutis* gen. n.

Fig. 5A–D

Type species. *Pilocutis mollis* sp.n. by monotypy and present designation.

Description. Female: Body robust, densely setose. Head subgloboid in lateral view and about subquadrate in dorsal view. Malar space shorter than mandibular proximal width. Malar sulcus narrow, subparallel to mandibular proximal margin. Mandible robust, dorsal margin not denticulate. Clypeus elevated medially, so that anterior margin seems to be thick and subtriangular in frontal view. Antenna with 10 flagellomeres. Eye densely setose. Gena hardly visible lateral to eye in dorsal view. Dorsal pronotal area ecarinate, trapezoidal. Notaulus and parapsidal signum present. Mesoscutum-mesoscutellar sulcus complete. First abdominal spiracle located at lateral surface of metapectal-propodeal complex. Propleural corners not prominent, in dorsal view. Prosternum small, smaller than ventral surface of procoxa. Macropterous. Forewing with anterior margin incurved, with only Radial (R) and First Cubital (1Cu) cells closed; costal vein absent; M+Cu vein complete; pterostigma linear, 2r-rs&Rs vein present; A vein tubular; cu-a vein present; 1Cu cell shorter than R cell. Hind wing with 3 hamuli irregularly spaced. Mesopleuron with posterior surface elevated. Femora with cross-section subcylindrical. Metasoma robust, cross-section subcylindrical, densely setose at posterior half, without tubercles; apical segments orientated downward. **Male**: Unknown.

Etymology. The generic epithet *pilo* + *cutis* refers to the head strongly setose of its type-species. Gender feminine.

Remarks. The genus runs to *Proplastanoxus* at the couplet 25 in the key by Azevedo et al. (2019), however in *Pilocutis* the forewings do not have Costal vein, so that the Costal cell is opened, whereas in *Proplastanoxus* the forewings have Costal vein and consequently the Costal cell is closed. Besides, *Pilocutis* has the clypeus with a triangular median area flat, unique among all genera Scleroderminae. Furthermore, this genus is easily recognized within Scleroderminae by having the body densely setose, unique in this subfamily.

3.4.10. *Pilocutis mollis* sp.n.

Description. Female: ***Measures***: Body 3.34 mm long; forewing 1.09 mm long; LH 0.62 mm; WH 0.58 mm; WF 0.34 mm; HE 0.25 mm; WOT 0.14 mm; OOL 0.09 mm. ***Color***: Body dark castaneous, anterior clypeal margin and mandible lighter, antenna and palpi castaneous, legs somewhat dark castaneous, except tibiae and tarsi castaneous; wings subhyaline, veins light castaneous. ***Head***: Mandible with two distal teeth, upper tooth rounded, lower tooth sharpened. Malar sulcus inconspicuous. Clypeus trapezoidal, median and lateral clypeal lobes not outlined. Toruli not covering anterior clypeal margin. Inter-torular space 2 × torular diameter. Pedicel about 1.6 × flagellomere I, flagellomeral pubescence short and subappressed, with some setae erect and as long as half thickness of flagellomeres. Frontal line inconspicuous. Frons coriaceous, densely punctuated, space among punctures

← **Fig. 4. A–D**: *Madanoxus patulus*, gen. et sp.n.: ♀. **A**: Head, dorsal view; **B**: Head, frontal view; **C–D**: Wings, dorsal view; **E–H**: *Mutatio mutata*, gen. et sp.n.: ♀. **E**: Habitus, lateral; **F**: Head, dorsal view; **G**: Wings, dorsal view; **H**: Habitus, dorsal view. ***Scale bars***: F–H – 200 µm; B–D – 500 µm; A, E – 1 mm.

smaller than punctures. Epistomal suture thick and boomerang-shaped. Eye subcircular, contour not protruding, setae much longer than ommatidium. WH 0.95 × LH. WF 0.58 × WH. WF 1.38 × HE. OOL 0.67 × WOT. Frontal angle of ocellar triangle acute. VOL shorter than HE. Anterior ocellus crossing supra-ocellar line. ***Mesosoma***: Notaulus complete, straight, evenly wide, converging posterad. Parapsidal signum complete, straight, inconspicuous, converging posterad. Mesoscutum-mesoscutellar sulcus not evenly wide. Metapectal-propodeal disc wider than long, metapostnotal median carina occupying anterior third of disc, transverse posterior and lateral carinae complete; first abdominal spiracle circular. Propodeal declivity without median carina. Mesotibia not spinose. Forewing with 2r-rs&Rs vein tubular and very long, about 0.33 × wing length; 1Cu cell narrower than R cell. Mesopleural subalar impression long, central pit deep.

Etymology. The specific epithet *mollis* from Latin means soft, it refers to the head excessively setose resembling soft velvet.

Material examined. Holotype ♀, THAILAND, Chaiyaphum, Tat Tone NP, Chaiyapoom forest, fire station, 16°0.809′ N 102°1.335′ E, 195 m, Malaise trap, 26.xii.2006 – 2.i.2007, Tawit Jaruphan & Orawan Budsawong leg. T1376. (QSBG).

3.4.11. *Thlastepyris marquisensis* (Fullaway, 1935) stat. et comb.n.

