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A new species of minute Scydmaenini (Coleoptera: Staphylinidae: Scydmaeninae) in mid-Cretaceous amber from Myanmar

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ABSTRACT
Fossil evidence of the ant-like stone beetle tribe Scydmaenini is extremely rare. To date, only one genus and species, †Kuafu borealis Yin, Cai and Huang, has been reported from mid-Cretaceous Burmese amber, which was treated as a stem group based on the rounded anterior margins of the scapes. Here we describe the second fossil species, †Scydmaenus minor Yin and Cai, sp. nov., from Burmese amber. The new species possesses a majority of characters typical of the extant genus Scydmaenus, and can be readily characterized by the minute body size, a unique form of the pronotum, and probably plesiomorphic short metatrochanters. Due to the current inadequate infrageneric classification of Scydmaenus, we place the new species as a stem-group taxon incertae sedis within Scydmaenus.

Keywords:
Scydmaenus
fossil
new species
miniaturization
Burmese amber
1. Introduction

The subfamily Scydmaeninae, or ant-like stone beetles, is a diverse group belong to the polyphagan family Staphylinidae, represented by more than 5350 extant species with a worldwide distribution (Yin et al., 2018a). A relatively rich fossil fauna of Scydmaeninae (over 50 species) has been documented from the Early Cretaceous to Miocene deposits, of which the research history has been summarized in detail by Jałoszyński and Perkovsky (2016), Jałoszyński et al., 2017, and Yin et al. (2018a–c).

Containing over 700 living species grouped in six modern genera, Scydmaenini is the second largest tribe of Scydmaeninae (Jałoszyński, 2016; Newton, 2019). In contrast to this impressive extant diversity, the intriguing absence of fossil evidence of the tribe (Jałoszyński et al., 2016) has become a major problem hindering a further understanding of early scydmaenine evolution. It was until only recently has the first definite fossil Scydmaenini been described. †Kuafu borealis Yin, Cai and Huang was the first reported fossil species of Scydmaenini known from a single specimen in mid-Cretaceous amber (ca. 99 Ma) of northern Myanmar (Yin et al., 2018b). This species has rounded apical margins of the scapes that lack any trace of an emargination or a notch; and mainly based on this feature, was it placed as a stem group within the tribe. Indeed, species belong to Scydmaenini are rarely represented in our amber collection containing more than 20,000 specimens, of which less than ten individuals were recognized. In this paper, we provide the description of the second fossil species of Scydmaenini based on an exquisitely preserved adult from Burmese amber. Our discovery sheds further light on the early morphological disparity of a diverse modern scydmaenine tribe otherwise poorly documented by fossils.

2. Material and methods

Depository, horizon, and specimen handling

The type material is deposited in the Insect Collection of Shanghai Normal University, Shanghai, P. R. China (SNUC). The fossil specimen described here was obtained from an amber deposit in the Hukawng Valley of Kachin, northern Myanmar (26°21′33.41″N, 96°43′11.88″E; Cruickshank and Ko, 2003; Grimaldi and Ross, 2017). Maps showing the amber-yielding locality and the amber forest some 99 million years ago were provided in Kania et al. (2015) and Yin et al. (2018b). The age of Burmese amber, once regarded as Eocene (Chhibber, 1934), has been recently established as the lowermost Cenomanian (98.79 ± 0.62 Ma) based on U-Pb dating of zircons (Shi et al., 2012),
which agrees with a general age predicted by Grimaldi et al. (2002) based on key bioinclusions. However, other workers have argued slightly older ages, either within the late Albian (Cruickshank and Ko, 2003; Ross et al., 2010) or near the Albian-Cenomanian boundary (Rasnitsyn et al., 2016; Mao et al., 2018).

