

A remarkable new fossil species of *Amplectister* with peculiar hindleg modifications (Coleoptera: Histeridae): further evidence for myrmecophily in Cretaceous clown beetles

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Abstract

Myrmecophily is a phenomenon of the symbiosis of organisms that depend on various ant (Formicidae) societies. Such interspecies associations are found in several unrelated lineages within the clown beetle family Histeridae. Recent studies have suggested that the origin of myrmecophily can be traced back to mid-Cretaceous based on a few fossil records from Kachin amber from northern Myanmar. Here, we describe a remarkable new species, *Amplectister terapoides* n. sp., from Kachin amber. This is the second species of the extinct genus *Amplectister* Caterino and Maddison, which has been found from the same amber deposit and has also been considered to be myrmecophilous. The new species here described has the most heavily modified hindlegs in any fossil histerids or even beetles discovered until now, indicating further evidence for ant colony association. Our discovery demonstrates that significant and diverse morphological adaptations to myrmecophily had already occurred during the Cretaceous.

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Keywords: Histeridae; mid-Cretaceous; palaeodiversity; inquiline; Kachin amber; Southeast Asia

1. Introduction

Myrmecophily is a symbiosis involving interspecies associations of organisms with various ant (Formicidae) societies (e.g., [Parker, 2016](#)). Myrmecophiles, organisms that make their living in the nests of ants, account for a surprising fraction of extant arthropod diversity ([Parker, 2016](#)), and they exhibit some of the most highly modified morphological characters seen in this most diverse phylum of all animal lineages (e.g., [Parker, 2016](#); [Maruyama and Parker, 2017](#)). Exaggerated glandular structures, or trichomes, on myriad parts of the body present chemicals to facilitate social integration, while fortified protective

structures may have enabled some of the earliest attempts to penetrate ants' defensive armada.

The rise of ants from the mid-Cretaceous is seen as a signal event in terrestrial ecology, prompting adaptations across the animal and plant kingdoms, particularly in associations with angiosperms ([Moreau et al., 2006](#); [Ward, 2014](#); [Barden and Grimaldi, 2016](#); [Boudinot et al., 2022](#); [Romiguier et al., 2022](#)), and palaeontologists have sought clues to the origins of some of these ancient symbioses in the fossil record. Direct evidence of inter-organismal dependencies is hard to come by in usually individually fossilised specimens, as indicated by [Jiang et al. \(2021\)](#) and [Skelley et al. \(2022\)](#). However, we may interpret as indirect evidence the presence of unusual morphological structures now found predominantly in living myrmecophiles. Thus, beetles like the mid-Cretaceous staphylinid genera

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Mesosymbion Yamamoto et al. (Yamamoto et al., 2016, 2017) and *Cretotrichopsenius* Cai et al. (Cai et al., 2017a, 2017b; Jiang et al., 2021) from Kachin amber of northern Myanmar have been hypothesised each as a specialised termitophile, exhibiting a defensive ‘limuloid’ habitus similar to that of many extant termite-colony inquilines. Another rove beetle, the lower Eocene pselaphine genus *Protoclaviger* Parker and Grimaldi from Indian Cambay amber, exhibits reduced mouthparts and well-developed trichomes, and is hypothesised to be a true, obligate myrmecophile (Parker and Grimaldi, 2014).

Histeridae, also known as the clown beetles, is a moderately large family in Coleoptera, with over 390 genera and 4300 species in one extinct and nine extant subfamilies worldwide (Mazur, 2011; Zhou et al., 2020). Histerids are predaceous and commonly found beetles in forested or arid environments, showing a cosmopolitan distribution. They are found in various cryptic habitats such as leaf litter, fungi, rotten wood, vertebrate dung or carrion. Several unrelated lineages of this family have converged on myrmecophilous habits, and they show significant diversity, both ecologically and morphologically, with the extreme examples seen in the following two subfamilies: Haeteriinae and Chlamydopsinae (e.g., Caterino and Degallier, 2007; Parker, 2016; von Beeren and Tishechkin, 2017). Given this, the histerids represent an ideal model system to elucidate the origin and evolutionary history of obligate behavioural symbioses with ants.

Considering the origin of myrmecophily in Histeridae, two previously hypothesised extinct myrmecophiles have been described. *Amplectister* Caterino and Maddison, found from Kachin amber, was presumed myrmecophilous on the basis of several external morphological features, especially the abdominal-metathoracic leg complex (Caterino and Maddison, 2018). Phylogenetic evidence may also serve as the basis for such hypothetical associations; the Cretaceous histerid *Promyrmister* Zhou et al., also from Kachin amber, represents the oldest putative member of the histerid subfamily Haeteriinae (Zhou et al., 2019), all of the extant species of which are obligate guests of social insects, primarily ants. As our understanding of the diversity and relationships of fossil insects grows, we will increasingly be able to integrate morphological and phylogenetic data in reconstructing the early evolution of such intriguing life histories.

