



The oldest aleocharine rove beetle (Coleoptera, Staphylinidae) in Cretaceous Burmese amber and its implications for the early evolution of the basal group of hyper-diverse Aleocharinae



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ABSTRACT

The subfamily Aleocharinae is a hyper-diverse group of Staphylinidae, accounting for nearly one-third of the diversity within the largest animal family on Earth. Here we describe *Cretodeinopsis aenigmatica* gen. et sp. nov., the first definitive Mesozoic aleocharine based on a well-preserved individual in the earliest Late Cretaceous (Cenomanian) amber from Myanmar (Burma). The new genus is clearly assigned to the 'basal' group of Aleocharinae based on its overall body shape, antennal insertions on the vertex of the head, and emarginate posterolateral margins of elytra. It is placed in the Recent tribe Deinopsini based on the strongly deflexed head, pectinate edge of abdominal segments III–V, tarsal structures, and non-pentamerous tarsi. The new discovery of the oldest known Aleocharinae from about 99 Mya represents a new aleocharine belonging to the 'basal' group of Aleocharinae, reinforcing the hypothesis that *Gymnusa*, *Stylogymnusa* and the tribe Deinopsini probably form a monophyletic lineage and suggest that the monophyly of Gymnusini is not supported based on the presence of 6 setigerous pores on the head. It indicates that the origin of the subfamily probably predates the Cenomanian. This new discovery is about 55 Ma older than the previously known Eocene-aged ones from Baltic amber, greatly broadening our knowledge on the early evolution of Aleocharinae.

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1. Introduction

The family Staphylinidae (rove beetles) is one of the remarkable radiations in the history of life; it currently includes over 58,500 described species placed in 32 extant subfamilies (Newton, unpublished data). With 12,851 described species placed in 1151 genera, the rove beetle subfamily Aleocharinae is a hyper-diverse group of staphylinids that accounts for approximately 27% of the diversity within the family Staphylinidae (Thayer, 2005). These mostly small to minute beetles are mainly predatory generalists that dominate leaf litter and soil communities (Ashe, 2007). Several groups of aleocharines have diversified in many unusual habitats, including mushroom, seashore, and tropical canopy habitats (Thayer, 2005). Notably, aleocharines are also known as the most successful group of inquilines in the nests of social insects (Seevers, 1978). The subfamily was first suggested as a monophyletic group by Hammond (1975) and later by Ashe (1994) based on unique characteristics of the aedeagus (presence of large lateral lobes on the aedeagus). Despite the seemingly endless diversity, the minute size of most adults, and the lack of illustrated keys and descriptions of aleocharines for most geographical regions, make the Aleocharinae

one of the most taxonomically difficult groups of beetles (Ashe, 2007). However, there is hope for this remarkable radiation of life as subfamilial and even tribal level phylogenetic studies are starting to shed light on the Aleocharinae (e.g., Ashe and Newton, 1993; Ahn and Ashe, 2004; Ashe, 2005). The subfamily Aleocharinae is robustly supported as a monophyletic group based on morphological phylogenetic studies using adult and larval characters (Ashe and Newton, 1993; Ashe, 2005).

The fossil record of Staphylinidae is substantial, and dozens of Jurassic and Cretaceous fossils have been described, with an increasing number of staphylinid fossils being described each year and many more under study. The oldest fossils placed in Staphylinidae are from the Late Triassic of Virginia (ca. 225 Ma), which have been formally described as *Leehermania prorova* Chatzimanolis et al., 2012 (Chatzimanolis et al., 2012). However, the systematic position of the supposed oldest polyphagan *Leehermania* has been recently questioned by Grebennikov and Newton (2012), and *Leehermania* share more features with some members of the extant myxophagan family Hydroscaphidae, especially the Early Cretaceous fossil *Hydroscapha? jeholensis* Cai et al. (2012a). Although a number of staphylinid fossils representing different extant subfamilies have been recorded from the Middle to Late Jurassic (e.g., Tikhomirova, 1968; Cai et al., 2012b; Cai and Huang, 2013; Cai et al., 2015a,b), no fossil aleocharines are known from the Mesozoic. Up to now, the described fossil aleocharines have been mainly confined to the Tertiary (20 species) and only three reported species are known