The ambers were cut using a handheld engraving tool and polished using sandpapers of different grits and rare earth polishing powder. Habitus pictures of the fossils were made either using a Canon EOS 5D Mark III digital camera, equipped with an Olympus Plan C 10× objective lens (Fig. 1A, 1B), and a wireless remote control Canon Speedlite 600EX II-RT flash as light source, or using a Zeiss Axio Imager 2 light microscope with an attached digital camera with fluorescent lighting (Fig. 1C). The morphology details of the sampled beetle were explored by using a Zeiss 710 Confocal Microscope with a 488 nm laser (Cai and Huang, 2014; Cai et al., 2017; Fig. 2A, 2D, 2E, 2G), or using a Canon G9 Camera mounted on an Olympus CX31 microscope (Fig. 2B). Montage photos were produced in Zerene Stacker ver. 1.04 or ZEN 2011 Microscope Software, and all images were optimized and grouped in Adobe Photoshop CS5 Extended.

Nomenclatural acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix “http://zoobank.org/”. The LSID for this publication is: urn:lsid:zoobank.org:pub:409A3FA4-D69A-4C3C-88D3-0C7BC31F75DB. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: LOCKSS, PubMed Central.

3. Systematic paleontology

Family Staphylinidae Latreille, 1802
Subfamily Scydmaeninae Leach, 1815
Tribe Scydmaenini Leach, 1815
Genus Scydmaenus Latreille, 1802
†*Scydmaenus minor* Yin and Cai, **sp. nov.**
urn:lsid:zoobank.org:act:72178C34-109F-47E4-9E71-4188EE30A490
Figs 1–2

**Type Material.** Holotype (SNUC-Paleo-0078), a possibly female adult in an approximately 8.3×4.9 mm clear, yellowish amber piece; deposited in SNUC.

**Diagnosis.** The new fossil species can be readily separated from all extant species of *Scydmaenus* by a combination of the following characters: 1) body small, approximately 0.8 mm long, 2) pronotum large in contrast to elytra, broadest near apical fifth, evenly narrowing from broadest point toward the base, 3) metatrochanters relatively short, such that the bases of mesofemora are close to coxal-trochanteral articulations.

**Description.** General body form (Fig. 1) elongate, length 0.82 mm; body relatively flattened, distinctly but not deeply constricted between head and pronotum and between pronotum and elytra; appendages elongate; vestiture covered by fine setae.

Head (Fig. 2A, 2E) in dorsal view sub-rectangular, with straight sides, broadest at cross section of temples, length of head from clypeal anterior margin to base 0.18 mm, maximum width 0.19 mm. Capsule divided by occipital constriction (Fig. 2F; occ) into large anterior and small posterior part (‘neck’ region), posterior part retracted into pronotum. ‘Neck’ region distinctly narrower than vertex, narrowest site of occipital constriction wider than half head width. Anterior part of head (Fig. 2F) strongly constricted and rounded. Vertex (Fig. 2A; vt) anteriorly confluent with strongly constructed frons (Fig. 2A; fr). Eyes (Fig. 2F; ce) located at anterolateral margins of vertex, small, each composing less than 20 facets. Antennal insertions located anterior to eyes, moderately separated. Clypeus with rounded anterior margin; anterior margin of labrum straight, mandibles each with broad subtriangular basal region and curved, markedly elongate apical tooth, and one slightly smaller, acute subapical tooth; head venter broadly and shallowly impressed at middle; lacking posterior tentorial pits. Maxilla of same structure of extant *Scydmaenus*; maxillary palpi (Fig. 2F; mpl1–4) short, palpomere I small, subtriangular, length 0.017 mm, palpomere II basally pedunculate and curved, broadest at apex, length 0.041 mm, palpomere III large, pedunculate at base for short distance, sub-oval, length 0.053 mm, palpomere IV short and transverse, dome-shaped, length approximately 0.004 mm.

Antennae (Fig. 1) slender and elongate, length approximately 0.32 mm; antennomeres
gradually broadened distally; scape (Fig. 2B; a1) strongly elongate, with distinct ventral and dorsal apical notches (pointed by red arrowheads), so antennomeres 2 (Fig. 2B; a2) and remaining segments are able to bent dorso-ventrally; flagellomeres relatively compactly assembled; antennal clubs well-formed by apical three antennomeres (Fig. 2C; a9–11).

