



The beetle fauna of mid-Cretaceous Kachin amber: a systematic synthesis

YAN-DA LI^{1,2,*} & CHEN-YANG CAI^{2,3,*}

¹Bristol Palaeobiology Group, School of Earth Sciences, University of Bristol, Bristol BS8 1TQ, UK

²State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China

³Nanjing College, University of Chinese Academy of Sciences, Nanjing 211135, China

✉ ydli@pku.edu.cn; <https://orcid.org/0000-0002-9439-202X>

✉ cycail@nigpas.ac.cn; <https://orcid.org/0000-0002-9283-8323>

*Corresponding authors

Abstract

Kachin amber from northern Myanmar, dated to the mid-Cretaceous (*ca.* 99 Ma), is an exceptional fossil Lagerstätte that preserves ancient terrestrial ecosystems in vivid, three-dimensional detail. Over the past decade, numerous beetle taxa representing a wide range of extant and extinct lineages have been described from this deposit, substantially expanding our knowledge of Cretaceous coleopteran diversity. Despite these discoveries, a comprehensive synthesis of the beetle fauna from Kachin amber remains unavailable. Here, we review the current record of beetles from Kachin amber and summarize the taxonomic composition of the fauna across major coleopteran groups. Particular attention is paid to fossils of evolutionary or ecological significance. This synthesis provides an updated overview of the diversity and systematic composition of the Kachin amber beetle fauna and highlights the importance of the deposit for future studies of beetle evolution and Cretaceous terrestrial ecosystems.

Keywords: Kachin amber, Coleoptera, Cretaceous, fossil, palaeodiversity

Introduction

Kachin amber (Burmese amber) from northern Myanmar, dated to the mid-Cretaceous (*ca.* 99 Ma), represents one of the most important fossil Lagerstätten for understanding terrestrial ecosystems of this period (Shi *et al.*, 2012). Like other amber deposits, it preserves organisms in three dimensions, often retaining fine morphological details that are rarely observable in adpression fossils. This exceptional preservation, combined with modern imaging techniques such as confocal microscopy and micro-computed tomography, allows detailed investigation of both external and internal structures (Fu *et al.*, 2021). Compared with other major amber deposits, Kachin amber offers a unique combination of taxonomic richness and

temporal significance (Penney, 2010). Earlier deposits, such as Lebanese or Spanish ambers (Lower Cretaceous), often yield limited available material; conversely, major Cenozoic deposits such as Baltic or Dominican ambers, while abundant, represent much later stages where the faunas already closely resemble extant lineages.

Beetles constitute a major component of the Kachin amber biota, exhibiting remarkable taxonomic and morphological diversity (Figs 1, 2). To date, representatives of all four extant suborders (Archostemata, Myxophaga, Adephaga, and Polyphaga), as well as all but three superfamilies in the hyperdiverse suborder Polyphaga, have been documented from this deposit. While the comprehensive checklists provided by Ross (2019–2026) offer an invaluable census of the taxa recorded from Kachin amber, the information in such lists is necessarily concise. Beutel *et al.* (2024) recently reviewed the Palaeozoic and Mesozoic fossil record of Coleoptera, including some discoveries from Kachin amber. However, as a broad-scale synthesis of the entire Palaeozoic and Mesozoic record, their work is necessarily selective in its treatment of Kachin amber taxa. Given the rapid influx of new discoveries and the increasing complexity of beetle systematics, there is a clear need for a more comprehensive and focused synthesis of the Kachin amber coleopteran assemblage. The following sections provide a systematic review of the beetle fossils from Kachin amber, emphasizing the diversity of families and discussing the broader implications of the key findings within each group.

Results

Systematic review

Archostemata

The families Cupedidae and Ommatidae, which exemplify the characteristic archostematan appearance with incompletely sclerotized elytra bearing window punctures, have both been found in Kachin amber (e.g., Y.D. Li *et al.*, 2019). Ommatidae are represented today by only three genera and seven species, exhibiting limited morphological disparity. In contrast, ommatids from Kachin amber, including representatives of the extant genus *Omma* Newman as well as numerous extinct genera such as *Clessidromma* Jarzembowski *et al.*, *Stegocoleus* Jarzembowski & Wang, and *Miniomma* Li *et al.*, are not only more diverse but also display substantially greater morphological variation (e.g., Li *et al.*, 2020b, 2021c; Tihelka *et al.*, 2020d; Li & Cai, 2021). The fossil genus *Notocupes* Ponomarenko was long considered a member of Ommatidae. Exceptionally well-preserved *Notocupes* specimens from Kachin amber have greatly facilitated interpretation of morphological features that are difficult to discern in adpression fossils. As a result, *Notocupes* was reinterpreted as the sister group to Cupedidae (Li *et al.*, 2023g, h). The enigmatic family Micromalthidae is represented today by a single species that reproduces via parthenogenetic paedogenesis, and its rarely observed infertile adults are weakly sclerotized (Perotti *et al.*, 2016). Adult Micromalthidae have been reported from Kachin amber (Tihelka *et al.*, 2020e; Yamamoto, 2021), supplementing previously known adult and larval records from other Cretaceous and Cenozoic ambers. These fossil adults share a similar body plan with the extant species and are likewise weakly sclerotized, although it is generally impractical to infer further details of the life cycle from fossil material.

Myxophaga

The suborder Myxophaga comprises four extant families, all of which are small-bodied and aquatic or semi-aquatic, each exhibiting a distinctive body form. Among them, Lepiceridae and Sphaeriusidae have been recorded from Kachin amber. The Kachin amber representatives of both families display the characteristic body plans of their extant counterparts, and in each case some species have even been assigned to extant genera (e.g., Jałoszyński *et al.*, 2017; Fikáček *et al.*, 2023; Li *et al.*, 2023f, 2024b), although certain authors expressed a different view regarding the generic attribution of the lepicerid fossils (Kirejtshuk *et al.*, 2023a).

Adephaga

The earliest diverging adephagan family, Gyrinidae, is aquatic in both adult and larval stages, and both life stages have been described from Kachin amber (Zhao *et al.*,

2019; Gustafson *et al.*, 2020; Liang *et al.*, 2020). Another aquatic family, Dytiscidae, has also been recorded from Kachin amber based on an adult specimen (Yang *et al.*, 2019).

