

Short communication

Last major gap in scydmaenine evolution filled (Coleoptera: Staphylinidae)

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ABSTRACT

The tribe Scydmaenini represents one of the most successful modern groups of the ant-like stone beetles (Scydmaeninae), displaying a high degree of species diversity (>750 species) and morphological disparity. Surprisingly, direct fossil evidence crucial for elucidating the origin and early evolution of Scydmaenini is lacking. This gap of knowledge is of particular interest as the Cretaceous origin of other major scydmaenine lineages, e.g., Mastigini, Eutheini, Cephenniini, and Glandulariini, were recently documented. Here, we report a new genus and species, *Kuafu borealis* gen. et sp. nov., from Cretaceous Burmese amber, pushing back the oldest definitive record of stem-group Scydmaenini to approximately 99 Ma. An affinity of the new taxon with recent Scydmaenini is strongly supported by the beetle's short, dome-like terminal (fourth) maxillary palpomeres, as well as an exposed metanepimera which are typical character states of the tribe. However, *Kuafu* possesses a plesiomorphic un-notched anterior margin of the scape, a character state unknown among living Scydmaenini, and suggesting a basal position of the fossil taxon. Our find provides firm evidence that stem-group Scydmaenini, like other major scydmaenine lineages, originated no later than the mid-Cretaceous, removing the possibility that Scydmaenini may had a young, Quaternary origin.

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1. Introduction

With more than 5200 extant species and a cosmopolitan distribution (Newton and Franz, 1998; A. F. Newton, pers. comm.), the ant-like stone beetles, or Scydmaeninae, represent a successful radiation of the rove beetle family Staphylinidae (Fig. 1C). A recent phylogenetic analysis based on both adult and larval characters suggested that Scydmaeninae is sister to Steninae + Euaesthetinae, in a monophyletic 'Staphylinine Group' (Grebennikov and Newton, 2009). Four supertribes are currently recognized within Scydmaeninae: Hapsomelinae, Cephenniinae, Mastigitae, and Scydmaenitae (Poinar and Brown, 2004; Grebennikov and Newton, 2009; Jajoszyński, 2014). However, due to the absence of a large-scale phylogeny for Scydmaeninae, it remains difficult to discern the higher-level relationships among these supertribes. This stems, in

part, from limited knowledge of the scydmaenine stem lineages. All fossil records of Scydmaeninae are currently known exclusively from amber. In contrast to the extant diversity, only 47 extinct species have been reported, from Early Cretaceous to Miocene depositories (summarized in Jajoszyński and Perkovsky, 2016, and subsequent additions by Jajoszyński et al., 2017a, 2017b; Yin et al., 2017). A major part of these fossil taxa, particularly those from Eocene Baltic amber published between the mid-19th to early 20th century, were usually accompanied by insufficient descriptions, lack of illustrations, and most unfortunately, loss or destruction of type material during World War II (Jajoszyński and Perkovsky, 2016), thus leading to one of the major challenges in fossil scydmaenine research.

Clear diagnoses and sufficient descriptions are provided only for recently described Mesozoic taxa, starting from O'Keefe's description of *Palaeoleptochromus* O'Keefe from late Campanian Canadian amber, a member belonging to Clidicini (O'Keefe et al., 1997). Subsequent works have yielded significant insights into the early evolution of Scydmaeninae and its major groups, including the