Pronotum (Fig. 2A; pr) elongate oval, broadest at apical fifth; length along midline 0.24 mm, maximum width 0.21 mm; sides rounded, lacking anterior and posterior corners; lacking any carinae, pits or impressions at base. Prosternal process very short and carinate, weakly projecting ventrally and not separating procoxae; procoxal sockets broadly open. Hypomera (Fig. 2E; hy) confluent with lateral portions of prosternite (Fig. 2E). Mesoventricle short, much broader than long, mesoventral intercoxal process (Fig. 2G; msvp) broad, nearly parallel-sided, weakly elevated; mesocoxae conical. Metaventrite much longer than mesoventrite, elongate, anteriorly fused with mesoventrite, posterior margin broadly concave at middle and forming broad and short metaventral intercoxal process (Fig. 2G; mtvp).

Elytra (Figs 1B, 1C, 2D; el) elongate, roundly sided, slightly broader than pronotum, broadest at apical two-fifths, length of elytra along suture 0.43 mm, maximum width 0.25 mm, elytral index (length/width) 1.72; lacking basal foveae or impressions, lacking humeral cali. Hind wings fully developed.

Abdomen (Fig. 2G) about as long as metaventrite; first visible sternite (III) (Fig. 2G; s3) longer than IV–VI combined along midline, sternites VIII (Fig. 2G; s8) contracted under precedent segment; suture between sternites VII and VIII distinct. Pygidium completely covered by elytra.

Legs (Fig. 1) moderately slender and elongate; pro- and mesocoxae (Fig. 2G; msc) subconical (Fig. 2E); metacoxae (Fig. 2G; mtc) transverse and protruding posteriorly, adjacent to metanepisterna (Fig. 2G; mtn); trochanters semicircular and short; femora strongly clavate distally, broadest near middle; tibiae distally broadened; tarsi (Fig. 2H) relatively short, tarsomeres I broader than II to V, tarsomeres I to IV (Fig. 2H; ts1–4) short, sub-quadracte, tarsomeres V (Fig. 2H; ts5) elongate. Protibiae with tiny apical tubercle. Protarsomeres not broadened, lacking ventral pads of spatulate setae. Pretarsal claws (Fig. 2H; tc) elongate and symmetric, acute apically.

Comments. The single specimen is possibly a female due to the small size of the eyes, and unbroadened protarsi. Hind wings are fully developed in the holotype.

Locality and horizon. Hukawng Valley, Kachin State, northern Myanmar; upper Albian to lower Cenomanian, mid-Cretaceous.
Etymology. The specific epithet refers to the small body size of the new species.

4. Discussion

The new species clearly belongs to the tribe Scydmaenini by possessing the following defining characters of the tribe (as discussed in Jałoszyński, 2012): 1) short, dome-like maxillary palpomeres IV have apical surface covered with fine setae (Fig. 2F); 2) deeply notched anterior margins of the scapes, which are distinctly elongate and much longer than the pedicels (Fig. 2B); 3) well-developed antennal clubs formed by apical three antennomeres (i.e., antennomeres IX–XI) (Fig. 2C); 4) pronotal hypomera fused with anterolateral parts of the prosternum (Fig. 2E); and 5) widely separated metacoxae which are laterally adjacent to the ventral margin of metanepisternum (Fig. 2G).

Among the six currently recognized genera of Scydmaenini (e.g., Adrastia Broun, Ceramphis Casey, Eudesis Reitter, Liliputella, Jałoszyński, Pseudoeudesis Binaghi, and Scydmaenus Latreille, 1802) (Jałoszyński, 2016a–b), the new fossil taxon seems to mostly fit the concept of the largest genus Scydmaenus, which contains over 700 living species worldwide (Newton, 2019). Aside from their shared small body size, †S. minor sp. nov. can be readily separated from all species of Eudesis, Pseudoeudesis, and Liliputella by a unique combination of characters: 1) absence of elytral calli; 2) fully developed hind wings; 3) absence of foveae on occipital constriction and elytral bases; and 4) lack of lateral carinae on metaventrite (Jałoszyński, 2016b; Fancello and Leo, 2018; Leo and Fancello, 2018). Of the remaining genera that lack humeral calli, †S. minor sp. nov. can be readily distinguished from the monotypic Ceramphis from the Neotropical region by the extremely small body size, and markedly different shape of the pronotum, which in Ceramphis is elongate and broadest near the base (O’Keefe, 1997).