Fig. 5E – H

Sierola depressa var. *marquisensis* Fullaway, 1935; FULLAWAY 1935; FOUTS 1936; GORDH & MÓCZÁR 1990.

Description. FEMALE: Body depressed. Body length 2.35 mm. LFW 1.40 mm. LH 0.58 mm. WH 0.43 mm. WF 0.25 mm. HE 0.23 mm. WOT 0.12 mm. OOL 0.26 mm. WH 0.74 × LH; WF 0.57 × WH; WF 1.07 × HE; OOL 2.13 × WOT. Head depressed, oval in lateral view, lateral margin straight, frons strongly coriaceous. Malar space absent. Medial clypeal lobe truncate, not carinate, longer than lateral ones, lobes not well delimited, anterior margin shape (anterior view) not angled. Inter-torular space absent or nearly so. Toruli covering anterior clypeal margin or nearly so. Gena not visible lateral to eye in dorsal view. Mandible slender with basal intercondylar lobe, four small distal teeth, upper margin not denticulate. Hypostomal carina not emarginate medially. Antenna with 11 flagellomeres, pedicel as long as distal flagellomere. Frontal line present. Eye subtriangular in lateral view, setose, contour not protruding. Frontal angle of ocellar triangle obtuse. VOL longer than eye. Ocellar triangle close to vertex crest. Anterior ocellus anterad to supra-ocellar line. Occipital carina absent. Pronotal flange inconspicuous. Dorsal pronotal area flat, longer than wide with anterior margin semicircular. Propleural neck and anterior angles visible in dorsal view. Prosternum size small. Anteromesoscutum medial length subequal than mesoscutellum. Scutellum apex widely rounded. Mesoscutum-mesoscutellar suture conspicuous, continuous, not evenly wide, deeper at lateral ends with lateral subcircular foveae. Metascutellum wide. Metapectal-propodeal disc flat, rugulose to areolate with transverse anterior, metapostnotal median and lateral carina of metapectal-propodeal complex; lateral margin straight, strongly convergent posteriorly; lateral carina of metapectal-propodeal complex outlined first abdominal spiracle. First abdominal spiracle lateral, circular, located below lateral carina of metapectal-propodeal complex. Metapectal-propodeal pleural postero-lateral corner rounded. Forewing anterior margin incurved near prostigma. Forewing venation with Sc+R vein; M+Cu tubular, basally incomplete; Rs&M complete; prestigmal abscissa of R1 longer than wide; pterostigma short; r-rs vein segment tubular; A vein present; cu-a vein present, length conspicuous, orientated proximally; 1Cu cell length less than half of R cell length; longitudinal fold simple; proximal venation reaching at most 0.2 × of forewing total length; membrane color hyaline to whitish. Mesopleural prepectal carina, two anterior small foveae present. Upper mesopleural fovea open. Subalar impression simple, long, connected with episternal groove, widened anteriorly. Metasomal tergite I lateral margins in contact each other ventrally. Metasomal second segment size short, apical segments orientated downward.

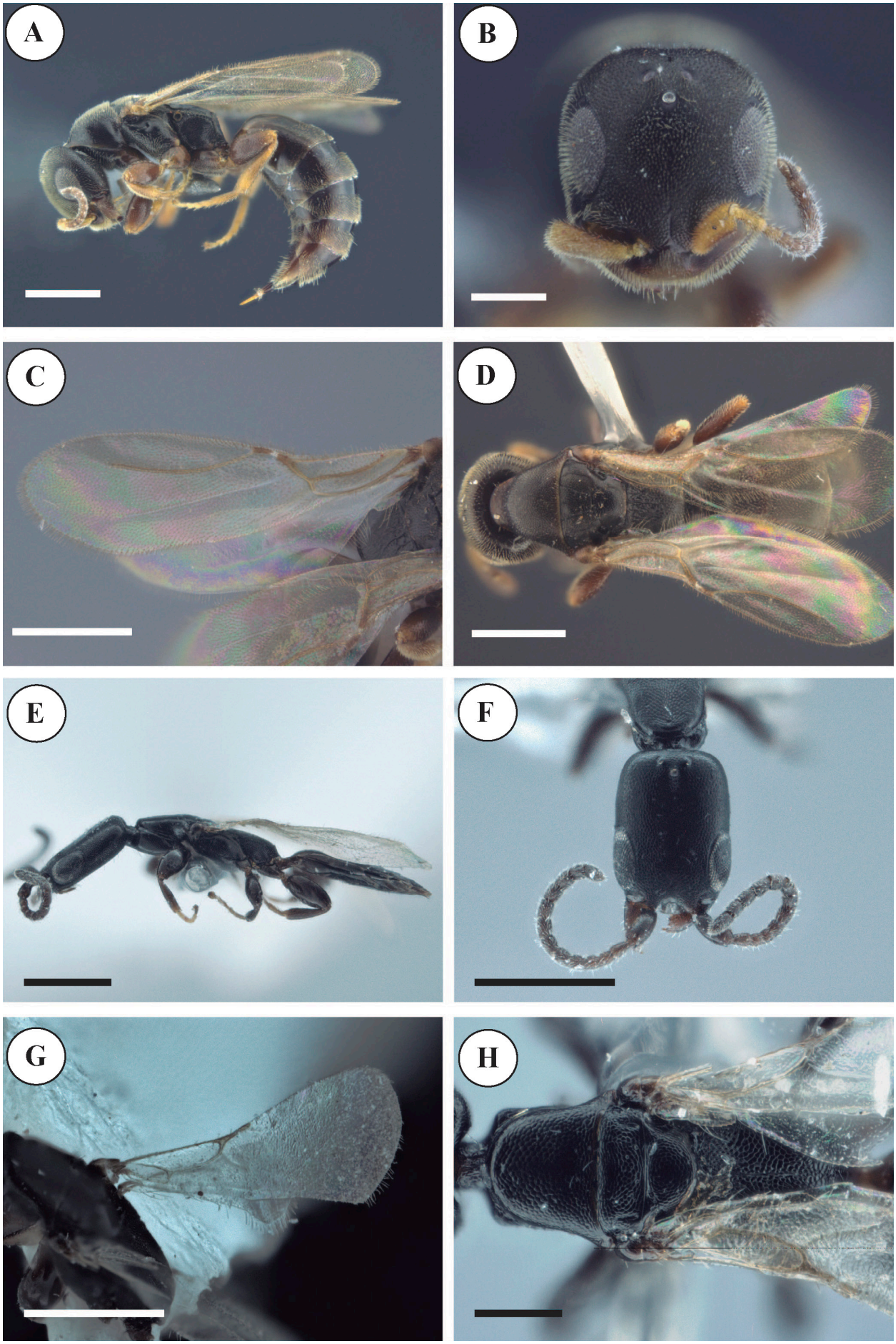
Remarks. This species is transferred to *Thlastepyris* due to the absence of clypeal carina, the forewing with R and 1Cu cells closed, proximally fused due the incompleteness of M+Cu and the presence of 2r-rs&Rs.

