

Phylogeny and placement of Boganiidae (Coleoptera, Cucujoidea) with a review of Australian and New Caledonian taxa

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Abstract. A phylogeny of the cucujoid family Boganiidae (Coleoptera) is inferred for the first time based on a parsimony analysis of 102 morphological characters (70 adult and 32 larval). The analysis resulted in a monophyletic Boganiidae divided into two main clades, Boganiinae and Paracucujinae, each supported by a series of synapomorphies. The Boganiinae genera recovered were *Afroboganium* Endrödy-Younga & Crowson and *Boganium* Sen Gupta & Crowson, whereas Paracucujinae includes *Paracucujus* Sen Gupta & Crowson, *Metacucujus* Endrödy-Younga & Crowson, *Athertonium* Crowson and the New Caledonian *Dzumacium caledonicum* **gen.n., sp.n.** New specimen data and biological information for the Australian taxa are summarized with overviews on biogeography and comments on the fossil Jurassic *Parandrexia* Martynov (Parandrexidae). Two new species of *Boganium*, primarily from the Australian mallee are described: *B. malleense* **sp.n.** and *B. medioflavum* **sp.n.** *Boganium malleense* is recorded from flowers of *Eucalyptus gracilis* F. (Myrtaceae). Adults and larvae of *Paracucujus rostratus* Sen Gupta & Crowson are redescribed. *Athertonium parvum* Crowson is redescribed and *Athertonium williamsi* **sp.n.** is described from coastal New South Wales. Several host records for *Athertonium* are also presented.

Introduction

Boganiidae are a small and poorly known family of cucujoid beetles that currently includes 5 genera and 11 species restricted to Australia, New Caledonia and southern Africa. Adults and larvae are pollenophagous, feeding on pollen of Cycadales and various Angiospermae (Myrtaceae, Meliaceae, Cunoniaceae, Elaeocarpaceae) and sharing several unique morphological features, possibly associated with this lifestyle (Endrödy-Younga & Crowson, 1986; Crowson, 1990) (Figs 1–11, Figures S1–S6). Adult boganiids have mandibles with large, setose cavities on the dorsal side (Figs 5D, E, 7B, 10C, Figures S1F, S4E) and usually have at least one ventrally lobed tarsomere (Figure S3D), whereas larvae have a falcate, basally articulated maxillary mala (Figure S6A) and elongate paired pygopods (Figs 9C, I, Figures

S5D, E), all features that are very rare in Cucujoidea. Some adults also have multipored outlets of possible glandular function located on the mandibles (Fig. 6E) and prothorax (Figs 3D, 7E, G) and/or paired, simple gland openings on abdominal ventrites (Fig. 11A). The only other pollenophagous group of Cucujoidea with comparable adult mandibular cavities is Meligethinae (Nitidulidae); the cavities in this group, however, are laterally placed and not concealed when the mandibles are in the closed position. Dorsal setose mandibular cavities also occur in Sphindidae and glabrous cavities in a similar position are known in some Phloeostichidae and Silvanidae; all of these taxa, however, feed on fungi or Myxomycetes and may utilize these structures for carrying spores (Crowson, 1988, 1991).

The family Boganiidae was originally proposed for two newly described Australian genera *Boganium* Sen Gupta & Crowson and *Paracucujus* Sen Gupta & Crowson (Sen Gupta & Crowson, 1966, 1969) and some other notogean genera now removed to Cavognathidae, Hobartiidae and Phloeostichidae. Endrödy-Younga & Crowson (1986) added two southern

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African genera, *Afroboganium* Endrödy-Younga & Crowson and *Metacucujus* Endrödy-Younga & Crowson, whereas Crowson (1990) described the third Australian genus, *Athertonium* Crowson in its own tribe – Athertoniini – and provided a key to the genera. The former classification of the family (Crowson, 1990; Lawrence & Newton, 1995) included two subfamilies: Paracucujinae for the genera *Metacucujus* (Africa) and *Paracucujus* (Australia); and Boganiinae with *Boganium* (Australia), *Afroboganium* (Africa) and *Athertonium* (Australia).

From its onset Boganiidae was a problematic group with an unclear relationship to other groups in Cucujoidea. Sen Gupta & Crowson (1966, 1969) and Crowson (1990, 1991) discussed various relationships with cucujoid families (Cucujidae, Silvanidae, Phloeostichidae) or even with Chrysomeloidea, the latter based primarily on the presence of a shared area of specialized microsculpture on the hindwing membrane (post-radial sclerite) and the articulated maxillary mala in the larvae. The same authors observed that the Jurassic fossil *Parandrexia* Martynov, originally placed in Cerambycidae, might occupy an intermediate position between Boganiidae and Chrysomeloidea (Sen Gupta & Crowson, 1966; Crowson, 1990, 1991).

Three phylogenetic studies have included Boganiidae in their taxon sampling but all failed to resolve its phylogenetic position adequately. Leschen *et al.* (2005) analysed relationships of various taxa included in ‘basal Cucujoidea’ and found that morphological analyses of adult and larval characters or adult characters alone, placed Boganiidae and Byturidae either at the base of the superfamily Cucujoidea or in a clade with two cleroid outgroups (Trogossitidae). In a cladogram based on larval characters alone, Boganiidae was recovered in a clade containing Silvanidae, Cucujidae, Priasilphidae and Phloeostichidae (Leschen *et al.*, 2005). A molecular study by Marvaldi *et al.* (2009) inferring phylogenetic relationships in Cucujiformia with an emphasis on Phytophaga, recovered a tree with a paraphyletic Cucujoidea and *Paracucujus rostratus* was placed in a clade with Erotylidae and Nitidulidae + Silvanidae + Cucujidae. Lawrence *et al.* (2011), in the most comprehensive phylogenetic analysis of Coleoptera based on morphological characters of larvae and adults to date, similarly resulted in a paraphyletic Cucujoidea, wherein *Paracucujus* (the only Boganiidae included) clustered with other families of Cucujoidea in a clade with *Sphindus* Dejean, *Protosphindus* Sen Gupta & Crowson (Sphindidae) and *Hobartius* Sen Gupta & Crowson (Hobartiidae).

Boganium, *Afroboganium* and *Athertonium* are associated with angiosperms. *Metacucujus* species are found exclusively in cones of *Encephalartos* Lehm. (Zamiaceae), and there is some evidence that they pollinate these cycads in South Africa (Donaldson *et al.*, 1995; Donaldson, 1997; Suinyuy *et al.*, 2009). The Australian *Paracucujus rostratus* Sen Gupta & Crowson is commonly found in male *Macrozamia* inflorescences in the south-west region of Western Australia, but its role as a cycad pollinator is unconfirmed (Endrödy-Younga & Crowson, 1986; Crowson, 1990; Ornduff, 1991; Connell & Ladd, 1993; Terry *et al.*, 2005).

The apparent relictual distribution of Boganiidae, as well as its uncertain relationship to other Cucujoidea, peculiar adult

and larval morphology, pollenophagous and anthophilous biology, and specific interactions with related cycads in southern Africa and the south-west region of Western Australia, makes this group an exceptional and significant element in current controversies regarding the evolution of insect–plant associations, diversification (e.g. Dodd *et al.*, 1999; Grimaldi, 1999; Labandeira, 2000, 2010; Grimaldi & Engel, 2005), contemporary biogeography (e.g. Lomolino *et al.*, 2010) and Coleoptera evolution (Crowson, 1960; Lawrence & Newton, 1982). We present the first phylogeny of the remarkable and enigmatic Boganiidae based on morphological characters of adults and larvae, and provide discussion regarding their classification and taxonomy.

Material and methods

Specimens examined and type specimens are deposited in: The Australian Museum, Sydney, NSW, Australia (AMS); Australian National Insect Collection, Canberra, ACT, Australia (ANIC); Natural History Museum, London, UK (NHML); California Academy of Sciences, San Francisco, California, USA (CAS); Institut Agronomique néo-Calédonien: Station de Recherches Fruitières de Pocquereux, New Caledonia (IACP); Institut de Recherche pour le Développement, Noumea, New Caledonia (IRD); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA (MCZ); Museum National d’Histoire Naturelle, Paris, France (MNHN); Museum of Natural History, University of Wrocław, Poland (MNHW); Upper Silesian Museum, Bytom, Poland (USMB); Museum of Victoria, Melbourne, VIC, Australia (MVM); Queensland Museum, Brisbane, QLD, Australia (QMB); South Australian Museum, Adelaide, SA, Australia (SAM).

For detailed study of morphological characters specimens were cleared in cold 10% KOH for 1 or 2 days, then disarticulated, stained with chlorazol black and transferred to glycerol on slides. In this medium it was possible to take digital photographs using a JVC digital camera attached to a Leitz microscope. Subsequently body parts were gold-coated to produce SEM images with a Zeiss EvoLS15 (Black Mountain Lab., CSIRO) and habitus images were generated with JVC and Nikon DS-Fi1 cameras mounted on a Leica M205C microscope. All images were edited with Adobe Photoshop.

The classification system for Coleoptera used here follows Ślipiński *et al.* (2011). Most of the terms used in the morphological descriptions and keys are based on Leschen *et al.* (2005) and Lawrence *et al.* (2010, 2011). The term transverse occipital carina is equivalent to low transverse occipital carina of Lawrence *et al.* (2011) and vertexal line used by Leschen (2003) for some Cucujoidea. The term median frontal endocarina is used here for an internal longitudinal ridge, usually visible externally as a fine line, extending anteriorly from the vertex (between the posterior edges of the eyes), crossing the frontal region and sometimes meeting the frontoclypeal suture. This structure is not homologous to the median occipital endocarina, which begins at the occipital foramen, and is unlikely to be a homologue of either the median frontoclypeal groove or the midcranial suture as used by Lawrence *et al.* (2011).

Total length (TL) was measured from above and includes the head; body length (BL) excludes the head; pronotal length (PL) was measured along midline and pronotal width (PW) is the greatest width; elytral length (EL) was measured along the midline and included the scutellar shield, whereas elytral width (EW) is the greatest combined width of the elytra in the closed position. Head length was measured dorsally at midline from the occipital foramen to the apex of the clypeus, and head width was measured immediately behind the eyes. Lengths of abdominal ventrites were measured along the midline but excluding the intercoxal process at the anterior edge of ventrite 1.

The morphological matrix used for the present analysis was originally extracted from that in Lawrence *et al.* (2011), with some corrections and/or additions based on the cucujoid analysis of Leschen *et al.* (2005) and a more detailed study of variation within Boganiidae. Unless otherwise stated, adult and larval taxa used are those listed in Lawrence *et al.* (2011). The Delta editor (Dallwitz, 1980) was used to build the morphological matrix. All six boganiid genera were included plus 28 outgroup genera from within the Cucujiformia series (15 cucujoids and 2 cleroids). The final matrix (Table S1) consisted of 23 terminal taxa and 102 morphological characters (70 adult and 32 larval); all characters were treated as unordered with equal weight, 57 were coded as binary (two-state) and 46 as multi-state. Eight characters (7, 11, 15, 25, 31, 48, 69, 90) identified as noninformative were included in the analysis. Some multistate characters could have been split into a series of binary characters, but we refrained from doing so before more information on their homologies is available.

Superfamilies, families, subfamilies and exemplar genera, as well as the morphological characters used in the analysis are included in Appendix S1.

Phylogenetic analysis

The phylogenetic reconstruction was inferred under parsimony as the optimality criterion, and performed with the software TNT, using Traditional Search (Goloboff *et al.*, 2003) with the branch-swapping algorithms, sub-tree pruning and re-grafting (SPR), and tree bisection and reconnection (TBR) with 1 000 random seeds and 10 replications. In order to observe the effect of ambiguous characters, the selected tree was optimized with fast (accelerated transformation, ACCTRAN) and slow (delayed transformation, DELTRAN) optimization in Winclada (Nixon, 2002).

Results and discussion

The phylogenetic inference using parsimony resulted in a single most parsimonious tree (Fig. 1, tree length, $L=410$ steps; consistency index, $CI=35$; retention index, $RI=54$). Each optimization (ACCTRAN, DELTRAN) recovered the same topology, supported by slightly different character states (Figure S7). Bootstrap and Bremer supports were estimated with TNT. The analysis show congruent relationships for the outgroups and supports the monophyly of Boganiidae (Fig. 1).

Family relationships of Boganiidae

Our taxon sampling comprised two superfamilies Cucujoidea and Cleroidea intending to recover the phylogenetic relationships of Boganiidae within Cucujoidea. The resulting tree was rooted with *Eronyxa* (Lophocaterinae: Trogossitidae) and recovered a well-defined Cucujoidea (Fig. 1A), a superfamily shown as paraphyletic by Lawrence *et al.* (2011). Boganiidae (Fig. 1B) was shown as monophyletic with high bootstrap and Bremer decay index supports nested in a clade with Byturidae as sister taxa, similar to the results obtained by Leschen *et al.* (2005) but in disagreement with Lawrence *et al.* (2011). The placement of Boganiidae in Cucujoidea is confirmed in our analysis, with further research needed to determine its relationships to other families of Cucujiformia, requiring broader taxon and character sampling.

