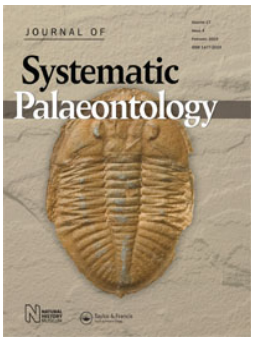


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# †Electrorubesopsinae, a new subfamily from Cretaceous Burmese amber, as the possible sister group of Dynamopodinae (Coleoptera: Scarabaeidae)

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# †Electrorubesopsinae, a new subfamily from Cretaceous Burmese amber, as the possible sister group of Dynamopodinae (Coleoptera: Scarabaeidae)

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A new subfamily of Scarabaeidae, †Electrorubesopsinae Bai & Wang subfam. nov., is described from Cretaceous amber of Myanmar (earliest Cenomanian, ~100 Ma) as the possible sister group of Dynamopodinae. †*Electrorubesopsis beuteli* Bai & Wang gen. et sp. nov. is the first species of this subfamily, which has probably been long extinct. Its external morphology was analysed and compared with all known genera of Dynamopodinae. A phylogenetic analysis based on 82 morphological characters suggests its placement in a sister relationship between †*Electrorubesopsis* and *Orubesa*. The hypothesis of a close relationship between *Orubesa* (Dynamopodini) and *Thinorycter* (Thinorycterini) is challenged. †*Electrorubesopsis* likely lived in a sandy environment or forest.

http://zoobank.org/urn:lsid:zoobank.org:pub:15351B5E-337C-49D4-90F0-619269BD1E5A

**Keywords**: Coleoptera; †*Electrorubesopsis*; phylogeny; Burmese amber; new taxa

## Introduction

Dynamopodinae is a small and poorly known subfamily of Scarabaeidae (Coleoptera) that comprises three modern genera (*Orubesa* Reitter, 1895, *Thinorycter* Semenov & Reichardt, 1925 and *Adraria* Villiers, 1956) (Semenov 1896; Arrow 1911; Semenov & Medvedev 1928, 1929). *Orubesa* ( = *Dynamopus* Semenov, 1896) was originally placed in Dynamopodinae (Arrow 1911). Alternative hypotheses are that *Orubesa* can be assigned to Hybosoridae (Balthasar 1971), and *Orubesa* ( = *Xanthelaeus* Fairmaire, 1897) to Dynastinae (Fairmaire 1897).

*Thinorycter* was originally placed in Aphodiinae (Semenov & Medvedev 1928). Nikolayev (1993) believed *Thinorycter* to be close to *Orubesa* on the basis of morphological evidence. *Orubesa* (Dynamopodini) and *Thinorycter* (Thinorycterini) constitute Dynamopodinae (Bouchard *et al.* 2011). *Adraria* was erected by Villiers (1956) on the basis of two specimens. No additional species of this genus have been reported since that time, and its systematic position is unclear.

Most lineages of Scarabaeoidea had appeared by the Mesozoic (Krell 2007; Nikolayev 2007; Bai *et al.* 2011, 2012a, b, 2013, 2016a; Yan *et al.* 2012, 2013; Boucher *et al.* 2016; Zhao *et al.* 2016). The discovery of a beetle that is apparently close to Dynamopodinae in mid-Cretaceous Burmese amber (~100 million years ago) is of great interest. Here we describe †*Electrorubesopsis beuteli* Bai & Wang gen. et sp. nov. in †Electrorubesopsinae Bai & Wang subfam. nov. of Scarabaeidae as the possible sister group of Dynamopodinae. A checklist of all species belonging to both subfamilies is provided in Supplemental Table S1. A phylogenetic analysis based on 82 morphological characters was conducted to infer the systematic position of †*Electrorubesopsis*.

## Materials and methods

### Material

The specimen was obtained from amber deposits in the Hukawng Valley of Myanmar (Kania *et al.* 2015). The locality is Noije Bum near Tanai Village (26°21′33.41″N, 96°43′11.88″E) (Grimaldi *et al.* 2002; Cruickshank & Ko 2003; Bai *et al.* 2016b), where many important fossils have been found, including vertebrates and invertebrates

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(Bai *et al.* 2016b, 2017; Oliveira *et al.* 2016; Jałoszynski *et al.* 2017; Lin & Bai, 2017; Xing *et al.* 2016a, b, 2017). The deposits were investigated in detail and dated by Cruickshank & Ko (2003) and Shi *et al.* (2012). We tentatively follow the age (98.8 ± 0.6 million years, Cenomanian) given by U-Pb dating of zircons from the volcaniclastic matrix of the amber (Shi *et al.* 2012).

