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The first fossil rove beetle from the middle Eocene Kishenehn Formation (North America) provides evidence for ancient Eocene relicts within the hyperdiverse Staphylinini (Coleoptera: Staphylinidae: Staphylininae)

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A new rove beetle (Coleoptera: Staphylinidae) is described from the middle Eocene Kishenehn Formation in Montana, USA. †*Tympanophorus greenwalti* Chatzimanolis, Brunke & Schillhammer sp. nov. is the oldest known definitive member of the subtribe Anisolinina (Staphylininae: Staphylinini) and the entire Staphylinini propria clade, which contains the majority of the tribe's over 5500 described extant species. In order to provide robust justification for the systematic placement of the Kishenehn fossil, all genera of the *Tympanophorus* lineage are reviewed and redefined. A key to these genera is provided for the first time. *Paratympanophorus* Lecoq becomes a junior synonym of *Trigonopalpus* Cameron, with the following new combinations: *Trigonopalpus africanus* (Lecoq), *Tr. peyrierasi* (Lecoq), *Tr. pubescens* (Lecoq), *Tr. punctatus* (Lecoq) and *Tr. steineri* (Lecoq). *Tympanophorus schenklingi* Bernhauer is moved to *Trigonopalpus* (comb. nov.) and *Ty. clavicornis* (Lecoq) is moved to *Barygnathus* (comb. nov.), and thus, the genus *Tympanophorus* no longer occurs in the Afrotropical region. *Tympanophorus* is shown to be at least as old as the middle Eocene, and its disjunct New and Old World lineages are hypothesized to have been separated in the early Eocene.

<http://zoobank.org/urn:lsid:zoobank.org:pub:CA1993B8-1251-45C3-877E-C4604F78E781>

Keywords: Palaeogene; Lutetian; biogeography; Montana; Anisolinina; *Tympanophorus*

Introduction

The last decade has seen a renaissance in fossil rove beetle systematics, with dozens of new species of Staphylinidae coming to light (for papers summarizing most of these fossils see: Chatzimanolis & Engel 2011, 2013; Chatzimanolis *et al.* 2012; Solodovnikov *et al.* 2013; Peris *et al.* 2014). One of the major barriers to the detailed integration of palaeontological taxa with extant rove beetle lineages is that the majority of the supra-specific taxa are poorly defined and are in need of revision. Recently, there has been renewed interest in reconstructing phylogenetic relationships within the tribe Staphylinini of Staphylininae (Chatzimanolis *et al.* 2010; Brunke & Solodovnikov 2013; Brunke *et al.* 2016), a hyperdiverse group of more than 5500 relatively large and predatory beetle species. While a consensus topology is emerging for Staphylinini and its higher classification is partially revised (e.g. Chatzimanolis *et al.* 2010; Brunke *et al.* 2016), the fossil record of this group is in need of revision as the majority

of taxa were either described in large polyphyletic genera or incorrectly placed systematically at the genus, subtribe or even subfamily level (Brunke, pers. obs.). One exception is the diverse Early Cretaceous (Yixian Formation, China) assemblage of Staphylinini described and placed in a phylogenetic context by Solodovnikov *et al.* (2013). However, with the evidence currently available, none of these taxa could be confidently placed within extant lineages and they are probably best treated as early diverging stem groups.

Resolving the position and demonstrating monophyly of the Staphylinini subtribe Anisolinina (*sensu* Schillhammer 2004) has been particularly problematical, though a recent analysis of molecular data suggests that it may be a natural group (Brunke *et al.* 2016). However, morphological character evidence for this group as a whole remains elusive (Brunke & Solodovnikov 2013), making the direct assignment of fossils to Anisolinina difficult. At present, Anisolinina is a group of 14 poorly known genera (Schillhammer & Brunke, in prep.) and just over 200 species, which is unknown from the fossil record (A. Newton,

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unpublished catalogue). The exclusion of *Algon* Sharp and *Philothalpus* Kraatz from the subtribe is supported by morphological (Schillhammer 2004) and molecular evidence (Chatzimanolis 2014), though their sister groups remain unknown. The systematic position of *Rientis* Sharp is also unknown but is thought to be near *Algon* (Schillhammer 2006).

Based on morphological characters of the mesoventrite, and maxillary and labial palpi, Schillhammer (2004) defined two groups of Anisolinina: the *Tympanophorus* and *Anisolinus* lineages. While the genera of the latter are diagnosable, the rarely collected genera of the *Tympanophorus* lineage are poorly defined and have never been critically re-evaluated. Nearly all genera of Anisolinina are restricted to the Afrotropical and Oriental regions (i.e. the Old World subtropics and tropics). *Misantlius* and *Tympanophorus* are exceptional in that they exhibit a disjunct subtropical to tropical distribution between the Old and New World: Oriental-Neotropical, or Oriental + east Palearctic (Japan and Korea) – Nearctic + Neotropical, respectively. The two Afrotropical species of *Tympanophorus* have not been re-examined since their descriptions and may belong to other genera. Although currently disjunct, these distributions in Anisolinina and other lineages of Staphylinini were hypothesized by Brunke & Solodovnikov (2013) to be formerly widespread in the northern hemisphere during the Palaeogene/early Eocene, becoming relictual after the cooling and polarization of global climate in the late Eocene/early Oligocene. However, evidence for an ancient Eocene age of these genera, from either fossils or divergence estimates, is currently lacking.

Evidence for boreotropical relictualism may be discovered amongst the diverse fossil insect faunas of subtropical to tropical Eocene North America (e.g. Archibald *et al.* 2011). We here report and describe the first fossil staphylinid from the middle Eocene Kishenehn Formation (c. 46 Ma, Constenius *et al.* 1989) in Montana, United States, that possesses morphological characters particular to some members of the *Tympanophorus* lineage of Anisolinina (Fig. 1). As this would currently be the only described fossil of Anisolinina, an accurate and taxonomically precise placement is critical for estimating divergence times within and testing biogeographical hypotheses about the Staphylinini super-radiation. Therefore, the morphological limits of several genera in the *Tympanophorus* lineage are revised based on the study of a broad taxon sample, and serve as robust justification for the taxonomic assignment of this fossil.