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from the Quaternary (Newton, unpublished data). The oldest aleocharine rove beetles known until now are from the middle-Eocene Baltic amber (ca. 37–54.5 Ma, see Ritzkowski, 1997) (Zerche, 1999; Pańnik and Kubisz, 2002; Wolf-Schwenniger, 2004; Pańnik, 2005). The Mesozoic fossil record, being of great significance for understanding the origin and early evolution of this subfamily, is still lacking. Here we report the new discovery of a definitive aleocharine beetle preserved in the earliest Cenomanian amber from northern Myanmar (Burma), which opens a window to understanding the origin and early evolution of Aleocharinae.

2. Material and methods

The material described here comes from amber deposits in the Hukawng Valley of northern Myanmar, once thought to be of Eocene origin, but currently considered to be of earliest Cenomanian age based on U–Pb dating of zircons (Grimaldi et al., 2002; Cruickshank and Ko, 2003; Shi et al., 2012). As mapped by the first two groups of workers, the extraction of amber is undertaken at a hill named Noiye Bum, near Tanai Village (26°21'33.41"N, 96°43'11.88"E). The material has been prepared, including being cut with a razor blade and polished with sand papers of different grain sizes and with diatomite mud. A polished slab of amber measuring 6.2 mm × 4.2 mm contains the beetle specimen. Observations and photographs were made using a Zeiss Discovery V20 stereo microscope (Fig. 1B, D) and a Zeiss Axio Imager 2 light microscope with a digital camera attached respectively. Photomicrographs with a green background (Figs. 1A, C; 2 and 3A–C) were taken using green fluorescence as a light source attached to a Zeiss Axio Imager 2 light microscope.

3. Systematic palaeontology

Order Coleoptera Linnaeus, 1758
 Family Staphylinidae Latreille, 1802
 Subfamily Aleocharinae Fleming, 1821
 Tribe Deinopsini Thomson, 1867
 Genus *Cretodeinopsis* gen. nov.

Type species

Cretodeinopsis aenigmatica new species, here designated.

Etymology

From the prefix *Creto-*, referring to the type species being from the Cretaceous, and the genus name *Deinopsis*; it is feminine in gender.

Diagnosis

Body small, sublumuloid. Head vertex with six setigerous pores. Antenna inserted on vertex of head, with eleven antennomeres, antennomere 11 with papilla. Mandible with preapical teeth. Pronotum transverse; posterior margin bisinuate. Elytra relatively short; posterolateral margins of elytra emarginated. All tarsi 4-segmented; with two pretarsal claws and three long setae surrounding the claws. Abdomen tapering from base to apex. Abdominal tergites, sternites and paratergites III–VI each with dense apical ctenidium of short comb-like cuticular projections of both sharp-pointed and apically rounded teeth. Tergite IX elongate.

Cretodeinopsis aenigmatica sp. nov.

(Figs. 1–3)

Etymology

Derived from the combination of the Latin adjectives *aenigmaticus*, *-a*, meaning enigmatic.