The piece of amber containing the material described was trimmed, polished and then examined using a LEICA MZ 12.5 dissecting microscope with a drawing tube attachment. Photographs were taken with a Nikon D610 digital camera fitted to a Zeiss Stemi 2000-C stereomicroscope and were processed using Helicon Focus 5.1 software and Adobe Photoshop CS5.

### Taxon sampling and phylogenetic analysis

We selected 38 species housed at the Institute of Zoology of the Chinese Academy of Sciences (IZAS) to represent all extant families of Scarabaeoidea (except Belohinidae), which included all traditionally accepted major lineages of Scarabaeidae. The nomenclature of family group names follows Bouchard *et al.* (2011). Additionally, we included Hydrophilidae and Histeridae as outgroups (Hunt *et al.* 2007; Ahrens *et al.* 2014).

Eighty-two morphological characters were selected for cladistic analysis to infer the phylogenetic position of †*Electrorubesopsis* gen. nov. The character list and matrix are can be found in the Supplementary material (S1 and S2). We used TNT (Goloboff *et al.* 2003, 2008) to perform heuristic searches to find the most parsimonious trees (MPTs; traditional search; 99,999 random seeds, 1000 replicates). Bremer support values were calculated in TNT with the TBR in 10 steps.

## Systematic palaeontology

Order **Coleoptera** Linnaeus, 1758
Superfamily **Scarabaeoidea** Latreille, 1802
Family **Scarabaeidae** Latreille, 1802
Subfamily †**Electrorubesopsinae** Bai & Wang subfam. nov.
urn:lsid:zoobank.org:act:4365EFF7-25B0-49DB-8413-DF65106FD28C

**Type genus.** †*Electrorubesopsis* Bai & Wang gen. nov.

**Diagnosis.** †Electrorubesopsinae subfam. nov. can be recognized by the following combination of characters: elongate-oval and convex; antennae 10-segmented with a short 3-jointed simple and compact club (Fig. 1E); mandible not exposed (Fig. 1C); elytra with striae; pro- and mesocoxae separated, metacoxae closed, mesocoxal cavities circular; outer edge of the protibia with one or more distinct teeth; outer apical angle of the mesotibia with one or more straight or outwardly facing teeth or spines; meso- and metatibia with two adjacent spurs at the apex, not separated by base of tarsomere 1, with setae respectively (Fig. 2C, E), metatibial spurs similar in form, differing distinctly in length and proximal spurs longer; mesotarsal claws paired and symmetrical; scutellum visible; abdomen 6-segmented.

**Remarks.** Three genera of the closely related Dynamopodinae are known: *Adraria*, *Orubesa* and *Thinorycter*. Comparisons of the characters of these genera with †*Electrorubesopsis* Bai & Wang gen. nov. are provided in Supplemental Table S2.

Genus †***Electrorubesopsis*** Bai & Wang gen. nov.
urn:lsid:zoobank.org:act:71AA9215-7D31-49A4-B501-FD00649330CE

**Type species.** †*Electrorubesopsis beuteli* Bai & Wang sp. nov.

**Etymology.** This name is a combination of *electr* ('amber' in Latin), *orubes* (from *Orubesa*) and *opsis* ('looks like' in Greek). Gender feminine.

**Diagnosis.** As for the subfamily.

†***Electrorubesopsis beuteli*** Bai & Wang sp. nov.
urn:lsid:zoobank.org:act:4D6EFABA-58B8-4CDE-969D-7813927BF7A0
(Figs 1, 2)

**Holotype.** Sex unknown, nearly complete specimen (NIGP157007); the piece of amber containing the specimen was cut and polished to a 13.5 × 17.1 × 6.1 mm cube (0.81 g in weight). The type specimen, currently housed in the Institute of Zoology of the Chinese Academy of Sciences (IZAS, Beijing, China), will eventually be deposited at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, PR China (the specimen is available for study by contacting MB or WB).

**Etymology.** This species is named in honour of Prof. Rolf G. Beutel (Institut für Spezielle Zoologie und Evolutionsbiologie, FSU Jena, Jena, 07743, Germany) in recognition of his extraordinary contributions to research on insects. Noun in the masculine genitive singular case.