Material and methods

Specimens were examined from the following institutions: **NHMUK**: Natural History Museum, London, UK; **CNC**: Canadian National Collection of Insects, Arachnids and Nematodes; **cRou**: Coll. G. de Rougemont, Oxford,

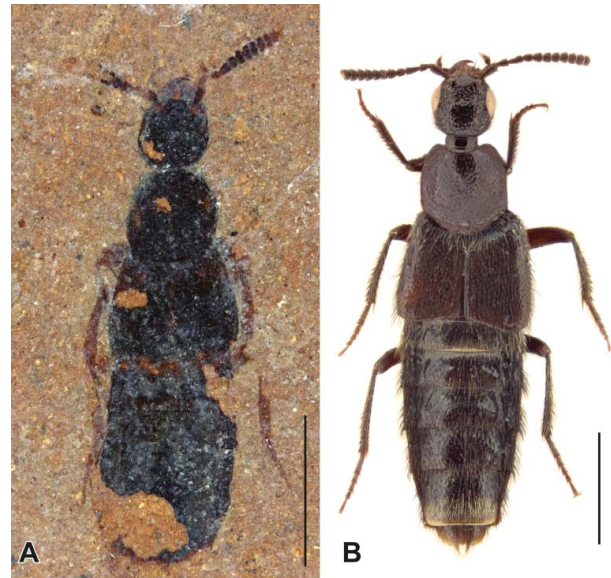


Figure 1. Dorsal habitus: **A**, *Tympanophorus greenwalti* Chatzimanolis, Brunke & Schillhammer sp. nov., USNM 595140; **B**, *Tympanophorus* sp. undescribed, from Mexico. Scale bars = 2 mm.

UK; **FMNH**: Field Museum of Natural History, Chicago, USA; **MHNG**: Natural History Museum, Geneva, Switzerland; **LNKD**: Landessammlung für Naturkunde, Karlsruhe, Germany; **NHMW**: Natural History Museum of Vienna, Vienna, Austria; **USNM**: National Museum of Natural History, Washington DC, USA.

Specimen examination and documentation

The fossil was examined submerged in 100% ethanol under an Olympus® SZX-12 stereomicroscope and measurements were made using an ocular micrometer. Photographs of the fossil were taken using a Cognisys® StackShot™ 3X macro rail and controller, a Canon® EOS40D and a Canon® MP-E 65 mm macro lens, and automountaged using Helicon Focus Pro™ 6. The age, taphonomy and biotic diversity of the middle Eocene Kishenehn Formation have been summarized by Constenius *et al.* (1989) and Greenwalt *et al.* (2015). Specimens of extant taxa were examined using a Nikon® SMZ 745T microscope. Photomontage was accomplished using a motorized Nikon® SMZ25 microscope and NIS Elements BR v. 4.5. Photographs were processed in Adobe Photoshop® CS6.

Systematic palaeontology

Family **Staphylinidae** Latreille, 1802
 Subfamily **Staphylininae** Latreille, 1802
 Tribe **Staphylinini** Latreille, 1802

Remarks. The Kishenehn fossil is clearly a staphylinid beetle based on its habitus, the presence of the exposed abdomen and the apically truncate and shortened elytra. All subfamilies of Staphylinidae can be excluded except Aleocharinae, Paederinae and Staphylininae based on the overall body shape. The exposed antennal insertions exclude the Paederinae. Although the habitus and extremely transverse antennomeres of the fossil resemble those of the diverse tribe Lomechusini of Aleocharinae (e.g. those genera near *Zyras*), the insertions of the antennae occur at the level of the anterior margin of the eyes (Fig. 2A, C) rather than distinctly posteriad of this level (Fig. 2B). In Aleocharinae, the mandibles in repose are nearly entirely covered by the labrum such that only the

lateral portions are normally visible from above (Fig. 2B). The anterior outline of the head capsule of the fossil is not abruptly narrowed and produced anteriorly as in the Aleocharinae (Fig. 2B). The fossil beetle is therefore most consistent morphologically with some Staphylininae.

The staphylinine tribes Diochini, Xantholinini, Maorothiini and Othiini can be excluded based on the antennal insertions of the fossil (Fig. 2A), which are each closer to the eye than to each other (Brunke *et al.* 2011). The fossil does not resemble the characteristically cylindrical members of the tribe Platyprosopini. The tribes Arrowinini and Thayeralini have a robust and parallel-sided body shape similar to Platyprosopini and lack accessory basal lines on the abdominal tergites.