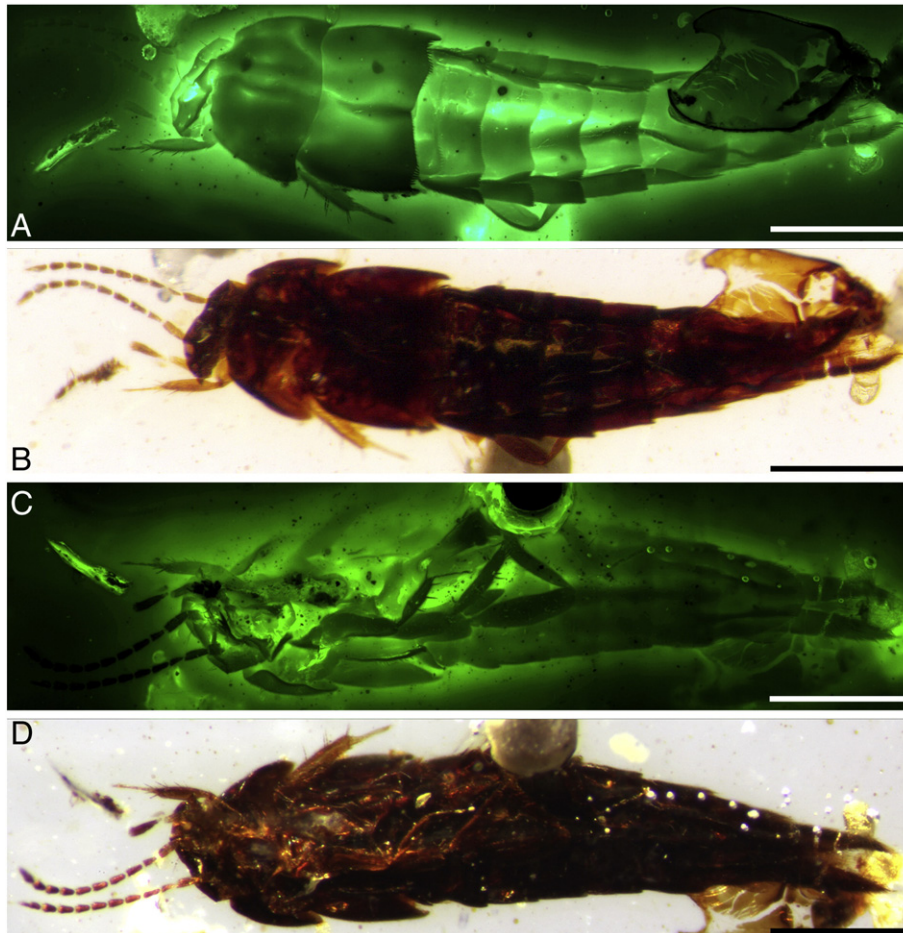


Fig. 1. *Cretodeinopsis aenigmatica* gen. et sp. nov., holotype. A. Dorsal view, under green fluorescence; B. dorsal view, under normal light; C. ventral view, under green fluorescence; D. ventral view, under normal light. Scale bars: 500 μ m.