**Description.** Body length 4.9 mm; width 2.7 mm. Elongate-oval and convex, with weak metallic reflection.

Clypeus short, with a rounded anterior margin. Mandible not exposed, anteriorly inwardly curved, with a sharp apex. Antennae 10-segmented, with a short 3-segmented simple and compact club. Compound eyes large and prominent, without anteriorly projecting genal processes.

Pronotum widest at the base, 1.82 times wider than long, without a median longitudinal groove or line. Lateral margin rounded, with long erect setae. Surface

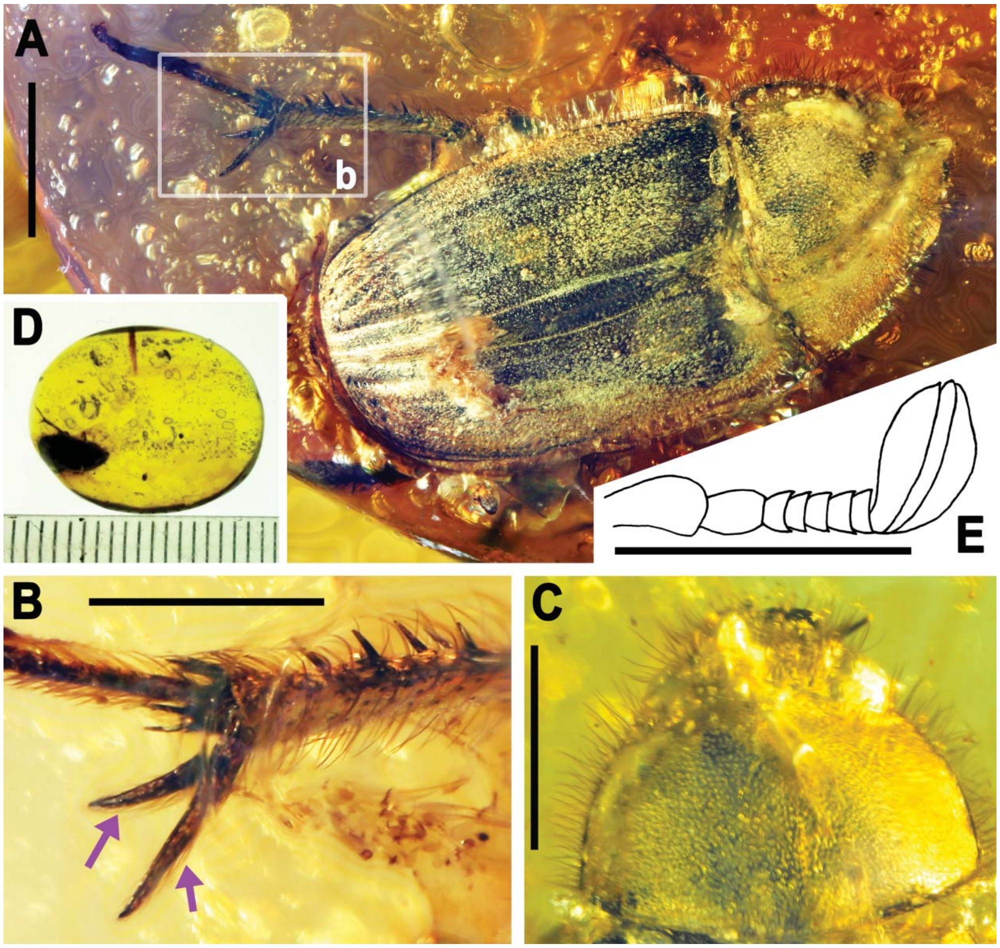


**Figure 1.** †*Electrorubesopsis beuteli* Bai & Wang gen. et sp. nov., holotype, NIGP157007. **A,** habitus photograph, in dorsal view (b, area enlarged in part B); **B,** distal portion of the left metatibia, arrows indicate the two spurs of the metatibia; **C,** head and pronotum in dorsal view; **D,** complete view of the amber cube with a ruler showing the scale; **E,** antennae. Scale bar = 1 mm.

densely covered with large punctures and oval scales. Scutellum triangular, round at the apex. Elytron elongate, 2.45 times longer than wide, with 10 rows of striae on each elytron. Stria 1 near the elytral suture clear, others clear only posteriorly. Interval 1 more convex and wider than the others. Surface covered with punctures and short, dense setae. Humeral umbone well developed.