Material examined. Holotype of *Sierola depressa* var. *marquisensis* Fullaway, 1935, ♀, MARQUESAS ISLANDS, Tapeata, E. Slope, Mt. Ootva, 5–25–29, Hiva['Oa], 2500 ft, On *Paspalum conjugatum*, Mumford & Adamson, Type 777, Pacific Entomological Survey (BPBM).

4. Discussion

Scleroderminae were recovered monophyletic and in agreement with LANES & AZEVEDO (2008), ALENCAR & AZEVEDO (2013), CARR et al. (2010) and JIANG et al. (2015). Although a small subfamily, Scleroderminae have several morphological patterns, and we were able to discover some additional patterns mostly from Madagascar, which deserve to be allocated in new genera due

→ **Fig. 5. A – D**: *Pilocutis mollis*, gen. et sp.n.: ♀. **A**: Habitus, lateral; **B**: Head, dorsal view; **C**: Wings, dorsal view; **D**: Mesosoma, dorsal view; **E – H**: *Thlastepyris marquisensis* (Fullaway, 1935) stat. et comb. nov.: ♀. **E**: Habitus, lateral; **F**: Head, dorsal view; **G**: Wings, dorsal view; **H**: Mesosoma, dorsal view. ***Scale bars***: B, G – 200 µm; A, C, D, E, F – 500 µm; H – 1 mm.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to the large morphological discontinuity in relation to the other genera. Most of these new patterns match with the old delimitation of Cephalonomiini sensu EVANS (1964), especially by the presence of ten flagellomeres or less in the antennae, a condition that characterized the tribe sensu EVANS (1964), along with other features like the forewing with prostigma, closed R cell and anterior margin slightly incurved proximally. However, this tribe was synonymized in order to eliminate the paraphyly of Sclerodermini (LANES & AZEVEDO 2008).

It is important to emphasize that the evolution of morphological character in Scleroderminae is still deeply incipient, because there is high intrageneric variability, and it is not rare new genera come to light. A complicating factor is the reduced number of specimens of Scleroderminae collected in field expeditions (MUGRABI & AZEVEDO 2010, for instance). This fact constrains our capacity for analyzing the alpha taxonomic limits of both inter- and intrageneric diversity, and sometimes results in many monotypic genera because few species or even specimens are found. Different sampling techniques are vital to face this kind of problem.

The large number of genera with few species and monotypic genera results in instability over the intergeneric relationship in Scleroderminae, because most of the genera have reduction of structures and polymorphism. During the course of this study, even slight modification in the search parameters resulted in major changes among intergeneric relationships. The same inconstancy happens when the addition or deletion of characters is applied. We have gotten very few similar results in comparison to LANES & AZEVEDO (2008), mainly because their study was focused on the Sclerodermini sensu EVANS (1964), i.e., those species with antennae 11-flagellomered. They performed analyses with 15 genera, whereas our analyses are based on all 30 genera of this subfamily. The only exception is *Discleroderma* and *Nothepyris* as sister-groups recovered in both studies. That emphasizes the instability. Future molecular analyses of these wasps are one possible approach to face the problem of reduction of structures and polymorphism in the group. Another feature that increases our difficulty in understanding the phylogenetic relationships among the sclerodermines is high degree of morphological diversity. The range of variation inside the subfamilies in Bethylidae is generally small when compared to sclerodermines.

