Megataxa 017 (2): 291–342
https://www.mapress.com/mt
Copyright © 2025 Magnolia Press

Article

ISSN 2703-3082 (print edition)
MEGATAXA
ISSN 2703-3090 (online edition)

https://doi.org/10.11646/megataxa.17.2.2
http://zoobank.org/urn:lsid:zoobank.org:pub:BC0D77D3-C302-4FED-B4FD-91D4885CE322

Staphylinoid beetles in Lower Cretaceous Hkamti amber from northern Myanmar (Coleoptera: Polyphaga: Staphylinoidea): An overview

SHÛHEI YAMAMOTO[1,*]
[1]*The Hokkaido University Museum, Hokkaido University, Kita 10-jo, Nishi 8-chome, Kita-ku, Sapporo 060-0810, Japan*
s.yamamoto.64@gmail.com; https://orcid.org/0000-0002-4162-8457
[*]*Corresponding author*

Table of Contents

Abstract

A super-rich and extremely diverse assemblage of insect fossils has been well-documented from mid-Cretaceous Kachin amber (*ca.* 99 Ma) in the Kachin State of northern Myanmar. In contrast, only four beetle (Coleoptera) species have formally been described from the slightly older Lower Cretaceous Hkamti (Khamti) amber (*ca.* 110 Ma), also originating from northern Myanmar's Sagaing Region. The polyphagan beetle superfamily Staphylinoidea, encompassing approximately 75,000 species, is among the largest superfamilies in the animal kingdom. This study records 11 staphylinoid fossils, providing a comprehensive overview of the Hkamti amber biota. These fossils were classified into three families (Hydraenidae, Colonidae, and Staphylinidae). The highest paleodiversity was observed in the rove beetle family Staphylinidae; nine specimens

Submitted: 21 Feb. 2025; accepted by Z.-Q. Zhang: 7 Jun. 2025; published: 24 Jun. 2025

from six staphylinid subfamilies (Osoriinae, Tachyporinae, Aleocharinae, Steninae, Solieriinae, and Scydmaeninae) were identified. With the exception of Steninae, all are reported for the first time from Hkamti amber. Notably, the discoveries of colonid, osoriine, aleocharine, and stenine (previously recorded) beetles represent the oldest known fossils for these groups. Additionally, the hydraenid and tachyporine fossils are the earliest biological amber inclusions reported for their respective familiy or subfamiliy. Three new species are herein described: *Colonellus* (*Colonellus*) *hkamtiensis* **sp. nov.** (Colonidae), *Cretochirus elongatus* **sp. nov.** (Staphylinidae: Osoriinae: Leptochirini), and *Prosolierius antennatus* **sp. nov.** (Staphylinidae: Solieriinae). These findings underscore the presence of a potentially diverse Staphylinoidea paleofauna in Hkamti amber, although it remains likely underestimated, warranting further investigation. This study highlights a striking similarity in entomofaunal composition between the Hkamti and Kachin amber deposits, supporting a previously suggested close affinity between the two. Additionally, the fossils described here provide valuable calibration points for future molecular dating analyses.

Key words: Staphyliniformia, fossil, Burmese amber, Albian, new species, paleontology

Introduction

Burmese (Myanmar) amber, with approximately 2,800 species documented (Ross 2024), harbors one of the most astonishing Cretaceous paleofaunas worldwide, particularly notable for its remarkable insect diversity. Although many of these species were described only in the 2010s and later, the exceptional diversity and abundance of biological inclusions in this fossilized tree resin are unparalleled. Burmese amber is further distinguished by the extraordinary preservation of its bioinclusions. Fine morphological details are often discernible (*e.g.* Cai *et al.* 2016, 2019; Yamamoto *et al.* 2017a; Ulitzka 2018; Li Y-D *et al.* 2023a), and in exceptional cases, even internal anatomical features have been preserved (Li Y-D *et al.* 2021a; Richter *et al.* 2022; Zhuang *et al*. 2022; Gautam *et al.* 2024). Myanmar amber has been known and traded with China for over 2,000 years (Ross *et al.* 2010; Grimaldi & Ross 2017). However, since the early 2000s, mining activities have intensified, and its geological age has been reassigned from the Cenozoic (Miocene-Eocene) to the Cretaceous (Ross *et al.* 2010). This reclassification has catalyzed a surge in research concerning fossil inclusions, sharply contrasting with the slow progress of earlier periods (Ross *et al.* 2010; Ross 2019). Burmese amber now becomes one of the most important sources of knowledge of fossil beetles (order Coleoptera) among worldwide amber deposits of any geological time or period.