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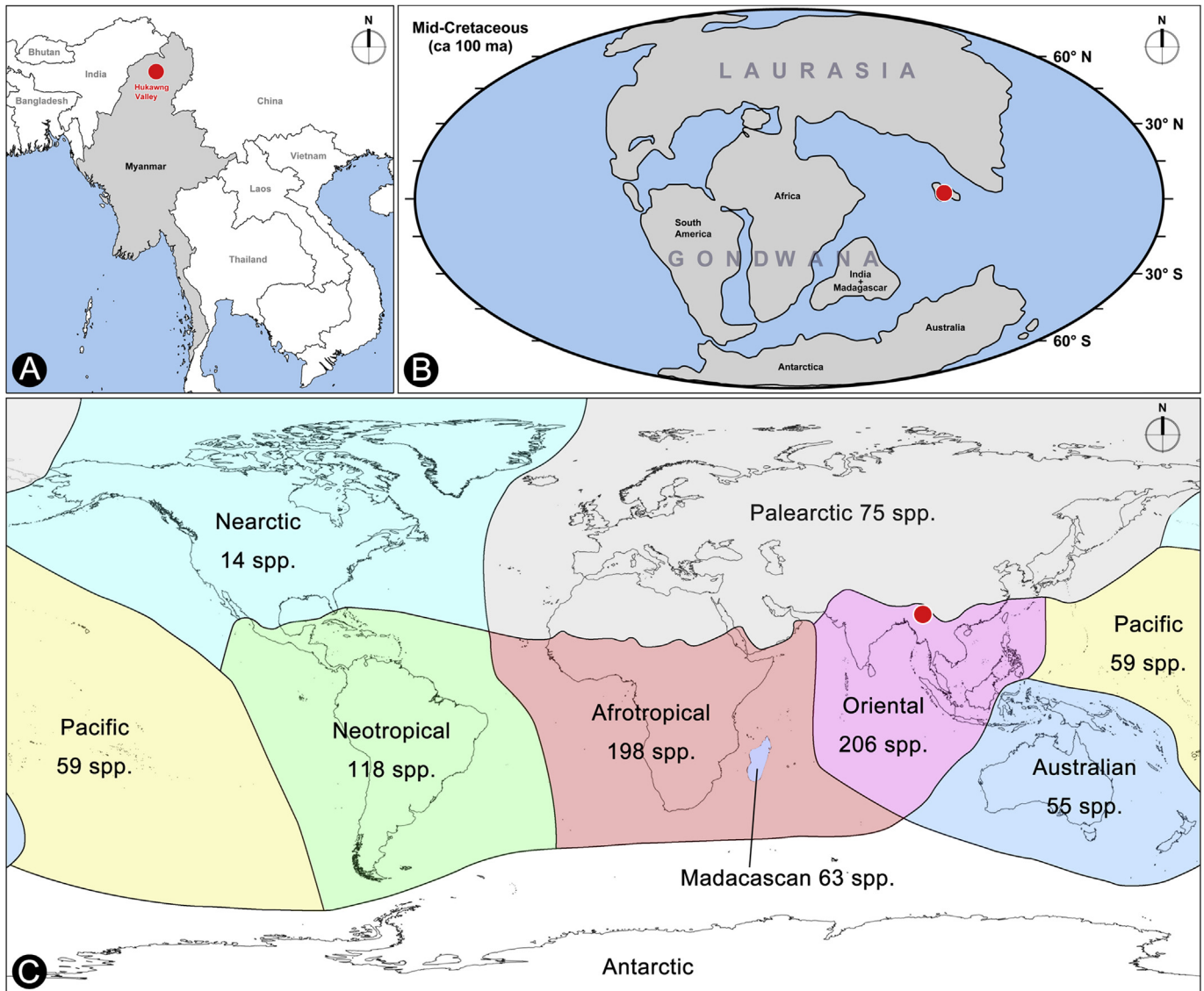


Fig. 1. The location (red dots) of the Burmese amber deposit in the present-day Myanmar (A), and in a paleogeographically reconstructed map of mid-Cretaceous (B); and distribution and species richness of present-day Scydmaenini (C). Map in Fig. 1B was based on Seton et al. (2012); background map of Fig. 1C was obtained from www.simplemapp.net, and data of species richness and distributional pattern provided by A. F. Newton (pers. comm.).

