New ant-like stone beetles in mid-Cretaceous amber from Myanmar (Coleoptera: Staphylinidae: Scydmaeninae)

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ABSTRACT

Three genera and species of Scydmaeninae (Staphylinidae) are described as new from mid-Cretaceous Burmese amber: Ektatotricha paradoxa Chatzimanolis, Engel & Newton gen. et sp. nov. and Electroatopos castaneus Chatzimanolis, Engel & Newton gen. et sp. nov. in the emended supertribe Hapsomelitae, and Kachinus antennatus Chatzimanolis, Engel & Newton gen. et sp. nov. in the supertribe Scydmaenitae. The supertribe Hapsomelitae is newly diagnosed and doubt cast on one of its putative apomorphies, with the development of a “patella” considered a misinterpretation by the original authors.

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1. Introduction

The staphylinid subfamily Scydmaeninae contains more than 4850 described species divided into three supertribes (one extinct) and nine tribes (O’Keefe, 2005; Jatoszynski, 2005; Grebennikov and Newton, 2009). The phylogenetic position of the subfamily has been problematic to say the least. Historically the subfamily has been treated as an independent family and was thought to be related to Leiodidae, Pselaphidae or Scaphidiidae (vide Newton and Franz, 1998 and O’Keefe, 2005 for reviews; the latter two families are now also considered staphylinid subfamilies). In two phylogenetic analyses of Staphyliniformia (Hansen, 1997; Caterino et al., 2005) the family was placed either in a polytomy with Silphidae and several families now included in Staphylinidae or within the family Staphylinidae, depending on the character weighting schemes. More recently, Hunt et al.’s (2007) molecular phylogenetic analysis using sparse exemplars of most coleopteran lineages recovered a peculiar placement of Scydmaeninae at the very root of the polyphagan clade. Conversely, Grebennikov and Newton (2009), in a much more extensive analysis of adults and larvae focused specifically on Staphylinidae, Scydmaenidae, and Silphidae, found strong support for placing the family within the staphylinine group of subfamilies of Staphylinidae, as a sister group to Steninae + Euaesthetinae. Based on these results, these authors proposed demoting the former family to a subfamily, Scydmaeninae, of Staphylinidae, and the three former scydmaenid subfamilies to the supertribes Hapsomelitae, Mastigitae, and Scydmaenitae of Scydmaeninae; this classification is adopted here.

A possible solution to these problems might be the discovery and identification of key fossil taxa that would shed new light into the interpretation of these relationships. Unfortunately, the fossil Scydmaeninae described until now appear to be more or less typical members of the family with the exception of Hapsomela Poinar and Brown (see below for details). The fossil record of Scydmaeninae was reviewed by O’Keefe et al. (1997) and Newton and Franz (1998) and most taxa have been described from Baltic amber, while others have been described from Mexican, Sicilian, and Dominican amber, all of mid-Tertiary age or much younger, and one species in Canadian amber of Late Cretaceous (Campanian) age. Since these two publications, three more taxa have been recorded: Aenictosoma doenitzi Schaufuss, which was originally described in Cerambycidae (Schaufuss, 1891) from mid-Eocene Baltic amber, but recently transferred to Scydmaeninae by Vitali (2006); Leptochromus palaeomexicanus O’Keefe (O’Keefe, 2002) from earliest Miocene Mexican amber; and Hapsomela burmitis (Poinar and Brown, 2004) from mid-Cretaceous Burmese amber.
Hapsomela burmitis was described in 2004 and placed in its own subfamily, Hapsomelinae (now supertribe Hapsomelitae), by Poinar and Brown owing to the putative presence of an extra foreleg podite (“patella”)1. Poinar and Poinar (2007: 75) suggested that owing to the presence of this “patella”, Hapsomela was a Cretaceous insect chimera. The simplistic figures provided by these authors do little to permit a critical evaluation of the leg structure in their specimen. However, the photomicrographs clearly showed a midventral hook of the tibia, similar to what is present among some groups of beetles (e.g., Curculionoidea, Staphylinoidea) (e.g., Vaurie, 1963; Campbell, 1994), which is also often associated with an internal costa or ridge strengthening the podite, and may even have associated external indentations but nonetheless represents a single podite. An apparently homologous hook is present in one of the new genera described herein, and clearly demonstrates that Poinar and Brown misinterpreted the hook of Hapsomela as an enlarged and modified spur and thereby assumed the remainder of the leg must represent a separate podite. As such, the “patella” is not a defining feature of this group. Although this character is erroneous, Poinar and Brown (2004) listed some other structures as diagnostic characters of their Hapsomelae (labial palpmere 3 “pointed” (= acicular); antennae not geniculate; antennomere 1 slightly longer than antennomere 2; only antennomere 11 forming a club), but these are all found in other genera of Scydmaenaeinae. One character of particular importance that was not used in the diagnosis of the subfamily is the greatly elongate and visible segments 5 and 6 (illustrated and discussed by Poinar and Brown, but not listed as diagnostic), a character state not found in any other Scydmaenaeinae, but also present in the two new hapsomelide genera described herein. Based on the characters employed by Poinar and Brown (2004) for establishing Hapsomelinae we could not support its recognition. However, we prefer to retain the supertribe based on the structure of the fifth and sixth visible abdominal sterna which is truly informative of a peculiar placement within the family. At present it is not possible to determine whether this is merely autopomorphic and the group belongs within a modern lineage, or whether this feature excludes Hapsomelae from the remainder of the subfamily. Further palaeontological and cladistic work will be needed in order to evaluate these two alternatives.