Pygidium small and triangular, with thick setae. Legs completely covered with setae. Pro- and mesocoxae separated, mesocoxal cavities circular, metacoxal cavities closed. Protibia broad, with one strong apical spur and three teeth on the outer margin. Meso- and metatibia flat, with more than 4 pairs of spines on the outer margin and two spurs at the apex, spurs covered with the same setae as the legs (Fig. 2C, E), spurs adjacent and not separated by base of tarsomere 1, metatibial spurs similar in form, differing distinctly in length and proximal spurs longer. Tarsi long and slender, paired claws extremely curved and symmetrical.

Abdomen with six visible ventrites.

## Phylogeny

A maximum parsimony analysis of 82 morphological characters from 41 species (Supplemental S2) yielded four MPTs (tree length = 447 steps, CI = 0.25, RI = 0.60), with two nodes collapsing in a strict consensus tree (Fig. 3). The morphological characters were optimized with parsimony based on the consensus of the four MPTs (Fig. 4), showing only unambiguous changes.

A strict consensus tree (Fig. 3) of four MPTs was obtained from parsimony analysis of 40 modern species and one fossil species of Hydrophilidae, Histeridae and all 12 families of Scarabaeoidea. All families with more than one representative were monophyletic. †*Electrorubesopsis* was unambiguously placed as a sister group of *Orubesa*. The other dynamopodine genus (*Thinorycter*) was not placed in the same lineage as *Orubesa.* The analysis suggests paraphyly within the family Scarabaeidae, which has been already highlighted by Ahrens *et al.* (2014). However, it should be noted that our dataset