discovery of a new supertribe Hapsomelitae from earliest Cenomanian Burmese amber (Poinar and Brown, 2004; Chatzimanolis et al., 2010), whose exceptionally elongate abdominal segments VII and VIII are absent in living scydmaenines; an extinct member of the extant genus *Clidicus* Laporte from latest Albian French amber (Kirejtshuk et al., 2015); an extinct species of *Eutheia* Casey (Eutheini) from Santonian Taimyr amber; a new genus *Archeutheia* Jałoszyński & Peris of the Cephenniitae: Eutheini from early Albian Spanish amber (Jałoszyński and Peris, 2016); and earliest records of the mega-diverse Glandulariini and highly distinct Mastigini from mid-Cretaceous Burmese amber (Jałoszyński et al., 2016, 2017a, 2017b; Yin et al., 2017). One of the notable features of these Mesozoic taxa attributes to the long-term morphological stasis over deep geological time, a phenomenon sometimes also interpreted as 'punctuated equilibrium' (Eldredge and Gould, 1972; Gould and Eldredge, 1977), which is well-known among numerous Jurassic and Cretaceous staphylinid and other beetle groups (for examples see Yue et al., 2014; Cai and Huang, 2015a, 2015b; Cai et al., 2015, 2017a, 2017b; Yamamoto, 2017; Yamamoto et al., 2017, and other

recently published papers). The distinct body plans, and sometimes unique behaviors, of most major scydmaenine lineages can thus be traced back to the Cretaceous period, indicating the antiquity of these groups. For example, the strongly elongate body form and greatly extended appendages in Recent Mastigini, indicative of a diurnal way of life, have been well-established for at least 99 million years (Yin et al., 2017; Jałoszyński et al., 2017b); and the specialized predation of extant *Stenichnus* Thomson on armoured mites also occurred in their 90-million-year-old ancestor (Jałoszyński et al., 2017c).

Surprisingly, standing as one of the most diverse scydmaenine groups and comprising over 750 extant species distributed all over the world (Jałoszyński, 2016a), the tribe Scydmaenini has not been known as fossils, even from younger Eocene to Miocene deposits. This is highly unusual given that older records from Baltic amber, and recent extensive investigations on Eocene Rovno amber had revealed a diverse scydmaenid fauna, covering all other major scydmaenine lineages. Thus existing accumulated data raise the question of whether Scydmaenini had a young, Quaternary origin

(Jałoszyński and Perkovsky, 2016). Recent Scydmaenini are cosmopolitan in distribution, but are particularly diverse in tropical areas (Fig. 1C; A.F. Newton, pers. comm.). These beetles, suggested to be a sister group to the Mastigitae (O’Keefe, 2005; Jałoszyński, 2014), are mainly characterized by their ant-like body form, a geniculation between the scape and pedicel, prosternum laterally fused with prothoracic hypomera, broadly separated metacoxae, and particularly short, dome-like maxillary palpomeres IV (Jałoszyński, 2012a). Here we report a well-preserved scydmaenine in mid-Cretaceous amber from Myanmar, and assign it to the stem-group Scydmaenini. This represents the first definite fossil Scydmaenini, and its old age may shed important light on the evolution of ant-like stone beetles.

2. Material and methods

The beetle described here is embedded in a piece of amber obtained from the Hukawng Valley in northern Myanmar (26°21’33.41”N, 96°43’11.88”E; Fig. 1A). The palaeohabitat was suggested to be moist tropical forest, with conifers of the families Cupressaceae and Pinaceae recognized as source of the resin (Grimaldi et al., 2002; Dutta et al., 2011, Fig. 1B). The map (Fig. 1C) summarizing the current distribution and species richness of Scydmaenini was based on data extracted from an unpublished database of the Staphyloidea (A.F. Newton, pers. comm.). The age of Burmese amber is now widely accepted as earliest Cenomanian (98.79 ± 0.62 Ma, Shi et al., 2012). The holotype (SNUC-Paleo-0012) is housed in the Insect Collection of Shanghai Normal University, Shanghai, China (SNUC).

The amber piece was cut using a handheld engraving tool, and polished using sandpapers of different grain sizes and rare earth polishing powder, allowing for detail observations and photography of the beetle. The habitus images (Fig. 2) were made using a Canon 5D Mark III camera with an Olympus Plan C 10× Objective Lens, and a Canon MT-24EX twin flash was used as light source. Images of morphological details (Fig. 3) were made using a Zeiss SteREO Discovery V20 stereomicroscope, or a Canon G9 Camera

mounted on an Olympus CX31 microscope. Montages were produced in Zerene Stacker Version 1.04. All images were modified and grouped in Adobe Photoshop CS5 Extended.