Among terrestrial adephagans, a member of Cicindelidae, *Hujia* Song *et al.*, was described from Kachin amber (Song *et al.*, 2022), though its further assignment to Manticorini by the original authors was later questioned by Schmidt *et al.* (2023). Carabidae, the most species-rich family within Adephaga, occupy a wide range of terrestrial habitats. Fossil carabids from Kachin amber also exhibit some intriguing ecological specializations. For example, *Burmapseudomorphus* Beutel *et al.*, similar to extant members of Pseudomorphini, possesses a flattened oval body and likely preferred living under bark (Beutel *et al.*, 2020), while *Kryzhanovskiana* Kataev & Kirejtshuk appears more specialized than its extant relatives in Metriini, being eyeless and presumably inhabiting dark enclosed interspaces (Kataev *et al.*, 2019). A larva of Ozaenini from Kachin amber possesses a characteristic terminal disk with branched urogomphi, closely resembling that of extant members of the tribe and likely representing an early adaptation for phragmotic defence and prey capture (Liu *et al.*, 2026). Notably, both adults and larvae of the extant genus *Loricera* Latreille have been recovered from Kachin amber (Li *et al.*, 2024h, i). In modern representatives of the genus, adults and larvae each possess specialized mechanisms for preying on collembolans, and the fossil specimens exhibit identical predatory adaptations. As predators and prey are generally expected under the Red Queen hypothesis to undergo continuous coevolution, the conserved predatory mechanism observed in *Loricera* represents an intriguing exception to this expectation.

Polyphaga

Scirtoidea. Scirtidae have been recorded from Kachin amber. Two of these fossils were subjected to phylogenetic analyses and respectively placed in the *Veronatus* group and the *Macrodescillus* group (Li *et al.*, 2022k, 2025i).

Clamboidea. Extant Clambidae generally exhibit a convex body form and are capable of conglobation as a defensive strategy; this morphotype is also present in Kachin amber (Cai *et al.*, 2019b). However, Kachin amber has additionally yielded a distinct clambid morphotype characterized by a flattened body with fully explanate margins, forming a shield-like appearance and implying an alternative defensive adaptation (Li *et al.*, 2026c). Extant Eucinetidae comprise two morphological groups: one with suctorial or semisuctorial mouthparts, and the other with normal non-suctorial mouthparts. Representatives of both groups have been discovered in Kachin amber (Jałoszyński, 2019; Li *et al.*, 2024a).

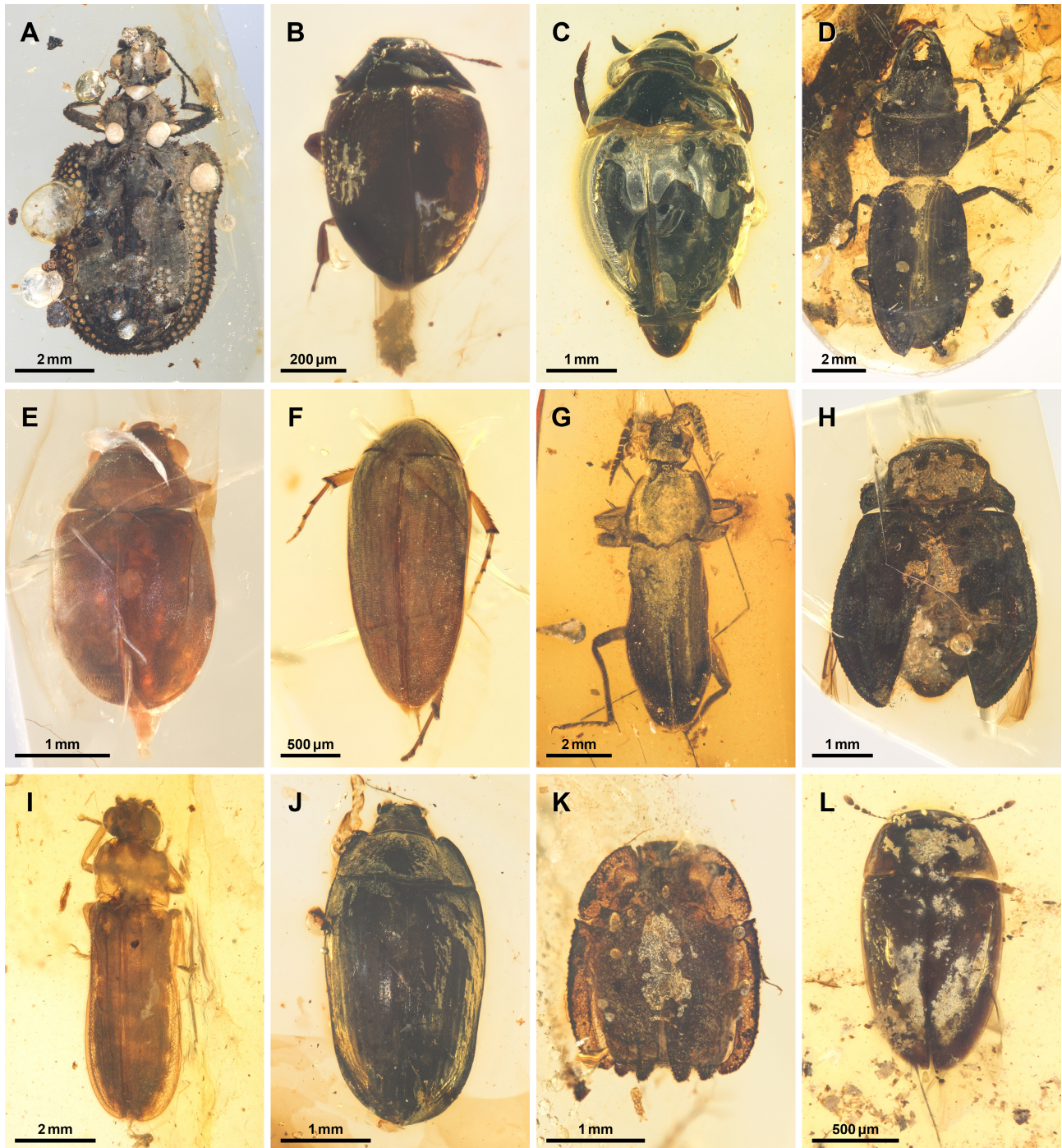


FIGURE 1. Representative beetles from mid-Cretaceous Kachin amber. **A**, *Stegocoleus arkonus* (Archostemata: Ommatidae). **B**, *Bezesporum huchengi* (Myxophaga: Sphaeriusidae). **C**, Gyrinidae sp. (Adephaga). **D**, Carabidae sp. (Adephaga). **E**, *Serracyphon philipsi* (Scirtoidea: Scirtidae). **F**, *Eucinetus zhenhuai* (Clamboidea: Eucinetidae). **G**, *Pagodocerus volkovitshi* (Dryopoidea: Mastigocoleidae). **H**, *Dictyorachys callidictyus* (Buprestoidea: Buprestidae). **I**, *Cretophengodes azari* (Elateroidea: Cretophengodidae). **J**, *Archaenosodendron remotidens* (Nosodendroidea: Nosodendridae). **K**, *Fantosmium qizhihaoi* (Histeroidea: Histeridae). **L**, Hydrophilidae sp. (Hydrophiloidea).