Boganiidae phylogeny

The monophyly of Boganiidae (Fig. 1B) is supported by six unambiguous synapomorphies: (i) median frontal endocarina present (character 3: states 2, 3; Fig. 10A, Figure S4A) (absent in *Athertonium*) – this character is present in several families of Coleoptera but it is more common in Chrysomeloidea (Lawrence *et al.*, 2011); (ii) phallobase asymmetrical (62: 2; Figs 10I, 11H, I); (iii) paired penile struts articulated (66: 2; Figs 11D–F, K, L, Figure S3G) – the distribution of this character in Coleoptera is poorly known; (iv) frontoclypeal suture complete and more or less distinct with internal epistomal ridge (74:2); (v) larva with maxillary articulated mala (89: 3; Figure S6A) – this uncommon character in Cucujoidea is present in many other families of beetles (Lawrence *et al.*, 2011); and (vi) larva with abdominal segment X with pygopods (99: 3; Figs 9C, I, Figures S5A–F) – this character is also present in some genera of Torridincolidae, Carabidae, Elateridae and Tenebrionidae (Lawrence *et al.*, 2011).

Boganiinae is supported by two putative homoplasious traits and by one synapomorphy, i.e. abdominal ventrites 1–4 with paired posterosublateral abdominal glands (56: 2; Fig. 11A). Paracucujinae is supported by three synapomorphies: (i) paired penile struts at least $0.33\times$ as long as body of penis (66: 3; Figs 11F, K, L, Figure S3G); (ii) apical maxillary palpomere cylindrical (20: 1, Fig. 6D, Figures S1D, S4B), apical labial palpomere more or less cylindrical (21: 1, Fig. 7A, Figure S1B); and (iii) paired penile struts articulated and at least $0.33\times$ as long as body of penis (66: 3, Figs 11F, K, L, Figure S3G). Within Paracucujinae one homoplasious character was identified for *Dzumacium*. Three unambiguous synapomorphies restricted to adults were identified for *Athertonium*: (i) lateral edge of mandible with gland opening (11: 2; Fig. 6C, E); (ii) anterolateral portion of pronotum with glandular pore or pores (26: 2; Fig. 7E); and (iii) paired posterosublateral abdominal glands present on ventrites 1–5 (56: 3). Several homoplasious traits and two synapomorphies were identified for the clade *Metacucujus* + *Paracucujus*: antennal flagellum appearing filiform, but with very weak three-segmented club (9: 2; Figs 2A, C,

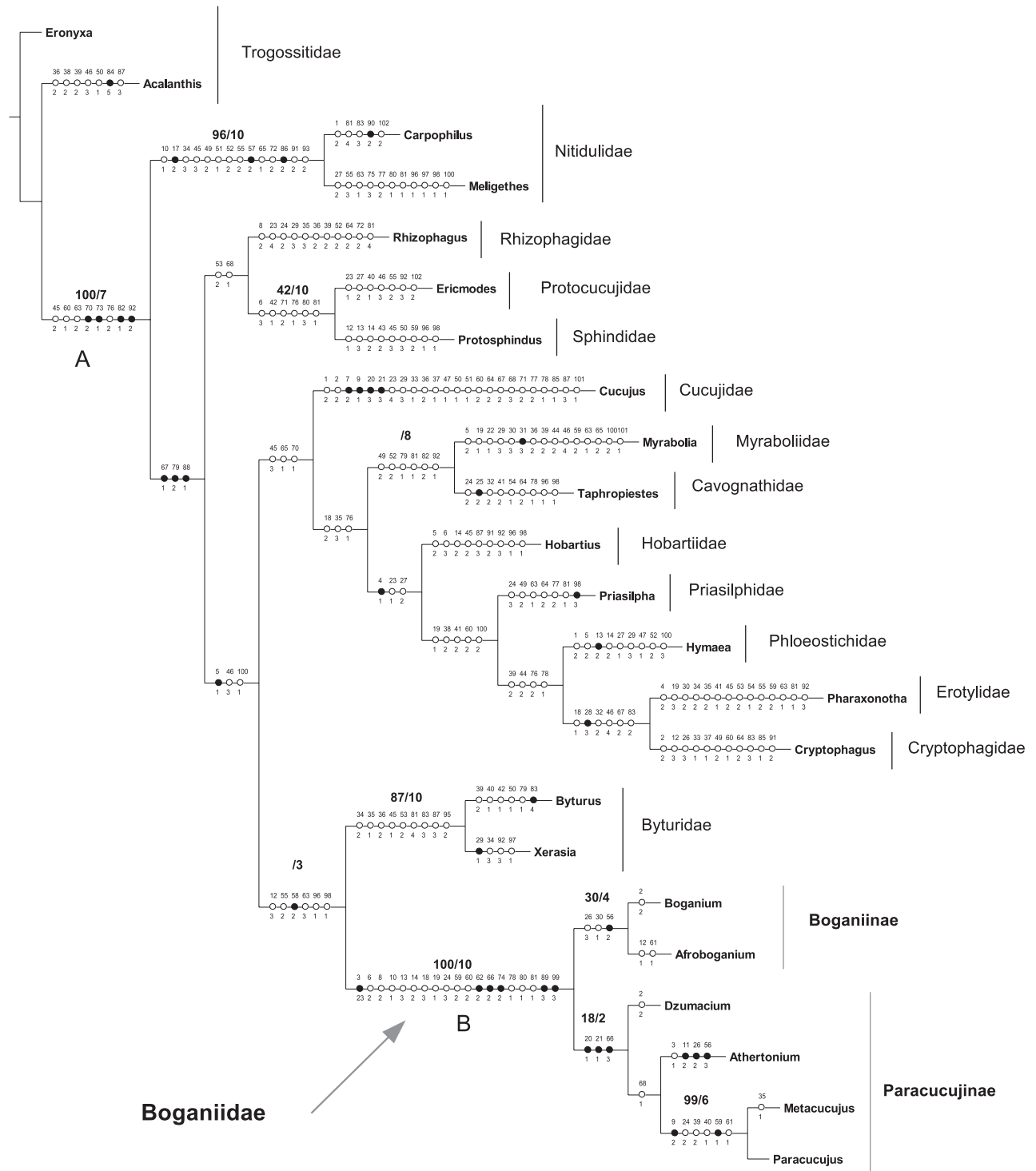


Fig. 1. Phylogenetic hypothesis for Boganiidae: single tree (L=410, CI=35, RI=54), obtained using Traditional Search in TNT with characters mapped on branches using unambiguous character changes in WinClada. Solid circles indicate nonhomoplasious changes, open circles indicate homoplasious changes; the numbers above and below each circle correspond to the character number and character state, respectively. The bold numbers above the clades represent Bootstrap/Bremer support respectively. Clades: (A) Cucujoidea (in part), (B) Boganiidae.

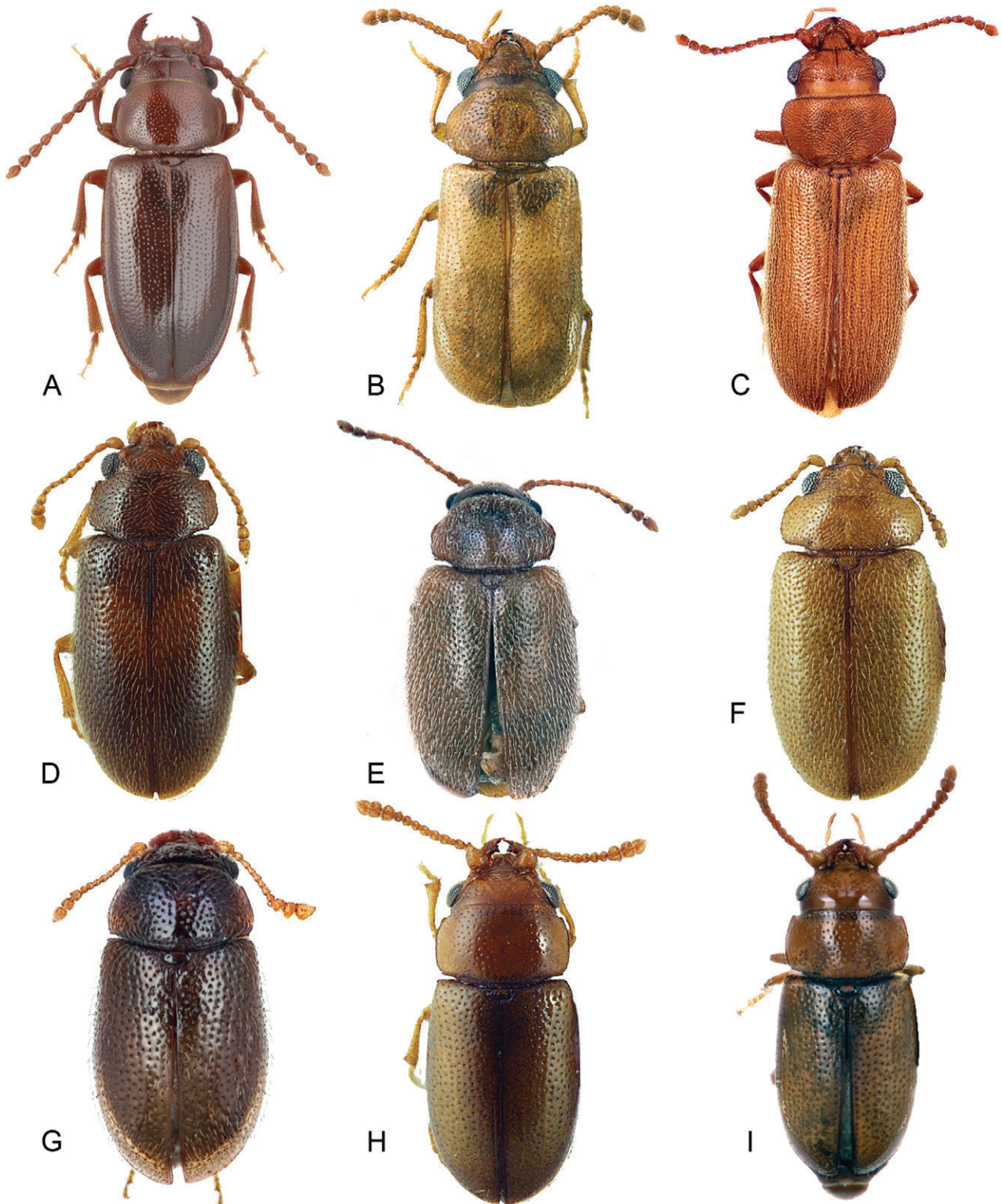


Fig. 2. Boganiidae adult habitus: (A) *Paracucujus rostratus* Sen Gupta & Crowson, © K. V. Makarov; (B) *Dzumacium caledonicum* gen. et sp.n.; (C) *Metacucujus encephalarti* Endrödy-Younga; (D) *Boganium medioflavum* sp.n.; (E) *Afroboganium proprium* (Grouvelle); (F) *Boganium malleense* sp.n.; (G) *Athertonium williamsi* sp.n.; (H, I) *Athertonium parvum* Crowson.

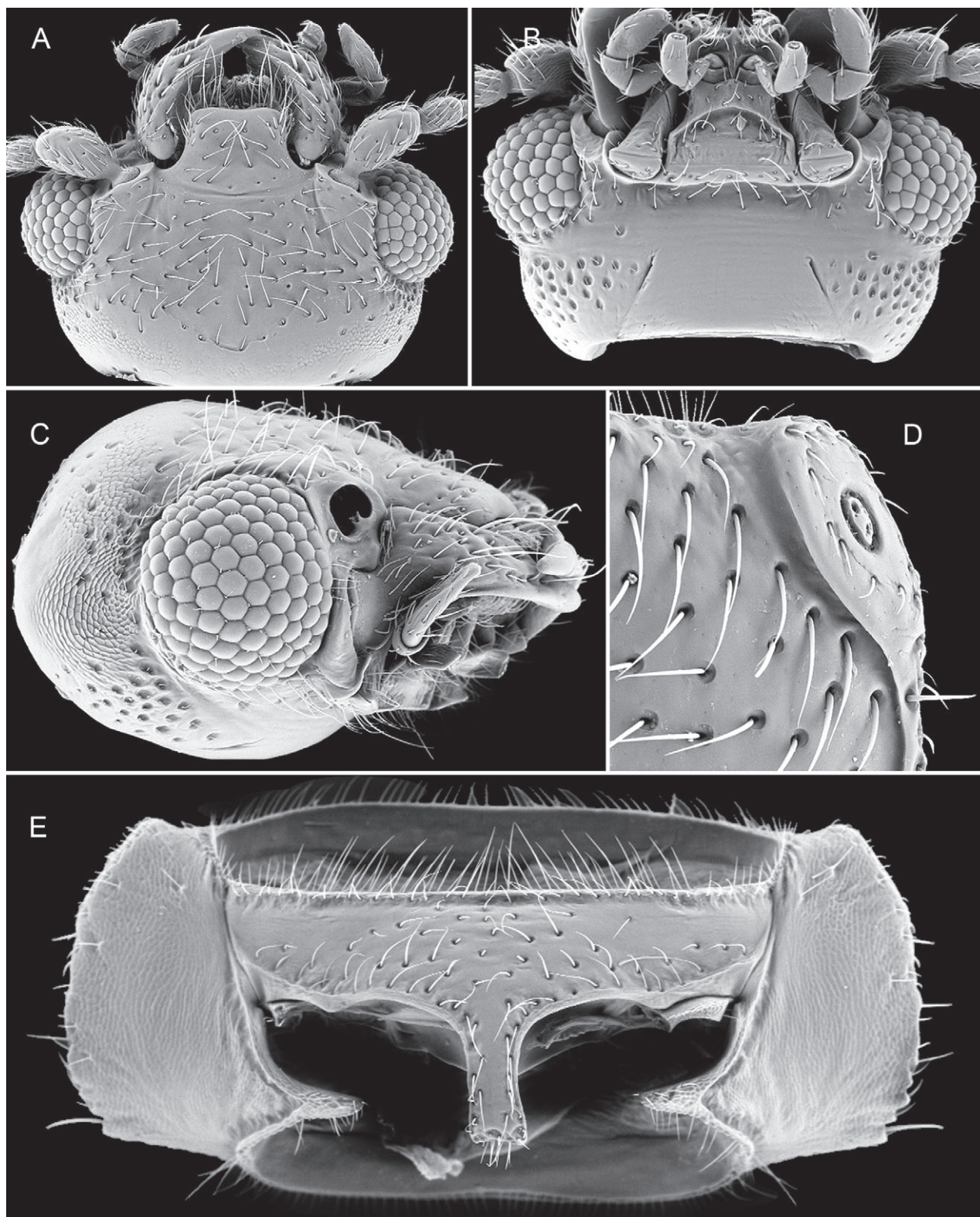


Fig. 3. *Boganium malleense* sp.n.: (A) head, dorsal, (B) head, ventral, (C) head, lateral, (D) pronotum, right anterior angle, dorsal, (E) prothorax, ventral.