Although, the situation is not favorable for recovering stable phylogenies of sclerodermines, the monophyly of the genera remains constant in these analyses. The only genus retrieved as polyphyletic is *Cephalonomia*. This genus is cosmopolitan with 42 species (AZEVEDO et al. 2018). Its species are very small, some can be less than 1 mm long, and have accentuated polymorphism, such as in *Cephalonomia perpusilla* Evans, where apterous, micropterous, brachypterous and macropterous forms are found (EVANS 1963). Recently, COLOMBO & AZEVEDO (2020) reinstalled the 8-flagellomered genus *Acephalonomia* from *Cephalonomia*, that helped reduce the high degree polyphyletism in the latter genus (Fig. 1).

The most inclusive genera are those with bodies with less reduction of structures, such as *Chilepyris*, *Glenosema*, *Discleroderma* and *Nothepyris*. They resemble Epyrinae in the general ground plan. Few genera with this style were positioned more apically in the tree, such as †*Celonophamia* and *Galodoxa*. The former is extinct with many unknown character states, so that its placement in the tree is a matter of fluidity, and the latter is a bizarre genus with ventral expansions on the metasoma (NAGY 1974) and unique wing venation (AZEVEDO & LANES 2009), which make it hardly comparable.

Morphological characteristics of the male genitalia are fundamental to the taxonomic and cladistic delimitation of the genera and species that comprise Bethylidae (AZEVEDO et al. 2018). However, the males of 18 genera of Scleroderminae are still unknown, which represent more than 50% of all genera of this subfamily. That is certainly another feature that generates fragility in our tree. Therefore, energy in associating conspecific males is crucial to future analyses, because that will doubtless improve the resolution of the tree.

4.1. Host inference

Although studies are scarce, the convergent morphology in parasitoid wasps is a result of ecological parameters, such as the kind of the host (e.g. SHAW 1988; TSCHOPP et al. 2013) and the different strata and habitats (BASSET & KITCHING 1991; CYR et al. 1997; ULRICH 1999). These features are important for discussing morphological plasticity in Scleroderminae because of their high number of homoplasies as indicated by our analysis (Figs. 1, 6).

The earliest form of parasitism found in the Hymenoptera is ectoparasitism of woodborer insects, and has an origin in the common ancestor of Orussoidea and Apocrita (WHITFIELD 2003). There is a series of stages by which a gradual transition from woodboring to ectoparasitism of woodborers might have taken place (PENNACCHIO & STRAND 2006).

The Bethylidae evolved to exploit small larvae occurring in cryptic situations like soil, stems, wood, or seeds (EVANS 1964). In general, the parasitic biological aspects of the subfamilies of Bethylidae are as follows: Pristocerinae parasitize larvae of myrmecophilous coleopterans (e.g. EVANS 1964), mainly Curculionidae (e.g. BAKER 1976), justifying, somehow, the convergent evolution of the female morphological characters, as absence of wings, small size, absence of ocelli and significant reduction of the eyes. Epyrinae are parasitoids of fossorial larvae, mainly Tenebrionidae (e.g. RUBINK & EVANS 1979), and Mesitiinae of larvae residing in close-fitting portable cases, built of faecal material of Chrysomelidae (ARGAMAN 2003). The parasitism of Coleoptera woodborers is the most widespread condition in Bethylidae, including Scleroderminae. Only Bethylinae are lepidopterophagous (CARR et al. 2010).

The most generalized feeding habit of Scleroderminae is to parasitize larvae of Coleoptera mainly in cryptic

habitats (e.g. Yang et al. 2012). However, there are records of parasitism in other groups, such as Hymenoptera: Cynipidae (Ashmead 1887), Diptera: Tephritidae (Pourhaji et al. 2018) and Lepidoptera: Cosmopterigidae (Bridwell 1920). Occasionally, it has reported that *Cephalonomia hyalinipennis* Ashmead is hyperparasitoid of other bethylid wasps (Perez et al. 2004). The Scleroderminae possess adaptations suited to explore such kind of habitats and hosts.

4.2. Homoplastic morphological traits

Many morphological characters used in our analysis are homoplasies. The most important alpha taxonomic ones are here highlighted.

Body flatness (Fig. 6A)**.** Some Scleroderminae such as *Megaprosternum* and *Platepyris* are much flattened, being the flattest within Bethylidae. Most of the flat bethylids are concentrated in Scleroderminae, with very few species of other subfamilies similarly flattened. Therefore, this character emerged independently within Bethylidae. However, our results show that the flatness evolved independently at least twice in the evolutionary history of the Scleroderminae, one in *Alloplastanoxus*, and other in clade A (Fig. 1).

Megaprosternum cleonarovorum Gupta & Azevedo explores galleries 2.6–2.7 mm in diameter made by the cerambycid host (Gupta et al. 2017), whereas, *Sclerodermus* explores host galleries 1.5–2.5 mm in diameter (Men et al. 2019). The body sizes of the parasitoids do not vary much (2.99–3.19 mm), but the flatness is remarkable. Gallery thickness seems to be important to the evolution of flatness in sclerodermines, but we need further information in this subject in order to explore such characteristics phylogenetically. There are flattened bodies in *Alloplastanoxus*, *Alongatepyris*, *Platepyris*, *Megaprosternum*, *Thlastepyris* and *Tuberepyris*, but only *Megaprosternum* has some information about its life history.