Buprestoidea. Legalov (2025) claimed that *Cretadystaxia* Legalov found in Kachin amber belongs to Schizopodidae. However, the published figures are not of sufficient quality to permit independent assessment of key familial diagnostic features, such as the deeply bilobed

tarsomere 4. Regarding Buprestidae, two adults have been described from Kachin amber (Jiang *et al.*, 2021a; Li *et al.*, 2023i). Of these, *Dictyorachys* Li *et al.* exhibits an unusual combination of characters that precludes confident placement within any known subfamily or

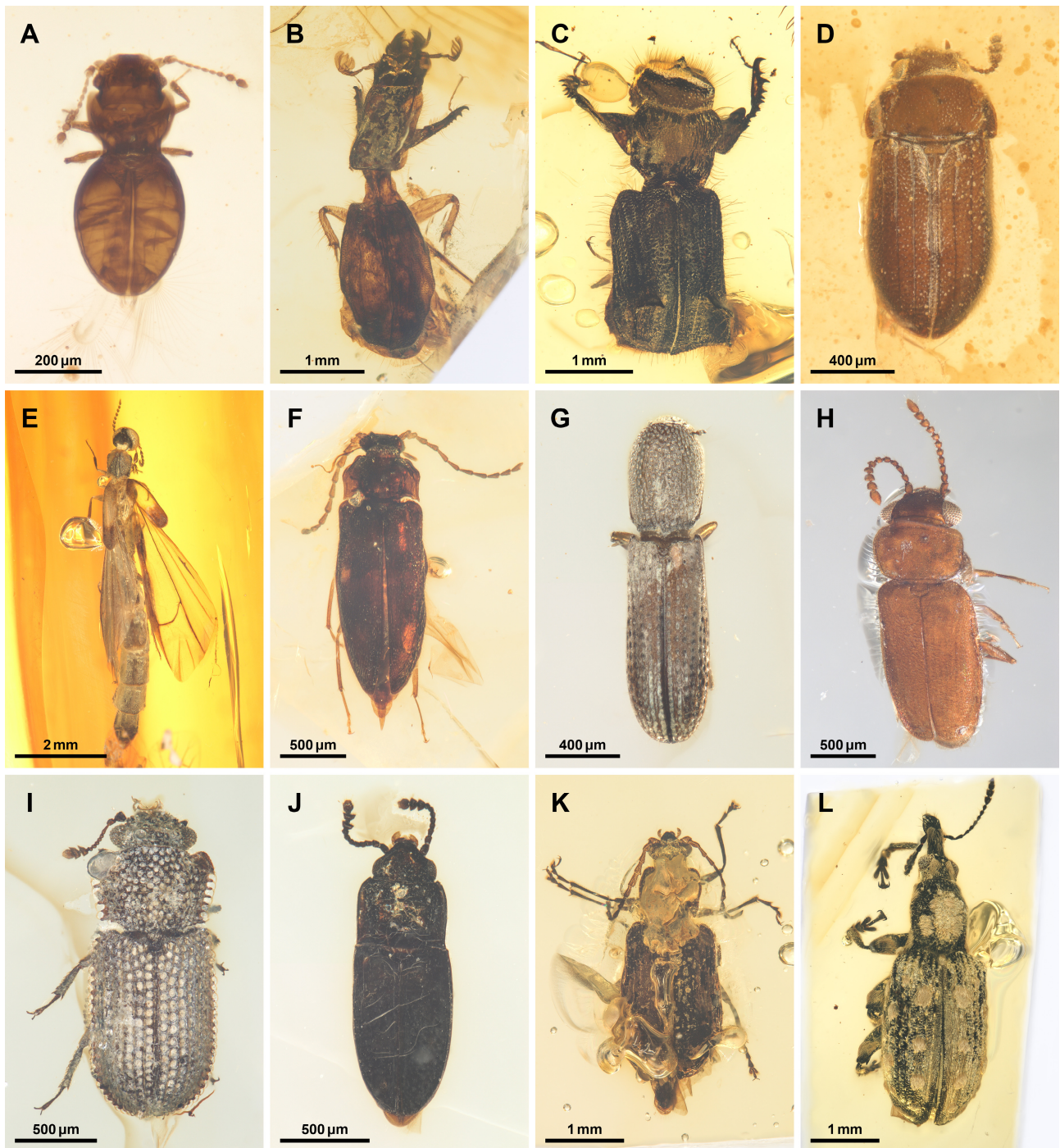


FIGURE 2. Representative beetles from mid-Cretaceous Kachin amber. **A**, *Kekveus brevisulcatus* (Staphylinoidea: Ptiliidae). **B**, *Passalopalpus cheni* (Scarabaeoidea: Passalopalpidae). **C**, *Poinarinius lesnei* (Bostrichoidea: Bostrichidae). **D**, *Foveapeltis rutai* (Cleroidea). **E**, *Cretoquadratus fossilis* (Lymexyloidea: Lymexylidae). **F**, *Glyphonotum hsiao* (Tenebrionoidea: ?Pythidae). **G**, *Delteredolaemus hei* (Coccinelloidea: Terebridae). **H**, *Isocryptophilus exilipunctus* (?Erotyloidea). **I**, *Trematosphindus newtoni* (Nitiduloidea: Sphindidae). **J**, *Alloterocucus atratus* (Cucujoidea: ?Lamingtoniidae). **K**, Chrysomelidae sp. (Chrysomeloidea). **L**, *Nugatorhinus chenyangi* (Curculionoidea: Mesophyletidae).

tribe (Li *et al.*, 2023i). In addition, wood-boring larvae attributable to Buprestidae have also been reported from Kachin amber (C. Haug *et al.*, 2021).