Fossil records of the Histeridae in the Cretaceous are rapidly increasing, with 10 species now described, and others in preparation or otherwise known (Poinar and Brown, 2009; Caterino et al., 2015; Caterino and Maddison, 2018; Caterino, 2021; Zhou et al., 2019, 2020; Jiang et al., 2022). These records have been invariably difficult to place in extant higher taxa, as all but the recently described *Anapleus kachinensis* Jiang et al., 2022 have represented new genera. Nonetheless, they have all helped show that the family had diversified considerably by the Cretaceous, pointing much further back in time for its initial origin. As mentioned above, only two taxa, *Promyrmis-*

ter Zhou et al. and *Amplectister* both found from Kachin amber, have been considered myrmecophilous, and they have exhibited more or less ‘modest’ modifications of external morphology.

Here, we describe a remarkable new *Amplectister* species from Kachin amber from northern Myanmar. The new species has the most dramatically and heavily modified hindlegs found so far in any fossil Histeridae, providing further evidence for early integration into ant societies. We discuss its unusual morphological characters, and the means by which these may represent adaptations to ant inquilinism.

2. Material and methods

2.1. Geological setting and material

The sole amber specimen studied herein originated from the Noije Bum hill mines, Hukawng Valley, Kachin State, northern Myanmar. It is housed in the Hokkaido University Museum, Hokkaido University, Sapporo, Japan (curator: M. Ôhara), under the assigned number of SEHU-0000121201. The holotype of *Amplectister terapoides* n. sp. is very well preserved, embedded in a narrowly elongate cuboid piece of yellowish transparent amber (17.4 × 4.7 × 3.6 mm). We adopt the mid-Cretaceous age (near Albian–Cenomanian boundary or slightly older) for Kachin amber, or previously called Burmese amber (Mao et al., 2018; Balashov, 2021).

2.2. Imaging, editing and Zoobank registration

Observations were made using two different binocular stereomicroscopes (Nikon SMZ745T, Nikon SMZ800). Detailed photomicrographs of the beetle fossil were taken using a Canon EOS 80D digital camera, mounted on a Canon MP-E 65 mm macro lens (F2.8, 1–5×), with the aid of Canon MT-24EX twin flash. The specimen was submerged in clove oil when it was photographed. Image stacks were carried out with Helicon Focus 8.1.0. All figures were edited and assembled using Adobe Photoshop Elements 15. The morphological terminology follows Caterino and Maddison (2018).

This published work and the nomenclatural acts it contains have been registered in ZooBank, the proposed online registration system for the International Code of Zoological Nomenclature (ICZN). The ZooBank Life Science Identifiers (LSIDs) can be resolved and the associated information viewed through any standard web browser by appending LSID to the prefix ‘http://zoobank.org/'. The LSID for this publication is: urn:lsid:zoobank.org:pub:4A91EC2A-234E-4777-A5D3-DBAB6E176855.

3. Systematic palaeontology

Superfamily Histeroidea Gyllenhal, 1808
Family Histeridae Gyllenhal, 1808

Genus *Amplectister* Caterino and Maddison, 2018

Amplectister terapoides n. sp.
(Figs. 1–5)

Zoobank LSID: urn:lsid:zoobank.org:act:AA54065C-8B C1-404E-A121-5D05C72C0607.

Etymology: The species name refers to the marked similarity in modifications of the posterior legs to those in the haeteriine genus *Terapus* Marseul, 1863 (see Fig. 6A). That name, in turn, translates to ‘mutant foot’.

Holotype: SEHU-0000121201, sex undetermined. The beetle inclusion can be observed from multiple angles, except the frontal one. Syninclusion: Diplopoda (ca. 2.65 mm long).

Stratigraphic position and age: Kachin amber, unnamed horizon, mid-Cretaceous (near Albian–Cenomanian boundary).

Type locality: The Noije Bum hill mines, Hukawng Valley, Kachin State, northern Myanmar.

Description: Sex undetermined. Total body (pronotum + elytra) length: 1.30 mm; maximum (humeral) width: 0.81 mm; head width: 0.32 mm; pronotal length: 0.39 mm; pronotal width: 0.76 mm; elytral length (from posterior margin of pronotum to elytral apices along midline): 0.91 mm.

Body small, subquadrate, oblong, dorsally irregularly flattened. Surface leathery, not shiny, generally glabrous without ground setae, lacking obvious punctures (ventral side partly with large, dense punctures). Colour uniformly dark brown to dark reddish brown.