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3. Systematic palaeontology

Order Coleoptera [Linnaeus, 1758](#)
 Superfamily Staphyloidea [Latreille, 1802](#)
 Family Staphylinidae [Latreille, 1802](#)
 Subfamily Scydmaeninae [Leach, 1815](#)
 Tribe Scydmaenini [Leach, 1815](#)

Kuafu Yin, Cai & Huang gen. nov.

Zoobank LSID urn:lsid:zoo-bank.org:act:3DF9B7C7-A8A1-485D-AA12-001D2DAC6663

Type species: Kuafu borealis Yin, Cai & Huang

Etymology. Kuafu is a giant in Chinese mythology who wished to chase and catch the Sun.

Diagnosis. A genus of Scydmaenini differing from all modern taxa of this tribe in the absence of an apical notch/emargination on the scapes, combined with the elongate overall body form; elongate and round-sided pronotum; anterior part of prosternum laterally fused with pronotal hypomera; and strongly elongate meso- and metatrochanters that widely separate the coxae and femora.

Description. General body form (Fig. 2A–C) elongate, body regularly flattened, distinctly but not deeply constricted between head and pronotum and between pronotum and elytra; appendages elongate; vestiture composed of fine setae.

Head (Fig. 3B) capsule divided by occipital constriction 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 subtriangular and rounded,

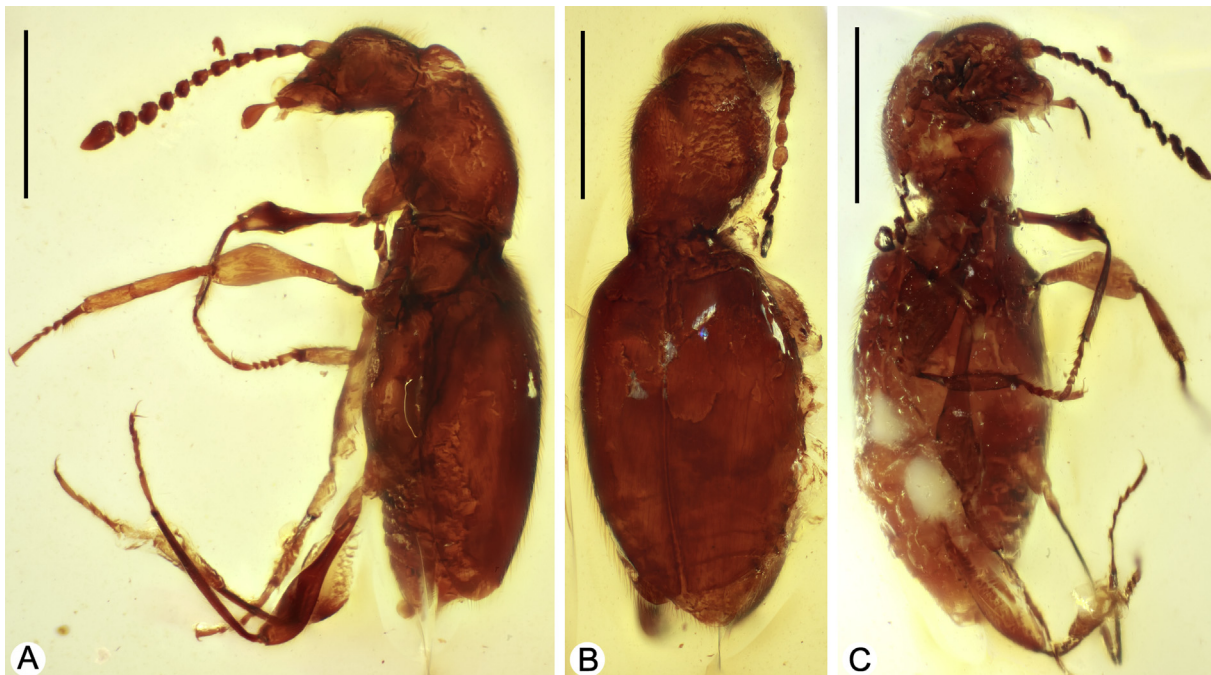


Fig. 2. Habitus of *Kuafu borealis* gen. et sp. nov. (holotype, SNUC-Paleo-0012) in lateral (A), dorsal (B), and ventral (C) view. Scale bars: 0.5 mm.