In the present paper we describe three enigmatic Scydmaenaeinae from Burmese amber. Two belong in the supertribe Hapsomelinae (as newly diagnosed), and the third is described as Scydmaenaeinae incertae sedis close to the tribes Eutheiini and Cephenniini. The abundance and diversity of scydmaenids in Burmese amber is unique, rarely do these beetles occur in other Cretaceous or younger ambers (D. Grimaldi, pers. observations).

2. Material and methods

Observations were made using Olympus SZX10 and SZX12 stereomicroscopes and measurements taken with an ocular micrometer. Most amber pieces were epoxy embedded prior to trimming and polishing following the procedure of Nascimbene and Silverstein (2000). Photomicrographs were taken using a Nikon DX1 Digital Camera attached to an Infinity K-2 long-distance microscopic lens. Total length of specimens was measured from the anterior margin of the head to the posterior margin of the elytra. All of the material derives from the mid-Cretaceous amber (latest Albian) deposits of northern Myanmar (e.g., Grimaldi et al., 2002; Cruickshank and Ko, 2003). Institutional abbreviations used herein are: AMNH, American Museum of Natural History, New York, New York, USA, and SEMC, Snow Entomological Collections, Division of Entomology, University of Kansas Natural History Museum, Lawrence, Kansas, USA.

3. Systematic paleontology

Family Staphylinidae Latreille

Subfamily Scydmaeninae Leach

Supertribe Hapsomelinae Poinar and Brown


Hapsomelae; Grebennikov and Newton, 2009: 288.

Revised diagnosis. Antenna not geniculate; first antennomere slightly longer than second. Labial palpmere 3 (P3) acicular. Visible abdominal sternum 5 and 6 greatly elongate.

Included genera. Hapsomela Poinar and Brown, Ektatotricha gen. nov., and Electrotropus gen. nov.

Comments. Given that the “patella” is clearly a misinterpretation we obviously have not used this upon which to base the supertribe. The other characters previously employed are not meaningful as they can be found in various scydmaenine genera. Instead, we have used the elongate visible fifth and sixth abdominal segments (morphological segments VII and VIII) as truly diagnostic for the group, present in all three of these genera but not found in other scydmaenids. As noted, however, this does not necessarily exclude the genera from being derived from within Scydmaenatae and the validity of this supertribe must await a more critical cladistic analysis of the subfamily. Accordingly, we retain Hapsomelae but with some hesitation.

Genus Ektatotricha Chatzimanolis, Engel & Newton gen. nov.

Type species. Ektatotricha paradoxa Chatzimanolis, Engel & Newton sp. nov.