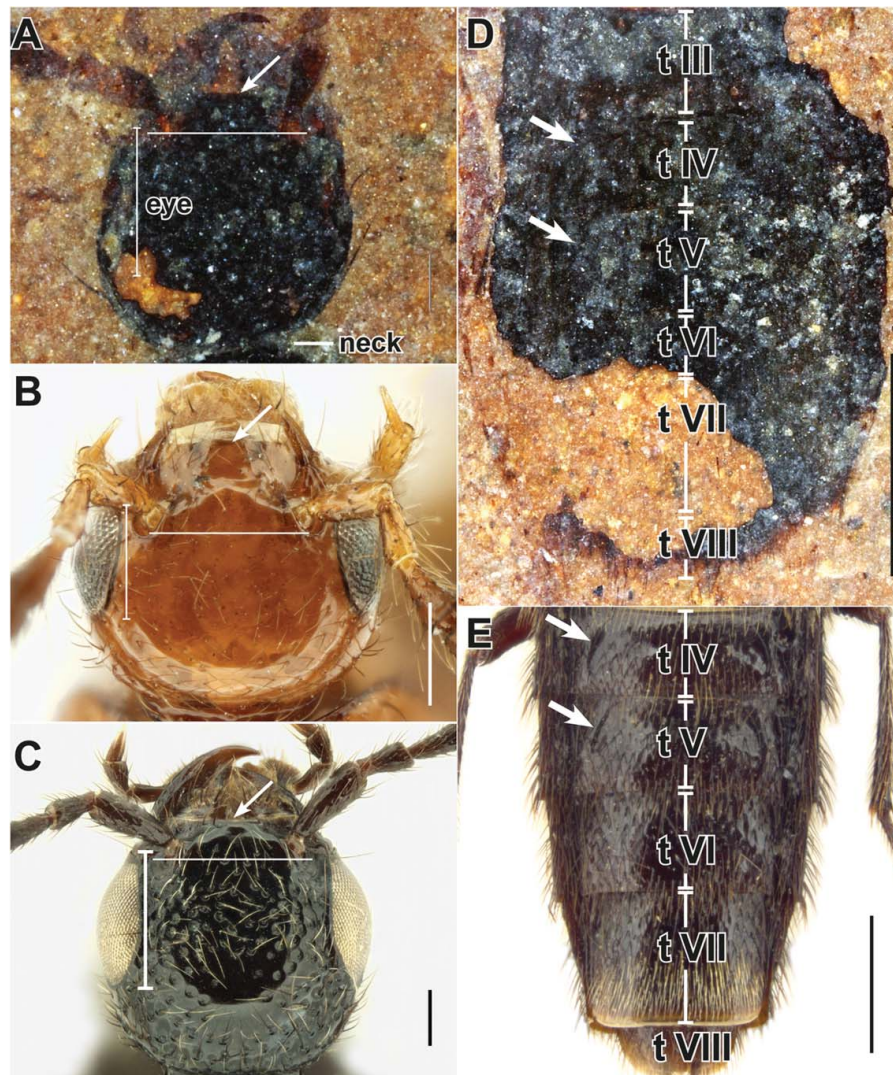


Figure 2. A–C, dorsal view of head capsules: A, *Tympanophorus greenwalti* Chatzimanolis, Brunke & Schillhammer sp. nov., USNM 595140; B, unidentified Lomechusini (Aleocharinae), CNC collection; C, *Tympanophorus* sp. undescribed, from Mexico, CNC collection. D, E, dorsal view of abdomen: D, *Tympanophorus greenwalti* sp. nov., USNM 595140; E, *Tympanophorus* sp. undescribed, from Mexico, CNC collection. Horizontal lines = level of antennal insertions; left facing arrows = anterior frontal margin; right facing arrows = accessory basal lines; t = abdominal tergite. Scale bars: A–C = 0.25 mm; D, E = 1.0 mm.

Thus, they can also be excluded, leaving the morphologically diverse Staphylinini.

Subtribe **Anisolinina** Hayashi, 1993

Remarks. Within the remaining tribe Staphylinini, the presence of accessory basal lines on the abdominal tergites (Fig. 2D, E) occurs in the subtribes Staphylinina (e.g. genera related to *Eucibdelus* and *Ocypus*) and Anisolinina (all genera), and the *incertae sedis* genera *Barypalpus*, *Rientis* and *Philothalpus*. The proportions of the body segments in the fossil are unusual for Staphylinini but among the above taxa, the broad abdomen relative to the narrow forebody is restricted to the *Tympanophorus* lineage of Anisolinina (*sensu* Schillhammer 2004), specifically to species of the poorly defined genera *Tympanophorus* and *Pammegus* (Fig. 3A, B). The position of these lines laterally rather than medially is also unique to the same lineage, though both states occur. In addition to the above differences, members of the *Anisolinus* lineage of Anisolinina possess long, rod-like palpi and a more

elongate body shape (Fig. 3F) (Schillhammer 2004) compared to the Kishenehn fossil. However, the genera of the *Tympanophorus* lineage are poorly defined and have never been critically evaluated. A revision of these generic concepts is provided below so that the Kishenehn fossil may be placed more confidently to a specific genus.

Generic revision of the *Tympanophorus* lineage. In this lineage, Schillhammer (2004) included the genera *Amelinus* Bernhauer, *Barygnathus* Bernhauer, *Bombylodes* Fauvel, *Diatrechus* Bernhauer, *Pammegus* Fauvel, *Tolmerinus* Bernhauer, *Turgiditarsus* Schillhammer and *Tympanophorus*. All members of this lineage differ from those of the *Anisolinus* lineage in the ridge of mesoven-trite, which extends close to its lateral margins, the broad and short mandibles and the basally placed setae on the medial margin of second labial palpomere (Schillhammer 2004). The genus *Turgiditarsus* should be excluded from Anisolinina entirely (Schillhammer & Brunke, in prep), lacks accessory basal lines and does not resemble the fossil specimen. We have examined the obscure