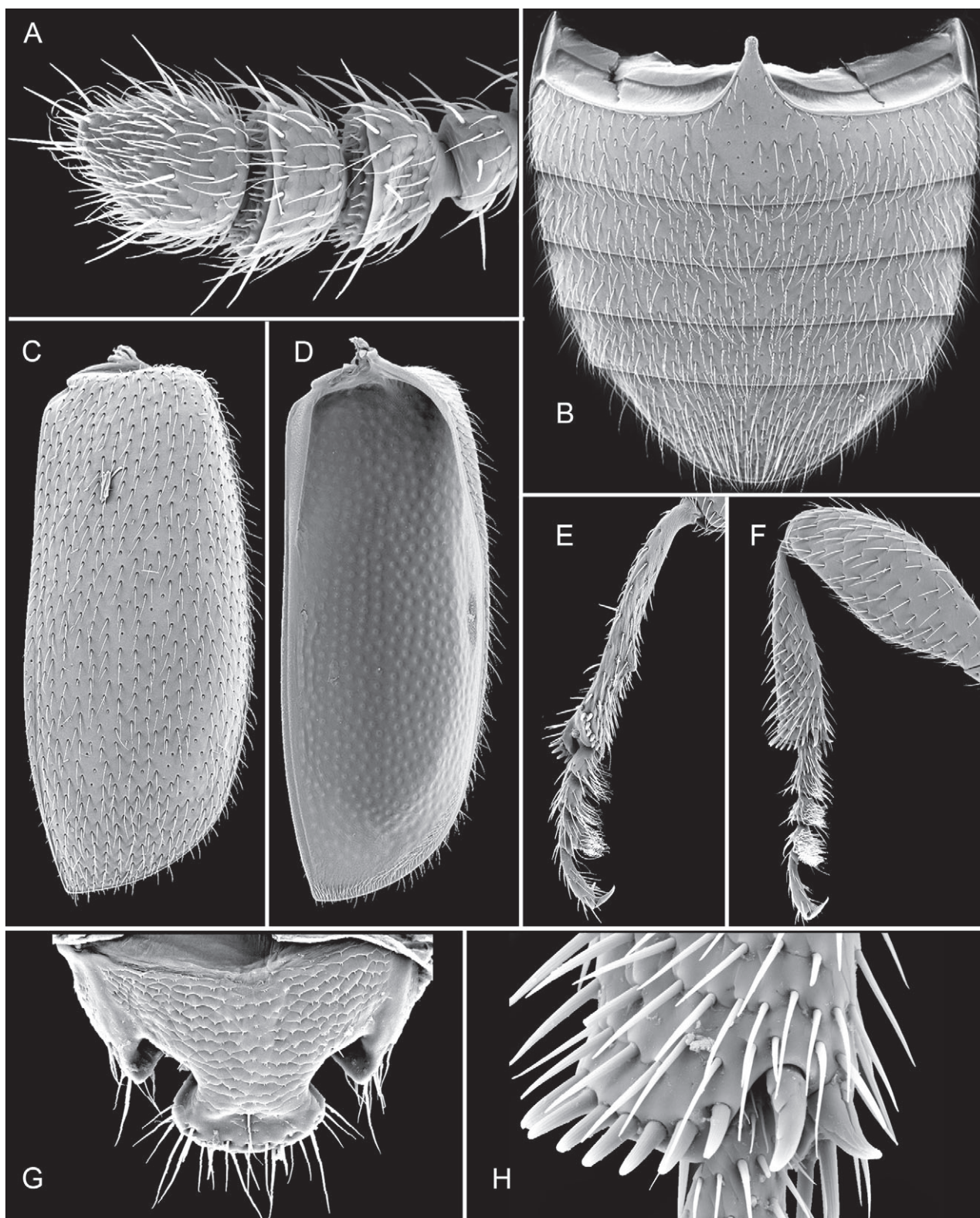


Fig. 4. *Boganium malleense* sp.n.: (A) antennal club, (B) abdomen, (C) elytron, dorsal, (D) elytron, ventral, (E) male protibia and tarsus, (F) mid leg, (G) male abdominal segments IX and X, ventral, (H) metatibial apex.

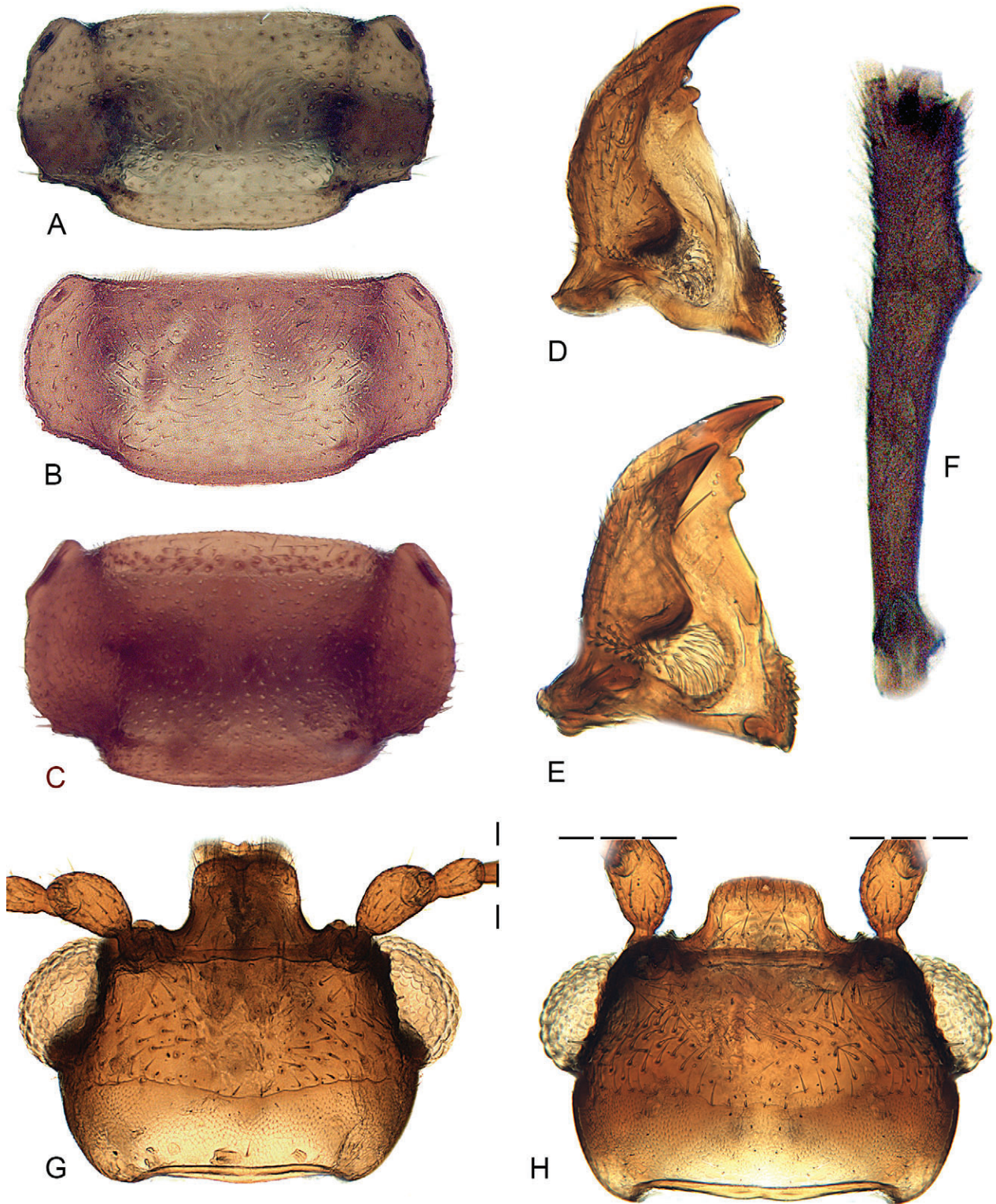


Fig. 5. *Boganium* spp.: (A) *B. medioflavum* sp.n., prothorax, dorsal; (B) *B. malleense* sp.n., prothorax, dorsal; (C) *B. armstrongi* Sen Gupta & Crowson, prothorax, dorsal; (D) *B. medioflavum* sp.n., mandible, dorsal; (E) *B. armstrongi* Sen Gupta & Crowson, mandible, dorsal; (F) *B. malleense* sp.n., male protibia; (G) *B. medioflavum* sp.n., head, dorsal; (H) *B. armstrongi* Sen Gupta & Crowson, head, dorsal.

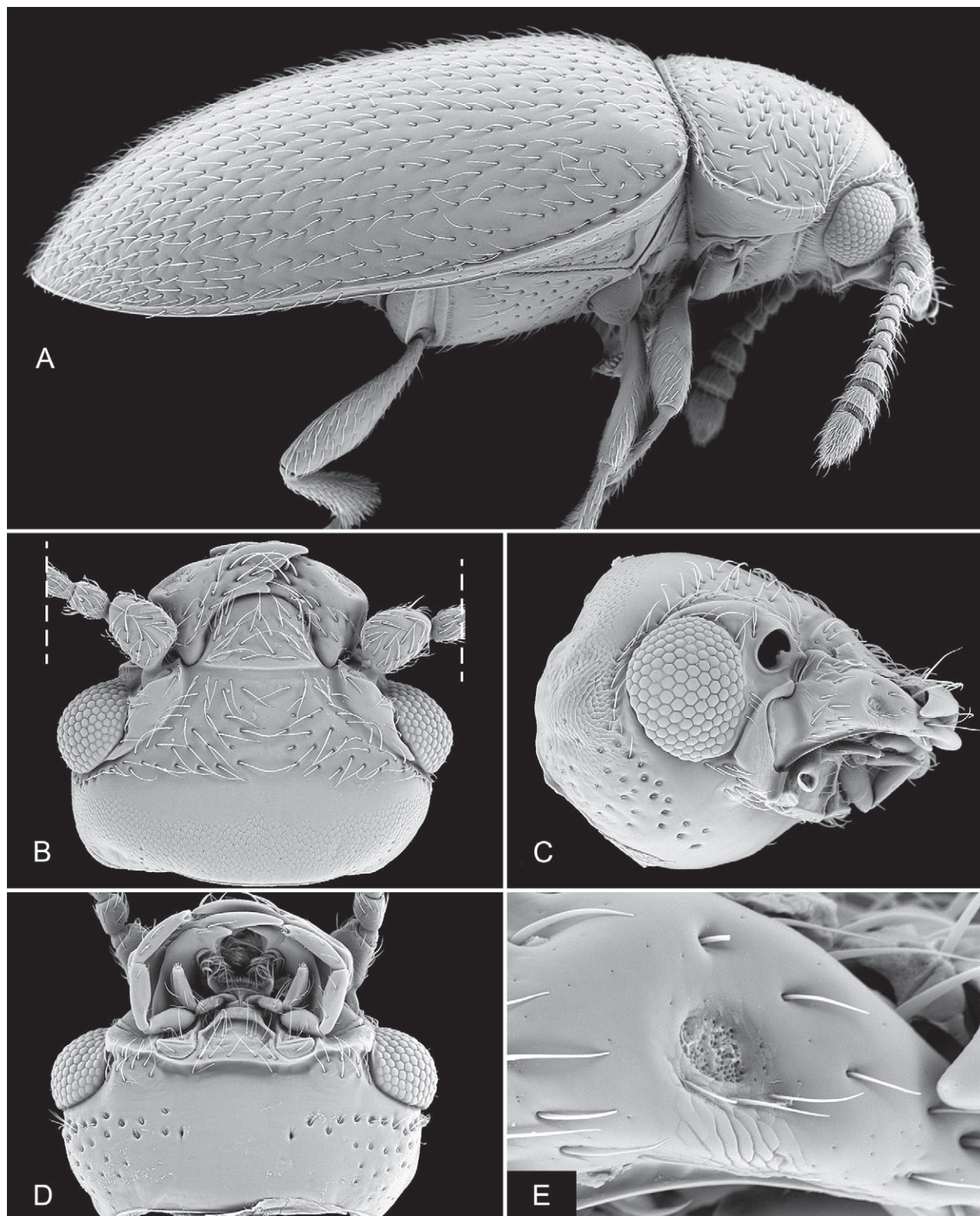


Fig. 6. *Athertonium williamsi* sp.n.: (A) habitus, lateral, (B) head, dorsal, (C) head, anterolateral, (D) head, ventral, (E) mandible, detail.