Head (Figs. 1, 3, 4A–C) small, mostly retracted, only partially exposed. Frons not well visible. Eyes present, large, located on sides of head. Mandibles apically acute, incisor edges short, without inner teeth. Antenna short; antennal scape elongate, curved, angulate at inner apical corner; pedicel short, expanded, moderately transverse; antennal funicle apparently with 6 moderately transverse antennomeres, gradually widening and lengthening distad, with antennomere 8 nearly as wide as club; antennal club elongate oval, subcylindrical, weakly truncate apically, surface setose with elongate setose patch on inner apical surface (Fig. 4C, ssp).

Pronotum (Figs. 1A, 3A) broad, strongly transverse (width/length = 1.95), with deep anterior emargination; sides broadly rounded, widest at near base; anterior corners rounded; posterior margin sinuate, rather strongly produced at obtuse angle; central part of pronotal disk convex dorsally, with moderately well-developed median ridge, rising to anterior margin, lateral areas widely depressed to broadly explanate, slightly reflexed. Scutellum small, narrowly triangular (Fig. 4A, sc).

Elytra (Figs. 1A, 3A) broad, moderately flattened, widest near shoulders, gently gradually narrowed apically, with truncate apical margin; posterolateral corners broadly rounded; each elytron with prominent marginal carina, depressed along its inner edge, also weakly carinate along sutural margin; each elytron with prominent marginal carina (Figs. 2, 5A); surface with several sparsely distributed erect setae, lacking distinct striae but with weak serial depressions; hindwings not visible.

Prosternum emarginate at base (Figs. 3B, 4C), without clearly separate prosternal lobe, i.e., presternal suture

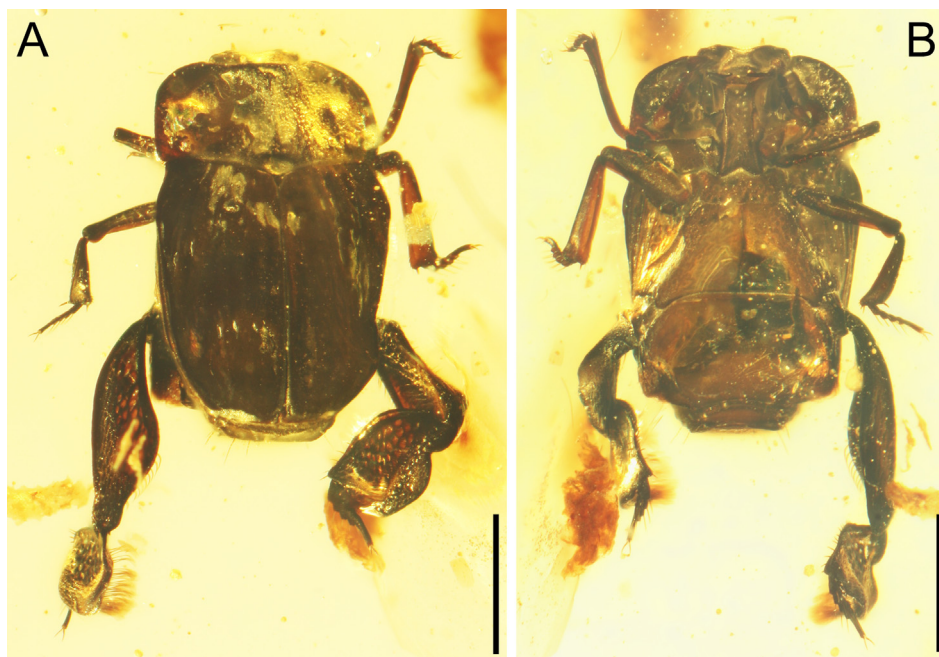


Fig. 1. *Amplectister terapoides* n. sp., holotype, SEHU-0000121201. (A) General habitus, dorsal view. (B) General habitus, ventral view. Scale bars = 0.5 mm.

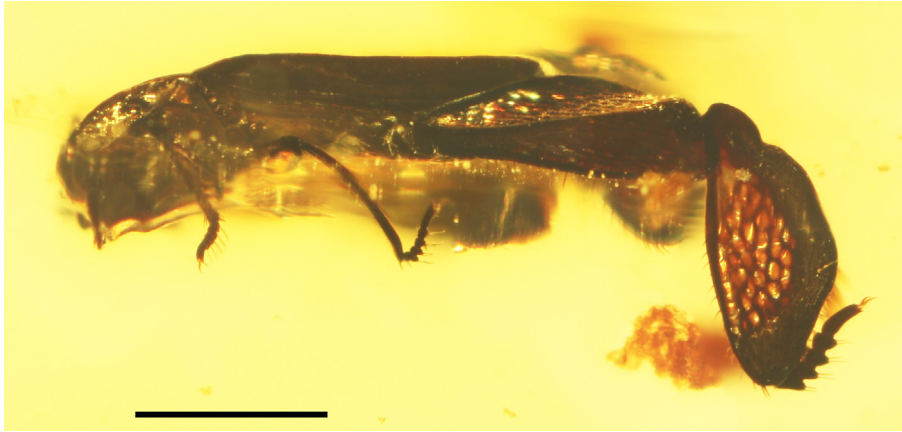


Fig. 2. *Amplectister terapoides* n. sp., holotype, SEHU-0000121201, general habitus, lateral view. Scale bar = 0.5 mm.