Currently, three major amber deposits are recognized in Myanmar: (i) mid-Cretaceous Kachin amber (commonly previously referred to as “Burmese amber” or “burmite”) (*ca.* 99 Ma) from the Hukwang Valley in Kachin State, northern Myanmar (Cruickshank & Ko 2003; Shi *et al.* 2012; Mao *et al.* 2018); (ii) Lower Cretaceous Hkamti (Khamti) amber (*ca.* 110 Ma) from the Sagaing Region in northern Myanmar (Xing & Qiu 2020); and (iii) Upper Cretaceous Tilin amber (*ca.* 72 Ma) from the Magway Region in central Myanmar (Zheng *et al.* 2018). Among these deposits, Kachin amber has been the most extensively mined and widely distributed commercially in the market. In contrast, Hkamti amber remains much less exploited, and Tilin amber has only been mined experimentally. Despite its lower market presence compared with Kachin amber, Hkamti amber is approximately 11 million years older and originates from a distinct geological context, making it an important locality, particularly in Asia (Xing & Qiu 2020). However, only 14 insect species have been formally described with certainty from Hkamti amber to date (Ross 2024; Mainda 2024; Simon-Pražák *et al*. 2024).

With 74,494 species across 4,600 genera (Newton 2022), the polyphagan beetle superfamily Staphylinoidea (Coleoptera: Polyphaga) is among the most species-rich groups in the animal kingdom (Lü *et al.* 2020). It belongs to the infraorder (series) Staphyliniformia and comprises seven families (Cai *et al*. 2022): Agyrtidae, Colonidae, Hydraenidae, Jacobsoniidae, Leiodidae, Ptiliidae, and Staphylinidae. Among these, the family Staphylinidae, commonly known as rove beetles, is the largest, encompassing 66,928 species in 4,038 genera (Newton 2022). The Staphylinoidea is currently considered monophyletic (McKenna *et al.* 2019; Cai *et al.* 2022). Several taxonomic revisions were recently proposed by Cai *et al.* (2022): Colonidae was elevated to a separate family, no longer considered a subfamily of Leiodidae; the large carrion and burying beetle family Silphidae was downgraded to a subfamily of Staphylinidae (as Silphinae), a change also supported by Sikes *et al.* (2024); and Jacobsoniidae was formally recognized as a member of the superfamily. Recent phylogenetic analyses based on genomic data have resolved relationships within Staphylinoidea as: (Jacobsoniidae + (Ptiliidae + Hydraenidae)) + ((Agyrtidae + Leiodidae) + Staphylinidae) (Zhang *et al.* 2018; McKenna *et al.* 2019; Cai *et al.* 2022). As one of the most species-rich coleopteran superfamilies, Staphylinoidea displays remarkable morphological and ecological diversity, representing a key radiation within the beetle Tree of Life. Unlike many other beetles, staphylinoids are predominantly non-phytophagous and exhibit diverse feeding modes such as predatory, saprophagy, and mycophagy (Thayer 2016). They are commonly found in cryptic microhabitats, including leaf litter, rotting wood, under bark, animal carcasses, dung, and nests of social insects (Newton *et al*. 2000).