Number of flagellomeres (Fig. 6B)**.** This character is an important matter at the level of the superfamily Chrysidoidea, and helps to define their families. Bethylidae are a sister group of Chrysididae, and this clade is a sister group of (Sclerogibbidae + (Dryinidae + Embolemidae)) (Brothers & Carpenter 1993). Dryinidae and Embolemidae have eight flagellomeres, Sclerogibbidae more than 12 flagellomeres and Chrysididae 10 or 11 flagellomeres. In Bethylidae, the Bethylinae are the sister group of all other bethylid Carr et al. (2010), and has 10 or 11 flagellomeres.

There is a general trend consisting of the miniaturization, venational reduction, enlargement of pterostigma, and reduction of number of the antennal flagellomeres based on observation of numerous fossil and extant lineages (Rasnitsyn 1969, 1980), which may suggest that the hypothetical ancestor of (Bethylidae + Chrysididae) had 11 or more flagellomeres. However, the understanding of the phenomena leading to the appearance of an additional antennomeres is poorly studied, so that we need precaution to affirm any trends on the evolutionary history of flagellomeres reduction. Therefore, ancestor of (Bethylidae + Chrysididae) had 11 flagellomeres is highly hypothetical.

Scleroderminae exhibit a wild range of variation in the number of flagellomeres, but many genera exhibit 11 flagellomeres (*Allobethylus*, *Alongatepyris*, *Bethylopsis*, *Chilepyris*, *Discleroderma*, *Galodoxa*, *Glenosema*, *Megaprosternum*, *Nothepyris*, *Platepyris*, *Sclerodermus*, *Solepyris*, *Thlastepyris* and *Tuberepyris*). These genera represent the old sense of Sclerodermini sensu Evans (1964). The condition with 10 flagellomeres appears in the genera *Alloplastanoxus*, †*Celonophamia*, *Cephalonomia*, *Israelius*, *Pararhabdepyris*, *Plastanoxus*, *Proplastanoxus* and *Prorops*. These genera represent the old sense of Cephalonomiini sensu Evans (1964).

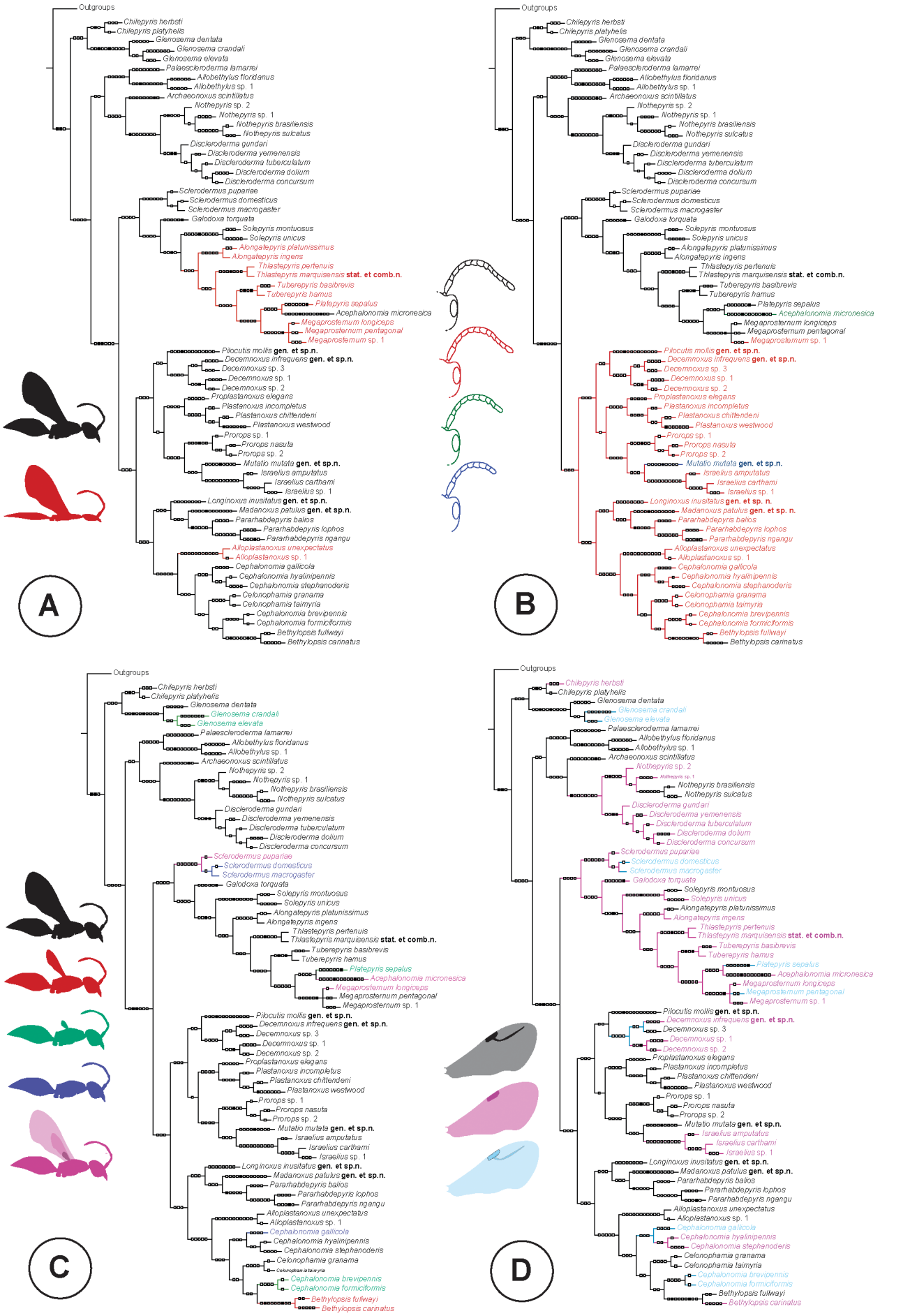
Our results indicate that antennae with 11 flagellomeres are the ancestral conditions, but reappears once in *Bethylopsis carinatus*. The condition of 8-flagellomeres of *Acephalonomia* arose once inside clade A (Fig. 1), so that the 11 flagellomeres characteristic is homoplastic. On the other hand, the antennae with 10 flagellomeres emerges twice, once in clade B (Fig. 1), and another in *Megaprosternum* sp. 1. The condition of seven flagellomeres in *Mutatio* gen. n. arose once inside clade C (Fig. 1), so that the 10 flagellomeres characteristic is also homoplastic.