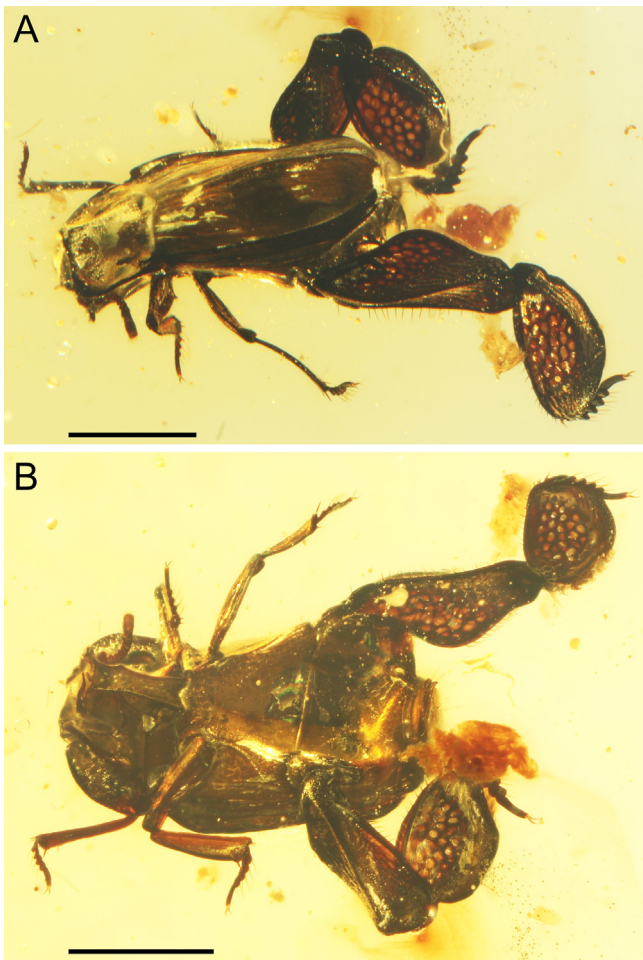


Fig. 3. *Amplectister terapoides* n. sp., holotype, SEHU-0000121201. (A) General habitus, dorsolateral view. (B) General habitus, ventrolateral view. Scale bars = 0.5 mm.

absent; lateral furrow present for passage of antennal funicle exposed; cavities for reception of antennal club located on prosternal sides, delimited by a distinct outer and posterior margin (Fig. 4C, ac); prosternal keel with two prominent carinae, subparallel-sided from base to near apex,

converging slightly above antennal cavities, uniformly distinctly depressed between; lateral carinae present on keel, from inner corner of front coxa anterad to join carinae on keel. Procoxal cavities widely separated. Mesoventrite (Figs. 1B, 3B, 4D) broad, anterior margin sinuate, weakly but distinctly produced at middle; surface uniformly densely punctured. Metaventrite with prominent, oblique postmesocoxal carinae extending from inner corners of mesocoxae to middle of metacoxa; middle of metaventrite increasingly depressed posterad, median longitudinal suture present; surface without with large punctures including lateral areas.

Legs (Figs. 1–3, 4D, E, 5) long, distinct, with significant modifications on hindleg. Procoxa moderately and obliquely transverse; profemur gradually narrowed apically; protibia slender, rod-like, widened weakly to apex, with two small apical spurs at inner corner, and a longer spine at outer corner (Fig. 4E); protarsomere 1 elongate, longer than each of protarsomeres 2–4; protarsomeres 2–4 each short, subequal; basal 4 tarsomeres each with pair of apicoventral setae; protarsomere 5 about three times longer than protarsomere 4, with pair of regular simple pretarsal claws. Mesocoxae small, rounded, widely separated; mesofemur moderately narrowed to apex; mesotibia slender, with short, thin apical spurs, outer edge slightly rounded, with single prominent spine at outer apical margin; mesotarsus as for protarsus. Metacoxae rounded, very broadly separated; metatrochanter small; metafemur broad and distinctly expanded, with prominent carina along outer medial surface obliquely, outer surface moderately setose, with honeycomb-like peculiar pattern of large punctures, inner surface weakly concave for reception of inner edge of metatibia; metatibia markedly broad and flat, elongate oval, significantly expanded, inner margin with scattered sparse setae, outer surface with honeycomb-like peculiar pattern of large punctures except along outer margin, inner surface with numerous stiff long setae along outer (= upper) margin of metatibia (Figs. 1A, 5C, D); metatarsus segmented as for meso- and protarsus, apparently received along apical half of outer edge of medial tibial face (Figs. 2, 5A, B).