Diagnosis. This genus belongs in the subfamily Hapsomelinae (as diagnosed above, vide supra) based on the extended visible abdominal sternum 5 and 6. Ektatotricha differs from Hapsomela in the structure of the maxillary palp (in Hapsomela maxillary P2 about half the length of P1, while in Ektatotricha maxillary P2 and P1 are subequal in length), the shape of the antennae (in Hapsomela all antennomeres are longer than wide; in Ektatotricha antennomeres 7 – 10 are subquadrate), and the structure of the elytra (in Hapsomela the elytra have shallow punctures, while in Ektatotricha the elytra have deep punctures).

Description. Body elongate, slightly convex, densely yellow pubescent. Head deflexed, slightly longer than wide; neck laterally and dorsally delimited; antennal insertion anterior to compound eyes, insertion points of antennae separated by distance subequal to first antennomere, antennae longer than head plus pronotum. Labrum broad; mandibles planar, acute; maxillary palpus 4-segmented, third palpmere (P3) strongly clavate, P4 short and truncate; labial palpmere 3-segmented, P3 subequal in length to P2, apex subacute. Pronotum in dorsal view convex anteriorly, almost flat in lateral view, laterally carinate, posterior part of pronotum as broad as elytra. Procoxae separated by small process, meso- and metacoxae not contiguous. Mesoscutellum small, triangular, darker than pronotum and elytra. Elytra longer than wide, truncate, with dense, deep, setose punctuation. Tarsal formula 5-5-5; protibia with pronotum and dorsomedial inflection at origin.

1 Poinar and Brown (2004) make an association of this putative structure with the similarly putative presence of patellae among some Paleozoic insects as interpreted by Kulakova-Pecck (e.g., modern review of such interpretations and models provided by Kulakova-Pecck, 2008). As has been noted elsewhere (e.g., Béthoux et al., 2008), Kulakova-Pecck’s interpretation of hexapod limb structures is exceedingly dubious and her models have collapsed under critical review. As such, making any tie between putative patellae in Hapsomela and those purported in Palaeodictyoptera or Archaeognatha (including Monura) is dubious at best.
of hook, pro- and mesofemora with deep U-shaped emargination ventromedially, metafemur with wide, shallow emargination. Abdomen with visible abdominal segments 5 and 6 extremely elongate.

_Etymology._ The genus-group name is a combination of _ektatos_ (Greek, meaning “extended” and referring to the fifth and sixth visible abdominal sterna) and _tricha_ (Greek, meaning “hair”). The name is feminine.

_Ektatotricha paradoxa_ Chatzimanolis, Engel & Newton sp. nov. Figs. 1–5

Staphylinoid sp.; _Grimaldi and Engel, 2005: 376, fig. 10.29._

_Holotype._ AMNH Bu-1464, labeled “Amber: Myanmar (Burma), Upper Cretaceous, Kachin: Tanai Village (on Ledo Rd. 105 km NW Myitkyna)” and “HOLOTYPE, _Ektatotricha paradoxa_ Chatzimanolis, Engel & Newton”. Deposited in the amber collection of the Division of Invertebrate Zoology, AMNH.

_Paratypes._ Twelve total paratypes: six in AMNH with locality data as above and catalogue numbers: Bu-073, Bu-259, Bu-374, Bu-1025, Bu-1046, and Bu-1579; four in SEMC (KU-NHM-ENT) and locality data “Amber: Myanmar (Burma), middle Cretaceous, Kachin: Tanai Village (on Ledo Rd. 105 km NW Myitkyna)” and voucher numbers: Bu-001, Bu-056, Bu-067, Bu-092; and two in J. Cornell private collection (JD2164 and unnumbered specimen) that eventually will be deposited in the Field Museum of Natural History, Chicago.

_Other material examined._ Two in AMNH with locality data as above and with catalogue numbers Bu-244 and Bu-1319.

_Diagnosis._ As for the genus (_vide supra_).

_Description._ Small, length 0.65–0.85 mm; brown to reddish brown throughout; with dense pubescence covering body, setae long.