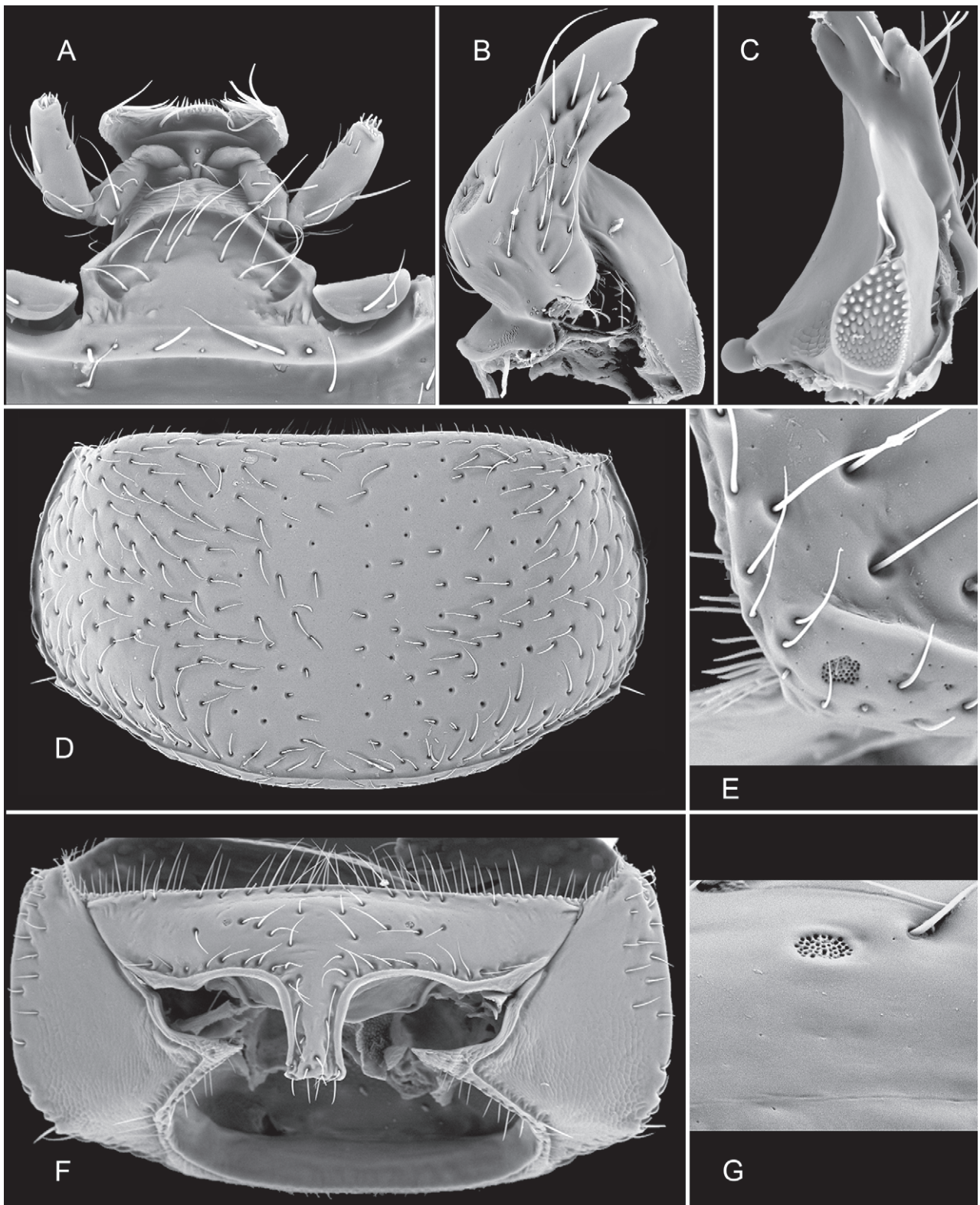


Fig. 7. *Athertonium williamsi* sp.n.: (A) labium, (B) mandible, dorsal, (C) mandible, mesal, (D) prothorax, dorsal, (E) prothorax, anterolateral angle, (F) prothorax, ventral, (G) prosternal disc, detail.

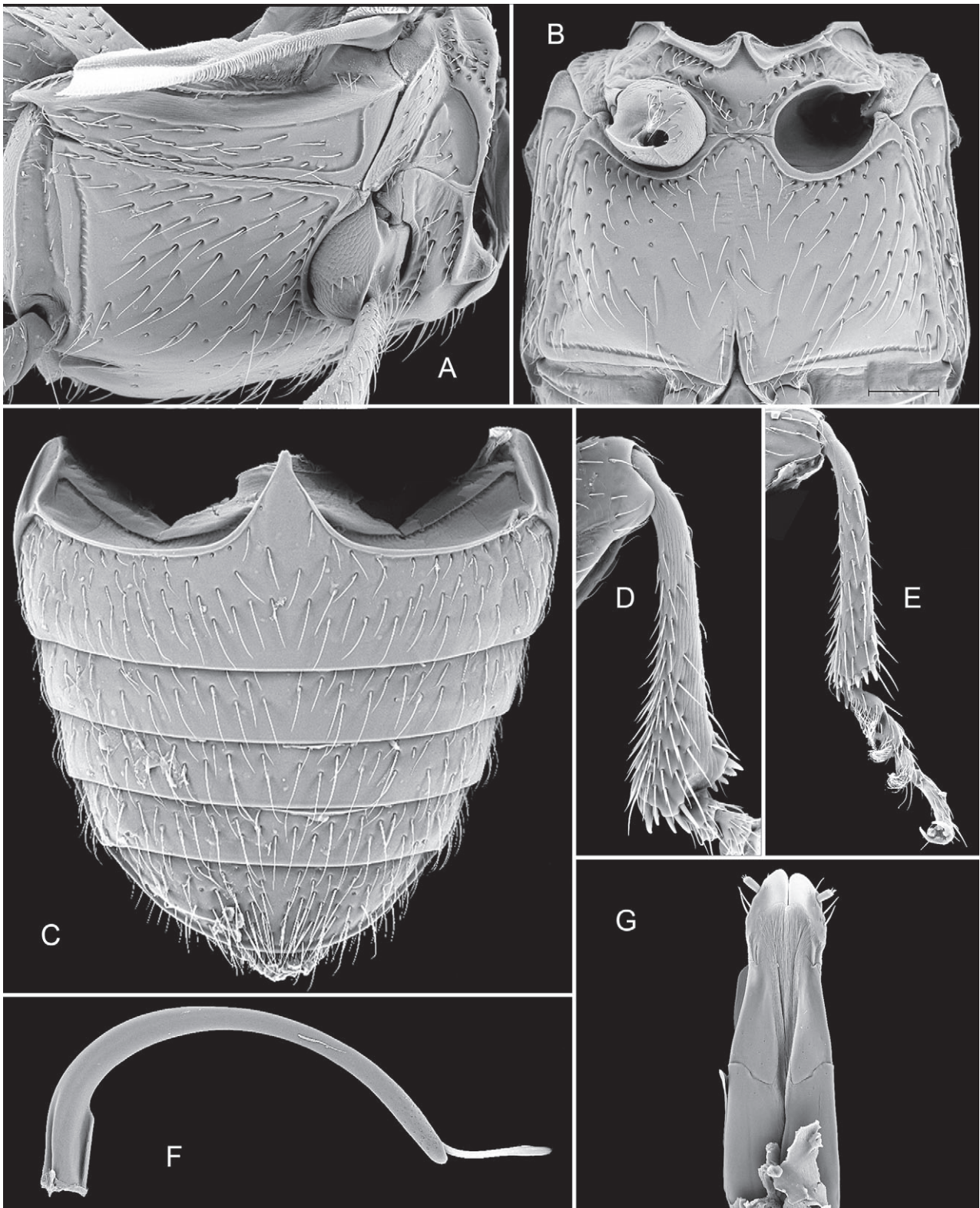


Fig. 8. *Athertonium williamsi* sp.n.: (A) pterothorax, lateral, (B) pterothorax, ventral, (C) abdomen, (D) protibia, (E) mesotibia and tarsus, (F) penis, lateral, (G) ovipositor.

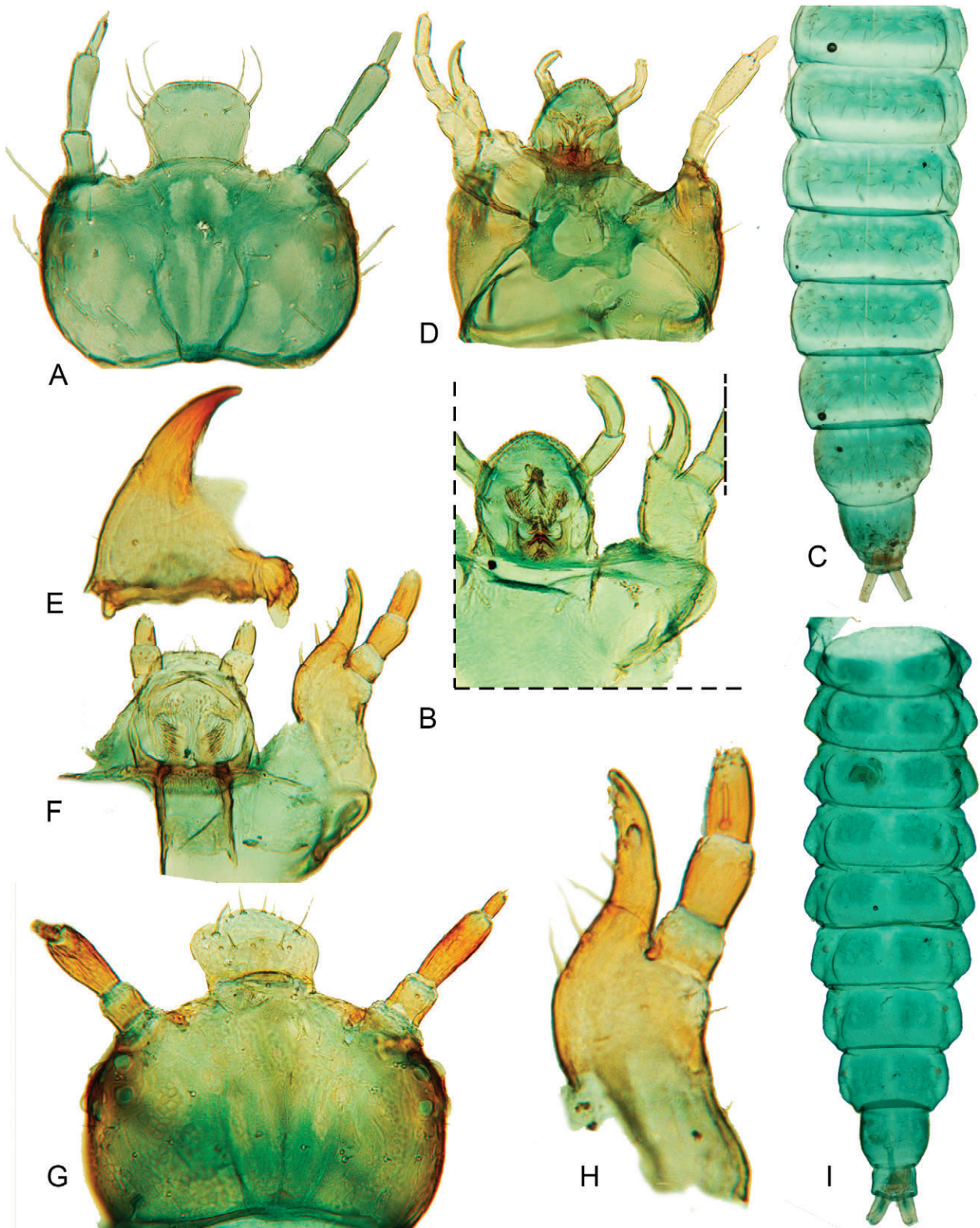


Fig. 9. (A–C) *Paracucujus rostratus* Sen Gupta & Crowson, larva: (A) head, dorsal, (B) labium and maxillae, dorsal, (C) abdomen, dorsal; (D) *Metacucujus encephalarti* Endrödy–Younga, head ventral; (E–I) *Boganium malleense* sp. n., larva: (E) mandible, (F) maxilla and labium, dorsal, (G) head, dorsal, (H) maxilla, (I) abdomen, dorsal.