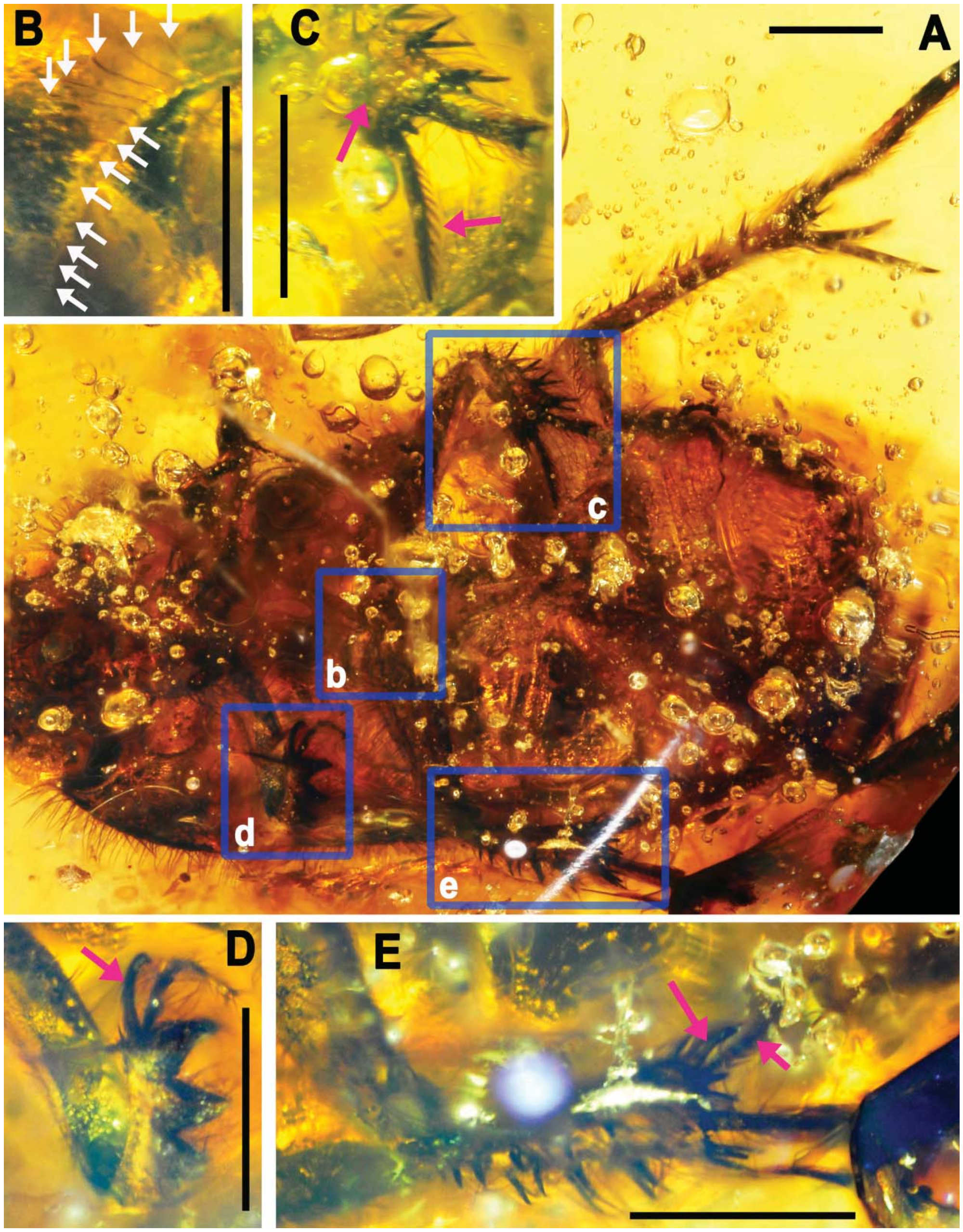


**Figure 2.** †*Electrorubesopsis beuteli* Bai & Wang gen. et sp. nov., holotype, NIGP157007. **A,** habitus photograph, in ventral view (b–e, areas enlarged in parts B–E); **B,** right mesocoxa, arrows indicate long setae near the margin of the mesocoxa; **C,** distal part of left mesotibia; **D,** right protibia; **E,** right mesotibia. Arrows indicate one or two spurs of the tibiae. Scale bar = 0.5 mm.

was not chosen to address either high-ranking Scarabaeoidea relationships or the phylogeny of the subfamilies within Scarabaeidea; the focus was specifically on the placement of †*Electrorubesopsis*.

## Synapomorphic support for selected clades of Scarabaeoidea

There is good support for the monophyly of the ingroup (extant and fossil Scarabaeoidea lineages), all lineages of scarabaeoid families (except Scarabaeidae), and most of the subfamilies (black star in Fig. 4). The monophyly of the ingroup (extant and fossil scarabaeoid lineages) is supported by nine character states, which are not homoplastic, including the following uncontroversial characters (Fig. 4): anterior or mesal edge of the eye shallowly emarginate or slightly divided by the canthus (char. 11: 1); antennal club lamellate (22: 1); lateral pronotal carinae with a raised margin or narrow bead (32: 1); anterior angles of the pronotum produced and broadly rounded or