_Fig. 1._ _Ektatotricha paradoxa_ Chatzimanolis, Engel & Newton gen. et sp. nov. (AMNH Bu-1496), Dorsal view.

_Fig. 2._ _Ektatotricha paradoxa_ Chatzimanolis, Engel & Newton gen. et sp. nov. (AMNH Bu-1496), Ventral view.

_Fig. 3._ _Ektatotricha paradoxa_ Chatzimanolis, Engel & Newton gen. et sp. nov. (AMNH Bu-1025), lateral view.
Head: Head subquadrate (excluding compound eyes), anterior margin of frons emarginate, ventral side not visible except gular sulci appearing united posteriorly. Compound eyes large, positioned medially. Antenna without defined club, setose, antennomeres 1–7 and 11 longer than wide, 8–10 subquadrate; antennomere 1 longer than 2 and antennomere 2 slightly longer than 3, antennomeres 3–6 subequal in size, antennomeres 8–10 gradually increasing in size, antennomere 11 acuminate, twice as long as antennomere 10. Labrum broad, twice as wide as long, with faint anterior emargination. Mandibles planar, strongly curved, acute, teeth not visible. Maxillary P1 and P2 subequal in size; P3 strongly clavate, longer and three times as wide as other palpomeres; P4 short and truncate, lacinia and galea setose. Labial palpus 3-segmented, P2 and P3 appearing subequal in length, apex of P3 subacute.

Thorax: Pronotum longer than wide, with dense, deep, setose punctures, distance between punctures as wide as puncture width. Pronotum strongly convex in dorsal view, almost flat in lateral view. Anterolateral sides of pronotum strongly deflexed ventrally; pronotum carinate laterally. Pronotum narrower anteriorly, as wide as elytra posteriorly, posterior margin faintly sinuate. Prosternum setose, with trapezoid basisternum; procoxae almost contiguous but furcasternum with small process. Mesepisternum and mesepimeron glabrous; mesocoxae not contiguous, separated by setose carina. Metasternum setose; metacoxae widely separated. Mesocutellum small, triangular, darker than remainder of body, as wide as length of three pronotal punctures. Elytra approximately twice as long as wide, without striae but with deep, dense, setose punctures, distance between puncture as wide as puncture width; humeri without foveae. Elytra wider anteriorly, slightly converging posteriorly. Hind wings fully developed, with series of setae forming fringe along margin; no distinct or nebulous veins present apically (exposed portions in AMNH Bu-374 and SEMC Bu-056), although numerous flexion lines are apparent for folding of wing under reduced elytra when in repose. Legs setose; trochanters small and rounded; protrochanteral setae present; femora weakly clavate; pro- and mesofemora with deep U-shaped emargination ventromedially; metafemora with wide, shallow emargination ventromedially; tarsomeres 1–4 gradually decreasing in length.

Abdomen: Pygidium (visible terga 5 and 6) exposed dorsally. Visible sternum 1 twice as long as visible sterna 2–4; visible sternum 5 3.5 times as long as visible sternum 4; visible sternum 6 2.5 times as long as visible sternum 4. Posterior margins of visible sterna 1–4 straight; posterior margins of visible sterna 5 and 6 arcuate; tergum 7 convex.

Etymology. The specific epithet derives from the Greek word *paradoxon* (meaning, “riddle”).

Genus *Electroatopos* Chatzimanolis, Engel & Newton gen. nov.

Type species. *Electroatopos castaneus* Chatzimanolis, Engel & Newton sp. nov.