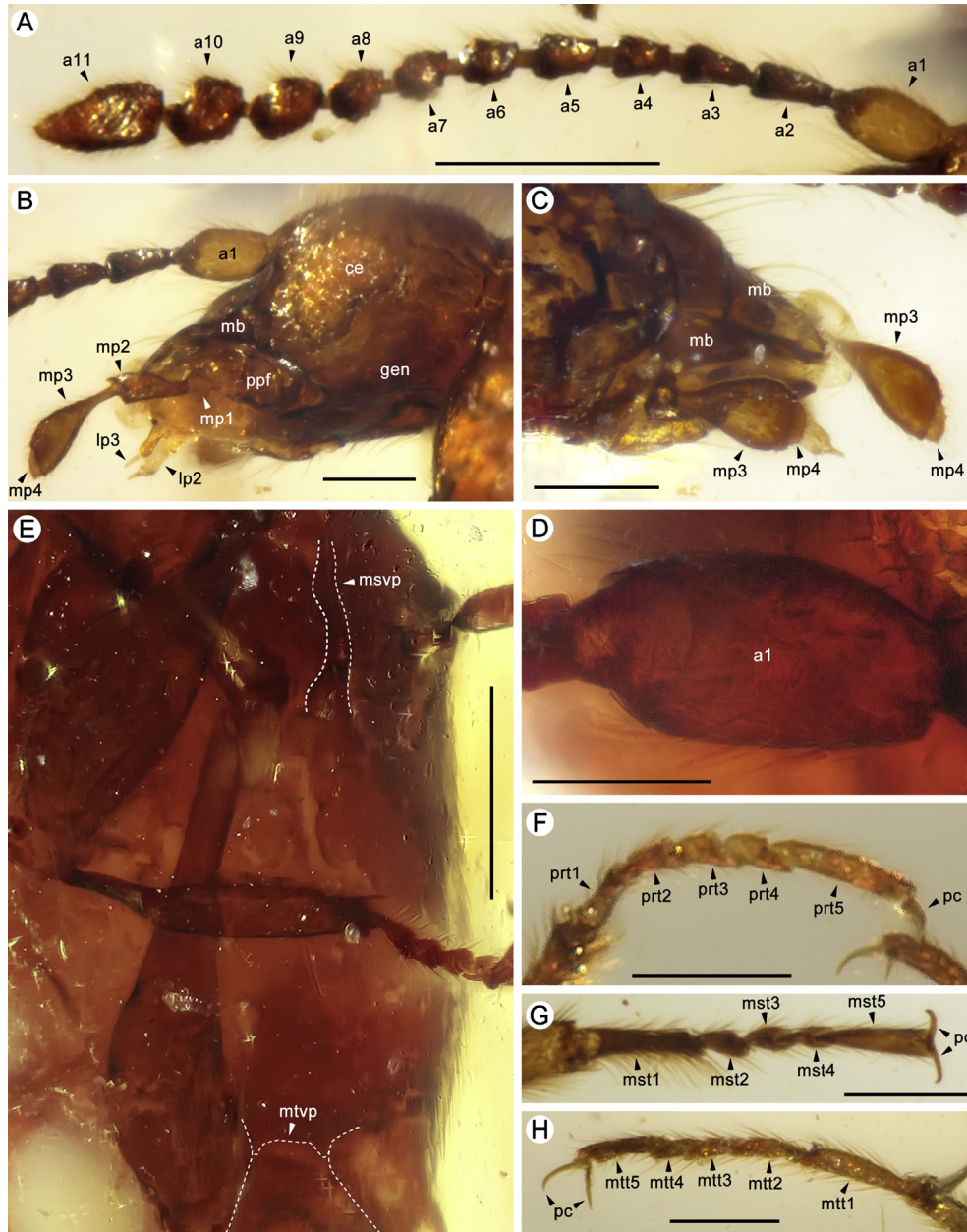


Fig. 3. Morphological details of *Kuafu borealis* gen. et sp. nov. (holotype, SNUC-Paleo-0012). A. Left antenna, in lateral view. B. Head, in lateral view. C. Mouthparts, in dorsolateral view. D. Left scape (antennomere I), in dorsal view. E. Meso- and metaventrite, showing meso- and metaventral process. F. Right protarsus and pretarsal claws. G. Left mesotarsus and pretarsal claws. H. Left metatarsus and pretarsal claws. Abbreviations: a1–a11, antennomeres I–XI; ce, compound eyes; gen, gena; mb, mandible; lp1–2, labial palpomeres I–II; mp1–4, maxillary palpomeres I–IV; mst1–5, mesotarsomeres I–V; msvp, mesoventral process; mtt1–5, metatarsomeres I–V; mtvp, metaventral process; pc, pretarsal claw; ppf, palpifer; prt1–5, protarsomeres I–V. Scale bars: 0.2 mm in A, E; 0.1 mm in B, F–H; 0.05 mm in D; 0.02 mm in C.

broadest across eyes. Vertex anteriorly confluent with roundly triangular frons. Antennal insertions located anterior to eyes, widely separated. Clypeus with rounded anterior margin; anterior margin of labrum slightly emarginate at middle, mandibles (Fig. 3B; mb) each with broad subtriangular basal region and curved, large apical tooth, and one to two slightly smaller, acute subapical teeth; head venter not observable in the holotype. Palpifer large (Fig. 3B; ppf), elongate. Maxillary palpi (Fig. 3B–C; mp1–4) short, palpomere I small, subrectangular, palpomere II clavate and curved, broadest at apex, large and broadened palpomere III broadest near apex, basally pedunculate, palpomere IV short and transverse, dome-shaped. Labial palpi (Fig. 3B; lp2–3) with short, transverse palpomere I, II strongly elongate, subcylindrical, III subconical with