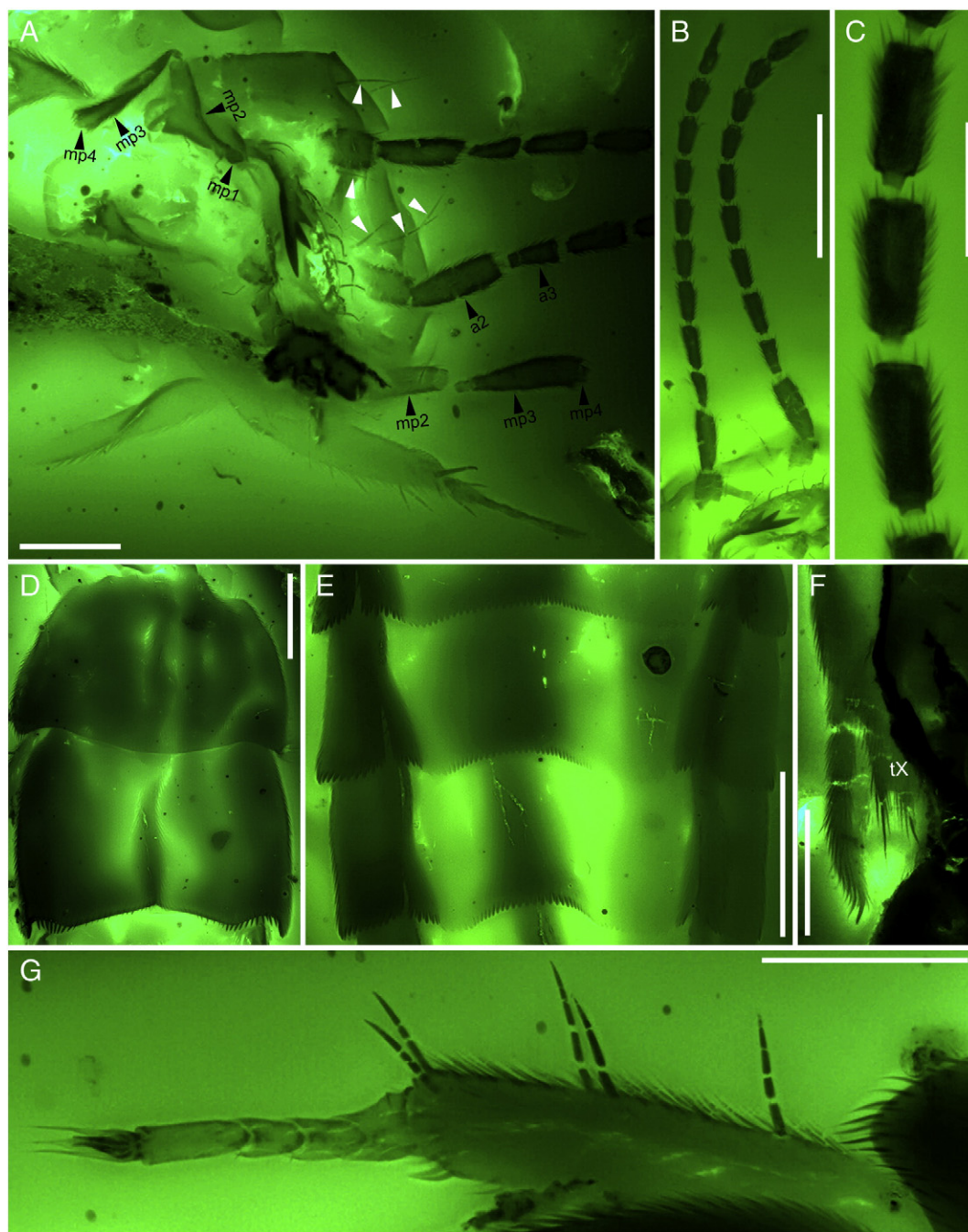


Fig. 2. Enlargements of *Cretodeinopsis aenigmatica* gen. et sp. nov., under green fluorescence. A. Enlargement of mouthparts, showing toothed mandible, long maxillary palpus, and six setigerous pores on the dorsum of the head (white arrows indicated); B. enlargement of antennae; C. enlargement of left antenna, showing antennomeres 5–7; D. enlargement of prothorax and elytra, showing emarginate posterolateral margin of elytron; E. enlargement of abdominal tergites and paratergites III–V, showing dense apical ctenidium of comb-like cuticular projections; F. enlargement of tergites IX and X, showing divided apical part of tergite X; G. enlargement of left mesotibia and mesotarsus. Abbreviations: a, antennomere; mp, maxillary palpomere; tX, tergite X. Scale bars: 50 μ m in C, 100 μ m in A and G, 200 μ m in others.

Material

Holotype, NIGP157736. The fossil beetle is a completely preserved adult. The type specimen is housed in the Nanjing Institute of Geology and Palaeontology, CAS, Nanjing, Jiangsu Province, China.

Occurrence

Lowest Upper Cretaceous (ca. 99 Ma; Shi et al., 2012) amber from the village of Tanai, Hukawng Valley, northern Myanmar.

Diagnosis

As for the genus (*vide supra*).

Description

Body (Fig. 1) 2.71 mm long, densely pubescent, dark brown.

Head (Fig. 2A) strongly deflexed, about 0.39 mm wide, gradually narrowed anteriorly, narrower than pronotum; head vertex glabrous, with three setigerous pores on each side: one just above antennal insertion, one near anterior margin of eye, and one behind eye; all situated toward midline (Fig. 2A). Frons obtusely, triangularly protruding (Fig. 2A). Labrum transverse, apparently with six anteriorly-directed setae (Fig. 2A). Eyes oval-shaped. Antennae (Fig. 2B) inserted near anterior margin of eye, densely setose (Fig. 2C), filiform; antennomere 1 (a1) slightly broader than a2; a2 elongate, slightly longer than a1; a3 narrower and distinctly shorter than a2, about 0.5 times as long as a2; a4 slightly longer than a3; a4–11 slightly widened and shortened

toward apex. Maxillary palpi (Fig. 2A) relatively long; palpomere 1 short and inconspicuous, palpomere 2 large and elongate, palpomere 3 large and elongate, gradually widened toward apex, palpomere 4 narrower than palpomere 3. Mandibles each with one small and two large and sharp preapical teeth.