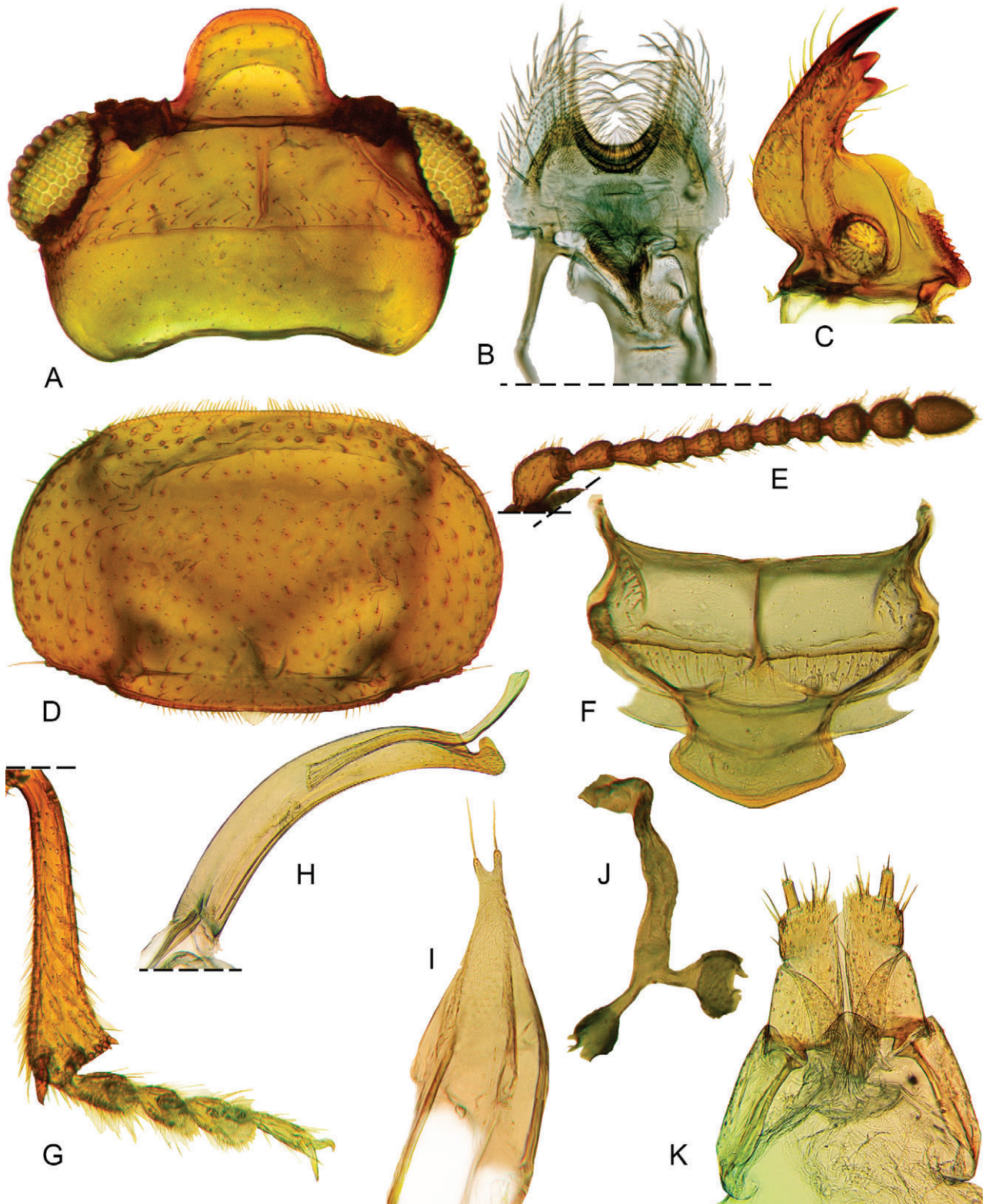


Fig. 10. *Dzumacium caledonicum* gen. et sp.n.: (A) head, dorsal, (B) labrum, (C) mandible, dorsal, (D) prothorax, dorsal, (E) antenna, (F) scutellum, (G) protibia and tarsus, (H) penis, lateral, (I) anterior portion of tegmen, (J) testes, (K) ovipositor, ventral.

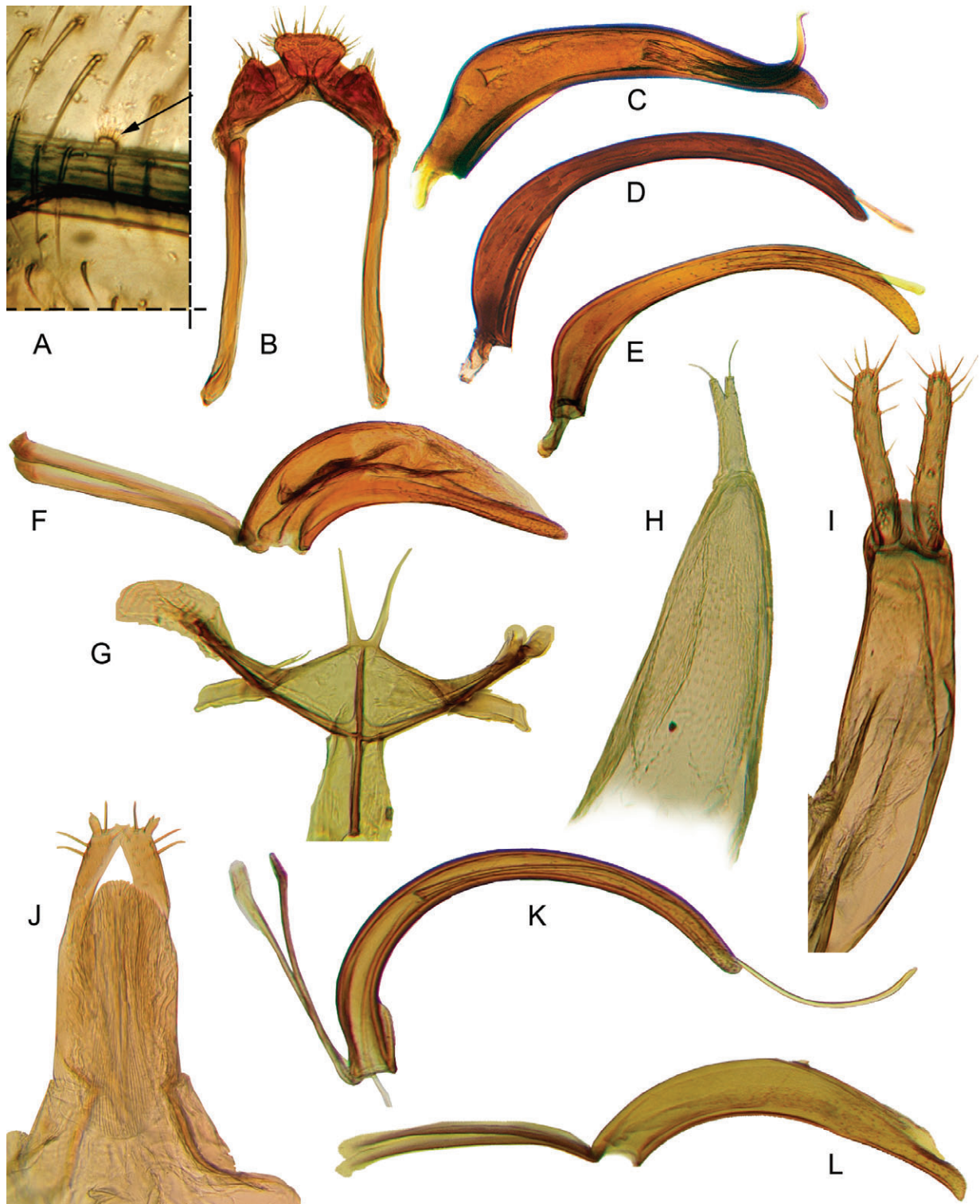


Fig. 11. (A–E) *Boganium* spp.: (A, B) *B. malleense* sp.n.: (A) apex of abdominal ventrite 2 (lateral portion) (B) male abdominal segments IX and X, ventral; (C) *B. armstrongi* Sen Gupta & Crowson, penis, lateral (paratype, ANIC); (D) *B. medioflavum* sp.n., penis, lateral (holotype, ANIC); (E) *B. malleense* sp.n., penis lateral; (F) *Paracucujus rostratus* Sen Gupta & Crowson, penis, lateral; (G) *Athertonium parvum* Crowson, metendosternite, posterodorsal; (H) *Paracucujus rostratus* Sen Gupta & Crowson, anterior portion of tegmen; (I) *Metacucujus encephalarti* Endrödy-Younga, anterior portion of tegmen; (J, K) *Athertonium parvum* Crowson: (J) ovipositor, dorsal, (K) penis, lateral (paratype, ANIC); (L) *Metacucujus encephalarti* Endrödy-Younga, penis, lateral.

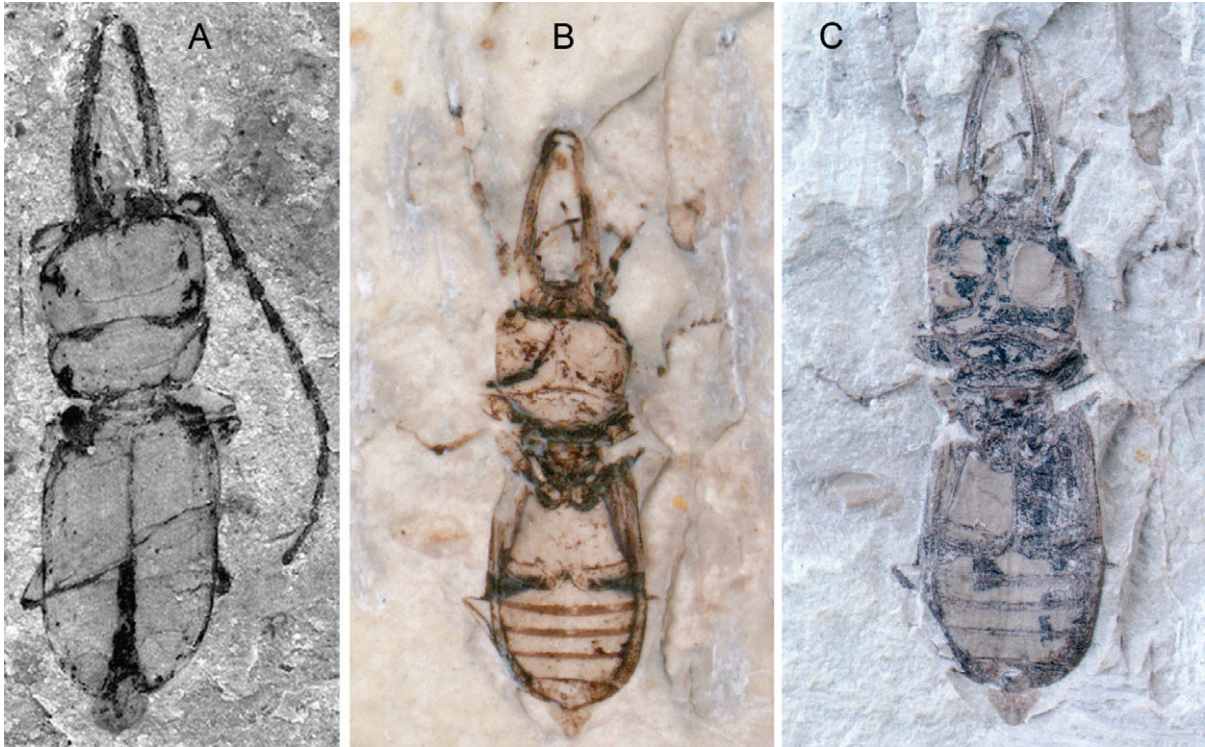


Fig. 12. (A–C) Undescribed representatives of Parandrexidae from the Middle Jurassic Jiulongshan Formation of Inner Mongolia, China; (B, C) same fossil covered with ethanol and dry respectively (© Capital Normal University, Beijing, photographs by Tangmei Lu & Huali Chang).

Figure S2A) and anteroventral edge of segment IX in male with broadly rounded, broadly truncate or emarginate subgenital plate (59: 1). The placement of *Dzumacium* in Paracucujinae is potentially affected by the lack of knowledge of its larvae. We recognized the genera *Metacucujus*, *Paracucujus*, *Boganium* and *Afroboganium* based on our current morphological diagnosis for each genus and their disjunct distributions. The classification of Boganiidae is shown in Appendix S1.

Taxonomy

Boganiidae Sen Gupta & Crowson

Type genus: *Boganium* Sen Gupta & Crowson, 1966

Diagnosis. Boganiidae can be distinguished from all other beetle families by a combination of characters: straight frontoclypeal suture, mandibles with dorsal tubercle and setose cavity, weak antennal club, lacinia with long, sickle-shaped uncus, bilobed ligula and asymmetrical double tegmen in the adult; and the presence of an articulated mala and paired, elongate pygopods on segment X in the larva. A family description for adults and larvae is presented in Appendix S1.

Distribution. Southern Africa, south and eastern Australia, and New Caledonia.

Comments. Additional morphological descriptions of larvae and adults are found in Lawrence & Ślipiński (2010, 2013). Other references for adult include Sen Gupta & Crowson (1966, 1969), Lawrence (1982), Crowson (1990), Lawrence & Britton (1991, 1994), Lawrence *et al.* (1999b) and Leschen *et al.* (2005), and for larvae Endrödy-Younga & Crowson (1986), Lawrence (1991), Lawrence & Britton (1991) and Lawrence *et al.* (1999a). Marvaldi *et al.* (2006) illustrated the propleurotrochantin of *Paracucujus rostratus* and compared it with *Xenocryptus tenebroides* Arrow (Erotylidae), and other Chrysomeloidea and Curculionoidea, identifying the presence of proprioceptor sensilla.

The function of the mandibular cavities for Boganiidae *sensu* Sen Gupta & Crowson (1966), including *Paracucujus* and *Boganium*, was originally postulated to be mycangia, in contradiction with their pollenophagous biology (Grebennikov & Leschen, 2010); more research is necessary to determine the function of these cavities.