The origin of Staphylinoidea has been suggested to date back to the Triassic or the Triassic-Jurassic boundary, based on molecular clock analyses (Zhang *et al.* 2018; McKenna *et al.* 2019; Lü *et al.* 2020; Cai *et al.* 2022). The purported oldest staphylinid, *Leehermania prorova* Chatzimanolis, Grimaldi, & Engel, 2012, from Upper Triassic strata (Chatzimanolis *et al*. 2012), was recently reclassified under Myxophaga by Fikáček *et al.* (2020). Consequently, no confirmed Triassic staphylinoid fossils are currently known. A diverse array of Jurassic and Cretaceous staphylinoid taxa has been identified as compression fossils from China, Russia, and Kazakhstan (summarized in Chatzimanolis 2018). The number of Mesozoic amber inclusions of the staphylinoids has been steadily increasing, with notable findings from Lower to Upper Cretaceous deposits, such as Lebanese, Spanish, Burmese, French, and New Jersey (USA) amber (Chatzimanolis *et al.* 2012; Peris *et al.* 2014; Chatzimanolis 2018; Ross 2019, 2024). To date, mid-Cretaceous Burmese (Kachin) amber has yielded by far the most diverse and abundant assemblage of Staphylinoidea, comprising six families, 74 genera, and 104 species as of 1 June 2025 (Ross 2024; Yamamoto 2024a, 2024b; Li Y-D *et al.* 2024a; Jałoszyński & Szawaryn 2024; Janák 2024; Liu *et al.* 2025; Chen *et al.* 2025; Reyes-Hernández *et al.* 2025; Yamamoto & Perreau 2025). These discoveries have greatly altered the overall understanding of the Mesozoic paleobiota within the superfamily, revealing an unexpectedly high faunal paleodiversity, particularly among rove beetles (Staphylinidae). The Lower Cretaceous Hkamti amber deposit from northern Myanmar represents another potentially important source of Mesozoic Staphylinoidea. However, only two staphylinid species, both belonging to the same genus of the subfamily Steninae, have been documented from this site to date (Mainda 2023, 2024).

This study provides a brief overview of the largely unexplored paleofauna of Staphylinoidea in the Lower Cretaceous (*ca.* 110 Ma) Hkamti amber from northern Myanmar, based on 11 specimens of 10 amber pieces. These newly analyzed specimens are critical for efforts to understand the evolutionary history of the superfamily and offer a valuable glimpse into the Cretaceous ecosystems preserved in amber. My findings also support the hypothesis of a very closely related entomofauna between Hkamti amber and the slightly younger (*ca.* 99 Ma) Kachin amber, both from northern Myanmar, as previously suggested (Balashov 2021; Caterino & Yamamoto 2023; Simon-Pražák *et al.* 2024).

Materials and methods

This study used 11 Staphylinoidea adult bioinclusions found in 10 amber pieces from the Hkamti (Khamti) excavation site in the Sagaing Region of northern Myanmar (Xing & Qiu 2020; Nyunt *et al.* 2020). The age of the amber in different mining pits from this site is estimated by the zircon U-Pb dating to be Lower Cretaceous (early Albian: 109.7 ± 0.4 Ma, *ca.* 110 Ma) (Xing & Qiu 2020). The Hkamti site is operated as a legal commercial mining venture, and amber fossils from this mine are not associated with recent armed conflicts in Myanmar (Haug *et al.* 2020; Peretti 2020, 2021). The specimens were legally acquired via the online platform eBay.com from an amber trader (burmite-miner, currently operating under the name of 'burmite-miner2025'). All specimens, including the holotypes, are housed in the Systematic Entomology collection (SEHU) at the Hokkaido University Museum, Hokkaido University, Sapporo, Japan, under the care of curator Dr. Masahiro Ôhara. They are cataloged with consecutive inventory numbers from SEHU-0000121240 to SEHU-0000121249. Some amber pieces were subjected to further preparation, including trimming and polishing with waterproof emery papers of varying grit sizes (#360 to #10,000). A plastic buffing cloth was used to achieve a final luster on the amber surfaces. For sorting and morphological examination, three stereomicroscopes were utilized: SMZ745T, SMZ800, and SMZ1500 (Nikon, Tokyo, Japan). To reduce surface reflections and improve image clarity, all amber pieces were submerged in clove oil, which has a refractive index similar to amber, during photography. Most photographs were captured using an EOS 6D Mark II digital camera (Canon, Tokyo, Japan) mounted on a Leica M205C stereomicroscope (Leica Microsystems, Wetzlar, Germany) with four lighting units (SPA2-10SW; Hayashi-Repic Inc., Tokyo, Japan). Additional images were taken using a Canon EOS 90D digital camera equipped with an MP-E 65mm F2.8 1–5× macro lens (Canon) and a Macro Twin Lite MT-24EX flash (Canon). Helicon Focus 8.2.0 software was applied for image stacking and processing; Adobe Photoshop Elements 15 was used for final editing, composition, and annotation of the images.