Given this arrangement, both Sclerodermini and Cephalonomiini (sensu Evans 1964) are polyphyletic, rather than paraphyletic and monophyletic respectively as indicated by Lanes & Azevedo (2008).

The morphological plasticity in the number of flagellomeres does not vary only between genera, but also inside some genera, as observed in *Bethylopsis* and *Megaprosternum* (Figs 1, 6B), or even at species level, as in *Cephalonomia formosiensis* Terayama & Ho, which has antennae with seven, eight, or 10 flagellomeres (Ho et al. 2020), which constitutes the most plastic scenario of this character in the family.

In summary, this character shows high plasticity to such an extent that is hard to understand its transformation series. To establish homologies in individuals with different numbers of flagellomeres, we should know the sequence of events by which the flagellum acquires segmentation (Minelli 2017). When numbers are different, only a detailed knowledge of the underlying segmentation processes would provide the ultimate background for determining positional homology, but unfortunately, current knowledge about this process is very poor for the holometabolous insects, from both the morphological and genetic points of view (Minelli 2017). The scenario in Bethylidae is even worse.

Wing forms (Fig. 6C)**.** Scleroderminae have all possible wing forms, apterous, micropterous, brachypterous and macropterous (Evans 1964). With the exception of the


Outgroups
Chilepyris herbsti
Chilepyris platyhelis
Glenosema dentata
Glenosema crandali
Glenosema elevata
Palaescleroderma lamarrei
Allobethylus floridanus
Allobethylus sp. 1
Archaeonoxus scintillatus
Nothepyris sp. 2
Nothepyris sp. 1
Nothepyris brasiliensis
Nothepyris sulcatus
Discleroderma gundari
Discleroderma yemenensis
Discleroderma tuberculatum
Discleroderma dolium
Discleroderma concursum
Sclerodermus pupariae
Sclerodermus domesticus
Sclerodermus macrogaster
Galodoxa torquata
Solepyris montuosus
Solepyris unicus
Alongatepyris platunissimus
Alongatepyris ingens
Thlastepyris pertenuis
Thlastepyris marquisensis stat. et comb.n.
Tuberepyris basibrevis
Tuberepyris hamus
Platepyris sepalus
Acephalonomia micronesica
Megaprosternum longiceps
Megaprosternum pentagonal
Megaprosternum sp. 1
Pilocutis mollis gen. et sp.n.
Decemnoxus infrequens gen. et sp.n.
Decemnoxus sp. 3
Decemnoxus sp. 1
Decemnoxus sp. 2
Proplastanoxus elegans
Plastanoxus incompletus
Plastanoxus chittendeni
Plastanoxus westwood
Prorops sp. 1
Prorops nasuta
Prorops sp. 2
Mutatio mutata gen. et sp.n.
Israelius amputatus
Israelius carthami
Israelius sp. 1
Longinoxus inusitatus gen. et sp.n.
Madanoxus patulus gen. et sp.n.
Pararhabdepyris balios
Pararhabdepyris lophos
Pararhabdepyris ngangu
Alloplastanoxus unexpectatus
Alloplastanoxus sp. 1
Cephalonomia gallicola
Cephalonomia hyalinipennis
Cephalonomia stephanoderis
Celonophamia granama
Celonophamia taimyria
Cephalonomia brevipennis
Cephalonomia formiciformis
Bethylopsis fullwayi
Bethylopsis carinatus
A
B
C
D

entirely apterous females of Pristocerinae, and some females of Scleroderminae like *Cephalonomia*, *Glenosema* and *Sclerodermus*, all other bethylid are winged (microbrachy- or macropterous) (Azevedo et al. 2018).

Some holopsenelline fossil such as *Holopsenella* Engel, Ortega & Azevedo, 2016 and *Cretabythus* Evans, 1973 from the Cretaceous are macropterous, the forewings have the most complete venation in comparison with other subfamilies, with tubular and pigmented veins defining seven closed cells: C, R, 1R1, 2R1, 1M, 1Cu and 2Cu (Engel et al. 2016). Besides, this subfamily is monophyletic (Colombo et al. 2020). With these features, this subfamily is the most plesiotypic bethylid subgroup and can help us understand the course of evolution of Bethylidae (Azevedo et al. 2018) and the subfamily is a useful terminal to root analyses of living subfamilies.