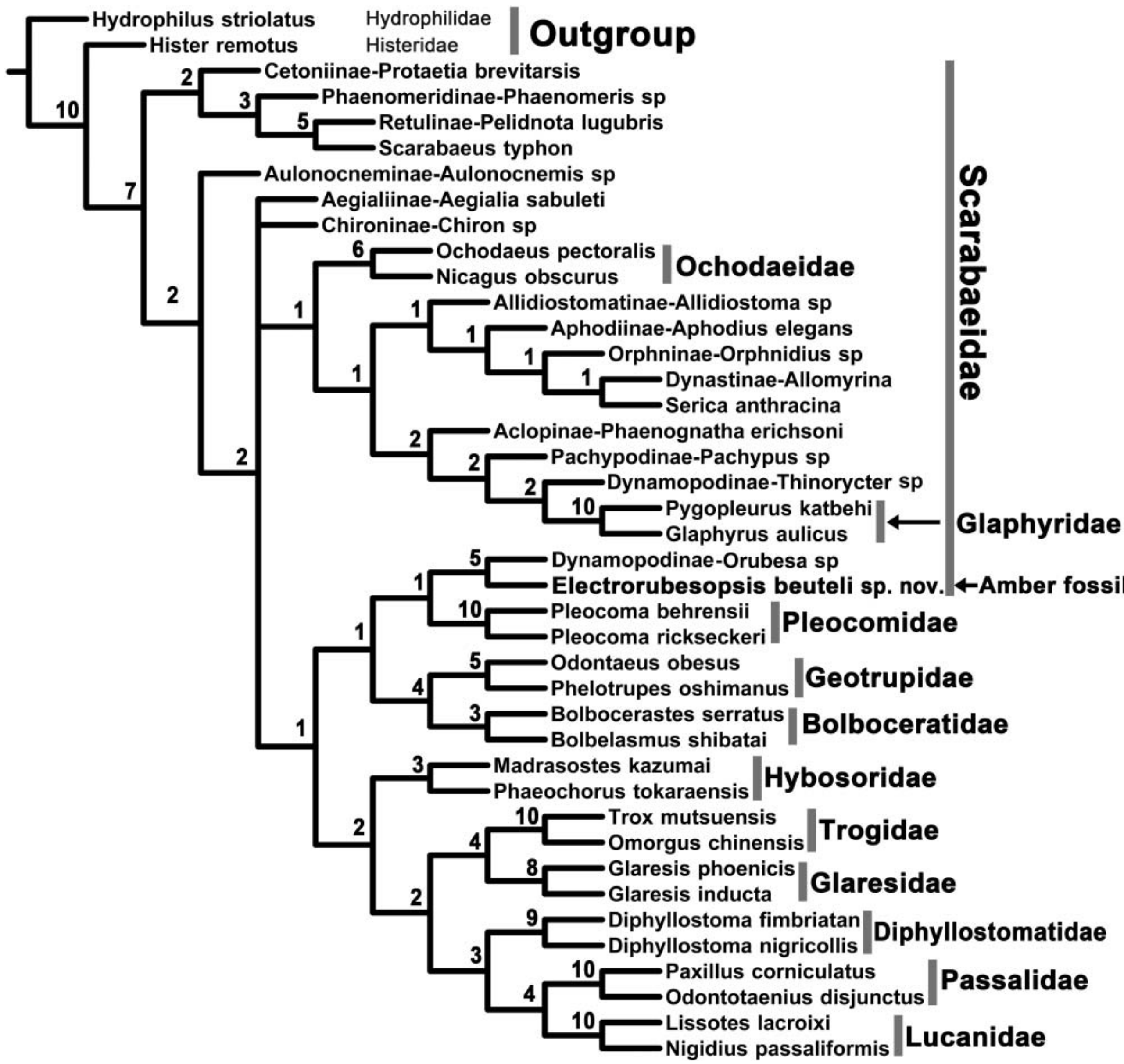


**Figure 3.** Strict consensus of the four most parsimonious trees obtained from the parsimony analysis of 40 modern species and one fossil species from Hydrophilidae, Histeridae and Scarabaeoidea. Bremer support values from 10 steps are given along the branches.

obtusely angulate (34: 1); ventral portion of the prothorax on each side with only notosternal sutures (43: 0); procoxal cavities externally closed (45: 1); scutellum not abruptly elevated (53: 0); mesotarsal empodium present and exposed (73: 0); outer edge of the protibia with one or more distinct lobes or teeth (74: 1).

The monophyly of the Dynamopodini lineage, including †*Electrorubesopsis* and *Orubesa*, is supported by six character states, one of which is not homoplastic: occipital region with a median longitudinal groove or line (endocarina) (8: 0); first antennomere (scape) less than 3 times as long as the second (pedicel) (18: 0); mandible enclosed in the mouth cavity or not visible in lateral view (27: 0); preapical surfaces of mesotibia with transverse or oblique ridges or combs (67: 1); metatibial spurs differing distinctly in length (79: 1); pygidium more or less horizontal (81: 0).

## Discussion

For reliable placement of a species within Scarabaeoidea, the taxon must show at least one synapomorphy that should ideally not be reduced in any terminal subordinated taxon in any period. As only imaginal characters are available for fossils, Krell (2000) has provided a list of