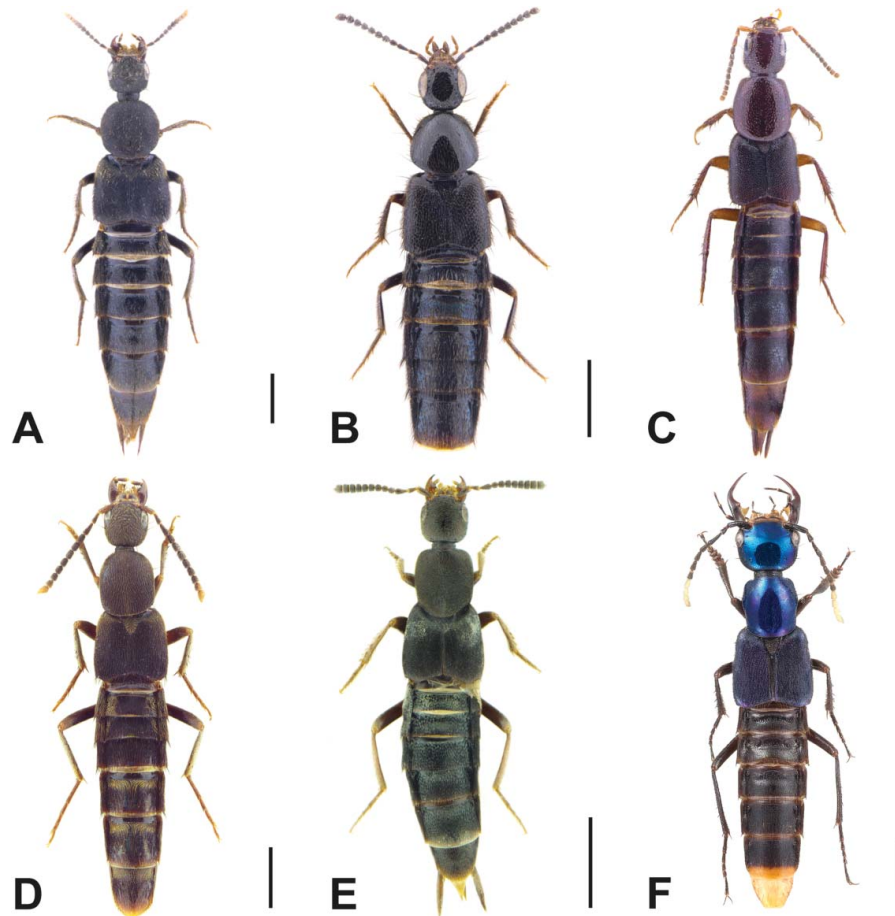


Figure 3. Dorsal habitus: **A**, *Tympanophorus* sp. undescrbed from China, NHMW collection; **B**, *Pammegus kachin* Schillhammer, NHMW collection; **C**, *Amelinus* cf. *collarti* Bernhauer NHMW collection; **D**, *Barygnathus* cf. *sasajii* (Hayashi), NHMW collection; **E**, *Barygnathus clavicornis* (Lecoq); **F**, *Hesperosoma brikatkaiseriae* Schillhamer, NHMW collection. Scale bars = 2 mm.

Staphylinini genera *Paratympanophorus* Lecoq and *Trigonopalpus* Cameron and conclude that the former is a junior synonym of the latter, and that they are almost morphologically indistinguishable from *Tympanophorus* (see below for details). The morphologically diverse and speciose genera *Diatrechus* Bernhauer and *Tolmerinus* Bernhauer differ from all other genera of the *Tympanophorus* lineage in the fusiform apical labial palpomeres. Based on the description of *Paradiatrechus* by Cameron (1944), this genus is similar to *Diatrechus* and *Tolmerinus*. These three genera need revision, as at present they cannot be separated by us, do not contain taxa with a distinctly narrow forebody relative to a broad abdomen, and are not redefined herein. The remaining genera are redefined based on a sample as representative as possible, especially given that some taxa are known from very few specimens.

Genus *Amelinus* Bernhauer, 1915

Type species. *Amelinus gestroi* Bernhauer, 1915.

Species examined. Ten specimens. ‘*Algon*’ *africanus* Bernhauer (photograph of holotype), two species near ‘*Algon*’ *africanus*, species near *Amelinus collarti* Bernhauer, species near *Amelinus densior* Bernhauer and five additional unidentified species.

Diagnosis. Species of *Amelinus* (Fig. 3C) can be recognized by the following combination of character states: labrum small and transverse; apical maxillary palpomere elongate, distinctly longer than previous segment and narrowed to pointed apex, not distinctly narrower than previous segment at widest point, not narrowed at base (Fig. 4A); apical labial palpomere distinctly dilated toward apex and flattened laterally, apical face narrow (similar to Fig. 4E); pronotum with median impunctate line (Fig. 3C); spines on hind tibia thickened (Fig. 3C); most species without secondary sexual structures on male sternite VII (see below). All species where male characters are known bear a short, compact aedeagus, with a short, broad paramere bearing many peg setae; this type of aedeagus also occurs in all species of *Barygnathus* and *Diatrechus* known to us.

Remarks. Currently, *Amelinus* consists of 19 species known from tropical mainland Africa and New Guinea. ‘*Algon*’ *africanus* Bernhauer and several similar undescribed species will key out as *Amelinus* here. As these species possess several character states not occurring in other *Amelinus* (reduced punctation on pronotal disc, a lateral group of setose punctures on pronotum and secondary sexual structures on male sternite VII), a new genus could be erected for them. However, this would require a more detailed morphological study that is outside of the scope of this paper. The single species from New Guinea, *A. punctus* Last, does not belong in this genus (or possibly

Anisolinina at all) based on the drawing of the aedeagus in Last (1989) but further taxonomic assignment is impossible at this point.

Genus *Barygnathus* Bernhauer, 1902

Type species. *Barygnathus opacus* Bernhauer, 1902.

Species examined. Six specimens. *Barygnathus clavicornis* (Lecoq) comb. nov., *Barygnathus opacus* Bernhauer, *Barygnathus sasajii* (Hayashi) and three undescribed species from Java, Borneo and Thailand.

Diagnosis. Species of *Barygnathus* (Fig. 3D, E) can be recognized by the following combination of character states: labrum expanded, each lobe less than 2 times wider than long and not widely separated medially (Fig. 4E); apical maxillary palpomere distinctly longer than previous segment, varying from weakly dilated fusiform (Fig. 4E) to slightly expanded at apex, about as broad as previous segment at widest point (Figs 4B); apical labial palpomere distinctly dilated toward the apex and flattened laterally, apical face narrow (Fig. 4E); spines on hind tibia thin (Fig. 3D, E). All known extant species bear a short, compact aedeagus, with a short, broad paramere bearing many peg setae; this type of aedeagus also occurs in all species of *Amelinus* and *Diatrechus* known to us.

Remarks. Prior to this study, the genus *Barygnathus* consisted of two highly similar species with a characteristic habitus due to elongate apical antennomeres, legs and pronotum: *B. opacus* Bernhauer described from Sri Lanka and later reported from China (Fujian, Sichuan) by Schilhammer (2004); and *B. sasajii* (Hayashi) from Borneo (Sabah, Malaysia). The morphological concept of *Barygnathus* is expanded here to include the Madagascan *B. clavicornis* (Lecoq) comb. nov. (see below), which possesses a less elongate pronotum, extremely transverse antennae and shorter legs. A new genus could be erected for this species, but without any pre-existing phylogenetic analyses for the *Tympanophorus* group we prefer to include it in *Barygnathus*. Based on the available material, *Barygnathus* occurs across southern China, Borneo, Java, Thailand, Sri Lanka and Madagascar. Due to the rarity of its species (fewer than a dozen specimens are known), *Barygnathus* may occur, albeit undetected, in continental Africa.

Barygnathus clavicornis (Lecoq, 2012) comb. nov.
(Fig. 3E)

2012 *Tympanophorus clavicornis* Lecoq: 197.