Diagnosis. This genus combines some characteristics of the supertribes Scydmaenitae and Hapsomelitae, suggesting that the latter is an artificial group and should be subsumed in the former. In particular, the last two visible abdominal segments are extended as in *Hapsomela* and *Ektatotricha*, but the forelegs are not modified with a midventral hook and dorsal inflection (misinterpreted by Poinar and Brown as indicating a separate podite). Although the genus superficially resembles *Ektatotricha*, it can be distinguished from it by the shape of the antennae (clubbed in *Electroatopos*, not clubbed in *Ektatotricha*), the shape of the lateral margins of the pronotum posteriorly (concave in *Electroatopos*, convex in *Ektatotricha*), and the longer mesocutellum. The structure of visible sterna 5 and 6 is known elsewhere only in *Hapsomela* and *Ektatotricha* and, moreover, *Electroatopos* does not seem to fit in any current tribe in Scydmaenitae, seemingly combining characteristics of *Euthieini* and *Cepheniiini* (as in the genus *Kachinus*, discussed below), with the addition of the antennae appearing clubbed. *Electroatopos* can be distinguished from other unplaced scydmaenid fossils by the combination of the clubbed antennae and the extremely extended visible abdominal segments 5 and 6.

Description. Minute; body slender, covered with dense yellow setae and dense punctuation; head subquadrate with small depression anteromedially. Antenna with strong club formed by antennomeres 9–11; maxillary palpus 4-segmented, P3 clavate; labial palpus 3-segmented. Pronotum subquadrate, lateral margin concave, converging posteriorly; elytra long and slender, truncate; Tarsal formula 5–5–5; femora weakly clavate. Abdomen with pygidium exposed vertically, visible sterna 5 and 6 greatly enlarged.
Etymology. The genus-group name derives from the word Greek words electron (amber) and atapos (strange). The name is masculine.

Electroatopos castaneus Chatzimanolis, Engel & Newton sp. nov. Fig. 6

Holotype. AMNH Bu-1596, labeled “Amber: Myanmar (Burma), Cretaceous, Kachin: Tanai Village (on Ledo Rd. 105 km NW Myitkyina)” and “HOLOTYPE, Electroatopos castaneus Chatzimanolis, Engel & Newton”. Deposited in the amber collection of the Division of Invertebrate Zoology, AMNH.

Diagnosis. As for the genus (vide supra).

Description. [Only dorsal side visible]. Minute, total length 0.65 mm; body reddish-brown with dense yellow setae.

Head: Head subquadrate, with small depression anteromedially, not constricted from vertex to occiput, with deep dense punctation; compound eyes large, positioned medially. Antenna long and setose, with strong club formed by antennomeres 9–11, antennomeres 1–2 not clearly visible, 3–4 longer than wide, antennomeres 5–6 slightly transverse, antennomere 7 subquadrate, antennomere 8 slightly transverse, antennomeres 9–11 transverse; antennomeres 5–6 smaller in size (both length and width) than antennomeres 4 or 7; antennomere 7 twice as wide and three times as long as antennomere 6; antennomere 8 smaller than 7, approximately 0.75 times as wide and as long as antennomere 7; antennomere 9 approximately equal in width to 7; antennomeres 9–11 gradually expanding but not clearly visible. Mouthparts not visible except maxillary P1 and P4, both appearing with dense setae; P3 enlarged, clavate; P5 small, truncate.

Thorax: Pronotum subquadrate, densely punctured, with long yellow setae; anterolateral corners deflexed downwards; lateral margins appearing concave; pronotum in dorsal view convex anteriorly and with depression posteriorly; posterior margin of pronotum with medial shallow U-shape emargination. Mesoscutellum clearly visible, triangular, punctured, with pointed apex. Elytra long and slender, truncate, with almost contiguous setose punctation, in dorsal view convex anteriorly and converging posteriorly. Legs setose; femora weakly clavate.

Abdomen: Pygidium (visible sterna 5 and 6 exposed dorsally), visible segments 5 and 6 greatly elongated (similar to Ektatotricha), with long yellow setae.

Etymology. The specific epithet derives from the Latin word castaneus and refers to the color of the body.

Supertribe Scydmaenitae Leach
Tribe Incertae sedis

Genus Kachinus Chatzimanolis, Engel & Newton gen. nov.

Type species. Kachinus antennatus Chatzimanolis, Engel & Newton sp. nov.