Pronotum (Fig. 2D) 0.39 mm long and 0.62 mm wide; sides arcuate, widest slightly before base, narrowed anteriorly; anterolateral angles obtuse rounded; posterolateral angles rounded. Surface with dense and fine microsetae.

Elytra (Fig. 2D) 0.47 mm long, each 0.32 mm wide; 0.82 times as long as pronotum at midline. Surface with dense, fine microsetae. Posterolateral margins of elytra emarginated, emargination with about thirteen relatively strong setae. Wings, if present, not preserved. Scutellum partly exposed; setose.

Legs relatively short. Procoxae conical, contiguous, with procoxal cavity open behind; profemora robust; protibiae widened toward apex, with at least five strong and long setae at outer and apical margins; protarsi (Fig. 3A) 4-segmented, tarsomere 1 broad and longer than wide, tarsomeres 2 and 3 almost the same length, thinner than tarsomere 1, tarsomere 4 longest. Mesocoxae oblique; mesotibiae (Fig. 2G) longer than protibiae, with five visible strong setae at outer and apical margins; mesotarsi 4-segmented (Fig. 3B), tarsomere 1 broad, tarsomere 2 slightly longer than tarsomere 3, tarsomere 4 longest (Fig. 3C). Metacoxae contiguous; metafemora long and robust, longer than mesofemora; metatrochanters large, fusiform; metatibiae gradually widened toward apex, elongate. Metatarsi 4-segmented, tarsomere 1 broad, tarsomeres 2 and 3 almost the same length, tarsomere 4 longest.

Abdomen triangular, covered with dense and fine setae; sides even tapering from base to apex; abdominal tergites lacking pruinose spots. Abdominal segments III–VII each with two pairs of paratergites. Abdominal tergites, sternites and paratergites III–VI each with dense apical

ctenidium of short comb-like cuticular projections of both sharp-pointed and apically rounded teeth (Fig. 2E). Abdominal tergite II well-developed, with a row of dense, strong and short setae at apex. Tergites VII and VIII long. Tergite IX elongate, densely setose, lateral tergal sclerites each with a strong setae at apex.

Male: Tergite VIII with apical margin rounded. Tergite X with apical part divided, terminating in two long setae (Fig. 2F).

5. Discussion

Within the large group of beetle family Staphylinidae, four informal and presumably monophyletic groups of subfamilies (the Omaliine group, Tachyporine group, Oxyteline group, and Staphylinine group) and one basal group (Apateticinae + Trigonurinae) have been recently recognized (Grebennikov and Newton, 2012). The new genus *Cretodeinopsis* can be easily placed in the Tachyporine group on the basis of its sublimuloid body shape and several defining features, including exposed antennal insertions, absence of distinct neck, and gradually tapered abdomen with six visible abdominal segments. The Tachyporine group currently comprises six subfamilies, viz. Aleocharinae, Habrocerinae, Olisthaerinae, Phloeocharinae, Tachyporinae, and Trichophyinae (Ashe, 2005). *Cretodeinopsis* can be readily separated from the two closely related subfamilies Habrocerinae and Trichophyinae by lacking the characteristic verticillate antennae. The subfamily Phloeocharinae is still not well defined and is not easy to characterize; it has been a 'dumping ground' for relatively primitive rove beetles that do not fit well elsewhere (Newton et al., 2000). Nevertheless, a couple of characteristics can be useful for recognizing it from other subfamilies, such as antennal insertion more or less concealed from above, and abdominal tergites IV and V each with a pair of distinctive cuticular combs (Newton et al., 2000). Obviously, *Cretodeinopsis* cannot be attributed to the Phloeocharinae due to its sublimuloid