Material examined. Holotype (male), FMNH 2819766 with labels: MADAGASCAR: Toliara: southern Isoky-Vohimena Forest, 22°41'S 44°50'E, 730 m, tropical dry forest, 21.i.1996 [white printed label]; FMHD

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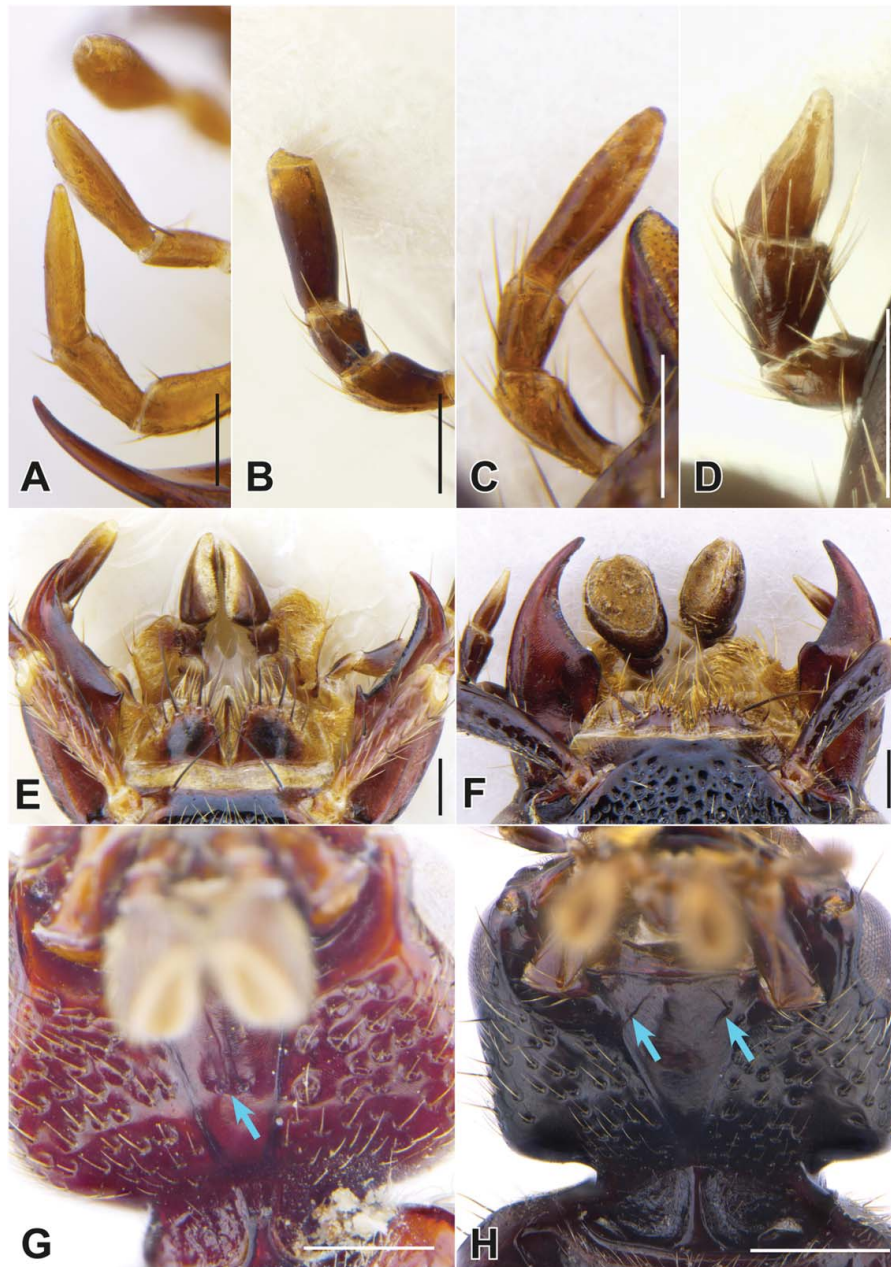


Figure 4. A–D, maxillary palpus: A, *Amelinus densior* Bernhauer, NHMW collection; B, *Barygnathus* sp., cRou collection; C, *Pamme-gus kachin* Schillhammer, NHMW collection; D, *Tympanophorus* sp. undescribed, from Panama, CNC collection. E, F, anterior head showing labial palpi: E, *Barygnathus sasajii* (Hayashi), NHMW collection; F, *Tympanophorus* sp., NHMW collection. G, H, ventral head and gular setae (arrows): G, *Trigonopalpus* sp., MHNG collection; H, *Tympanophorus concolor* Sharp, NHMW collection. Scale bars: = A–F = 0.2 mm; G, H = 0.5 mm.

310 #96-204, pitfall traps, Sylvain, B. L. Fisher, #1313 (1-50), FIELD MUS. Nat. HIST. [white printed label]; Staphylinini ?genus det A. Newton 2002 [white written label]; HOLOTYPE [red printed label]; *Tympanophorus clavicornis* n.sp. Lecoq det. 2011 [white printed label]; PHOTOGRAPHED Kelsey Keaton 2015 Emu Catalog [blue printed label]; HOLOTYPE teste M. K.

Thayer 2015 GDI Imaging Project [purple printed label]; FMNH INS 2819766 FIELD MUSEUM [printed barcode label].

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Remarks. Despite the strongly transverse antennomeres typically associated with most species of the genus *Tympanophorus*, *Tympanophorus clavicornis* Lecoq possesses

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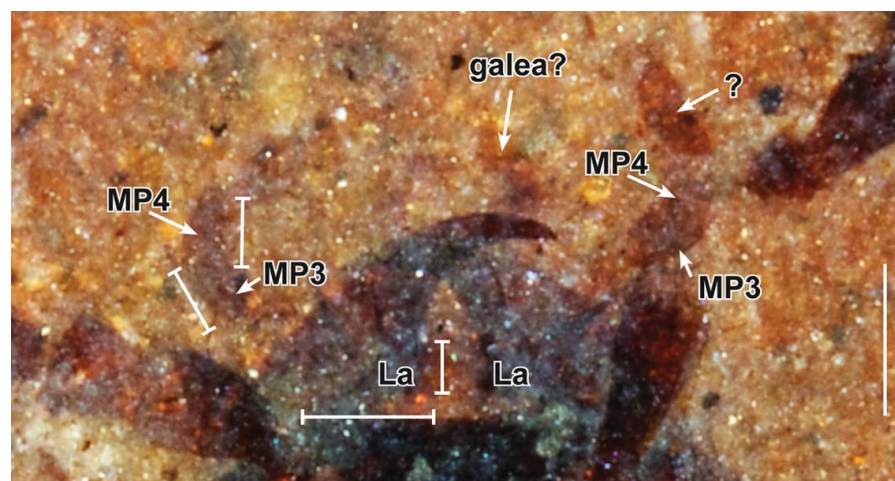