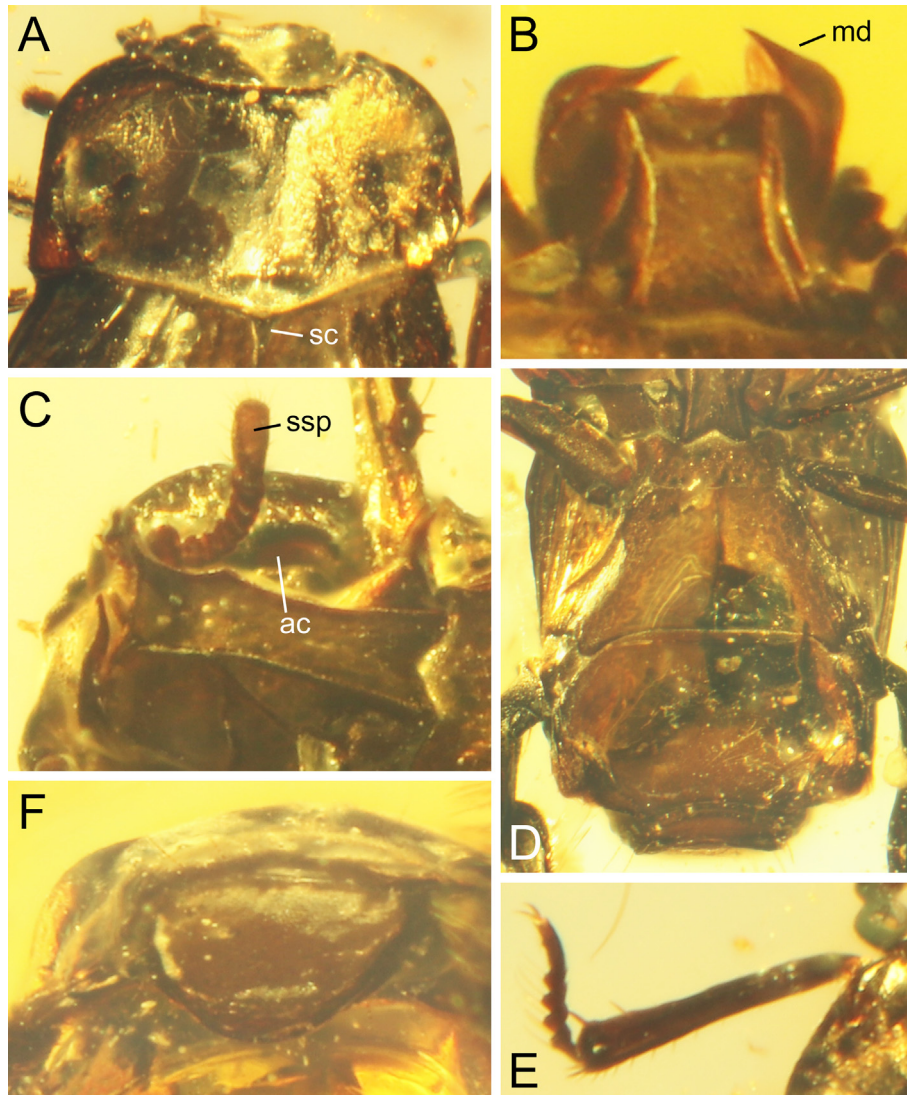


Fig. 4. *Amplectister terapoides* n. sp., holotype, SEHU-0000121201. (A) Head and pronotum with scutellum, dorsal view. (B) Head, ventral view. (C) Prothorax and antenna, left, ventral view. (D) Mesothorax, metathorax and abdomen. (E) Protibia and protarsus, right, dorsal view. (F) Propygidium, posterior view. Abbreviations: ac, antennal cavity on the prosternum; md, mandible; sc, scutellum; ssp, a specialised setose patch on the inner apical surface of the terminal antennomere.

Abdominal venter (Figs. 1B, 3B, 4D) deeply concave medially; sides of first ventrite elevated behind metacoxae; subsequent ventrites transversely depressed, with abdomen deeply arched to pygidial apex. Propygidium (Fig. 4F) exposed, half-moon shaped; pygidium subtriangular, with rounded sides and apex. Genitalia not visible.