The pore fields (Figs 3D, 6E, 7E, G) occurring on mandibles and thorax, and the minute openings on the abdomen (Fig. 11A) of Boganiidae are assumed to be ectodermal or integumentary glands, but the true nature and function of these structures requires further study. Crowson (1990) attributed a defensive nature to the glands found in the prothorax of *Boganium* and the mandibles of *Athertonium*, similar to those of some genera of Erotylidae (*Pharaxonotha* Reitter, *Leucohimatium* Rosenhauer), given that their presence in both sexes makes any pheromonal function unlikely. Crowson (1990) also referred to glands in the mandibles in the African *Boganium* and *Paracucujus*, but so far

the only similar structure found by the present authors is a single deep pit in *P. encephalarti*.

Crowson (1990) pointed out the striking parallelism between adults and larvae of Boganiidae and those of Meligethinae (Nitidulidae). These two groups share a pollenophagous biology, adults and larvae developing in flowers or inflorescences, adults with mandibular dorsal cavities and an emarginate labral apex, larval mandibles with a hyaline, acute prostheca (Hayashi, 1978) (whereas in most Nitidulidae the prostheca is often complex with comb-hairs or fringed membranes; Lawrence, 1991) and labrum fused to the head capsule.

Natural history. Adults and larvae of Boganiidae appear to be pollenophagous. Adults and larvae of *Paracucujus* and *Metacucujus* feed on male cones of *Macrozamia riedlei* (Gaudich.) and *Encephalartos* spp. Adults and larvae of *Boganium malleense* have been collected in the flowers of *Eucalyptus gracilis* F. (Myrtaceae). *Athertonium* adults have been found in the blossoms of Myrtaceae [*Syzygium* Gaertn., *Rhodomyrtus* (DC.) Rchb. and *Waterhousea* B.Hyland], Elaeocarpaceae (*Elaeocarpus* L.), Cunionaceae (*Caldcluvia* D.Don), Meliaceae [*Toona* (Endl.)] and Lauraceae (*Cryptocarya* R.Br.). Pupation almost certainly takes place in the soil, but no pupae have been described (Lawrence & Ślipiński, 2010). *Paracucujus rostratus* is usually found in male cones of *Macrozamia riedlei* in south-west Western Australia. Although a single record from female cones is cited below, the role of this species in pollination is unclear (Endrödy-Younga & Crowson, 1986; Crowson, 1990; Ornduff, 1991; Connell & Ladd, 1993; Terry *et al.*, 2005).

Based on the assumption that Boganiidae and *Parandrexis* were related, Crowson (1981) supposed that *Parandrexis* hosts were cycads. He speculated further that Boganiidae, Pharaonothinae (Erotylidae), and the weevils *Rhopalotria* Chevrolat and *Antliarhis* Billberg, were descendants of groups that once frequented cycadeoid flowers – implying a role in the evolution of Jurassic conifers and cycadeoids, and ultimately the origin of the angiosperms (cycads, in contrast to most gymnosperms, seem to be largely insect-pollinated). Crowson (1988, 1990) suggested that the dorsally setose mandibular cavities might serve to carry pollen grains between host plants. Donaldson *et al.* (1995) stated that cycad association of sister genera of Boganiidae in Africa and Australia (*Metacucujus* and *Paracucujus*) may suggest that this beetle lineage includes the first insect pollinators of cycads. Labandeira (2000) suggested that cycad host plant associations in Boganiidae, Curculionidae and other beetles (e.g. Palophaginae, Chrysomelidae) are of Mesozoic origin. The notion that closely related cycads (*Encephalartos* and *Macrozamia*) hosting closely related taxa of Boganiidae in southern Africa and south-west Western Australia are remnants of a very primitive association is very attractive and fascinating, but more direct evidence and definitive fossil Boganiidae are necessary to confirm such a notion.

Biogeography. The distribution of Boganiidae is clearly relictual and disjunctive (Grimaldi & Engel, 2005; Lomolino *et al.*, 2010), with taxa scattered in southern South Africa,

Western Australia and New Caledonia. Lawrence (in Austin *et al.*, 2004) mentioned that they represent a link between Australia and South African beetle faunas. Crowson (1981) considered boganiids as a relic taxa, together with several other beetle groups, and speculated that modern superfamilies of beetles were most likely already distinctive during the middle Jurassic (c. 175 Ma). Endrödy-Younga & Crowson (1986) suggested that Boganiidae were present during the initial break-up of Gondwana and rifting of Pangaea during the early Jurassic (c. 205–180 Ma) and their current distribution is mainly the result of vicariant events – a reasonable argument based on their adult and larva morphology, and current restricted distribution.

The New Caledonian *Dzumacium* is a novel element in the rich and highly endemic New Caledonian biota (Ladiges & Cantrill, 2007). The distribution of *Dzumacium* fits the vicariant distributional pattern between eastern Australia and New Caledonia known in different organisms (Heads, 2010); for example, the Myrtaceae clade *Arillastrum* (New Caledonia) and *Corymbia*, *Angophora* (Eastern Australia) and *Eucalyptus* associated with vicariant events in the Late Cretaceous (Ladiges *et al.*, 2003).

Parandrexidae. The family Parandrexidae is an extinct group of beetles with five species described from Russia, China and Spain. The first species described, *Parandrexis parvula* Martynov, 1926 from the Karatau formation, Kazakhstan, was initially thought related to Prioninae (Cerambycidae). Crowson (1975, 1981, 1990, 1991) recognized that some fossils of the Karatau formation resemble Boganiidae and later commented on similarities between *Parandrexis* and boganiids, particularly *Paracucujus rostratus*. Kirejtshuk (1994) placed *Parandrexis* in a new family, Parandrexidae, close to Cucujoidea with ‘anthophagous’ biology, rejecting relationships between Parandrexidae and Boganiidae. Later (Kirejtshuk *et al.*, 2010) considered Parandrexidae as a cleroid family near Peltidae (Trogossitidae) based on new Mesozoic beetle fossil data from Asia. We were able to examine a few specimens of Parandrexidae from China (Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences and College of Life Sciences, Capital Normal University, Beijing) (Fig. 12A–C) and concluded that some of their morphological features were very similar to Boganiidae, but, in contrast to Kirejtshuk’s observations, we were not able to support a definitive relationship between *Parandrexis* and Boganiidae or with any Cucujiformia.

Key to subfamilies and genera of Boganiidae

1. Lateral pronotal carina with ovate, glandular callosity containing multipored gland opening, at or just behind anterior angle (Figs 3D, 5A–C); apical maxillary palpomere <3× as long as wide, more or less fusiform (Fig. 3A); elytra evenly but irregularly punctate, without puncture rows (Fig. 2D–F); antenna with distinct three-segmented club (Figs 2D–F, 4A); protibia not expanded at apex (Fig. 4E); inner ventral edge of mandible without or with short fringe of hairs; penile struts <0.2× as long as body of penis (Fig. 11C–E) **Boganiinae, 2.**

– Lateral pronotal carina without anterior callosity; apical maxillary palpomere $>4\times$ as long as wide, parallel-sided (Fig. 6D, Figures S1C, D); elytral punctation more or less seriate (Fig. 2A, C); antennal club indistinct and inner ventral edge of mandible with long fringe of hairs (Figure S4E), OR, protibia distinctly expanded at apex (Figs 8D, 10G); penile struts $>0.33\times$ as long as body of penis (Figs 11F, K, L, Figure S3G)

Paracucujinae, 3.

2. Pronotal callosity located well behind anterior pronotal angle; clypeus not deeply constricted at base; mesal edge of mandible without or with one preapical tooth; tarsomere 3 not or only slightly lobed beneath; Republic of South Africa and Namibia

Afroboganium Endrödy-Younga & Crowson.

– Pronotal callosity contiguous with anterior pronotal angle and at least slightly projecting anteriorly (Fig. 5A–C); clypeus deeply constricted at base (Fig. 3A); mesal edge of mandible with two preapical teeth (Fig. 5D–E); tarsomere 3 distinctly lobed beneath; Australia

Boganium Sen Gupta & Crowson.

3. Elytral punctures more or less seriate (Fig. 2A, C); protibia not expanded at apex; median endocarina meeting frontoclypeal suture (Figure S4A); antennomeres 9 and 10 at least slightly elongate (Figures S2A, B, S4D); inner ventral edge of mandible with long fringe of hairs (Figure S4E); southern Africa and south-west Western Australia

4.

– Elytral punctures not seriate (Fig. 2B, G–I); protibia distinctly expanded at apex (Figs 2B, H, 8D); median endocarina, if present, not meeting frontoclypeal suture (Fig. 10A); antennomeres 9 and 10 not elongate (Fig. 10E); inner ventral edge of mandible without or with short fringe of hairs; eastern Australia and New Caledonia

5.

4. Clypeus anteriorly narrowed and broadly rounded at apex (Figure S4A); elytral striation indistinct, blurred by dense punctation of interstriae (Fig. 2C); occiput with transverse impression touching posterior edges of eyes (Figure S4A); entire dorsal surface conspicuously pilose (Fig. 2C); parameres separate, much longer than wide and articulated at base (Fig. 11I); southern Africa

Metacucujus Endrödy-Younga & Crowson.

– Clypeus with subparallel sides and truncate apex bearing two small teeth (Figure S1A); elytra clearly punctate-striate, interstriae with a few scattered punctures (Fig. 2A); occiput without transverse impression (Figure S1A); dorsal surface glabrous; parameres partly fused together but articulated at base (Fig. 11H); south-west Western Australia . . . **Paracucujus Sen Gupta & Crowson.**

5. Anterior and posterior pronotal angles without glandular pores (Fig. 10D); sides of pronotum strongly curved (Fig. 10D); vertex with median endocarina (Fig. 10A); mandible without ventral accessory tooth (Fig. 10C); without gland openings on prosternum and abdomen; New Caledonia

Dzumacium gen.n.

– Anterior and posterior pronotal angles with small, multipored gland openings (Fig. 7E); sides of pronotum weakly curved (Fig. 7D, F); vertex without median endocarina (Fig. 6B); mandible with ventral accessory tooth (Fig. 7C); prosternum with paired multipored gland openings (Fig. 7F, G) and abdomen

with simple gland on ventrites 1–5 (Fig. 11A); Australia: eastern New South Wales and Queensland . . . **Athertonium Crowson.**

Boganiinae Sen Gupta & Crowson

Boganiidae Sen Gupta & Crowson, 1966: 63.

Diagnosis. Members of this subfamily differ from other boganiids in the presence of pronotal callosities (Figs 3D, 5A–C), shorter and broader, fusiform apical maxillary palpomeres (Fig. 3A, B), paired posterolateral gland openings (Fig. 11A) on ventrites 1–4 but not on 5, and short penile struts (Fig. 11C–E). The pronotal callosities resemble those of some Cryptophagidae, and *Afroboganium proprium* (Grouvelle) was originally described in the cryptophagid genus *Micrambe* Thomson.

Included genera. *Afroboganium* Endrödy-Younga & Crowson, *Boganium* Sen Gupta & Crowson.

Boganium Sen Gupta & Crowson

(Figs 2D, F, 3–5, 9E–I, 11A–E)

Boganium Sen Gupta & Crowson, 1966: 70. Type species: *Boganium armstrongi* Sen Gupta & Crowson, 1966 (original designation).

Diagnosis. The Australian species of *Boganium* may be distinguished from the southern African species of *Afroboganium* by the more well-developed pronotal callosities located at, but not behind, the anterior pronotal angles, the more deeply constricted clypeal base, the mandible with two preapical teeth and tarsomere 3 distinctly lobed below. Parameres in *Boganium* are either absent or represented by very small fixed lobes, whereas in *Afroboganium elmeae* they are partly fused together but basally articulated. Male protibia with small posteromesal tooth at apical third (Fig. 5F).

Distribution. South Australia, Victoria, Tasmania and south-east Western Australia.

Natural history. Specimens have been collected on flowers of *Eucalyptus gracilis* F. (Myrtaceae) and other angiospermae of the Australian Mallee, whereas some others have been collected from leaf litter and moss of *Nothofagus* and *Eucalyptus* forest.

Key to species of Boganium

1. Dorsal surface of mandible with accessory tooth (Fig. 5E); occiput with scalloped and interrupted transverse carina (Fig. 5H); vertex with weak median endocarina (not always visible externally in dried specimens); anterior pronotal angles distinctly produced forward; callosities prominent and sides of pronotum immediately behind them more or less parallel (Fig. 5C); pronotal punctures usually smaller than those on

elytra; Tasmania and Victoria
 ***B. armstrongi* Sen Gupta & Crowson.**
 – Dorsal surface of mandible without accessory tooth (Figs 3A, 5D); occiput with or without transverse carina; vertex without median endocarina (Fig. 5G); anterior pronotal angles only slightly produced; callosities less prominent and sides of pronotum immediately behind them distinctly curved; pronotal punctures about the same size as those on elytra **2.**
 2. Pronotum $>0.5\times$ as long as wide, with sides weakly irregularly curved behind callosities which are more than a fourth as long as pronotum (Fig. 5B); occiput with transverse carina (Fig. 5G); right mandible with well-developed, setose prostheca; colour usually dark brown with yellow macula crossing elytral suture at about anterior 1/3 (Fig. 2D); South Australia, Western Australia and New South Wales ***B. medioflavum* sp.n.**
 – Pronotum $<0.5\times$ as long as wide, with sides more strongly, evenly curved behind callosities, which are $<1/4$ as long as pronotum (Fig. 5B); occiput without transverse carina (Fig. 3A); prosthecae on both mandibles reduced and nonsetose; colour usually yellow (Fig. 2F), sometimes with dark macula crossing elytral suture; South Australia and Western Australia
 ***B. malleense* sp.n.**

***Boganium malleense* sp.n**

(Figs 2F, 3–5B, F, 9E–I, 11A, B, E)

Diagnosis. This species differs from *B. armstrongi* in lacking the dorsal mandibular tooth and from both *B. armstrongi* and *B. medioflavum* in having a shorter and broader prothorax (Figs 2F, 5B) with relatively small callosities and strongly, evenly rounded sides and a simple, nonsetose prostheca on both mandibles, and in lacking a transverse occipital carina (Fig. 3A). The colour is often uniformly yellow, but in some specimens there is a dark median macula crossing the elytral suture.