Diagnosis. This genus does not belong in the supertribe Hapso- melitae because it lacks the elongated visible abdominal segments 5 and 6 (in addition, the protibia is not modified). It also does not belong in the supertribe Mastigitae because the first antennomere is not elongate, the antennae are not elbowed between antennomeres 1 and 2, and maxillary P4 is not large. It may be included in the supertribe Scydmaenitae but cannot be classified easily into any of the existing tribes. In many details it can be excluded from the Chevolatini because it lacks the raised medial carina on the pronotum; from the Leptoscydmini because the antennal insertion points are widely separated and not contiguous; from the Plau- mannio I ni and Cyrtoscydmini because maxillary P4 (MxP4) is not broadly triangular to narrow and acuminate; from the Scydmaenini because the apex of the elytra are not entire and the pygidium is exposed; and from the Cephenniini because the overall shape is not broad and the head is only slightly recessed. Kachinus does have most of the general characteristics of Eutheini (e.g., truncate elytra, slender, more or less flat body, general habitus), but the head apparently is not constricted between the vertex and the occiput (vide Jasoszyński and Hoshina, 2004). It can be diagnosed from the remaining unplaced scydmaenid fossils based on the unique antennal shape (see description below and Fig. 9), apparent absence of MxP4, and the truncate elytra.

Description. Minute, body slender, elongate and setose. Head subquadrate, apparently not constricted between vertex and occiput (deflexed position of head makes this difficult to confirm); compound eyes large and coarsely faceted. Antenna 11-segmented, antennal insertions not contiguous but separated by length sub-equal to first antennomere; antennomeres 9–11 forming weak club. Maxillary palpus 3-segmented, P3 strongly clavate, apex not acute, P4 apparently absent or indistinctly separated from apex of P3; labial palpus 3-segmented. Pronotum subquadrate, widest at anterior third, lateral margins converging posteriorly. Elytra long and slender, truncate, with rows of small, shallow punctures, anterolateral corners appearing flexed upwards; hind wings present. Tarsal formula 5–5–5; femora clavate.. Abdomen with exposed pygidium (visible sterna 5, part of visible segment 5).

Etymology. The genus-group name derives from the name Kachin, the state in northern Myanmar (Burma) from which the amber originates. The name is masculine.
**Kachinus antennatus** Chatzimanolis, Engel & Newton sp. nov.

Figs. 7–9

Scydmaeninae sp.; Grimaldi and Engel, 2005: 372, fig. 10.21.

**Holotype.** AMNH Bu-113, labeled “Amber: Myanmar (Burma), Cretaceous, Kachin: Tanai Village (on Ledo Rd. 105 km NW Myitkyina)” and “HOLOTYPE, Kachinus antennatus Chatzimanolis, Engel & Newton”. Deposited in the amber collection of the Division of Invertebrate Zoology, AMNH.

**Diagnosis.** As for the genus (*vide supra*).

**Description.** Minute, length 0.6 mm; body light brown with yellowish brown legs and antennae.

**Head.** Head subquadrate, head apparently not constricted from vertex to occiput, with shallow punctures. Compound eyes large, coarsely faceted, occupying most of side of head. Antenna long and setose; antennal insertion points relatively close to each other, separated by distance equal to length of first antennomere; antennomeres 1–3 longer than wide, 4–8 subquadrate, 9–10 transverse, 11 longer than wide; antennomeres 9–11 forming weak club; antennomere 1 slightly longer than 2, antennomere 3 approximately half length and width of antennomere 2, antennomeres 4–6 as long as 3 but twice as wide, antennomeres 7–10 gradually increasing in size, antennomere 11 as wide as antennomere 10 but four times as long. Mandibles planar, acute. Maxillary P2 slender,

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Fig. 7. *Kachinus antennatus* Chatzimanolis, Engel & Newton gen. et sp. nov (AMNH Bu-113). Dorsal view.

Fig. 8. *Kachinus antennatus* Chatzimanolis, Engel & Newton gen. et sp. nov (AMNH Bu-113). Ventral view.

Fig. 9. *Kachinus antennatus* Chatzimanolis, Engel & Newton gen. et sp. nov. Antennae, scale bar represents 0.07 mm. (AMNH Bu-113).
subequal in length to P3; P3 strongly clavate, with rounded apex, base narrowed (not quite ovoid), greatest width about 3x width of P2; labial palpus 3-segmented; apex of P3 (LP3) subacute.