Figure 5. Anterior head of *Tympanophorus greenwalti* Chatzimanolis, Brunke & Schillhammer sp. nov. (USNM 595140), showing proportions of the labral lobes and maxillary palpomeres. Abbreviations: MP3, maxillary palpomere III; MP4, maxillary palpomere IV; La, lobe of labrum. Scale bar = 0.25 mm.

all generic characters of the genus *Barygnathus* (see diagnosis of both genera) and is therefore moved to this genus.

Genus *Bombylodes* Fauvel, 1904

1902 *Bombylius* Fauvel: 42 [preoccupied].

Type species. *Bombylodes mimeticus* (Fauvel, 1902).

Species examined. The redescription by Schillhammer (2002) of the single known specimen was used in this study.

Diagnosis. This genus can be recognized easily by the triangular head with temples almost straight and converging strongly posteriad of eyes, and the areas of dense golden and silvery pubescence on the pronotum, elytra and abdominal tergites. Male characters are unknown.

Remarks. The generic concept of *Bombylodes* (Schillhammer 2002) remains unchanged. This apomorphy-rich and monotypic genus known only from Sumatra might be phylogenetically nested within *Pammegus*, to which it is similar.

Genus *Pammegus* Fauvel, 1895

Type species. *Pammegus flavipes* (Fauvel, 1884).

Species examined. Twelve species. All described species were available for study.

Diagnosis. Species of *Pammegus* (Fig. 3B) can be recognized by the following combination of character states: labrum weakly transverse, lobes not broadly separated; apical maxillary palpomere elongate fusiform, about as twice as long as previous segment and about as broad at widest point (Fig. 4C); apical labial palpomere distinctly

dilated, not flattened laterally and with broad apical face (similar to Fig. 4F); spines on hind tibia thin (Fig. 3B); abdomen broad (Fig. 3B). The paramere of *Pammegus* is also uniquely shaped among Anisolinina: in parameral view with lateral expansion at midlength and long slender apical portion.

Remarks. *Pammegus*, with 12 described species, is restricted to the Oriental region as far as is known (Schillhammer 2002). Species of the genus are easily distinguished from *Tympanophorus* and *Trigonopalpus* Cameron by shape of the maxillary palpi alone.

Genus *Trigonopalpus* Cameron, 1951

2002 *Paratympanophorus* Lecoq: 117, syn. nov.

Type species. *Trigonopalpus pilosus* Cameron, 1951.

Species examined. Four species. *Trigonopalpus africanus* (Lecoq) comb. nov., *Tr. pilosus* Cameron, *Tr. schenklingi* (Bernhauer) comb. nov., and an undescribed species from Kenya.

Diagnosis. Species of *Trigonopalpus* (habitus variable and overlapping with that of *Tympanophorus*) can be recognized by the following combination of character states: lobes of labrum distinctly transverse to, in some species, reduced, lobes distinctly separated by U-shaped emargination (similar to Fig. 4F); apical maxillary palpomere distinctly constricted apically and entirely setose, at most slightly longer than and always narrower than previous segment, with acuminate apical portion (similar to Figs 2C, 4D); apical labial palpomere distinctly dilated, not flattened laterally and with broad apical face (similar to Fig. 4F); spines on hind tibia variable; ventral surface of head with pair of gular setae approximate and placed in

middle of gula (Fig. 4G); prosternum rounded in lateral view, not projected acutely ventrad.

Remarks. The genus *Trigonopalpus* had remained more or less in obscurity since its description by Cameron (1951) based on a single species from Uganda. An examination of the only known syntype in the NHMUK revealed that it was morphologically similar to *Tympanophorus* and the Afrotropical genus *Paratympanophorus* recently described by Lecoq (2002). The type species of *Trigonopalpus* was found to possess a setose apical maxillary palpomere and medially placed gular setae, both features of *Paratympanophorus* given by Lecoq (2002) to differentiate it from *Tympanophorus*. As we cannot find any morphological evidence to maintain separate generic concepts, we herein synonymize *Paratympanophorus* with *Trigonopalpus*. Of the diagnostic character states given by Lecoq (2002), only the approximate gular setae were found to be truly diagnostic. A pubescent apical maxillary palpomere was also observed in two undescribed species of *Tympanophorus* from New Guinea and Australia that do not bear medially placed gular setae. In the four species of *Trigonopalpus* available for study, the prosternum was observed to be rounded rather than projected ventrad as in all studied species of *Tympanophorus* and *Pammegus*. It is possible that *Trigonopalpus* is phylogenetically nested inside *Tympanophorus*, as all known unique character states of the latter genus are shared by the former genus. Currently, *Trigonopalpus* consists of seven species distributed in the Afrotropical region, mostly in Madagascar.

Trigonopalpus schenklingi (Bernhauer, 1912)
comb. nov.

1912 *Tympanophorus schenklingi* Bernhauer: 204.

Material examined. Syntype (female), FMNH specimen with labels: Südost-Kamerun [= Southeast Cameroon], Lolodorf, L. Couradt 95 [blue printed label]; Deutsch. Entom. National Musm. [white written label]; Schenklingi Bernh. Typus. [yellow written label]; Chicago NHMus, M. Bernhauer Collection [yellowed printed label].

Remarks. Lecoq (2002) mentioned that *Tympanophorus schenklingi* may belong in his new genus *Paratympanophorus* (here = *Trigonopalpus*) but did not study the type. Based on the study of a female syntype (FMNH) we confirm that this species should be moved to *Trigonopalpus* based on the approximate positions of the gular setae. *Trigonopalpus schenklingi* is easily distinguished from other two continental African species by the elongate pronotum alone.