The forewing fully developed and with seven closed cells is probably the plesiomorphic condition in the family (Colombo et al. 2020). The absence or reduced wing occurred several times independently in Bethylidae, and consequently in Scleroderminae, as observable in the figure 6C. A biological explanation would be to save developmental resources as well as miniaturization, as suggested by Dudley (2002) when exploring the biomechanics of insect flight (Žikić et al. 2017).

The wing reduction can be driven by selection pressure induced by extreme climate conditions and short seasonal activity rather than direct influence of aphid hosts (Žikić et al. 2017), such as reported for *Diaeretellus svalbardicum* Chaubet & Tomanović (Chaubet et al. 2013), an arctic braconid with both macropterous and micropterous conditions. However, in the Scleroderminae, it seems to be associated with exploring cryptic environments such as wood galleries and barks.

Recent studies have examined the effect of major abiotic factors such as photoperiod, with various photoperiods associated with different light intensities (Hu et al. 2019) and temperature, biotic factors such as maternal wing morph on the wing dimorphism (Wang et al. 2016), and other life-history parameters of *Sclerodermus pupariae* Yang & Yao (Yang et al. 2012).

These studies suggest that long photoperiods and strong light promotes the development of winged females. However, only one species of host, *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), was used, while the different hosts could contribute to the results of wing differentiation (Hu et al. 2019). Additional work is needed to examine the effects of abiotic and biotic factors on the production of wing phenotypes in parasitoid wasps.

In the case of the Pristocerinae, in which females of all genera are apterous and very similar to each other, the hypothesis of host influence on morphology seems more plausible. In Scleroderminae, we cannot support either hypothesis since we do not currently have enough information to do so. Thus, wing polymorphism can be an adaptation for several environmental conditions.

The morphological phylogeny (Bethylinae + (*Lancepyris* + (Scleroderminae (Epyrinae + Pristocerinae + Mesitiinae))) by (Azevedo & Azar 2012) showed groups with six closed cells deriving early in the tree. The molecular phylogeny (Bethylinae + ((Scleroderminae + Mesitiinae) + (Pristocerinae + Epyrinae)) by Carr et al. (2010) also showed the trend of wing reduction, with loss of six closed cells to three closed cells in Pristocerinae, Mesitiinae, Epyrinae and in some groups of Scleroderminae (*Chilepyris*, *Glenosema* macropterous forms, †*Celonophamia*, *Galodoxa*, *Allobethylus* and *Proplastanoxus*). Nevertheless, Scleroderminae have different expressions of secondary losses and gains of closed cells, mostly because of presence or absence of the costal vein, for instance, *Galodoxa* and †*Celonophamia*, which returned the condition of three closed cells (Fig. 1).

2r-rs&Rs of forewing (Fig. 6D)**.** Another historically important character in the forewing is the 2r-rs&Rs, called the radial vein by Evans (1964, p. 13). This vein is present in all subfamilies of Bethylidae, with the exception of some species in *Laelius* (Epyrinae) and some clades in Scleroderminae, and is clearly the ancestral condition in both Bethylidae and Scleroderminae. Within the evolutionary history of Scleroderminae, this vein became absent several times (Fig. 6D), so that it is highly homoplastic throughout the phylogeny. In several genera, such as *Solepyris* and *Alongatepyris* for instance (Fig. 6D), both conditions are present, which make this character little convenient for phylogenetic analyses.

4.3. Synapomorphy-less genera

Some genera are not supported by apomorphies, as indicated in figure 1. We have listed some possible reasons for that. First, the inclusion of fossils as terminal taxa. The fossil record can make significant contributions to phylogeny reconstruction (Donoghue et al. 1989; Novacek 1992; Smith 1998). However, it is hard to extract information from fossil taxa, as seen in this study for †*Celonophamia* and †*Paleoscleroderma*. Although the incompleteness of fossil data sets can lead to problems (Novacek 1992; Smith 1998; Kearney & Clark 2003), judicious use of fossil data can make important contributions as well and for that reason, we included these terminal in our analyses. Besides, general problems of character analysis with morphological data (for more details, see Wiens 2001), as reductionism, morphological convergence, polymorphism, and sexual dimorphism.

← **Fig. 6.** Phylogenetic character mapping. **A**: Body thickness: robust in black and strongly flattened in red; **B**: Number of flagellomeres: seven in blue, eight in green, ten in red, eleven in black; **C**: Wings forms: apterous in blue, micropterous in green, brachypterous in red, macropterous in black and ambiguous in pink; **D**: 2r-rs&Rs vein in the forewing: present in black, absent in red, polymorphic in blue

Second, the reduction of different morphological variants, already explained in this text, is extreme, as in *Cephalonomia* and *Sclerodermus*, with a potential loss of phylogenetic information, obscuring relationships of homology and thus introducing unnecessary constraints in the process of translating anatomical observations into phylogenetic characters (KELLER 2011). Also, potentially problematic is the morphological convergence between some genera, like apterous forms of *Cephalonomia* and *Sclerodermus*, with other bethylids, such as the Pristocerinae females other than sclerodermines. Convergence is a critical issue in Systematics because it can potentially mislead phylogenetic reconstruction methods, for example, causing analyses to group distantly related organisms that share similar habitats (WIENS et al. 2003). The accentuated polymorphism and sexual dimorphism constrain the range of shared conditions in all terminals of the genera, as seen in *Alloplastanoxus* and *Decemnoxus*. Many of the morphological polymorphisms may not represent the phylogeny because they do not have a strictly genetic basis, as these polymorphisms could be the result of environmental or epigenetic effects in ontogeny or even ambiguities or errors in scoring characters (WIENS 1995). According to WIENS (1995) the relationship between polymorphism and the increase of homoplasies in phylogenies is positive.