Comparison: *Amplectister terapoides* n. sp. is closely similar to the nominotypical species, *Amplectister tenax* Caterino and Maddison, 2018, in general appearance. In fact, *A. tenax* bears numerous unmistakable similarities that speak to a close relationship between it and *A. terapoides* n. sp. Indeed the significant differences are almost entirely confined to the remarkable hind legs of the latter. While the hind legs of *A. tenax* are also highly modified, its hind femur and especially hind tibiae are much more slender. The abdomen of *A. terapoides* n. sp. is also much more deeply depressed than that of *A. tenax*, in which the depression

only barely extends anterad onto the metaventricle. In *A. terapoides* n. sp. the metaventricle is depressed all the way to the meso-metaventral suture, and the metaventral surface lacks distinct punctation that is evident on the central part of the metaventricle of *A. tenax*. The marginal carina on each elytron is much more prominent in *A. terapoides* n. sp. (Figs. 2, 5A) than it is in *A. tenax* (Caterino and Maddison, 2018, fig. 4). The general body form of *A. terapoides* n. sp. is flatter, with little to no dorsal convexity, than is that of *A. tenax*. There are few sparsely scattered erect setae on the elytral surface of *A. terapoides* n. sp., whereas such setae are completely absent in *A. tenax*.

Together, the above character differences seem sufficient to support distinct species status for *A. tenax* and *A. terapoides* n. sp. We had initially considered whether the extremes seen in *A. terapoides* n. sp. might represent sexual (presumably male) characters, only poorly developed in *A.*

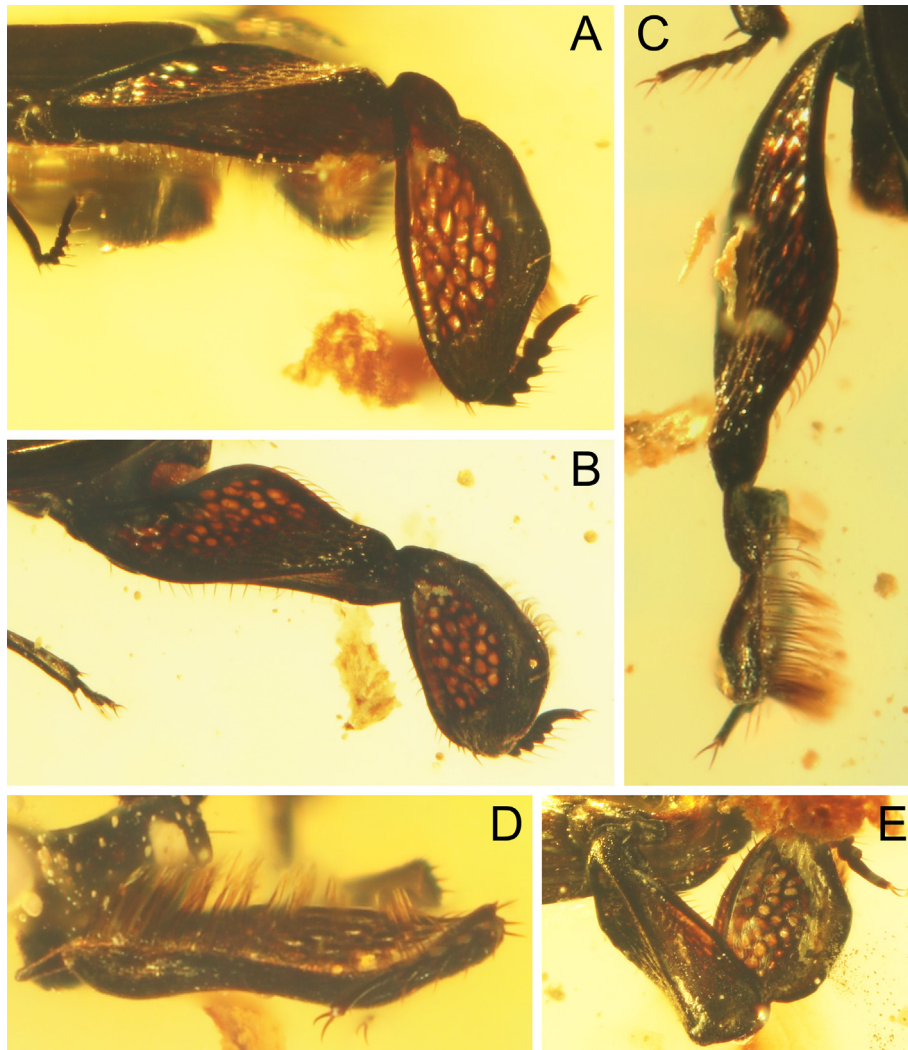


Fig. 5. *Amplectister terapoides* n. sp., holotype, SEHU-0000121201, hindleg, left. (A) Lateral view. (B) Dorsolateral view. (C) Dorsoposterior view. (D) Posterior view. (E) Ventrolateral view.

tenax. However, while leg dimorphisms are known in Histeridae (e.g., *Saprinus alienus* LeConte, 1851; *Vaquerister cantador* Caterino and Tishechkin, 2022), the females are invariably unmodified, while the shapes of the males depart from the norm. The legs and venter of *A. tenax* are unmistakably modified relative to plesiomorphic histerid morphology, and seem more likely to be species level characters. The differences also seem to preclude any kind of minor/major intraspecific polymorphism, especially given differences in overall body shape. Instead, there is every indication that the genus *Amplectister* had diversified by the time these examples were fossilised.