Tympanophorus Nordmann, 1837

Type species. *Tympanophorus canaliculatus* Nordmann, 1837.

Species examined. Twenty species. *Tympanophorus* species near *canaliculatus* Nordmann, *Ty. concolor* Sharp, *Ty. jacobsoni* Bernhauer, *Ty. javanus* Cameron, *Ty. longiceps* Bernhauer, *Ty. puncticollis* (Erichson), *Ty. rugosus* (Waterhouse) (Sumatra), and at least 13 undescribed morphospecies.

Diagnosis. Species of *Tympanophorus* can be recognized by the following combination of character states: lobes of labrum distinctly transverse more than twice as long as wide, or strongly reduced, lobes distinctly separated by U-shaped emargination (Fig. 4F); apical maxillary palpomere distinctly constricted apically, rarely setose, with acuminate apical portion, at most slightly longer than and always narrower than previous segment (Figs 2C, 4D, F); apical labial palpomere distinctly dilated, not flattened laterally and with broad apical face (Fig. 4F); accessory basal lines placed laterally and well developed, reaching at least half the length of each tergite (Fig. 2E); ventral surface of head with pair of gular setae distant, placed in each anterior corner (Fig. 4H); prosternum projected acutely ventrad. Aedeagus usually asymmetrical.

Remarks. A large variation in size (6.7 mm in an undescribed Caribbean species, to nearly 16 mm in *Ty. canaliculatus*), head shape (entirely rounded and convergent to strongly angular hind angles) and body shapes (dilated toward apex to parallel-sided) was observed between species of *Tympanophorus* despite consistent shapes of the maxillary and labial palpi, the labrum and the strong development of the accessory basal lines. In many species, the antennae were removed from the margin of the frons such that they were positioned about halfway between the margin and the eye, a character state also occurring in *Pammegus*. We also observed a distinct tendency toward more transverse antennal segments and a more triangular apical maxillary segment in the smallest species. The 12 described species of *Tympanophorus* are distributed in the Oriental, Palearctic (Korea and Japan), Nearctic and Neotropical Regions. The African species originally described in this genus belong to *Barygnathus* and *Trigonopalpus*. We herein report *Tympanophorus* and the entire subtribe Anisolinina from the Caribbean subregion for the first time based on one male specimen of an undescribed species from Jamaica (CNC).

†***Tympanophorus greenwalti*** Chatzimanolis,
Brunke & Schillhammer sp. nov.
(Figs 1A, 2A, D, 5)

Holotype. Sex unknown; USNM 595140. Collected at the Spring site along the Middle Fork of the Flathead River near Pinnacle, Montana.

Diagnosis. Among most species of *Tympanophorus*, †*Ty. greenwalti* can be distinguished by the small size alone. From the few *Tympanophorus* smaller than 9 mm in body length (all undescribed), it can be easily distinguished by the extremely transverse antennomeres 5–9 (more than 3 times as wide as long).

Description. Total length at least 6.0 mm, probably about 6.5 mm (body strongly contracted); body colouration dark brown to black except antennae, mouthparts, legs and tip of segment VIII reddish brown. Body elongate, with head and pronotum both distinctly narrower than elytra and abdomen. Head ovoid, hind angles entirely rounded. Head 0.9 mm long and 0.9 wide (at middle). Eyes moderately large, positioned anteriorly and slightly longer than temples. Mandibles prominent, broad, curved, sharp distally; as long as half the length of head. Maxillary palpi short, labial palpi not preserved; last maxillary palpomere triangular and distinctly constricted apically, glabrous, slightly longer and narrower at base than previous segment, apical segment of right palpus apparently broken at about midlength, palpomeres 1 and 2 not clearly preserved. Labrum with lobes transverse, more than twice as long as wide and broadly separated. Antennal inserts situated about halfway between frontal margin and eye. Antennomeres 1–3 longer than wide, 4 subquadrate, 5–9 extremely transverse, antennomeres 10 and 11 not preserved. Antennomere 1 longer than antennomere 2; antennomere 3 slightly longer than 2; antennomere 4 wider than 3 but narrower than 5; antennomere 4 slight longer than 5; antennomeres 5–9 subequal in length and width. Head constricted, neck only partially visible but about one-third of posterior head width. Head and pronotum with dense small punctures. Pronotum widest medially, anterolateral corners curved ventrad; lateral sides slightly concave after middle, pronotum constricted posteriorly. Pronotum slightly longer than wide; 1.2 mm long and 1.1 wide (at widest part); on lateral sides with long seta near anterior 2/3. Elytra wider than long; 1.2 mm long and 1.7 mm wide (at widest part). Meso- and metatibia slightly curved; metatibia slender, not conspicuously spinose; mesofemur and mesotibia setose; mesotibia with coarse apical spines; metatarsi slender; apical metatarsomere long, longer than previous two tarsomeres. Abdomen broad, compact, setose; with prominent paratergites; abdominal tergites VI and V (III obscured) with laterally positioned and well-developed accessory basal lines that extend beyond half the length of tergite.

Etymology. The species is named in honour of Dr Dale Greenwalt who provided the specimen to us and has been instrumental in uncovering Kishenehn fossils.

Remarks. According to the new diagnoses and limits of the genera given below under '*Tympanophorus* lineage', the fossil specimen can be placed within *Tympanophorus* or *Trigonopalpus* based on the posteriorly shifted antennal

insertions, strongly developed and laterally positioned accessory basal lines, short, triangular and glabrous apical maxillary palpomere (best visible on left palpus) and strongly transverse labral lobes. The combination of the antennal insertions and accessory basal lines are unique to *Tympanophorus/Trigonopalpus* and are sufficient to make a confident identification, even though the diagnostic mouthpart characters are less than optimally preserved in the fossil. Although the position of the gular setae is the only definitive diagnostic difference between *Tympanophorus* and *Trigonopalpus*, the apical maxillary palpomere of the fossil specimen is certainly not entirely setose, excluding the latter. The fossil bears transverse subapical antennomeres, consistent with *Tympanophorus* but far more transverse than any other known species. It is possible either that these segments have become compressed during fossilization or that the unusual antennal morphology reflects an association with social insects as in other members of host-reliant Staphylinini (e.g. *Quedius (Velleius)* Leach, *Haematodes* Laporte, *Agacerus* Fauvel). In general, the biology of all *Tympanophorus* is unknown, though they have been collected in forests in decaying wood and leaf litter (Brunke, pers. obs.).