Thorax: Pronotum subquadrate, appearing convex anteriorly and with depression at posterior margin; widest at anterior third, lateral margins converging posteriorly; pronotum with shallow punctation. Mesoscutellum small, triangular. Elytra long and slender, lateral margins slightly curved, truncate, with seven rows of small shallow setose punctures each; punctures spaced with distance of about 5–6 punctures from each other within row and with a distance of 3–4 punctures across; anterolateral angles slightly folded upward; elytra approximately three times as long as wide; humeri without foveae; elytral setae as long as distance between punctures in each row; hind wings developed. Legs setose; procoxae narrowly separated by slender prosternal process; mesocoxae moderately separated by strongly elevated acute keel-like process; posterior margin of metasternum carinate; metacoxae separated by less than half of transverse width of a metacoxa; trochanters small and rounded; femora clavate; tibiae slender, slightly curved; tarsis with tarsomeres 2–4 subequal in length, slightly shorter than 1 and half as long as 5; pretarsal claws simple.

Abdomen: Pygidium (visible segment 6) exposed; visible sternum 1.5 times as long as visible sterna 2–4; visible sternum 5 1.5 times as long as visible sternum 2; visible sternum 6 smaller, subequal to 2; apical margins of visible sterna 5 and 6 arcuate.

Etymology. The specific epithet derives from the Latin word antenna.

Remarks. Kachinus appears to intermingle features of the tribes Cephennini and Eutheini. In particular, it shares with Cephennini the traits that the elytra and pronotum are not clearly discontinuous and that the head is apparently not constricted from the vertex to the occiput (a key characteristic of Cephennini, the labium with suction discs, is not clearly visible). It shares with Eutheini the truncate elytra and the general shape of the body, especially that of the pronotum. Indeed, in the key to genera of Eutheiini by Jaoszyński and Hoshina (2004), Kachinus is most similar to the genus Paranesethia Franz (moved in that work from Cephenniini to Eutheiini), sharing with that genus both the absence of MxP2 and an acutely elevated mesosternal keel. But Kachinus differs from that genus in several characters including narrowly separated procoxae, less widely separated metacoxae, and a more flattened body form, as well as the absence of the neck constriction common to Eutheini. Jaoszyński and Hoshina (2004) also noted the tendency to reduction of MxP4 in other genera of Eutheini.

Kachinus sp. indet.

Material. AMNH Bu-026, labeled “Amber: Myanmar (Burma), Cretaceous, Kachin: Tanai Village (on Ledo Rd. 105 km NW Myitkyina)”. Deposited in the amber collection of the Division of Invertebrate Zoology, AMNH.

Comment. This specimen is remarkably similar to K. antennatus but the ventral view of the specimen as well as the antennae are not clearly visible, and a confident determination is not possible. It appears to represent a second species but is not sufficiently well preserved to permit a formal description.

4. Discussion

One of the new species described here (Ektatatricha paradoxa) has leg structures that are homologues with the hooks seen in Hapsomela. These hooks may be used in mating to allow a male to forcefully hold on to the female, or in male-male combat, or could possibly be used in prey capture as suggested by Poinar and Brown (2004). The latter suggestion is reinforced by the study of modern scydmaenines by Schmid (1988). Schmid found that except for Cephennini (which have labial suction discs to hold prey) both sexes of all of the diverse scydmaenines he studied relied on the prehensile feet to help capture and hold prey, and often had modifications of these legs such as patches of adhesive setae for this purpose; further reinforcement is the assertion of Poinar and Brown (2004), if correct, that the Hapsomela type is a female with protruding ovipositor. However, Jaoszyński and Hoshina (2004) reported a similar denticle at the middle of the male protibia only in Paranesethia paradoxa (Sawada) of the scydmaenite tribe Eutheini (missing in males of some other species of that genus).