4. Discussion

4.1. Taxonomic placement

Among all fossil Histeridae, our new specimen found in mid-Cretaceous Kachin amber can be very easily separated from all others by having markedly modified hindlegs (see

Figs. 1–3, 5). Regardless of their significant structures, the general habitus and other body parts of the specimen are almost fully congruent with those of Histeridae. Therefore, the familial placement under Histeridae is strongly supported. We placed the specimen into the extinct genus *Amplectister* previously solely known from Kachin amber based on the general similarities as follows: elongate and flattened overall body form, elevated prosternal keel with antennal cavities lying along its sides, general pronotal shape with its sinuate posterior margin, and deeply concave abdomen (Caterino and Maddison, 2018).

Amplectister terapoides n. sp. is the second record of the genus and it also represents the second species of *Amplectister* known to date. Our finding provides new insight into the morphological diversity of *Amplectister*, as stated in the ‘Comparison’ section such as the more flattened general body, distinctly modified metatibiae, presence of sparsely scattered erect setae on the elytra, etc. (cf. Caterino and Maddison, 2018). Since the sole specimen of *A. tenax* is largely encrusted with whitish granular thin film (Caterino

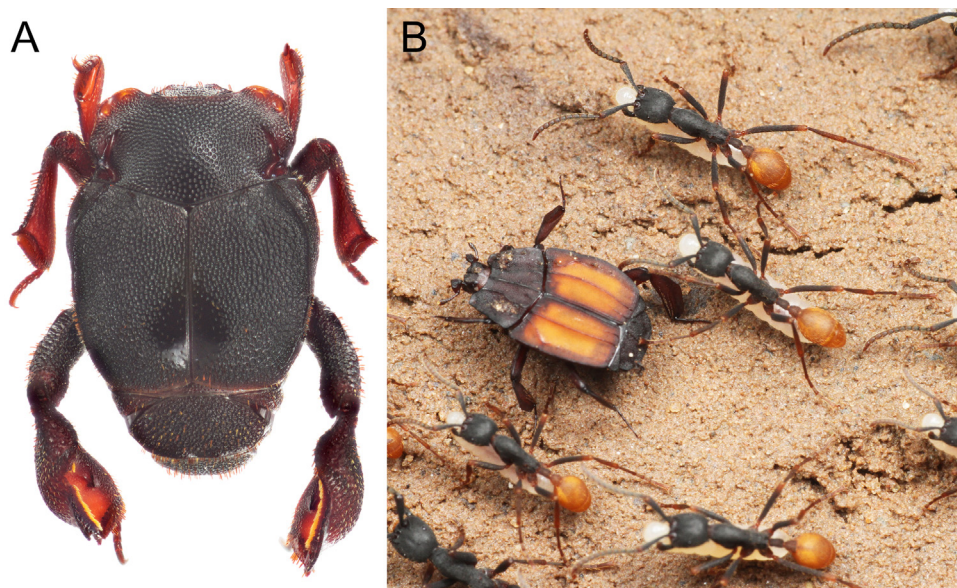


Fig. 6. Extant Haeteriinae associated with Neotropical army ants (Ecitonini). (A) *Terapus* sp. (probably undescribed) from Cerrado habitats, with a pronotal-elytral length of 4.8 mm. (B) *Colonides* beetle with *Eciton burchellii* army ants in Peru. Photo credit for (B): ©Taku Shimada (AntRoom, Tokyo), used with permission.

and Maddison, 2018), the holotype of *A. terapoides* n. sp. provides more detailed information on the body surfaces, especially on the ventral side.

Caterino and Maddison (2018) considered the possibility that *A. tenax* belonged in or near the extant subfamily Sapriniinae, which today contains few myrmecophiles. Those that are known, like *Phoxonotus* Marseul or *Myrmecites* Marseul, do not show such extreme modifications as *Amplectister*, which as the name of the new species implies, are much more similar to those in the morphologically diverse Haeteriinae. In contrast, Zhou et al. (2020) alternatively suggested this genus could be included in an expanded and redefined Onthophilinae. No new light is shone on these higher level relationships by characters visible in *A. terapoides* n. sp. The saprinine-like prosternal keel remains suggestive of a relationship to Sapriniinae, while other characters that one might expect in an early member of the subfamily are not evident (see Caterino and Maddison, 2018 for specifics). Nevertheless, more specimens and further analyses to reveal genitalic characters, particularly the degree to which the concealed abdominal segments 8–10 are modified, would be extremely useful in revealing characters pertinent to higher level placement of *Amplectister*.