The higher classification of Coleoptera adopted in this study follows Cai *et al.* (2022) and Bouchard *et al.* (2024). Morphological terminology is based on the works of Yamamoto *et al.* (2017b) for Hydraenidae, Yamamoto and Takahashi (2018) for Colonidae, and Yamamoto & Takahashi (2019) for Staphylinidae.

Results

Based on 11 Staphylinoidea bioinclusions from Hkamti amber, the fossil beetles were classified into three families: Hydraenidae, Colonidae, and Staphylinidae. Among these, Staphylinidae exhibited the highest paleodiversity, represented by 9 specimens spanning six subfamilies: Osoriinae, Tachyporinae, Aleocharinae, Steninae, Solieriinae, and Scydmaeninae. Consequently, only one specimen was identified each for Hydraenidae and Colonidae. The overall results with their taxonomic assignments are briefly summarized in Table 1. Detailed analyses and classifications are outlined below, the Systematic Paleontology section.

Some taxa, such as "Hydraenini gen. et sp. indet." and "Mesoporini gen. et. sp. indet.", lack critical diagnostic features due to their fossil positions and difficulty of observing minute morphological features. Additionally, a few more specimens have preservation issues including direct damage to the fossils or several huge cracks in amber (*e.g. Festenus* sp., *Mesallotrochus* sp.). For those reasons, I decided to hold off until additional evidence or well-preserved specimens will be secured for these staphylinoids, and only three species are described as new to science in this paper. The above mentioned two taxa, namely the hydraenin and mesoporin, failed to be identified at a generic level, since several important characters were not clearly discernible from the fossils (although both taxa should probably be considered as undescribed genera).

TABLE 1. A summarized result of the Staphylinoidea species from Lower Cretaceous Hkamti amber (Albian, *ca*. 110 Ma) found in the present study. Three taxonomic ranks, *i.e*. supertribe, subtribe, and subgenus, were omitted. Abbreviation: N/A, not applicable.