Third, genera with a turbulent taxonomic history, like *Cephalonomia*, *Plastanoxus* and *Sclerodermus*. The former is probably the genus with the most taxonomic problems within Scleroderminae. This was the only polyphyletic genus in our analysis. These genera urgently need studies based on the world's fauna, to refine and increase the morphological information, similar to AZEVEDO et al. (2020) for *Discleroderma*.

Finally, while there are genera within Bethylidae that currently lack synapomorphies, characteristics that are shared by all members of a genus are still useful for alpha taxonomy, such as agricultural entomologists identifying bethylids attacking crop pests to a genus. However, unless a characteristic uniquely defines a genus and is found nowhere else within Bethylidae, that characteristic is not a synapomorphy. It is an unfortunate reality that we currently have bethylid genera that lack clear synapomorphies, but one that will hopefully resolved by a combination of morphological and molecular phylogenetic work in the future.

5. Conclusions

The addition of all extant and extinct genera and the parsimony criterion under implied weighting analyses have generated a better resolution of the topology of Scleroderminae, compared with previous phylogenies. The morphological data provided informative evidence for the monophyly of all genera, except *Cephalonomia*.

We define here five new genera of Scleroderminae, amount corresponding to about 20% of the previous number and almost duplicating the number of the 10-flagellomered genera, becoming a considerably bigger clade exhibiting new and complex relationships. Our results are far different from previous studies, and do not retrieve the monophyly of Cephalonomiini sensu EVANS (1964), contrary to the phylogeny proposed by TERAYAMA (2006), LANES & AZEVEDO (2008), CARR et al. (2010), ALENCAR & AZEVEDO (2013) and JIANG et al. (2015).

The hypotheses of linear tendency of morphological reduction by Evans (1964) from taxa more generalized in Epyrini to more specialized taxa in Cephalonomiini is rejected, since the latter are spread and fragmented across the tree. That is the case of antennal metamerism, where the ground plan is 11 flagellomeres, a plastic multistate transformation series that includes ramifications and reversions. Certain groups had this number modified. Another example is the wing venation and cells that follow the same direction. Body flatness is also a homoplastic character, and illustrates an array of convergent strategies suitable to live in different degrees of fossorial and cryptic micro-environments, like galleries in trees.

Finally, three frontiers are necessary in order to enhance the Systematics of Scleroderminae. First, alpha-taxonomic revision of the main speciose genera such as *Cephalonomia*, *Plastanoxus* and *Sclerodermus* is urgent. Second, investing energy in molecular analyses in order to get more well-supported trees. Better sampling strategies are fundamental to resolve these challenges. Third, addressing the issue of the lack of both sexes. It is quite possible that species known from one-sex only might actually be the conspecific of another described species. We will never know unless specimens are caught reproducing, or they are matched via molecular phylogenies.

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***Decemnoxus infrequens* Vargas, Colombo & Azevedo** sp.n.: http://zoobank.org/urn:lsid:zoobank.org:act:DF5148E5-23A7-4682-86A9-123B481F59B7

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***Mutatio* Vargas, Colombo & Azevedo**, gen.n.: http://zoobank.org/urn:lsid:zoobank.org:act:1B864BDD-30B5-405C-9043-E21B-7013C03A

***Mutatio mutata* Vargas, Colombo & Azevedo**, sp.n.: http://zoobank.org/urn:lsid:zoobank.org:act:E1638992-A153-44F4-97C9-129A01B38700

***Pilocutis* Vargas, Colombo & Azevedo**, gen.n.: http://zoobank.org/urn:lsid:zoobank.org:act:E028A368-8233-473F-A039-36EFB7B04701

***Pilocutis mollis* Vargas, Colombo & Azevedo**, sp.n.: http://zoobank.org/urn:lsid:zoobank.org:act:7A2AA874-F692-4D88-A02D-0402D8A7F320

***Thlastepyris marquisensis* (Fullaway, 1935) stat. et comb.n.**: http://zoobank.org/urn:lsid:zoobank.org:act:3202F178-D13E-4273-913E-CC7535AD763C

Authors' contributions

All authors performed the study of morphology, analyzed the data and write the text. J.M.V.R. and W.D.C. run the analyses on T.N.T. and prepared and edited the images. C.O.A. designed the study, got financial add and facilities.

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File 1: Vargas_etal _S1.xlsx — **Appendix S1.** Character scoring of Scleroderminae.

File 2: Vargas_etal _S2.nex — **Appendix S2.** Morphological matrix in nexus format.