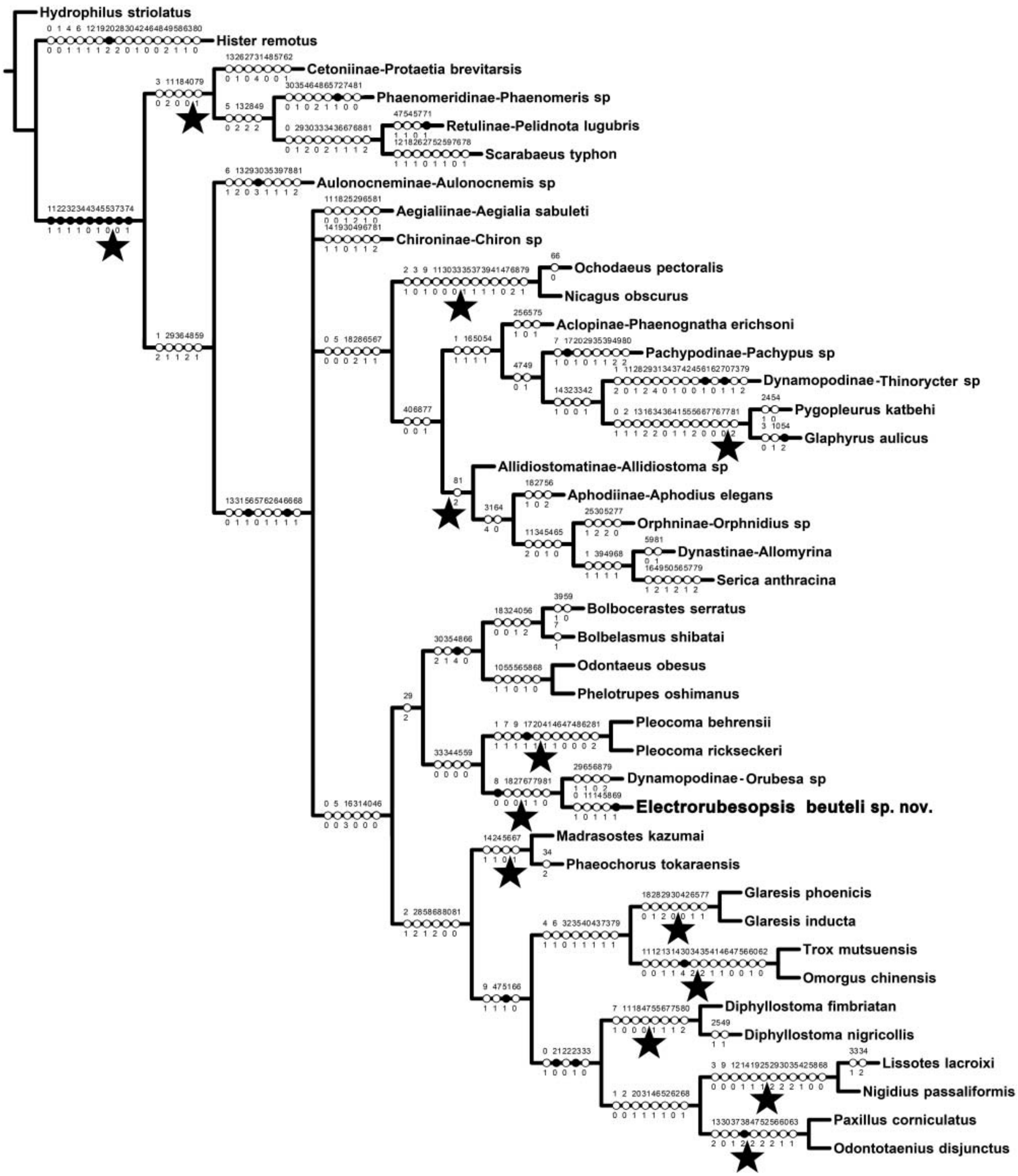


**Figure 4.** Strict consensus of the four most parsimonious trees, optimized with morphological characters, from the parsimony analysis of 40 modern species and one fossil species from the Hydrophilidae, Histeridae and Scarabaeoidea. Black circles indicate non-homoplasious changes, and white circles indicate changes in homoplasious characters. The numbers above the branches are character numbers, and those below are character states. Black stars indicate good support for the monophyly of the lineages.

Scarabaeoidea synapomorphies that are suitable for identifying scarab fossils. †*Electrorubesopsis beuteli* Bai & Wang gen. et sp. nov. can be classified within Scarabaeoidea based on its antennae with a lamellate club and protibiae with teeth on their outer margins. With the diagnosis provided above, †*Electrorubesopsis* Bai & Wang gen. nov. can be classified as belonging to †Electrorubesopsinae Bai & Wang subfam. nov. Together with the *Orubesa* species sampled in this study, †*Electrorubesopsis beuteli* is placed within the same lineage according to our phylogenetic analysis supported by six character states: (8: 0), (18: 0), (27: 0), (67: 1), (79: 1), (81: 0) (see Fig. 4).

On the basis of one genus and four species known at the time, Arrow (1911) erected Dynamopodinae based on a combination of several characters. The clypeus producing a sharp point in the middle and the genae producing a pair of long processes are specifically mentioned in the diagnosis of Dynamopodinae Arrow, 1911. However, the morphology of the clypeus and genae of *Adraria* and *Thinorycter* are different from those of *Orubesa* (Semenov & Medvedev 1928; Villiers 1956), and these characters must be reconsidered for Dynamopodinae. The head preservation of the type specimen of †*Electrorubesopsis beuteli* is of insufficient quality, and the detailed morphology of the head (e.g. the mouthparts) is difficult to observe, as is the presence of any clypeal projection. Nevertheless, we could still determine that the head of †*Electrorubesopsis beuteli* lacks anteriorly projecting genal processes. The right antenna of the holotype of †*Electrorubesopsis beuteli* is incomplete and has a damaged club. However, the 10-segmented left antenna is complete and the short 3-jointed lamellate and compact club can be clearly recognized (Fig. 1E).