Key to genera of the *Tympanophorus* lineage

1. Apical labial palpomere slender, fusiform...*Tolmerinus/Diatrechus/Paradiatrechus* 560
 - Apical labial palpomere distinctly dilated apically and almost always securiform (Fig. 4E, F) 2
2. Apical labial palpomere laterally flattened with narrow apical face (Fig. 4E); aedeagus short and oval-shaped, paramere short and broad 3 565
 - Apical labial palpomere not laterally flattened, with broad apical face (Fig. 4F); aedeagus and paramere more elongate 4 570
3. Labrum expanded, lobes less than twice as wide as long (Fig. 4E); apical maxillary palpomere weakly to moderately expanded subapically or apically, apex never pointed (Fig. 3D, E); pronotum punctate across entire disc (Fig. 3D, E)..... *Barygnathus* 575
 - Labrum not expanded, lobes distinctly more than twice as wide as long (as in Figs 2C, 4F); apical maxillary palpomere evenly converging posterior to pointed apex (Fig. 4A); pronotum with median impunctate line (Fig. 3C)...*Amelinus* 580
4. Apical maxillary palpomere fusiform, not conspicuously constricted apically, at least twice as long as previous segment (Fig. 4C)..... 5
 - Apical maxillary palpomere conspicuously constricted apically (Figs. 2C, 4D, F), at most slightly longer than previous segment (as in Fig. 4D) 6

- 585 5. Head with temples nearly straight and strongly con-
verging to neck; body with areas of long golden
pubescence; male unknown *Bombylodes*
– Head with temples rounded (Fig. 3B); body
without conspicuous areas of golden
590 pubescence; paramere characteristic: symmetri-
cal, with long apex and distinct expansion at
midlength.....*Pammegus*
6. Ventral surface of head with gular setae
approximate (Fig. 4G); prosternum not projected
595 ventrad; occurring in continental Africa and
Madagascar.....*Trigonopalpus*
– Ventral surface of head with gular setae distant
(Fig. 4F); pronotum projected ventrad; occurring
600 in Oriental, far east Palearctic, Nearctic and Neo-
tropical Regions*Tympanophorus*

Discussion

605 †*Tympanophorus greenwalti* sp. nov. is the first rove bee-
tle described from the Kishenehn Formation, and the old-
est definitive representative (middle Eocene) of both the
subtribe Anisolinina and the broader Staphylinini Propria
clade. The slightly older *Leistotrophus patriarchicus*
Scudder from the early Eocene Green River Formation is
610 poorly described (Scudder 1876) and its higher taxonomic
placement should be reconsidered. Based on the rede-
scription and illustration included in Scudder (1890), this
taxon does not belong to the otherwise monotypic genus
Leistotrophus, nor does it belong to its subtribe Staphylini-
615 nina. Based on the wide neck and overall shape of the pro-
notum, this taxon could be either a true member of
Staphylinini propria as something similar to *Algon* (cur-
rently *incertae sedis*) or any one of the non-Staphylinini
propria subtribes Acylophorina, Cyrtocuediina, Indoque-
620 diina or Quediina. Aside from the Kishenehn fossil, the
next oldest definitive members of the Staphylinini Propria
clade are known from the Eocene–Oligocene boundary
Q2 (34 Ma) based on Florissant fossils (e.g. *Platydracus bre-
viantennatus* Cai *et al.* 2014). A slightly older, unde-
625 scribed fossil from the early Eocene (Green River
Formation, 51 Ma (Brunke, pers. obs.) is similar to †*Ty.*
greenwalti, but that specimen is far less preserved. Given
that †*Ty. greenwalti* could be placed in an extant genus,
the true ages of the Anisolinina and, especially, the large
630 Staphylinini propria clade are suspected to be far older.
Other species of Staphylinidae are present in the Kishenehn
Formation (Greenwalt *et al.* 2016; Chatzimanolis,
unpublished data) from multiple subfamilies (e.g. Oxyteli-
nae, Omaliinae, Paederinae), though their generic assign-
635 ment is uncertain. The reason for this is mostly due to the
state of the rove beetle taxonomy (limited or not up-to-
date genus-level revisions of extant taxa that render the

placement of a fossil uncertain) rather than the preserva-
tion of the fossils.

A revision of the generic concepts of the *Tympanophorus* lineage revealed that all African species of *Tympanophorus* belonged to other genera, and that the revised 640
distribution of this genus is disjunct in a similar way to
other Staphylinini that were hypothesized to be previously
widespread across the northern hemisphere during the
early Eocene (see Introduction). The discovery of
645 †*Tympanophorus greenwalti* provides evidence that *Tym-*
panophorus is at least as old as the middle Eocene, mak-
ing it possible that the divergence between disjunct New
and Old World lineages dates to the early Eocene. The
genus *Tympanophorus* occurs in the Recent fauna of
650 North America and is represented by two species: eastern
Tympanophorus puncticollis (Erichson) and south-west-
ern *Ty. concolor* Sharp, which extends into Central Amer-
ica. The small body size, strongly transverse
antennomeres, elongate pronotum and posteriorly inserted
655 antennae of †*Ty. greenwalti* suggest that it is related to
undescribed species of *Tympanophorus* from Jamaica,
Costa Rica and Panama (not illustrated here) rather than
to *Ty. puncticollis* LeConte or *Ty. concolor*, which are
much larger, and have a broad and circular pronotum, reg-
660 ular antennal insertions and much less transverse antenno-
meres. The Eocene was a period of globally warmer
temperatures and radically different faunal distributions
compared to the present (Archibald *et al.* 2011), and the
presence of a tropical group of *Tympanophorus* in the
665 middle Eocene of North America is congruent with the
discovery of small tarsier-like primates (Ni *et al.* 2010)
and tropical ant groups (LaPolla *et al.* 2015) from the
Kishenehn Formation.

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