Description. Total length 2.1–2.6 mm. Body about 1.65–1.77 \times as long as wide. Colour of fully pigmented specimens yellow, sometimes with a large dark brown macula crossing elytral suture and extending to posterior 1/3. Head about 0.8 \times as long as wide. Occiput without transverse carina or microsculpture. Frons without median endocarina. Antennomeres 7–9 not longer than wide. Dorsal surface of mandible without accessory tooth; prostheca without setal fringe. Pronotum about 0.47–0.51 \times as long as wide. Anterior pronotal angles barely produced forward and callosities not prominent; sides behind callosities strongly and evenly curved; posterior pronotal angles not produced laterally. Elytra about 1.25–1.40 \times as long as wide and 3.00–3.75 \times as long as pronotum. Dorsal curvature of penis (on left side in abdomen) at basal 1/3 much sharper than ventral curvature (on right side), remainder of penis evenly curved (Fig. 11E).

Holotype, ♂, AUSTRALIA: South Australia, Canopus HS, Danggali Cons. Park (33.30°S, 140.42°E), 21.v.1996, at light, T. Weir, K. Pullen (ANIC). *Paratypes*, AUSTRALIA: South Australia: same data as holotype (22, ANIC); Brookfield

Cons. Park, 11 km E of Blanchetown, 14.v.1999, on flowers of *Eucalyptus gracilis*, C. Reid (6, ANIC); Ceduna, 67 mi. E, 3.v.1968; I. Common, M. Upton (14, ANIC); Mildura, 13 km SE, 20.v.1969, flowers of *Eucalyptus gracilis*, C. Reid (4, ANIC); Kimba, 40 km E (NSW on label), 22.ix.1985, R. Bejsak (AMS, K358272–274); Mt. Remarkable, towards Terka, 1800 ft., 16.v.1968, forest trees and dense scrub, H. M. Cooper (2, SAM); Port Lincoln, 15.viii.1950, C. Oke (6, MVM); same locality, Blackburn Coll. (2, NHML); Swan Reach, 10 km SW, 13.v.1986, flowering mallee, C. Reid (1, ANIC). **Victoria:** Birchip, J. C. Goudie (2, SAM; 2, MVM). **Western Australia:** Balladonia HS, 7 mi. EbyN, 13.x.1968, E. Britton, M. Upton, J. Balderson (1, ANIC); Madura Pass (31.54°S, 127.01°E), 19.v.1984, E. S. Nielsen, E. D. Edwards (1, ANIC); Newman Rock (32.07°S, 123.10°E), 7.v.1983, E. S. Nielsen, E. D. Edwards (1, ANIC); Norseman, 61 mi. E, 29.iv.1968, I. Common, M. Upton (8, ANIC); Scaddan, 12 km N (33.20°S, 121.43°E), 16.v.1984, E. S. Nielsen, E. D. Edwards (1, ANIC).

Distribution. South Australia, Victoria and south-east Western Australia.

Natural history. Adults and larvae have been collected on flowers of the Myrtaceae *Eucalyptus gracilis* F. and flowering plants of the Australian Mallee.

Etymology. Derived from the predominant vegetation group where this species is distributed, the semi-arid mallee woodlands and shrublands in southern Australia.

***Boganium medioflavum* sp.n**

(Figs 2D, 5A, D, G, 11D)

Diagnosis. This species differs from *B. armstrongi* in having a continuous transverse occipital carina (Fig. 5G) and in lacking the dorsal mandibular tooth (Fig. 5D). The pronotal callosities are more prominent and slightly produced laterally as in *B. armstrongi*, whereas the sides of the pronotum behind the callosities are slightly, irregularly curved, usually with small teeth or angulations (Fig. 5A), unlike the straight sides in *B. armstrongi* or the strongly, evenly curved sides in *B. malleense*. The species also differs from *B. malleense* in having a less transverse prothorax (more than 0.5 \times as long as wide) and in the presence of a transverse occipital carina. The colour is darker than in *B. malleense* and more like that of *B. armstrongi*, but the elytra often have a median yellow macula crossing the elytra at the anterior 1/3 (Fig. 2D).

Description. Total length 2.5–3.2 mm. Body about 1.87–2.00 \times as long as wide. Colour of fully pigmented specimens, dark reddish-brown, often with large yellow macula crossing elytra at about basal 1/3. Head about 0.8 \times as long as wide. Occiput with continuous, even transverse occipital carina behind which there is microsculpture of fine spicules. Frons without median endocarina. Antennomeres 7–9 at least slightly

elongate. Mandible with well-developed setose prosthema on right mandible, reduced or absent on left mandible. Pronotum about 0.50–0.59× as long as wide. Anterior pronotal angles with moderately prominent callosities slightly produced laterally beyond lateral curvature, sides behind callosities distinctly curved and with several small teeth. Elytra about 1.45–1.60× as long as wide and 3.18–4.00× as long as pronotum. Dorsal curvature of penis (on left side in abdomen) at basal 1/3 about the same as ventral curvature (on right side) (Fig. 11D).

Holotype, ♂, **AUSTRALIA: Western Australia:** Norseman, 61 mi. E, 29.iv.1968, I. F. B. Common, M. S. Upton (ANIC). *Paratypes*, **AUSTRALIA, Western Australia:** same data as holotype (11, ANIC); Coolgardie, 29 km SE by E (31.07°S, 121.24°E), 5.v.1983, E. S. Nielsen, E. D. Edwards (1, ANIC); Eucla, 7 km EbyN (31.40°S, 128.57°E), 29.iv.1984, E. S. Nielsen, E. D. Edwards (2, ANIC); Norseman, 61 mi. E, 29.iv.1968, I. F. B. Common, M. S. Upton (11, ANIC). **South Australia:** Belair, Waverley Ridge Rd., 21.iv.1973, P. McQuillan (5, SAM Database No. 25-035734); Brookfield Cons. Park (32.21°S, 139.29°E), 3–12.ix.1991, at light, J. Lawrence, T. Weir, W. Dressler (1, ANIC); Mt. Remarkable, towards Terka, 1800 ft., 16.v.1968, H. M. Cooper (2, SAM); Port Lincoln, 15.viii.1950, C. Oke (6, MVM); Port Lincoln, Lea (6, SAM Database No. 25-035735); same locality, A. M. Lea (2, SAM). **New South Wales:** Bogan River (2, ANIC); The Rock Nature Res. 20.viii.1985, *Ac. pycnantha*, C. Reid (1, ANIC).

Distribution. South Australia, Victoria and south-east Western Australia.

Comments. One specimen was collected on *Acacia pycnantha* Bentham (Fabaceae).

Etymology. Derived from the Latin words *medius*, middle, and *flavus* yellow, referring to the yellow elytral macula crossing the suture at about the middle of the dark brown elytra.

***Afroboganiium* Endrödy-Younga & Crowson**

(Fig. 2E)

Afroboganiium Endrödy-Younga & Crowson, 1986: 258. Type species: *A. capense* Endrödy-Younga in Endrödy-Younga & Crowson, 1986 (= *Micrambe proprium* Grouvelle, 1899) (original designation).

Diagnosis. *Afroboganiium* species differ from those of *Boganiium* in having somewhat smaller pronotal callosities located well behind the anterior pronotal angles, the clypeus not or weakly constricted at base, the mandible often with only one preapical tooth, and tarsomere 3 not or only barely lobed beneath. The parameres in at least one species (*A. elmeae*) appear to be articulated at base, unlike those of any *Boganiium* species.

Distribution. South Africa (Transvaal, southern and south-western Cape Province) and Namibia (extreme south-west).

Included species. *A. proprium* (Grouvelle, 1899) (= *A. capense* Endrödy-Younga, 1986), *A. elmeae* Endrödy-Younga, 1986, *A. namibense* Endrödy-Younga, 1986, *A. transvaalense* Endrödy-Younga, 1986, *A. major* Endrödy-Younga, 1986.

Paracucujinae Endrödy-Younga & Crowson

(Figs 2A–C, G–I, 6–9A–D, 10, 11F–L, Figures S1–S6)

Athertoniini Crowson, 1990: 91.

Diagnosis. Paracucujinae includes the remaining boganiid genera which lack the pronotal callosities (Fig. 10D) and have longer and more slender, cylindrical apical maxillary palpomeres and much longer penile struts (Fig. 11F, K, L). Crowson (1990) proposed the tribe Athertoniini for the Australian genus *Athertonium*, differing from *Paracucujus* and *Metacucujus* in lacking a median frontal endocarina and having apically expanded protibiae, glands at both anterior and posterior pronotal angles, irregular elytral punctation and toothed pretarsal claws. The New Caledonian genus *Dzumacium* **gen.n.** also has expanded protibiae and irregular elytral punctation, but differs in other respects.

Included genera. *Athertonium* Crowson, *Dzumacium* **gen.n.**, *Metacucujus* Endrödy-Younga & Crowson, *Paracucujus* Sen Gupta & Crowson.

***Paracucujus* Sen Gupta & Crowson**

(Figs 2A, 9A–C, 11F, H, Figures S1–S3, S5, S6)

Paracucujus Sen Gupta & Crowson, 1966: 67. Type species *Paracucujus rostratus* Sen Gupta & Crowson, 1966 (original designation).

Diagnosis. *Paracucujus rostratus* resembles the South African species of *Metacucujus* in several respects, but differs in having the clypeus with sub-parallel sides and bidentate apex, the occiput without a transverse impression behind the eyes, the upper surfaces sub-glabrous, the elytral punctation distinctly seriate, and the parameres more or less fused together.

Distribution. South-west region of Western Australia.

Natural history. Adults and larvae are pollenophagous. The only known host is the cycad *Macrozamia riedlei* (Gaudich.).

***Metacucujus* Endrödy-Younga & Crowson**

(Figs 2C, 9D, 11I, L, Figure S4)

Metacucujus Endrödy-Younga & Crowson, 1986: 255. Type species *Metacucujus encephalarti* Endrödy-Younga in Endrödy-Younga & Crowson, 1986 (original designation).

Diagnosis. *Metacucujus* species are densely clothed with fine, decumbent hairs, unlike *Paracucujus rostratus*, and the elytral punctation is less obviously seriate, due to dense interstitial

punctuation. In addition, there is a transverse impression joining the posterior edges of the eyes, the clypeus is anteriorly narrowed and rounded at apex and the parameres are separate, narrowly elongate and basally articulated.

Distribution. South Africa (Transvaal, Natal, eastern Cape Province).

Included species. *M. encephalarti* Endrödy-Younga, 1986, *M. transvenosi* Endrödy-Younga, 1991, *M. goodei* Endrödy-Younga, 1991.

Natural history. *Metacucujus* species have been found in male cones of *Encephalartos transvenosus* Stapf & Burtt-Davy, *E. lanatus* Stapf & Burtt-Davy, *E. natalensis* Dyer & Verdoorn and *E. friderici-guilielmi* Lehm. (Endrödy-Younga, 1991).

Comments. Endrödy-Younga (1991) mentioned relatively common teratogenesis in some species.

Athertonium Crowson

(Figs 2G–I, 6–8, 11G, J, K)

Athertonium Crowson, 1990: 92. Type species *Athertonium parvum* Crowson, 1990 (original designation).

Diagnosis. The species of *Athertonium* may be distinguished from species of *Paracucujus* and *Metacucujus* by the distinctly expanded protibial apex (Fig. 8D), nonseriate elytral punctuation, lack of a median endocarina, transverse ninth and tenth antennomeres, and simpler prosthema, not involving a tuft of long hairs. From *Dzumacium caledonicum* they differ in being smaller (less than 2.2 mm) and having a number of cuticular gland openings, either simple as on abdominal ventrites 1–5 or compound (multipored) as on the outer edges of the mandibles, anterior and posterior pronotal angles and prosternum.

Distribution. East Australia.

Natural history. Adults are pollenophagous and the larva is unknown. The known host includes plant of families Lauraceae, Elaeocarpaceae, Cunoniaceae and Meliaceae.