Dryopoidea. Adults of several dryopoid families have been described from Kachin amber, including

Ptilodactylidae (Chatzimanolis *et al.*, 2012), Psephenidae (Cai & Huang, 2018a; Li *et al.*, 2022e), Elmidae (Cai *et al.*, 2018b), Limnichidae (*e.g.*, Kirejtshuk & Prokin, 2022; Li *et al.*, 2022m, 2025b), and Heteroceridae (Li *et al.*, 2020a). Among these, the heterocerid *Excavotarsus*

Li *et al.* is morphologically distinctive, possessing fore legs with robust 2-segmented tarsi and stout claws, which likely represents an alternative burrowing adaptation compared with that seen in extant representatives of the family. The characteristic flattened disc-like larvae of Psephenidae have also been reported from Kachin amber (Bao *et al.*, 2018a). Additionally, Tihelka *et al.* (2022) established a new family, Mastigocoleidae, based on material from Kachin amber and other compression fossil deposits, and proposed it as the sister group to Lutrochidae + Dryopidae. However, recent evidence from transitional material suggests that Mastigocoleidae share a closer affinity with Dryopidae and might eventually be synonymized with the latter (Li *et al.*, 2026a; R. Kundrata, pers. comm.).

Elateroidea. Hard-bodied elateroids are generally well represented in Kachin amber, with definitive adult records for Armatopodidae (Li *et al.*, 2022f), Brachypsectridae (Qu *et al.*, 2020; Li *et al.*, 2022g), Throscidae (Li *et al.*, 2021b, 2021j), Eucnemidae (Muona, 2020; Li *et al.*, 2025d), Cerophytidae (Yu *et al.*, 2019), and Elateridae (*e.g.*, Kundrata *et al.*, 2021, 2023, 2024). Among these groups, Eucnemidae and Cerophytidae appear to be particularly common. Notably, with respect to Eucnemidae, Muona (2020) described 20 new species purportedly from Kachin amber. However, most of these fossils were poorly illustrated, hindering reassessment of their morphology and systematic placement by other researchers. Furthermore, there are concerns that certain specimens may not have originated from Kachin amber deposits at all (Li *et al.*, 2025d). Recent molecular studies have demonstrated that Elateridae also encompass several soft-bodied lineages, including Plastocerinae, Omalisinae, and Drilini (Kusy *et al.*, 2018). Li *et al.* (2021d) reported a soft-bodied genus, *Anoema* Li *et al.*, from Kachin amber, which shares morphological similarities with extant Omalisinae. Nevertheless, given the complex convergent evolution of soft-bodiedness across Elateroidea, this genus is currently treated as Elateroidea *incertae sedis*. Taxonomic uncertainty is also reflected in Mysteriomorphidae, a largely hard-bodied family so far known only from Kachin amber (Alekseev & Ellenberger, 2019). While its family-level status is provisionally maintained, the possibility that it represents a specialized lineage of Elateridae cannot be ruled out (Peris *et al.*, 2020b).

Among the soft-bodied Elateroidea, numerous genera and species of Cantharidae have been described from Kachin amber (*e.g.*, Hsiao *et al.*, 2021), and evidence suggestive of potential chemical defence has also been reported (Poinar *et al.*, 2007). However, the present taxonomic situation of Kachin amber Cantharidae appears particularly chaotic and problematic. Two main groups of researchers have engaged in ongoing disputes

over generic delimitations (*e.g.*, Fanti & Müller, 2022, 2025; Yang *et al.*, 2022, 2024). Some genera, such as *Sanaungulus* Fanti *et al.*, contain an excessively high number of described species, at least some of which were proposed based on inadequate diagnoses that fail to sufficiently consider intraspecific variation or differences resulting from taphonomy or viewing angle. The placement of *Sanaungulus leniae* Fanti & Müller is especially problematic. In addition to features inconsistent with the generic concept of *Sanaungulus*, such as the non-dehiscent elytra lacking clear puncture rows, its non-bilobed tarsomere 4 further indicates that it may not belong to Cantharidae at all (Fanti & Müller, 2022: fig. 14). We instead suggest that this species may have affinities with Melyridae. Beyond issues of taxonomic assignment, certain specimens claimed to originate from Kachin amber may have been misattributed to this deposit, as indicated by their characteristic Baltic moulds (*e.g.*, Fanti & Müller, 2022: fig. 17; see also Li *et al.*, 2025d). Lycidae are represented in Kachin amber by four described genera and species, all of which are based on non-neotenic female specimens (Bocak *et al.*, 2019; Tihelka *et al.*, 2019; Li *et al.*, 2021g; Motyka *et al.*, 2025). Another important, primarily soft-bodied lineage is the bioluminescent lampyroid clade, which includes Sinopyrophoridae, Phengodidae, Rhagophthalmidae and Lampyridae (Kusy *et al.*, 2021). One phengodid and three lampyrid fossils have been reported from Kachin amber, with all three lampyrid specimens preserving abdominal photic organs (Kazantsev, 2015; Roza *et al.*, 2023; Cai *et al.*, 2024a; Yuan *et al.*, 2026). Additionally, the extinct family Cretophengodidae was erected based on Kachin amber material (Li *et al.*, 2021e). This family also possesses a luminous organ on the abdomen and may be allied to Phengodidae and Rhagophthalmidae, but differs in being markedly less soft-bodied.

A few elateroid larvae have also been documented in Kachin amber, including typical, visually distinctive larvae of Brachypsectridae featuring branched protrusions (Zhao *et al.*, 2020; J.T. Haug *et al.*, 2021), as well as larvae assigned to Eucnemidae (Muona & Teräväinen, 2023; Zippel *et al.*, 2023b; Muona, 2025), Cantharidae (Haug & Haug, 2026), and Elateridae (Zippel *et al.*, 2024; Haug *et al.*, 2025a, 2026; Kundrata *et al.*, 2025). The cantharid larva bears paired gland openings presumed to have a defensive function (Haug & Haug, 2026). Haug *et al.* (2023) also documented larviform fossils comparable to extant Lampyridae and Lycidae.

Nosodendroidea. Three extinct genera of Nosodendridae have been discovered in Kachin amber (*e.g.*, Li *et al.*, 2021f). Compared with extant members of Nosodendridae, these fossils differ in that the prosternum in front of coxae is better developed, and the lateral portions of the prosternum are not distinctly depressed to accommodate the folded forelegs.