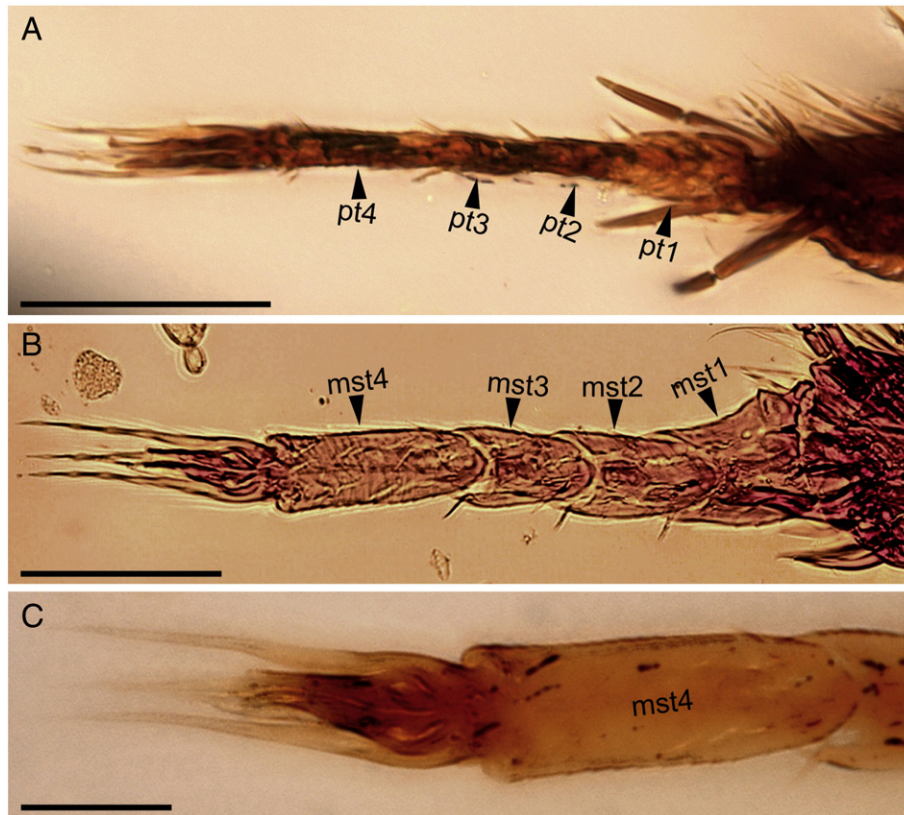


Fig. 3. Enlargements of *Cretodeinopsis aenigmatica* gen. et sp. nov., under normal light. A. Enlargement of left protarsus, showing four tarsomeres and three long setae surrounding claws; B. enlargement of left mesotarsus, showing four tarsomeres; C. enlargement of left mesotarsomere 4 and pretarsal structures. Abbreviations: pt, protarsomere; mst, mesotarsomere. Scale bars: 20 μ m in C, 50 μ m in others.

shape and lacking the two characteristics mentioned above. The monogeneric subfamily Olisthaerinae, morphologically very similar to Phloeocharinae, is characterized by the pronotal postcoxal process, which is separated by a suture from the rest of the pronotum and is slightly movable (Newton et al., 2000). Olisthaerine beetles usually have sub-parallel bodies. The placement of *Cretodeinopsis* to Olisthaerinae is clearly unsupported based on the overall shape of the body, and more importantly, the absence of the characteristic postcoxal process. In superficial appearance, *Cretodeinopsis* appears related to the subfamily Tachyporinae, especially the modern tribe Tachyporini. However, it can be readily distinguished from Tachyporinae by the antennae inserted posterior to a line drawn along the anterior margins of the eyes, and the sinuate posterolateral margins of the elytra. Although the posterolateral margins of the elytra of *Megarhropsis* (tribe Megarhropsini of Tachyporinae) are distinctly emarginate, the new genus can be separated from it by the antennal insertions, setose elytra, non-emarginate abdominal tergite and sternite VIII and characteristic mouthparts. Considering the discussion above, *Cretodeinopsis* is placed in the mega-diverse staphylinid subfamily Aleocharinae, mainly based on the two characteristic traits: the antenna inserted on the head vertex (near the anterior margin of the eye) and the emarginate posterolateral margin of elytron.