Key to species of *Athertonium*

1. Dorsal surfaces of pronotum and elytra clothed primarily with very short, fine setae barely longer than a puncture diameter (Fig. 2H, I), with scattered longer, sub-erect setae along sides of elytra; pronotal punctuation sparser, with most punctures separated by more than a puncture diameter; total length 1.7–2.2 mm; fully pigmented specimens reddish-yellow to reddish-orange (Fig. 2H), sometimes with dark elytral suture (Fig. 2I) but very rarely darker in colour; penile struts apically expanded (Fig. 11K); distal lobe of gonocoxite about 4× as long

as wide and parallel-sided (Fig. 11J); central coastal New South Wales to northern Queensland ***A. parvum* Crowson.**
– Dorsal surfaces of pronotum and elytra clothed with longer, fine, decumbent setae, several times as long as a puncture diameter (Figs 2G, 6A, 7D); pronotal punctuation denser, with most punctures separated by much less than a puncture diameter; total length 1.3–1.7 mm; fully pigmented specimens dark reddish-brown (Fig. 2G); penile struts narrowly acute at apex; distal lobe of gonocoxite about twice as long as wide with convex outer edge (Fig. 8G); New South Wales
. ***A. williamsi* sp.n.**

***Athertonium williamsi* sp.n**

(Figs 2G, 6–8)

Diagnosis. This species may be distinguished from *A. parvum* by the somewhat denser pronotal punctuation, with most punctures separated by much less than a puncture diameter, the dorsal vestiture which consists of fine decumbent hairs much longer than a puncture diameter, the slightly smaller size – usually less than 1.7 mm in length – the apically acute penile struts and shorter, broader, apically expanded distal lobe of the gonocoxite. The colour of fully pigmented specimens is dark yellowish-brown, in contrast to the more reddish-yellow or orange colour of *A. parvum*.

Description. Total length: 1.3–1.7 mm. Body about 1.75–1.95× as long as wide. Colour yellow to dark brown, with pronotum darker and elytra lighter or pronotum with more reddish in colour and elytra more yellowish. Dorsal surfaces clothed with decumbent to sub-erect setae distinctly longer than a puncture diameter. Pronotum about 0.48–0.61× as long as wide; punctuation moderately dense with most punctures separated by less than a puncture diameter. Elytra about 1.28–1.44× as long as wide and 2.65–3.42× as long as pronotum; punctuation similar to that on pronotum. Aedeagus with penile struts narrowly acute at apex. Ovipositor about 2.75× as long as wide; paraprocts about 0.85× as long as gonocoxites, each of which is indistinctly divided into proximal and distal lobes, the former slightly longer than the latter, which is about twice as long as wide with distinctly curved outer edge and angulate apex; gonostylus about 0.15× as long as distal lobe, narrowly cylindrical and sub-apical.

Holotype, ♂, **AUSTRALIA: New South Wales:** Lansdowne, 0.5 km SE, via Taree, 12.xi.1990, ex *Acmena smithii* flowers, G. Williams (ANIC). *Paratypes*, **AUSTRALIA: New South Wales:** Acacia Plateau, J. Armstrong (1, ANIC); Brindle Creek, Border Ranges N.P., 3–14.x.1984, ex pantraps, I. Naumann, J. Cardale (1, ANIC); Gloucester, c24 km NNW, 25.xi.1990, ex *Acmena smithii*, G. & T. Williams (3, AMS K358269–70); Lansdowne, 0.5 km SE, via Taree, 29.x.1990, on *Elaeocarpus obovatus* blossom, G. Williams (1, ANIC); same locality, 6.xi.1990, on *Acmena smithii* blossom, G. Williams (2, ANIC); same locality, 12.xi.1990, ex *Acmena smithii* flowers, G. Williams (10, ANIC); same locality, 15.xi.1990, ex *Acmena smithii* flowers, G. Williams (7, ANIC); same locality,

19.xi.1990, ex *Rhodomyrtus psidioides* blossoms, G. Williams (4 ANIC); Lansdowne, 3 km N, 13.xi.1990, ex flowers *Elaeocarpus reticulatus*, G. Williams (17, ANIC); same locality, 6.xi.1990, ex flowers *Elaeocarpus reticulatus*, G. Williams (1, ANIC); same locality, 17.xi.1990, *Rhodomyrtus psidioides*, G. Williams (2, AMS K358268); same locality, 20.xi.1990, on *Caldcluvia paniculosa* blossoms, G. & T. Williams (2, AMS K358267); Wingham, 22.xi.1990, riparian rainforest, on *Waterhousea floribunda* blossoms, G. Williams (2, ANIC).

Distribution. This species is restricted to coastal New South Wales, where it overlaps with the more widely distributed *A. parvum*.

Natural history. Several specimens have been collected on flowers of *Syzygium smithii* (Poir.) Nied. (= *Acmena smithii* (Poir.) Merr. & L. M. Perry), *Rhodomyrtus psidioides* (G. Don) Benth. and *Waterhousea floribunda* F. Muell. B. Hyland (Myrtaceae), *Elaeocarpus obovatus* G. Don. and *Elaeocarpus reticulatus* Sm. (Elaeocarpaceae) and *Caldcluvia paniculosa* F. Muell. Hoogl (Cunoniaceae). Abundant pollen was found in the digestive track of the adults dissected.

Etymology. The species is named in honour of Geoff Williams, an Australian naturalist who collected most of the specimens.

***Dzumacium* gen.n.**
(Figs 2B, 10)

Type species. *Dzumacium caledonicum* sp.n.

Diagnosis. This genus may be distinguished from both *Paracucujus* and *Metacucujus* by the nonseriate elytral punctation, distinctly expanded protibial apex (Fig. 10G), shorter median endocarina not meeting the frontoclypeal suture (Fig. 10A), sub-quadrate ninth and tenth antennomeres and simpler prostheca, not involving a tuft of long hairs. The genus differs from *Athertonium* in its consistently larger size (more than 2.5 mm) and more elongate and parallel-sided elytra, with sides narrowing only at apical fifth, and in the lack of a ventral accessory tooth on the mandible and cuticular glands on the anterior and posterior pronotal angles, prosternum, abdominal ventrites and outer edges of the mandibles.

Description. Length 2.7–3.0 mm; body about 2.06–2.16× as long as wide. Surfaces clothed with short decumbent fine setae, with scattered, slightly longer erect setae. Head and pronotum reddish-yellow, elytra and under surfaces yellow.

Head (Fig. 10A) about 0.78× as long as wide, slightly declined, slightly convex dorsally. Occipital region with continuous transverse occipital ridge, behind which is an area of fine microsculpture. Frontal region with short median endocarina extending between transverse occipital carina and frontoclypeal

suture but meeting neither one. Antennal insertions slightly concealed from above by frontal ridges; sub-antennal grooves short, shallow; oblique supraorbital groove on each side beginning at frontoclypeal suture just mesal to frontal ridge and ending at posterior edge of eye. Clypeus about 0.65× as long as wide at base, slightly narrowing anteriorly and broadly rounded at apex. Labrum (Fig. 10B) lying beneath clypeus and barely visible from above, deeply emarginate anteriorly. Antennae (Fig. 10E) slightly longer than width of pronotum; scape robust and asymmetrical, antennomeres 2 and 3 sub-equal in length, elongate and about 0.62× as long as scape; antennal club weak, three segmented, antennomeres 9 and 10 sub-equal in length and about as long as wide. Mandible (Fig. 10C) about 1.55× as long as wide at base; outer edge strongly rounded, without cuticular gland; dorsal surface with relatively small tubercle and large, setose cavity; apex unidentate, with two large sub-apical teeth partly joined at base, so that apex may appear tridentate; mola well-developed, basal; prostheca simple, finely setose but without fringe or tuft of setae. Maxilla with galea apically expanded and densely setose and lacinia short, with typical sickle-shaped double uncus; apical palpomere about 5× as long as wide, sub-cylindrical. Mentum about 0.5× as long as wide, rounded at apex; ligula apically expanded and emarginated forming two setose lobes; apical palpomere about 2.5× as long as wide, narrowly fusiform. Gular sutures short.

Pronotum (Fig. 10D) about 0.58–0.61× as long as wide; apical edge weakly curved; anterior pronotal angles not produced; sides evenly and broadly rounded; lateral pronotal carinae very fine, complete, continued along posterior edge; posterior angles rounded; disc slightly convex. Prosternum in front of coxae about 1.2× as long as mid length of coxal cavity. Prosternal process complete, slightly expanded apically, surface flat, extending well beyond posterior edges of coxae, apex truncate, microcrenulate and setose. Notosternal suture complete. Procoxal cavities transverse, separated by about 0.3× mid width of coxal cavity, lateral extensions narrow.

Scutellum (Fig. 10F) strongly transverse, expanded and rounded laterally, broadly angulate posteriorly. Elytra about 1.60–1.64× as long as wide and 3.15–3.48× as long as pronotum; sides parallel for most of their lengths, converging at posterior eighth and broadly rounded apically; punctation confused; epipleura narrow, extending to apical 1/3. Mesocoxal cavities separated by about 0.5× shortest diameter of a cavity. Metaventrite about 0.6× as long as wide and slightly convex; transverse metakatepisternal suture long, extending on each side of midline to lateral fifth; discrimen about 0.7× as long as ventrite. Legs slender; tibiae (Fig. 10G) setose, with two apical spurs differing slightly in length; all tibiae expanded at apex, but protibiae especially so; apical edges of all tibiae fringed with spines; tarsomeres 1–3 similar in length, penultimate much shorter than the rest, tarsomeres 1–3 narrow at base but expanded apically, each with ventral, setose, membranous lobe, that on tarsomere 1 reduced and that on tarsomere 3 extending beyond apex of tarsomere 4; pretarsal claws with weak basal tooth; empodium not observed.

Abdomen about 1.1× as long as wide at base; ventrite 1 slightly longer than 2, with acute intercoxal process; 2–4 more

or less equal in length; 5 about 1.4× as long as 4 and densely setose, especially in male. Aedeagus with tegmen (Fig. 10I) about 2.8× as long as wide, twisted; basoventral strut slender, parallel-sided, its base broadly irregularly rounded; cap piece gradually but distinctly narrowed posteriorly; parameres very small, fused together at base but articulated with apex of cap piece; penis (Fig. 10H) in lateral view evenly curved, its body slightly shorter than tegmen; penile struts about 0.33× as long as body of penis. Apex of penis dorsally notched forming a small, sharply curved apical process. Linear endophallic sclerite distinctly protruding. Ovipositor (Fig. 10K) about 1.2× as long as wide; paraprocts sub-equal in length to gonocoxites, each of which is divided into short, broad proximal lobe and distal lobe about 2× as long as wide with somewhat angulate apex and sub-apical, gonostylus about 0.33× as long as distal lobe. Internal tract with sharply curved spermathecal capsule attached to long duct and with spermathecal gland attached to duct entering capsule at its base.

Etymology. Derived from Dzumac Mts., the type locality north Noumea, New Caledonia. Gender masculine.

Dzumacium caledonicum sp.n.

(Figs 2B, 10)

Description. As for genus.

Holotype, ♂, **NEW CALEDONIA**: Dzumac Mts. (22.03188°S, 166.46738°E), Mt. Ouin Rd. Jct., 910 m, 30.x.2008, at light, M. Wanat (MNHN). *Paratypes*, **NEW CALEDONIA**: Dzumac Mts. (22.03188°S, 166.46738°E), Mt. Ouin Rd. Jct., 910 m, 30.x.2008, at light, 10 exs, M. Wanat (ANIC, IRD, IACP, MNHW); same locality, 28.xii.2006, at light, 2 exs, R. Dobosz (USMB).

Distribution. Known only from the type locality, Dzumac Mts., North of Noumea, New Caledonia.

Natural history. Unknown, the few specimens of the type series were collected at light. Some specimens were dissected and their digestive track was empty.

Etymology. Derived from New Caledonia.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12126

Figure S1. *Paracucujus rostratus* Sen Gupta & Crowson: (A) head, dorsal, (B) head, ventral, (C) head, anterolateral, (D) maxilla, ventral, (E) labrum, ventral, (F) mandible, dorsal.

Figure S2. *Paracucujus rostratus* Sen Gupta & Crowson: (A) antenna, (B) antennomeres 10–11, (C) scutellum, (D) prothorax, ventral, (E) pterothorax, ventral, (F) prothorax, lateroventral, (G) abdomen, ventral.

Figure S3. *Paracucujus rostratus* Sen Gupta & Crowson: (A) pygidium, (B) hind leg, (C) ovipositor, (D) tarsus, lateral, (E) tarsus, dorsal, (F) mesotibial apex and mesotarmere 1, (G) penis, lateral.

Figure S4. *Metacucujus encephalarti* Endrödy–Younga: (A) head, dorsal, (B) maxilla, ventral, (C) maxilla, detail, showing crescent-shaped lacinial uncus, (D) antenna, (E) mandible, dorsal, (F) mandible, mola, (G) scutellum.

Figure S5. *Paracucujus rostratus* Sen Gupta & Crowson, larva: (A) habitus, lateral, (B) habitus, ventral, (C) habitus, dorsal, (D) abdominal apex, ventral, (E) abdominal apex, posterolateral, (F) abdominal apex, lateral.

Figure S6. *Paracucujus rostratus* Sen Gupta & Crowson, larva: (A) head, ventral, (B) mandible, ventral, (C) mandible, mola, (D) mid leg, (E) abdominal spiracle.

Figure S7. Selected phylogenetic hypothesis for Boganiidae with (a) ACCTRAN and (b) DELTRAN optimizations.

Table S1. Data matrix used in the cladistic analysis.

Appendix S1. Superfamilies, families, subfamilies and exemplar genera used in the analysis, morphological characters used in the analysis, Boganiidae classification and description of Boganiidae adult and larvae.

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