Histeroidea. Jiang & Wang (2021) reported the first fossil record of Synteliidae from Kachin amber and assigned it to the only extant genus of the family, *Syntelia* Westwood. Histeridae are well represented in Kachin amber, with numerous genera and species described to date (e.g., Simon-Pražák *et al.*, 2023, 2024). Some taxa have been interpreted as subcortical (Simon-Pražák *et al.*, 2023), whereas some others have been suggested to be myrmecophilous (Zhou *et al.*, 2019; Yamamoto & Caterino, 2023). The latter are of particular interest as myrmecophily represents one of the most specialized ecological adaptations in extant Histeridae. Simon-Pražák *et al.* (2024) further discussed the evolution of antennal concealment in Histeridae. Notably, all four genera assigned to Onthophilinae from Kachin amber possess ventrally open antennal cavities, which may represent a transitional condition between the plesiomorphic state of indistinct cavities and the ventrally closed cavities behind prosternal alae characteristic of extant Onthophilinae (Simon-Pražák *et al.*, 2024; Li *et al.*, 2025e).

Hydrophiloidea. Hydrophiloidea appear to be exceptionally rare in Kachin amber. To date, only a single species of Hydrophilidae, *Cretocrenis burmanicus* Fikáček *et al.*, has been formally described from this deposit (Fikáček *et al.*, 2017).

Staphylinoidea. The systematic position of Jacobsoniidae was historically disputed, but the family is now confidently placed within Staphylinoidea (McKenna *et al.*, 2019; Cai *et al.*, 2022). The family is represented in Kachin amber by two species assigned to the extant genera *Sarothrias* Grouvelle and *Derolathrus* Sharp (Yamamoto *et al.*, 2017b; Cai *et al.*, 2018c). Ptiliidae, renowned for their minute body size and feather-like hindwings, are represented in Kachin amber by one genus from each of the two subfamilies (Yamamoto *et al.*, 2018; Li *et al.*, 2022i, 2023j). The primarily aquatic Hydraenidae are known from one genus and species described from Kachin amber (Yamamoto *et al.*, 2017a). A few genera and species belonging to Leiodidae and Colonidae have also been described from Kachin amber (e.g., Cai & Huang, 2017a, b; Yamamoto & Perreau, 2025).

Reflecting the family's modern hyperdiversity, Staphylinidae in Kachin amber are notably abundant and have been extensively studied. Nearly one hundred species have been described to date, spanning 22 of the 34 extant subfamilies, namely Piestinae (Yamamoto *et al.*, 2019), Osoriinae (e.g., Cai & Huang, 2015b; Yamamoto & Takahashi, 2019; Yamamoto, 2024b), Oxytelinae (e.g., Lü *et al.*, 2017; Makranczy *et al.*, 2018; Chen *et al.*, 2023a, b, 2025a, b), Proteininae (Cai *et al.*, 2016b), Micropeplinae (Cai & Huang, 2014), Dasycerinae (Yamamoto, 2016b; Cai *et al.*, 2018d; Yin *et al.*, 2021), Protopselaphinae (Y.C. Liu *et al.*, 2020b, 2021), Pselaphinae (e.g., Parker, 2016; Yin *et al.*, 2019a, 2019b), Mycetoporinae (Yamamoto, 2023a),

Tachyporinae (Yamamoto, 2016a, 2024a), Phloeocharinae (Li *et al.*, 2023d, 2024f; Yamamoto & Newton, 2023), Trichophyinae (Yamamoto & Newton, 2021), Aleocharinae (Cai & Huang, 2015a; Yamamoto *et al.*, 2016; Cai *et al.*, 2017a), Oxyporinae (Yamamoto, 2017), Megalopsidiinae (Yamamoto & Solodovnikov, 2016), Steninae (Żyła *et al.*, 2017), Euaesthetinae (Clarke & Chatzimanolis, 2009; Li *et al.*, 2025a), Solieriinae (e.g., Thayer *et al.*, 2012), Scydmaeninae (e.g., Jałoszyński *et al.*, 2016; Yin *et al.*, 2018a, b, 2019c, d), Pseudopsinae (Y.C. Liu *et al.*, 2020a), Paederinae (e.g., Żyła *et al.*, 2019; Tokareva *et al.*, 2023), and Staphylininae (Jenkins Shaw *et al.*, 2022; see also Reyes-Hernández *et al.*, 2025). Additional material attributable to Silphinae has also been reported, although no formally described species are currently available (Cai *et al.*, 2014). Among them, several taxa have yielded notable ecological and evolutionary insights. For instance, certain members of Aleocharinae with a limuloid body shape, such as *Mesosymbion* Yamamoto *et al.* and *Cretotrichopsenius* Cai *et al.*, have been interpreted as non-integrated social parasites of termites (Yamamoto *et al.*, 2016; Cai *et al.*, 2017a; Jiang *et al.*, 2021b). In Steninae, *Festenus* Żyła *et al.* possesses a prey-capture apparatus formed by a protrusible labium almost identical to that of its extant relative *Stenus* Latreille, adapted for preying upon collembolans or other small invertebrates (Cai *et al.*, 2019a). In Pselaphinae, *Cretobythus* Yin *et al.* features enlarged maxillary palpi that likely performed a function similar to that of its extant relatives in capturing collembolans (Yin *et al.*, 2018c). In Scydmaeninae, the genus *Clidicostigus* Jałoszyński *et al.* possesses dense stout setae on the antennal scape and pedicel, which have been interpreted as a convergence with the antennal setal trap of the carabid *Loricera* and were likewise utilized for collembolan predation (Yin *et al.*, 2017). In Proteininae, *Vetuproteinus* Cai *et al.* bears an apparent spore brush on the galea, suggesting a specialized diet of fungal spores (Cai *et al.*, 2016b). Larvae assigned to Staphylinidae have also been reported from Kachin amber (Haug *et al.*, 2022, 2025b).