According to Jałoszyński (2016b), the New Zealand endemic genus Adrastia is morphologically similar to certain subgenera of Scydmaenus, whereas other subgenera of Scydmaenus may retain full generic rank in the future due to their distinct morphological discrepancy. In the present, †S. minor sp. nov. cannot be ruled out from Scydmaenus by many shared morphological similarities. The sub-parallelled sides of the head, the anteriorly broadened pronotum, and the short metatrochanters of †S. minor sp. nov. appear to be unusual for the general Scydmaenus morphology. However, considering the age of †S. minor sp. nov. which is dated back to some 99 million years ago, these can be reasonably considered as representing plesiomorphic states of corresponding features. Moreover, it is notable that the shape of the pronotum of †S. minor sp. nov. is not uncommon in Mastigitae, a group postulated to be sister to Scydmaenini (O’Keefe,
2005). This character indicates that the ancestral form of the pronotum in some early lineages of Scydmaenini may be indeed more ‘mastigite’-like than their extant relatives.

The new species described here exhibits a remarkable small body size (0.82 mm long), which is comparable to members of the extant genera Pseudoeudesis, Eudesis, and Liliputella. Unlike its extant companions that are flightless and eyeless, †S. minor sp. nov. clearly possesses well-developed eyes, complete hindwings, as well as considerably long mandibles. These features collectively indicate a probable free-living and predaceous lifestyle of the new species in leaf litter layer or other cryptic habitat of forest floor. Accordingly, the origin of body miniaturization of modern Scydmaenini can be traced back to mid-Cretaceous, by the latest.

The discovery of †S. minor sp. nov. in Myanmar amber further broadens our knowledge about the early morphological evolution of Scydmaenini. Nevertheless, due to the unsatisfactory infrageneric classification of Scydmaenus that includes 30 illy-defined subgenera, we refrain from erecting a new taxon above a species level, and therefore tentatively regard the new fossil species as a basal form incertae sedis within the genus Scydmaenus.

5. Conclusion

The ant-like stone beetle tribe Scydmaenini is a diverse group of more than 700 living species. Fossil evidence of this tribe, however, is extremely rare, and little has been known regarding their origin, early divergence, and paleoecology. In this paper, we describe the second extinct species of Scydmaenini, †Scydmaenus minor sp. nov., in mid-Cretaceous amber from northern Myanmar. We place it as a stem-group taxon within the extant genus Scydmaenus based on the plesiomorphic short metatrochanters, and unusual forms of the head and the pronotum. Our find throws new light on the early morphological evolution of Scydmaenini, which may be of particular interest for future phylogenetic analyses aiming to solve the relationship between Scydmaenini and Mastigitaec.

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Fig. 1. Habitus of †Scydmaenus minor sp. nov. A. Ventral view. B–C. Dorsal view. Scale bar: 0.3 mm.
Fig. 2. Morphological details of *Scydmaenus minor* sp. nov. A. Head dorsum and pronotum. B. Antennomeres I–II. C. Antennal clubs. D. Elytra. E. Head venter and prosternum. F. Head venter, showing mouthparts. G. Pterothorax, sternites, and hind leg. H. Protarsus. Scale bar: 0.2 mm in A, C–F; 0.05 mm in B; 0.02 mm in H. Abbreviations: a1–2, 9–11 = antennomeres I–II, IX–XI; ce = compound eye; el = elytra; fr = frons; hy = hypomeron; mp1–4 = maxillary palpomeres I–IV; msc = mesocoxa; msvp = mesoventral intercoxal process; mtc = metacoxa; mtn = metanepisternum; mtvp = metaventral intercoxal process; mtt = metatrochanter; pr = pronotum; occ = ocular constriction; s3, 8 = sternite III, VIII; tc = tarsal claw; ts1–5 = tarsomeres I–V; vt = vertex.