Family	Subfamily	Tribe	Genus	Species	Differential diagnosis
Hydraenidae Mulsant, 1844	Hydraeninae Mulsant, 1844	Hydraenini Mulsant, 1844	Genus *incertae sedis*	Hydraenini gen. et. sp. indet.	"Hydraenini gen. et. sp. indet." is closely similar to *Archaeodraena cretacea* Jäch & Yamamoto, 2017 (in Yamamoto *et al*. 2017b) from Kachin amber in general appearance, but it can be easily distinguished from the latter by the shorter maxillary palpomere 3, simplified labrum, strongly explanate epipleural gutter, and glabrous metatarsi lacking nanatorial setae.
Colonidae G.H. Horn, 1880 (1859)	N/A	N/A	*Colonellus* Szymczakowski, 1964	*Colonellus* (*Colonellus*) *hkamtiensis* **sp. nov.**	The new species can be separated from *Colonellus* (*Pentacolonellus*) *burmiticus* Cai & Huang, 2017 from Kachin amber by its antennal club composed of only four antennomeres and larger body size. Furthermore, it is distinguishable from extant members of *Colonellus* (subgenus *Colonellus*) by the comparatively smaller body size and elongate antennomeres 8 and 9.
Staphylinidae Latreille, 1802	Osoriinae Erichson, 1839a	Thoracophorini Reitter, 1909	*Mesallotrochus* Cai & Huang, 2015	*Mesallotrochus* sp.	"*Mesallotrochus* sp." can be separated from the other species of the genus, *Mesallotrochus longiantennatus* Cai & Huang, 2015 from Kachin amber, by the more transverse and shorter pronotum, along with a comparatively smaller body size. However, it is difficult to properly evaluate the species's status due to several huge cracks in the amber piece.
		Leptochirini Sharp, 1887	*Cretochirus* Yamamoto, 2019 in Yamamoto & Takahashi (2019)	*Cretochirus elongatus* **sp. nov.**	This new species appears to be most similar to *Cretochirus newtoni* Yamamoto, 2019 (in Yamamoto & Takahashi 2019) from Kachin amber in its simplified protibiae and peculiar cephalic modification, but is distinguished from the latter by the much more elongate and larger body, together with the structures of its mandibles and mentum.
	Tachyporinae W.S. MacLeay, 1825	Vatesini Seevers, 1958	*Procileoporus* Yamamoto, 2016	*Procileoporus* sp.	"*Procileoporus* sp." is most similar to the other *Procileoporus* species from Kachin amber, *Procileoporus burmiticus* Yamamoto, 2016. However, it is challenging to unambiguously identify this specimen as *P. burmiticus* due to its smaller body size and the poor state of the preservation of the fossil.
	Aleocharinae Fleming, 1821	Mesoporini Cameron, 1959	Genus *incertae sedis*	Mesoporini gen. et. sp. indet.	"Mesoporini gen. et. sp. indet." is similar to *Mesosymbion compactus* Yamamoto, Maruyama & Parker, 2016 from Kachin amber in general appearance including the thick and clavate antennal flagellae, but may be distinguished from it by a combination of the following character states: a larger, narrower, and less flattened body; a non-opisthognathous head visible dorsally; and merely transverse antennomeres (non-saucer shaped), not fully concealing the antennal stem, or base, at least for apical four segments of flagellum in lateral view.

......*continued on the next page*

TABLE 1. (Continued)

Family	Subfamily	Tribe	Genus	Species	Differential diagnosis
	Steninae W.S. MacLeay, 1825	N/A	*Festenus* Żyła, Yamamoto, Wolf-Schwenninger & Solodovnikov, 2017	*Festenus* sp.	Among the congeners, "*Festenus* sp." is most similar to *F. annodutt* Mainda, 2023 from Hkamti amber based on its slender habitus and the coloration of the elytra. However, it is difficult to assign it to *F. annodutt* due to the preservation problem of the fossil.
	Solieriinae Newton & Tayer, 1992	N/A	*Prosolierius* Thayer, Newton & Chatzimanolis, 2012	*Prosolierius antennatus* **sp. nov.**	This new species is closely related to *Prosolierius thayerae* Yamamoto, 2023 from Kachin amber in general appearance with distinctly modified antennomeres 3 and 4, but is easily distinguished from it by the only single modified antennal segment (antennomeres 3).
		N/A		*Prosolierius* sp.	"*Prosolierius* sp." somewhat resembles with either *P. tenuicornis* Thayer, Newton & Chatzimanolis, 2012 or *P. mixticornis* Thayer, Newton & Chatzimanolis, 2012 (both from Kachin amber), but it cannot be reliably assigned to each of the species due to observation issues.
	Scydmaeninae Leach, 1815	N/A	*Hapsomela* Poinar & Brown, 2004	*Hapsomela* cf. *burmitis* Poinar & Brown, 2004	Based on the available morphological characteristics including the protibiae, metatibiae, and male genitalia, it can be assumed that the fossil taxon is a close relative of *Hapsomela burmitis* Poinar & Brown, 2004 from Kachin amber, or even itself. Nevertheless, after the consideration of Yin (2020), the structure of the male aedeagus of this Hkamti specimen seems to be slightly different from that of the Kachin amber *H. burmitis*. Given this uncertainty, I have provisionally identified the Hkamti fossil as *Hapsomela* cf. *burmitis*.
		N/A	*Ektatotricha* Chatzimanolis, Engel & Newton, 2010	*Ektatotricha* sp.	The Hkamti fossil can unambiguously placed in the Kachin-amber endemic genus *Ektatotricha* Chatzimanolis, Engel & Newton, 2010, which contains the type species, *Ektatotricha paradoxa* Chatzimanolis, Engel & Newton, 2010, only. Due to the slight difference found in the configuration of the antennae, I tentatively identified it as "*Ektatotricha* sp.", since there is a possibility that it actually represents an undescribed species.