Scarabaeoidea. Several genera and species of Lucanidae have been described from Kachin amber (e.g., Cai *et al.*, 2017b; Li *et al.*, 2023b; Yu *et al.*, 2024). Notably, these include the smallest known member among the approximately 1,500 extant and extinct species of Lucanidae (Yamamoto, 2023b). Tihelka *et al.* (2021a) described the genus *Kresnikus* Tihelka *et al.* from Kachin amber and assigned it to a new subfamily within Trogidae. Although *Kresnikus* indeed resembles extant Trogidae in its general dorsal appearance, its mesocoxal cavities are separated and laterally open. Given that contiguous and laterally closed mesocoxal cavities are actually two key diagnostic characters of Trogidae (Lawrence & Ślipiński, 2013), the familial placement of *Kresnikus* may require

further evaluation. Boucher *et al.* (2016) described *Passalopalpus* Boucher & Bai from Kachin amber and established the new family Passalopalpidae, interpreting it as the sister group of Passalidae. Boucher *et al.* (2017) subsequently also reported two true members of Passalidae from Kachin amber. Bai *et al.* (2016) documented a typical representative of Hybosoridae in Kachin amber. In addition to forms exhibiting a typical scarabaeoid appearance, this family includes the distinctive subfamily Ceratocanthinae, which is characterized by a specialized morphology enabling conglobation. Representatives of this subfamily have also been identified in Kachin amber (Lu *et al.*, 2022). Glaresidae (Cai & Huang, 2018b), Diphylostomatidae (Yamamoto, 2024c), Bolboceratidae (Bai *et al.*, 2017), and the hyperdiverse Scarabaeidae (S. Li *et al.*, 2019) are each represented by a single species reported from Kachin amber. In addition, Li *et al.* (2025f) described *Crassiungula* Li *et al.* from Kachin amber, a scarabaeoid of uncertain familial placement characterized by the highly modified mesotarsus and mesopretarsal claws.

Bostrichoidea. Several fossils of Dermestidae have been reported from Kachin amber and were recently reassessed by Ślipiński *et al.* (2025). Their phylogenetic analyses supported the placement of the unusual genus *Cretodermestes* Deng *et al.* in a separate subfamily, Cretodermestinae. Dermestid larvae bearing the characteristic defensive setae have also been recorded from Kachin amber (Háva, 2023; Le Cadre *et al.*, 2025). Bostrichidae in Kachin amber are mainly represented by the species-rich genus *Poinarinus* Legalov (*e.g.*, Legalov & Háva, 2022), a taxon assigned to its own monogeneric subfamily, Alitrepaninae (Peng *et al.*, 2022). Regarding Ptinidae, the Kachin amber record includes typical members of Eucradinae and Ernobiinae (Li *et al.*, 2023e, 2025h), as well as *Cretasernus* Peris & Philips, which possesses unusual antennae and metacoxae and cannot be assigned to any currently recognized subfamily (Peris *et al.*, 2020a).

Cleroidea. Several basal lineages of Cleroidea were previously united in a broadly defined Trogossitidae (*sensu* Kolibáč, 2013) based on morphological studies. However, molecular data have demonstrated that this group is not monophyletic, resulting in its dissolution into seven distinct families (Gimmel *et al.*, 2019a). Four trogossitid-like genera from Kachin amber have been assigned to Lophocateridae (Kolibáč & Peris, 2021; Lyubarsky *et al.*, 2021; Yu *et al.*, 2021a, b), but given that these trogossitid-like lineages are notoriously difficult to delimit morphologically, such assignments should be regarded as tentative. Indeed, Li *et al.* (2024d) conducted a phylogenetic analysis of *Foveapeltis* Li *et al.*, another trogossitid-like fossil possessing a large cavity on each pronotal hypomerite, to evaluate its affinities with

various lineages formerly included in Trogossitidae *sensu lato*. Their results were inconclusive and did not allow a definitive placement of the fossil within any particular family. Fossils that can be confidently attributed to Trogossitidae *sensu stricto* have nevertheless been discovered in Kachin amber (Li *et al.*, 2021h, 2025g). Notably, the genus *Rutrizoma* Li & Cai appears to be a predator adapted to moving through narrow wood galleries, yet it also possesses a specialized abdominal declivity likely utilized for defence against higher-level predators or competitors (Li *et al.*, 2025g).

The melyrid lineage in Kachin amber is currently represented by an adult of Prionoceridae (Zhao *et al.*, 2022) and a larva tentatively attributed to Rhadalidae (Kolibáč *et al.*, 2023). In addition, “*Sanaungulus*” *leniae* discussed above may represent another putative member of this lineage. Three members of Thanerocleridae have been described from Kachin amber (Yu *et al.*, 2017; Cai & Huang, 2018c; Peris *et al.*, 2022), whereas unequivocal representatives of Cleridae have not yet been found in this deposit. Although Poinar & Brown (2020) claimed to have found clerid larvae attached to a bee in Kachin amber, Kolibáč & Perkovsky (2025) questioned this interpretation and suggested that these larvae may not even belong to Cleroidea.

Lymexyloidea. This superfamily contains a single family, Lymexylidae, whose members exhibit a distinctive morphology among beetles. In particular, species of Atractocerinae possess strongly reduced elytra, with hind wings almost completely exposed and lacking transverse folds (Lawrence, 2020). Known larvae of lymexylids feed primarily on symbiotic fungi cultivated within their wood galleries (*i.e.*, ambrosia fungi) (Wheeler, 1986). Several fossils of Atractocerinae have been reported from Kachin amber (Yamamoto, 2019; Chen & Zhang, 2020). This relatively high Cretaceous diversity suggests that lymexylids may have served as important early vectors of ambrosia fungi before the evolution of the specialized fungal relationships seen in modern Scolytinae and Platypodinae (Peris *et al.*, 2021; Li *et al.*, 2022j).

Tenebrionoidea. In Ripiphoridae, subfamilies Pelecotominae, Ripiphorinae, and Ptilophorinae have been documented in Kachin amber (Batelka *et al.*, 2016; Hsiao & Huang, 2018; Batelka & Prokop, 2021), but the most noteworthy records concern Ripidiinae. While all extant Ripiphoridae with known life histories possess an endoparasitic larval stage, Ripidiinae are further distinguished by adult males with reduced mouthparts and females larviform. In addition to morphologically diverse adult males of Ripidiinae described from Kachin amber (Batelka *et al.*, 2018; Cai *et al.*, 2018e; Batelka & Prokop, 2023; Li *et al.*, 2025c), one remarkable specimen preserves multiple males of the genus *Paleoripiphorus* Perrichot *et al.*, together with a larviform female, two

free-living longipede larvae, and a possible cockroach host (Batelka *et al.*, 2021). Although the parasitic stage itself is not directly documented, this assemblage offers rare insights into the complex life cycle of ancient ripidiines, particularly regarding the potential host-seeking mechanism of the longipede larvae. Crown-group Mordellidae are known from Kachin amber as a single described species (Bao *et al.*, 2019a). Additionally, the extinct subfamily Apotomourinae from Kachin amber, characterized by a short pygidium and the absence of a subapical metatibial ridge, has been interpreted as a stem group of Mordellidae (Bao *et al.*, 2018b; Batelka *et al.*, 2025). Modern mordellids often exhibit specialized pollen-feeding behaviours associated with angiosperm pollination. Bao *et al.* (2019b) interpreted an apotomourine specimen from Kachin amber bearing attached pollen as a crown-group mordellid and therefore proposed it as a specialized pollinator of angiosperms. A subsequent re-examination by Li *et al.* (2026b) refuted this taxonomic interpretation and further noted a co-preserved pollen-carrying thrips, instead suggesting a potential mixed-visitor or generalist pollination context. Zippel *et al.* (2022b) assigned a larva from Kachin amber to Mordellidae, but later studies suggest that it actually belongs to Hymenoptera (Batelka & Engel, 2022; Rasnitsyn & Müller, 2023).