The monophyletic Aleocharinae is informally divided to two groups: the 'basal' and the 'higher' groups (Ashe, 2005). The former comprises four tribes (Deinopsini, Gymnusini, Mesoporini, and Trichopseniini); the latter contains the remaining majority of Aleocharinae (Ashe and Newton, 1993; Ashe, 2005). Morphological phylogenetic analyses have shown that a monophyletic 'higher' Aleocharinae lineage was strongly supported based primarily on the presence of a tergal gland in both larvae and adults; 'basal' aleocharine beetles do not possess this structure (Ashe and Newton, 1993; Ashe, 2005). *Cretodeinopsis* is readily placed in the most basal lineage including the tribes Deinopsini and Gymnusini by having the characteristic apical centridium of short comb-like projections on abdominal tergites and sternites III–VI. Adults of modern Gymnusini and Deinopsini share a number of features, such as a deflexed head; lack of a tergal gland opening on abdominal tergum VII; pectinate edge of abdominal segments III–V, and distinctive mouthparts (for details see Klimaszewski, 1979). Extant members of the Gymnusini bear 6 setigerous pores on the dorsal surface of the head and entire male tergum IX, while in members of Deinopsini the male tergum IX is divided and the head lacks setigerous pores (e.g., Klimaszewski, 1979; Ashe, 2002). *Cretodeinopsis* appears to combine features belonging to the two basal tribes. It shares with extant members of Gymnusini the presence of 6 setigerous pores on the vertex of the head. Compared to Gymnusini, *Cretodeinopsis* shares more characters with members of Deinopsini, including the overall sublimuloid body shape, antennomere 11 with papilla, bisinuate posterior pronotal margin, emarginate posterolateral margin of elytra (non-emarginate in *Stylogymnusa* Hammond of Gymnusini), non-pentamerous tarsi (tarsal formula 4–4–4), and abdominal tergite X with apical part divided in the male. In addition, *Cretodeinopsis* has some unique characters that are not present in extant members of Gymnusini or Deinopsini, such as the 4-segmented tarsi and the exposed scutellum. We placed *Cretodeinopsis* in the Recent tribe Deinopsini, rather than Gymnusini, based on its overall body shape, the peculiar presence of three long setae surrounding the claws, and 4-segmented tarsi.

Phylogenetically, the monophyly of the tribe Gymnusini (*Gymnusa* Gravenhorst and *Stylogymnusa* Hammond) is supported by the shared apomorphic characteristics of a large mentum, 6 setigerous pores on the dorsum of the head, and similarities in the mouthparts (e.g., Hammond, 1975; Klimaszewski, 1979, 1982). However, a monophyletic Gymnusini is weakly supported, although a monophyletic lineage consisting of *Gymnusa*, *Stylogymnusa* and the tribe Deinopsini is strongly supported (Ashe, 2000). The mouthparts of *Gymnusa* share many derived features with the mouthparts of members of the Deinopsini; most derived features presumably shared between *Gymnusa* and *Stylogymnusa* as

proposed by Hammond (1975) and Klimaszewski (1979) were suggested to be based on misinterpretations (Ashe and Chatzimanolis 2003). It was furthermore suggested, that *Gymnusa* and *Stylogymnusa* uniquely share the presence of 6 setigerous pores on the dorsum of the head, a feature not known to occur among any other lineage of basal aleocharines, or among other potential out-groups within the Tachyporine group (Ashe, 2000). Thus, the supporting characters for a monophyletic Gymnusini are contradictory, and the issue is still unresolved. Our new find of a new genus bearing an enigmatic combination of characteristics sheds new light on the phylogenetic relationships between the basal tribes Deinopsini and Gymnusini. The supposed uniquely shared character by *Gymnusa* and *Stylogymnusa* (6 setigerous pores on the dorsum of the head) is also found in the new genus *Cretodeinopsis*. The new finding reinforces the hypothesis that *Gymnusa*, *Stylogymnusa* and the tribe Deinopsini probably form a monophyletic lineage as indicated in Ashe (2000). Furthermore, the monophyly of Gymnusini is not supported based on the presence of 6 setigerous pores on the head.

The discovery of a definitive aleocharine beetle from the Late Cretaceous (Cenomanian, ca. 99 Ma) of Myanmar indicates that the origin of the subfamily Aleocharinae probably predates the Cenomanian. It represents the first Mesozoic member of the diverse subfamily Aleocharinae. The new genus is about 55 Ma older than the previously known Eocene-aged ones from Baltic amber (e.g., Wolf-Schwenniger, 2004), which greatly broadens our knowledge on the early evolution of the Aleocharinae.

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