The recent phylogenetic analysis of Grebennikov and Newton (2009), based on a large sample of adults and larvae of staphylinids and allied taxa including six genera of Scydmaeninae representing five tribes, found strong evidence for monophyly of Scydmaeninae and for placement of scydmaenines among the Staphylininae Group of staphylinid subfamilies. This revelation lead to their proposed demotion of the former Scydmaenidae to a subfamily within this group, as a sister group to the Steninae + Euaesthetinae. Their analysis supported the conclusion that the long elytra of Scydmaeninae were a synapomorphy for this subfamily within the otherwise short-elytra members of the Staphylininae Group, rather than a primitive condition of long elytra from which all other tribes are derived. They noted the minimal age of Scydmaeninae as Cretaceous based on the extinct genus Hapsomela from mid-Cretaceous Burmese amber (Poinar and Brown, 2004), placed in the extinct group Hapsomelitae and Palaeoleptochromus from late Cretaceous Canadian amber (O’Keefe et al., 1997), placed in Mastigita: Clidicini. Our discovery and description here of three additional genera of Scydmaeninae from mid-Cretaceous Burmese amber, including two further genera placed in Hapsomelitae and one in Scydmaenitae, confirms the minimal age of the group and extends the known Cretaceous diversity to include all three currently recognized superfamilies. Moreover, our extended and emended concept of the extinct group Hapsomelitae shows that common characteristics of this group include elytra that are shorter and more abruptly truncate, an abdomen that is more elongate and apparently flexible, than in any previously known extinct or recent scydmaenines. The discovery of such characteristics among the earliest known Scydmaeninae is exactly what one would expect if this group is derived from within a group of staphylinids characterized by short elytra and an elongate and flexible abdomen, thus reinforcing the conclusions of Grebennikov and Newton (2009) about the placement of Scydmaeninae and the derived rather than primitive nature of long elytra within this clade.

Within Scydmaeninae, the validity of the three recognized superfamilies and relationships between and within them remains unclear. Given the above discussion, the more abruptly truncate elytra and more elongate and flexible abdomen of Hapsomelitae are likely to be retained symplesiomorphies that do not establish the monophyly of this group, but the great elongation of visible abdominal segments 5–6 is a unique condition not only within Scydmaeninae but also within the Staphylininae Group of subfamilies (in which the abdominal segments are generally subequal in length) and thus is likely to be a synapomorphy supporting the monophyly of Hapsomelitae, with Electrurus possibly being basal therein owing to the absence of the tibial hook. It then follows that the more complete elytra (generally exposing at most one tergite) and compact abdomen of the other extinct and recent scydmaenines are synapomorphies uniting these taxa in the supertribes Scydmaenitae plus Mastigita. O’Keefe (2005), based on an unpublished cladistic analysis of all included tribes of both groups, found good evidence for monophyly of Mastigita (e.g., presence of geniculate antennae), and for monophyly of most tribes within Scydmaenitae, but suggested that the latter group was likely to be paraphyletic with respect to Mastigita (citing evidence that the
scydmaenite tribe Scydmaenini might be a sister group to Mastigitaee). He also found that Euthenei and Cephenniini were basal clades within Scydmaenitae = Mastigitaee, consistent with earlier suggestions of other authors (e.g., Brown and Crowson, 1980, based on larval characters). Our placement of the new genus Kacinbus, the oldest known member of the Scydmaenitae to date, in the vicinity of Euthenei and Cephenniini but not clearly a member of either tribe as defined by recent taxa, is consistent with such a basal position of these tribes. In contrast, in their most parsimonious tree based on morphological data, Grebennikov and Newton (2009) found weak support for a more basal position of their exemplars for Mastigitaee and Scydmaeniini and a more derived position of Euthenei + Cephenniini. Clearly a more rigorous phylogenetic analysis focused on phylogenetic relationships within Scydmaeninae is needed to resolve such discrepancies.

Acknowledgements

Partial support for this work was provided by NSF DEB-0542909 (to M.S. Engel), NSF DEB-0741475 (to S. Chatzimanolis and M.S. Engel), and NSF DEB-0542726 (to D.A. Grimaldi). This is a contribution of the Division of Entomology, University of Kansas Natural History Museum.

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