The femora and tibiae of modern dynamopodines are massive; in particular, the ends of the metatibiae are broad in *Orubesa* (Semenov & Medvedev 1929). The legs of †*Electrorubesopsis*, *Adraria* and *Thinorycter* are not as massive as those of *Orubesa* (Semenov & Medvedev 1928; Villiers 1956). Several straight or outwardly facing strong spines are present on the outer apical angle of the meso- and metatibiae of †*Electrorubesopsis*. The spines on the tibiae of modern dynamopodines are much shorter and thinner and occasionally become setae. Both the meso- and metatibial spurs of †*Electrorubesopsis* possess setae and are similar in form but differ distinctly in length (Figs 1B, 2C, E). In modern dynamopodines, meso- and metatibial spurs are glabrous and are never distinctly different in length (see Supplemental Table S2 for details).

Due to the lack of material, *Adraria* was not included in the phylogenetic analysis reported in this study. Based on the available evidence, we are of the opinion that *Adraria* could be classified within Thinorycterini according to the following combination of characters: antennae 8-segmented; anterior or mesal edge of the eye not or only barely emarginated; mesotibial spurs glabrous; elytra apunctate, irregularly punctate, or with five or fewer distinct punctate rows or striae (Supplemental Table S2). The phylogenetic analysis conducted in this study (Figs 3, 4) suggests that *Thinorycter* does not belong to the same lineage as *Orubesa.* Therefore, the hypothesis of a close relationship between *Orubesa* (Dynamopodini) and *Thinorycter* (Thinorycterini) is challenged (Nikolayev 1993). As the phylogenetic position of Thinorycterini is beyond the focus of this study, further work addressing this issue is warranted.

*Orubesa* (Dynamopodini) was not included in Hybosoridae or Dynastinae in the phylogenetic analysis performed in this study (Figs 3, 4), which did not support the hypotheses of Fairmaire (1897) (Hybosoridae hypothesis) or Balthasar (1971) (Dynastinae hypothesis). The Dynamopodini lineage (including Dynamopodini and †Electrorubesopsinae) and Pleocomidae are sister groups. For some reason, dynamopodines have not been included in phylogenetic reconstructions of the Scarabaeoidea based on modern approaches (Hunt *et al.* 2007; Ahrens *et al.* 2014). As in previous studies (Hunt *et al.* 2007; Ahrens *et al.* 2014), all of the subfamilies of Scarabaeidae included in this study do not form a monophyletic group. The systematic status of the *Orubesa* lineage (e.g. Dynamopodini, Dynamopodinae or Dynamopodidae) could not be resolved based on available evidence. In this case, the subfamily status (Scarabaeidae: Dynamopodinae) is tentatively followed here.

The species of *Orubesa* from Asia and Africa are desert dwellers or inhabit sandy environments (Endrödi 1970). The morphological adaptations of broad legs and long hairs on the dorsal and ventral body can be found in beetles living in a similar environment (e.g. Tenebrionoidea or Glaresidae) (Bai *et al.* 2010, 2014). Many long hairs are found on the surface of †*Electrorubesopsis beuteli*, and long hairs are even present on the mesocoxae (white arrows in Fig. 2B). Although the legs of †*Electrorubesopsis beuteli* are not greatly expanded, many strong and densely distributed spines occur on the meso- and metatibiae (Figs 1, 2), which may play a similar role to broad legs. Considering the evidence together, it is possible that †*Electrorubesopsis beuteli* inhabited a similar sandy environment to that of modern *Orubesa*. Alternatively, forest is another possible interpretation for the living environment of †*Electrorubesopsis*, because amber is fossilized tree resin.

## Conclusions

†Electrorubesopsinae Bai & Wang subfam. nov. from Cretaceous Burmese amber is the possible sister group of Dynamopodinae. A phylogenetic analysis suggests that †*Electrorubesopsis* should be placed as a sister to

*Orubesa*. The hypothesis of a close relationship between *Orubesa* (Dynamopodini) and *Thinorycter* (Thinorycterini) is challenged. *Orubesa* (Dynamopodini) was not found to be close to Hybosoridae or Dynastinae in our phylogenetic analysis. Based on its external morphology, †*Electrorubesopsis* likely lived in sandy environments or forests.

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## Supplemental data

Supplemental material for this article can be accessed here: https://doi.org/10.1080/14772019.2018.1427638

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