Adults assigned to Scaptiidae (Alekseev *et al.*, 2025), Ischaliidae (Telnov *et al.*, 2023), Aderidae (Bao *et al.*, 2022), Prostomidae (*e.g.*, Li *et al.*, 2022a), Oedemeridae (Vitali & Ellenberger, 2019; Vitali & Legalov, 2020), Pythidae (Li *et al.*, 2024g), Salpingidae (Jiang *et al.*, 2024), and Anthicidae (Molino-Olmedo, 2017) have also been described from Kachin amber. In some cases, the familial assignment is relatively straightforward. For example, *Vetuprostomis* Engel & Grimaldi is confidently placed within Prostomidae due to the presence of diagnostic jugular processes visible in the fossil material (Li *et al.*, 2022a). However, in other cases the familial assignment is more challenging, as many extant tenebrionoid families exhibit high morphological heterogeneity and lack a clear set of diagnostic characters. For example, Li *et al.* (2024g) tentatively assigned *Glyphonotum* Li *et al.* to Pythidae based partly on the results of phylogenetic analyses, although alternative affinities with other tenebrionoid lineages, such as Melandryidae, cannot be confidently excluded. The case of *Prototrichalus* Molino-Olmedo *et al.* is even more complicated. The original authors misinterpreted the number of metatarsomeres and placed *Prototrichalus* in Lycidae (Elateroidea) (Molino-Olmedo *et al.*, 2020). Bocak *et al.* (2022) later corrected its placement to Tenebrionoidea, and a subsequent study by Telnov *et al.* (2023) formally placed it in Ischaliidae, while also suggesting that a relationship with Pyrochroidae remains possible. Larvae assigned to Scaptiidae are also known from Kachin amber, some of which were previously

misidentified as Haliplidae (Zippel *et al.*, 2022a; Beutel & Vondel, 2024). In addition, Poinar & Brown (2014) reported a triungulin larva attached to a hemipteran host in Kachin amber and attributed it to Meloidae.

Melandryidae are morphologically highly heterogeneous (Nikitsky & Pollock, 2010), and molecular studies have demonstrated that the family as currently circumscribed is not monophyletic (McKenna *et al.*, 2019; Cai *et al.*, 2022, 2024b). This lack of a cohesive familial identity may partly explain why, despite their potentially higher diversity, only two species of the tribe Serropalpini have been formally described from Kachin amber to date (Tihelka *et al.*, 2020b; Li *et al.*, 2022b). Tihelka *et al.* (2021d) also described *Kulindrobor* Tihelka *et al.* from Kachin amber, which may be related to Melandryidae according to the phylogenetic analysis, but the authors refrained from formally assigning it to the family as it exhibits several features unusual for melandryids. Within Zopheridae, at least six genera of the subfamily Colydiinae have been reported from Kachin amber (*e.g.*, Deng *et al.*, 2017; Cheng *et al.*, 2021; Li *et al.*, 2021a). These fossils range from forms closely resembling extant taxa, including one placed in a living genus (Li *et al.*, 2024c), to unusual and eye-catching forms such as *Stegastochlidus* Poinar & Vega (Poinar & Vega, 2020). Tetratomidae have also been reported from Kachin amber, with four genera described to date (Cai *et al.*, 2016a; Yu *et al.*, 2016; Hsiao *et al.*, 2018; Jiang & Chen, 2025). Curiously, Tenebrionidae, despite being hyperdiverse in the extant fauna, are represented in Kachin amber by only a single record (Bao & Antunes-Carvalho, 2020).

Coccinelloidea. Teredidae (Li *et al.*, 2022c), Bothrideridae (Li & Cai, 2024), and Corylophidae (Li *et al.*, 2022n) are each represented in Kachin amber by a single described genus and species. Anamorphidae (Arriaga-Varela *et al.*, 2024) and Endomychidae (*e.g.*, Tomaszewska *et al.*, 2018, 2022; Arriaga-Varela *et al.*, 2023) have also been reported from Kachin amber. Anamorphidae (together with Mycetaeidae and Eupsilobiidae) were long included in Endomychidae until molecular evidence supported their recognition as distinct families (Robertson *et al.*, 2015). Accordingly, distinguishing among these endomychid-like families in the fossil record can be taxonomically challenging, as limited morphological characters may not always reliably indicate familial affinity. For instance, despite possessing laterally broadly closed mesocoxal cavities, a key diagnostic feature of Anamorphidae, *Rhomeocalpsua* Li *et al.* was tentatively placed in Endomychidae by Li *et al.* (2022i) based on an overall assessment of its morphology. In another case, the unusual genus *Yassibum* Li *et al.* was tentatively assigned to Anamorphidae based on phylogenetic analyses, yet the authors left open the possibility that it may belong to another family or even

an extinct family of its own (Li *et al.*, 2024j). Notably, the fossils from Kachin amber currently represent the earliest definitive records of all the coccinelloid families mentioned above. Potential coccinelloid larvae have also been reported from Kachin amber (Zippel *et al.*, 2023a).