blunt apex, strongly elongate, much shorter and narrower than palpomere II.

Antennae (Fig. 3A) slender and elongate, antennomeres (Fig. 3A; a1–11) gradually broadened distally; scape (Fig. 3A, D; a1) strongly elongate, lacking ventral and dorsal apical emarginations or notches; flagellomeres relatively loosely assembled, antennomeres VII and VIII subequal in size.

Prothorax (Fig. 2B) in dorsal view elongate oval, broadest in front of middle; anterior corners indistinct, posterior corners obtuse-angled and blunt. Sides of hypomera confluent with pronotum (Fig. 2C). Pronotum lacking any carinae, possibly with pits or impressions at base. Prosternal process narrow and carinate, weakly projecting ventrally and not separating procoxae; procoxal

sockets broadly open. Mesoventrite short, much broader than long, mesoventral intercoxal process (Fig. 3E; msvp) nearly parallel-sided, weakly elevated; mesocoxae elongate. Metaventricle much longer than mesoventrite, elongate, anteriorly fused with mesoventrite, at middle posterior margin broadly concave and forming broad and short metaventral intercoxal process (Fig. 3E; mtvp).

Elytra elongate, possibly with basal foveae and impressions, humeral calli indistinct or lacking.

Abdomen about as long as metaventricle; sternite III (first visible) nearly as long as IV–V combined; suture between sternites VII and VIII distinct. Pygidium exposed.

Legs slender and elongate; pro- and mesocoxae subconical; metacoxae oval and transverse; all trochanters subtriangular and elongate; all femora strongly clavate distally; tibiae thin and long; tarsi (Fig. 3F–G) relatively long, tarsomeres I and V elongate, II–IV subquadrate.

Kuafu borealis Yin, Cai & Huang sp. nov.