4.2. Morphological and probable behavioural adaptations as inquilines with ants

Overall, *Amplectister terapoides* n. sp. is extremely unusual when compared to the other putative fossil symbionts of termite/ant colonies from the Cretaceous so far discovered. In fact, *A. terapoides* n. sp. has a pair of remarkably expanded and modified hindlegs with several specialised features that include honeycomb-like punctures and the

presence of combs of stiff long setae along the inner marginal surfaces. These specialised anatomical and morphological features on the hindlegs are rather frequently observed in the Recent haeteriine clown beetles (Fig. 6A). In fact, many of them are associated with army ants as myrmecophiles (see, ecological photo of Fig. 6B). Here we consider these characteristics in the fossil as specialised structures that are hallmarks of social symbionts. On the other hand, two putatively inquilinous aleocharine rove beetle species from Kachin amber exhibit a much simpler, typical defensive ecomorphology without significantly protruding legs (Yamamoto et al., 2016; Cai et al., 2017a; Jiang et al., 2021), and thus, they have a completely different body plan from *A. terapoides* n. sp. A fossil haeteriine, *Promyrmister kistneri* Zhou et al., 2019, also from Kachin amber embodies a form indicative of true behavioural symbiosis (Zhou et al., 2019), but it lacks such greatly modified hindlegs. Given the extremely derived features of the hindlegs, it may even stand as one of the most bizarre-looking beetles ever found from the Mesozoic.

The most intriguing question about *Amplectister* remains: what purpose(s) were served by the enlarged hind legs? To answer this fundamental question, Caterino and Maddison (2018) examined a range of possibilities, all centered on grasping, either between the sexes, as defense, or for phoresy. The much more deeply concave venter of *A. terapoides* n. sp. seems to further substantiate the last possibility — these structures are adaptations to hold on to something, but what? The strong similarity of the legs of *A. terapoides* n. sp. to its namesake, haeteriine histerids in the genus *Terapus* (Fig. 6A), suggests associations with ants, as all *Terapus* species are obligate myrmecophiles, with the genus *Pheidole* (Hinton, 1945). Yet, no biological observations have ever been published to suggest a more

specific function for its exaggerated hind legs. Some other Haeteriinae with enlarged hind legs, however, have been observed to ride their hosts, including *Euxenister* Reichen-sperger; *Chrysetaerius* Reichen-sperger and *Pulvinister* Reichen-sperger. Similar, though convergent, adaptations are found in the ant-riding chlamydopsine histerid *Chlamy-dopsis loculosa* Lea, 1925, sometimes known as the ‘jockey beetle’ (McMillan, 1950). Akre (1968) has described many of these behaviours in Haeteriinae in detail. It is noteworthy that most of these have dense setal brushes on the inner sides of the tibiae, as seen in *A. terapoides* n. sp. (Figs. 5C, D), which are used in a ‘grooming’ behaviour that seems to help transfer ant colony odors to the beetles (Akre, 1968). The most unusual feature of *Amplectister*, with no analog among extant enlarged-legged myrmecophilous histerids, is the deeply concave venter. It is tempting to hypothesise an association that would also have no extant analog, perhaps with the extinct ant subfamily Haidomyrmecinae, the so-called ‘hell ants’, which exhibit remarkable taxonomic and morphological diversity in Kachin amber (e.g., Perrichot et al., 2020).

5. Conclusions

A remarkable new fossil species of clown beetles, *Amplectister terapoides* n. sp., is described from mid-Cretaceous Kachin amber from northern Myanmar. Based on the well-preserved adult specimen, we could observe many morphological characters from various angles. The overall morphological characters found in the hindlegs are exceptional; they are markedly expanded and enlarged, also possessing dramatic features such as the presence of numerous peculiar, honeycomb-like large punctures on the metafemora and metatibiae, together with stiff long setae along the inner marginal surface on the metatibiae. We hypothesise that these specialised anatomical features strongly suggest the Mesozoic beetle was a true myrmecophile, a symbiont in some Cretaceous ant’s nest. Along with previous studies (Caterino and Maddison, 2018; Zhou et al., 2019), our discovery further reinforces an ancient origin of obligate behavioural symbioses between clown beetles and ants, and that these associates had diversified considerably by mid-Cretaceous.

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