Erotyloidea. Within Boganiidae, the genera *Cretoboganium* Cai & Huang and *Cretoparacucujus* Cai & Escalona from Kachin amber were assigned to Boganiinae and Paracucujinae, respectively (Cai *et al.*, 2018a; Cai & Huang, 2019b). *Cretoparacucujus* possesses specialized mandibular cavities and occurs in association with cycad pollen in the amber specimen. Considering this evidence together with pollination and pollinivory observed in its extant relatives, *Cretoparacucujus* has been interpreted as an ancient pollinator of cycads (Cai *et al.*, 2018a). It should be noted that Kirejtshuk *et al.* (2023b) transferred *Cretoparacucujus* to the extinct family Parandrexidae, which they considered to be related to Nitiduloidea. However, the status of Parandrexidae itself may be problematic, as the group shows considerable morphological similarity to Boganiidae (Crowson, 1981; Escalona *et al.*, 2015) and may eventually be synonymized with the latter. While definitive representatives of Erotylidae have yet to be identified in Kachin amber, the genus *Isocryptophilus* Li & Cai has been suggested to have possible affinities with that family (Li *et al.*, 2024e). However, its atypical combination of characters complicates its familial placement, and affinities with other cucujiform families cannot be excluded.

Nitiduloidea. Representatives of Helotidae (Liu *et al.*, 2019a; Tihelka *et al.*, 2020a; Li *et al.*, 2023c), Sphindidae (Kirejtshuk *et al.*, 2019; Li *et al.*, 2021i), Monotomidae (Peris & Delclòs, 2015; Z.H. Liu *et al.*, 2020; Li *et al.*, 2022d), and Smicripidae (Cai & Huang, 2016) have been reported from Kachin amber. Most of these fossils exhibit the typical appearance of their respective families and can be confidently assigned to them. *Lobatihelota* Li *et al.*, although possessing some features unusual for Helotidae, such as nitidulid-like legs, nevertheless bears submental furrows, the most important diagnostic character of Helotidae, and its placement there is further supported by phylogenetic analysis (Li *et al.*, 2023c).

The situation in Nitidulidae and Kateretidae is more complicated. Extant members of the two families are often morphologically similar, and molecular evidence indicates that they are sister groups (Cai *et al.*, 2022). While a few species in Kachin amber have been consistently attributed to Nitidulidae since their discovery (Kirejtshuk & Chetverikov, 2018; Kirejtshuk *et al.*, 2023b), many others were initially described as Kateretidae. These taxa assigned to Kateretidae are frequently found in association with pollen (Peris *et al.*, 2020c; Zhao *et al.*, 2026), and one specimen preserved together with pollen-laden coprolites has been proposed as direct evidence

of angiosperm pollinivory (Tihelka *et al.*, 2021c). However, Kirejtshuk *et al.* (2023b) considered none of these taxa to belong to Kateretidae and transferred them to a newly established extinct family, Apophisandridae. Alternatively, Peris *et al.* (2024) interpreted these fossils as members of Nitidulidae and treated the group as the nitidulid subfamily Apophisandrinae. Consensus on their familial placement has yet to be reached, with some recent studies such as Zhao *et al.* (2026) continuing to treat them as members of Kateretidae.

Cucujoidea. Within Silvanidae, two genera of the tribe Brontini have been discovered in Kachin amber, both characterized by remarkably long antennae and mandibular horns in males (Liu *et al.*, 2019b). The sexual dimorphism of *Protoliota antennatus* Liu *et al.*, along with the intraspecific variation among its males, was further documented by Cai & Huang (2019a). Poinar *et al.* (2023) also claimed to have discovered another species of *Protoliota* Liu *et al.*, but its morphology does not appear to fall clearly outside the range of variation observed in the series of *P. antennatus* specimens reported by Cai & Huang (2019a), and the establishment of a new species is therefore doubtful and potentially unnecessary. Cyclaxyridae are today restricted to New Zealand and are strictly associated with sooty moulds (Gimmel *et al.*, 2009). The discovery of cyclaxyrids in both Kachin and Baltic amber indicates that the family was once far more widespread (Gimmel *et al.*, 2019b; Tihelka *et al.*, 2021b). Passandridae are represented in Kachin amber by a single record, *Mesopassandra* Jin *et al.*, which has been interpreted as sister to all other Passandridae (Jin *et al.*, 2019). As in other cucujiform superfamilies, convergent external appearance is also common in Cucujoidea and sometimes complicates the classification of fossil taxa. For example, *Alloterocucus* Li *et al.* possesses a combination of characters not fully consistent with any known cucujoid or erotyloid family. Li *et al.* (2022h) thus employ phylogenetic analyses, which tentatively suggested an affinity with Lamingtoniidae. Another problematic taxon from Kachin amber, *Pleuroceratos* Poinar & Kirejtshuk, was originally placed in Silvanidae (Poinar *et al.*, 2008), a placement subsequently rejected by Liu *et al.* (2019b). While Kirejtshuk *et al.* (2019) later transferred *Pleuroceratos* to Sphindidae, the phylogenetic analysis by Tihelka *et al.* (2020c) suggested that it might instead belong to Phloeostichidae.

Chrysomeloidea. The hyperdiverse superfamily Chrysomeloidea is conspicuously scarce in Kachin amber, as well as in the Mesozoic fossil record more broadly. Lin & Bai (2017) described the only fossil of Cerambycidae known from Kachin amber, *Qitianniu* Lin & Bai, which was considered by Vitali (2019) to belong to the subfamily Prioninae. Likewise, the family Chrysomelidae is represented by a single described fossil in Kachin amber,

Myanmarops Legalov & Kirejtshuk, which was assigned to the subfamily Bruchinae (Legalov *et al.*, 2020).

Curculionoidea. Clarke *et al.* (2019) systematically studied the Curculionoidea from Kachin amber, reviewing previously described taxa and establishing numerous new genera and species. In their treatment, only three genera were assigned to Nemonychidae. With the exception of *Palaeocryptorhynchus* Poinar (treated as family *incertae sedis*), all other genera that had previously been placed in various families were assigned to Mesophyletidae, a newly recognized extinct family potentially related to Attelabidae, Caridae, or Brentidae. However, a group of researchers led by Legalov has largely ignored this arrangement, continuing to assign newly described taxa to a so-called Ithyceridae (Poinar *et al.*, 2019, 2021). According to Legalov (2023), this Ithyceridae also include a subfamily Mesophyletinae, although its exact generic composition has not been clearly specified. It should be noted that Legalov does not adhere to the principle of monophyly when defining taxa. In his interpretation, Ithyceridae are a descendant of Nemonychidae, and Brentidae and Curculionidae are descendants of Ithyceridae (*e.g.*, Legalov, 2018). This reliance on evolutionary grades rather than clades makes his taxonomic framework inherently incompatible with the widely accepted, phylogeny-based classification of Curculionoidea (*e.g.*, Shin *et al.*, 2018; Li *et al.*, 2023a).

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