Zoobank LSID urn:lsid:zoobank.org:act:2FB2C88F-C370-483E-9A21-C2B251677BF8

Etymology. The specific epithet is derived from the Greek ‘βορέας’, meaning ‘northern’, and referring to the distribution of the new species in the northern Laurasia landmass during the mid-Cretaceous period.

Type Material. Holotype (SNUC-Paleo-0012), sex undetermined, a complete adult preserved in Burmese amber, collected from an amber mine located in northern Myanmar; deposited in SNUC.

Type locality and horizon. Hukawng Valley (26°21′33.41″N, 96°43′11.88″E), Kachin State, northern Myanmar; lowermost Cenomanian (98.79 ± 0.62 Ma), mid-Cretaceous.

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

Description. Body elongate and slender, regularly flattened; BL 1.92 mm. Head in dorsal view subtriangular with rounded sides, broadest across eyes, length of head 0.42 mm, width not possible to be measured; vertex anteriorly confluent with subtriangular frons. Dorsal surface of head covered with short, moderately dense suberect setae. Antennae long and slender, with flagellum gradually thickened distally; length of antenna 0.82 mm; antennomeres I–V elongate, VI–X successively broadened, XI about 1.5 times as long as broad, narrowing distally from middle. Pronotum in dorsal view lengthily oval, with rounded sides, broadest near anterior third; length of pronotum 0.5 mm, width 0.34 mm; anterior margin rounded; posterior margin nearly flat. Setae on pronotal disc fine, suberect. Elytra roundly sided, much broader than pronotum, broadest slightly at middle, length of elytra 0.1 mm, width 0.07 mm, elytral index 1.45. Humeral calli present, weakly developed. Elytra covered with setae longer than those on head and pronotum, sparse, nearly recumbent. Legs long and slender; all tibiae almost straight, with elongate tarsomeres.

4. Discussion

Within the mega-diverse rove beetle subfamily Scydmaeninae, one extinct and three extant supertribes have been recognized, viz., Hapsomelitae, Cephenniitae, Mastigitae, and Scydmaenitae (Poinar and Brown, 2004; Grebennikov and Newton, 2009; Jałoszyński, 2014). The new genus *Kuafu* can be readily ruled out from the extinct Hapsomelitae by the abdominal segments VII and VIII not being exceptionally elongate, from Cephenniitae by the more slender rather than oval (Cephennini) or distinctly compact (Eutheini) general body form, and from Mastigitae by the short antennal scapes in relation to the head length, and relatively much shorter antennomeres and maxillary palpomeres. The supertribe Scydmaenitae currently comprises four tribes: Chevrolatiini (one

genus), Leptoscydmini (one genus), Glandulariini (about sixty genera), and Scydmaenini (six genera) (Jałoszyński, 2016b). Chevrolatiini is a well-defined group that has a posteriorly depressed head, and distinct dorsal and ventral setae in front of and behind the occipital constriction directed towards the constriction (O’Keefe, 1997; Jałoszyński and Kubisz, 2016); Leptoscydmini has never been properly diagnosed, but the terminal maxillary palpomeres appear to be pointed (but not acute) (Jałoszyński, 2005: 565); Glandulariini harbors the greatest diversity of extant scydmaenines, but all members are presumed to embody subconical maxillary palpomeres IV usually with a pointed apex (Jałoszyński et al., 2017a). An affinity of *Kuafu* with Scydmaenini is strongly supported by the fossil’s short and dome-like maxillary palpomere IV with setose distal surface, and metanepimera not covered by the elytra. Within Scydmaenitae this combination of characters are typical for Scydmaenini, and present in all six genera included in the tribe. Other characters found in *Kuafu* and indicative of a Scydmaenini are (although sometimes found also in other related groups): overall elongate body form, with an elongate and round-sided pronotum; anterior part of prosternum laterally fused with pronotal hypomera; and strongly elongate meso- and metatrochanters that widely separate the coxae and femora. Within Scydmaenini, *Kuafu* seems to be more similar to *Scydmaenus* and *Adrastia* Broun than to *Eudesis* Reitter, *Pseudoeudesis* Binaghi, and *Liliputella* Jałoszyński. The latter three genera are relatively compact in overall body form, minute in size, blind and wingless, and have strikingly short tarsi suggesting an endogean life style. Despite the fact that *Kuafu* possesses a number of characters typical of Scydmaenini, it also displays some plesiomorphic traits not found in extant Scydmaenini. The most notable is that *Kuafu* has the anterior margin of the scape normally developed, devoid of any notch or emargination. An apically notched or emarginate scape is widely considered as a synapomorphy of the Scydmaenini (Franz and Besuchet, 1971; Franz, 1975, 1986; O’Keefe, 1997; Jałoszyński, 2005, 2012a), thus lacking such character in a Mesozoic taxon appears to bear great importance for elucidating the origin and early evolution of this group. Jałoszyński (2016c) described and illustrated an unusual character found in extant Scydmaenini, i.e., the dorsal surface of propygidium (tergite VII) bearing a median longitudinal impression flanked with complex sculpturing fields. This character is present only in Scydmaenini, Chevrolatiini, and Leptoscydmini, and seems to be a synapomorphy for these groups (A. F. Newton, pers. comm.). The tergite VIII and part of tergite VII in *Kuafu* is exposed from elytra (Fig. 2B), but we were not able to find a similarly-structured median impression on tergite VII. Thereby, this structure is either truly absent in *Kuafu* representing a plesiomorphic state, or less likely, became invisible due to the fossilization of the specimen.

Recent phylogenetic studies based on morphological characters suggested a sister group relationship between Scydmaenini and Mastigitae, raising questions about the monophyly of Scydmaenitae as currently composed (O’Keefe, 2005; Jałoszyński, 2012b, 2014). O’Keefe (2005) listed three synapomorphies that link Scydmaenini and Mastigitae: 1) emarginate anterior margin of the labrum, 2) prosternal-pleural suture completely fused, and 3) notched apical margin of the scape. The latter two characters also carried a heavy weight in a phylogenetic tree according to Jałoszyński (2014). In *Kuafu*, the anterior margin of the labrum is slightly emarginate, and the prosternum indeed seems to fuse with the hypomera, without trace of a lateral prosternal sulcus that separate these parts. However, in contrast to its modern relatives, *Kuafu* has a much shorter scape, with the anterior margin lacking a notch or an emargination, so that the antenna is not able to bend between the scape and the pedicel. The plesiomorphic state of this character indicates that the antennal geniculation among Recent

Scydmaenini may be secondarily derived from their ancestors without this structure. A similar condition of this character in Mastigitae may only reflect convergent or parallel evolution, rather than indicative of a close relationship to Scydmaenini, noting the highly modified antennal structure in Mastigitae was already well-established in their Cretaceous and Eocene ancestors (Jałoszyński, 2012c; Cai and Huang, 2016; Yin et al., 2017; Jałoszyński et al., 2017b). Consequently, inclusion of *Kuafu* in existing phylogenetic analysis would probably result in contradictory results, and greatly change the currently obtained topologies.

The discovery of a stem-group Scydmaenini from the mid-Cretaceous (Cenomanian, ca. 99 Ma) of Myanmar indicates the origin of this tribe probably predates the Cenomanian, similar to other major scydmaenid groups. It represents the first extinct member of the diverse tribe Scydmaenini, filling a major gap in the evolution of Scydmaeninae, and may shed important new light on the early evolution and systematics of this subfamily.

5. Conclusion

Our discovery of *Kuafu borealis* gen. et sp. nov. from mid-Cretaceous Burmese amber dates back the definitive oldest record of Scydmaenini, a highly successive scydmaenine lineage previously lacking any fossil record, to at least the Cenomanian, some 99 million years ago. *Kuafu* possesses a short, dome-like terminal maxillary palpomere, a character shared by all extant genera of Scydmaenini, but lacks an apical notch or emargination on the scape that has been considered a synapomorphy of the tribe. We thus place the new genus as a member of the stem-group Scydmaenini, with a possible sister group relationship to all of its modern counterparts.

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