X-ray micro-computed tomography (or so-called 'micro-CT scanning') (*e.g.* Peris *et al*. 2020; Li Y-D *et al.* 2020, 2025; Richter *et al.* 2022) and synchrotron radiation based micro-computed tomography (SR-μ-CT) (*e.g.* Chatzimanolis *et al*. 2013; Peris *et al*. 2014; Jałoszyński *et al*. 2020; Tihelka *et al*. 2022) may help resolving these obscured structures of the fossils, as exampled by fine details of the ventral head, mandibles, or mesosternal intercoxal process of the mesocoxae. Future studies using advanced imaging techniques may reduce morphological ambiguities of the staphylinoid fossils reported here, although they are not necessarily successful and helpful in our previous experiences, particularly those of Cretaceous ambers (*e.g.* Jałoszyński *et al*. 2018 and Yamamoto *et al*. 2022 *versus* Żyła *et al.* 2017: supplementary fig. S3 and Hirano *et al*. 2019: supplementary fig. S2).

Systematic Paleontology

Order Coleoptera Linnaeus, 1758

Suborder Polyphaga Emery, 1886

Series Staphyliniformia Lameere, 1900

Superfamily Staphylinoidea Latreille, 1802

Family Hydraenidae Mulsant, 1844

Subfamily Hydraeninae Mulsant, 1844

Tribe Hydraenini Mulsant, 1844

Hydraenini gen. et. sp. indet.

(Fig. 1)

Material examined. SEHU-0000121240, sex undetermined, a complete adult (Fig. 1), preserved in a pale yellow, triangular piece of amber measuring 11.3 × 7.7 × 3.2 mm, housed in the Systematic Entomology collection (SEHU), Hokkaido University Museum, Hokkaido University, Sapporo, Japan. The holotype is exceptionally well-preserved; however, observing the ventral surface of the forebody, particularly the head, is somewhat challenging due to the beetle's positioning and the shape of the amber piece.

Locality and horizon. Hkamti site, Hkamti District, Sagaing Region, northern Myanmar; Early Albian (*ca.* 110 Ma), Early Cretaceous.

Systematic placement. The specimen can be assigned to the family Hydraenidae, commonly known as minute moss beetles, based on its small size (body length: 1.49 mm), flattened and elongate oval body shape, conspicuously long maxillary palpi, short "hydrophiloid-like" antennae with an antennal club composed of five pubescent antennomeres, and the presence of a well-developed intercoxal sternite between the metacoxae (Perkins 2000; Jäch *et al.* 2016; Yamamoto *et al.* 2017b). Overall, the fossil closely resembles the external morphology of the genus *Hydraena* Kugelann, 1794, one of the most speciose water beetle genera globally (over 1,000 species; Newton 2022). Based on these morphological features, the fossil can be provisionally assigned to both the subfamily Hydraeninae and the tribe Hydraenini, to which *Hydraena* belongs. Two specific characteristics of the fossil further support this taxonomic placement (Perkins 2000): the prosternal intercoxal process is expanded laterally behind the procoxae, and the second maxillary palpomere is elongated and slender.

Comparison. As noted above, the morphological features of the fossil closely resemble those of the extant genus *Hydraena*. However, it was not possible to confirm two autapomorphies of the genus due to the unclear details of the ventral side of head in the fossil specimen: (i) the presence of a labral-mandibular interlocking device (see fig. 7 in Perkins 1989); (ii) the mentum with an acute median projection anteriorly (see fig. 8 in Perkins 1989). Considering the extensive morphological variability within *Hydraena* and the limited morphological information available from the fossil, confident assignment of the specimen to *Hydraena* is challenging. Furthermore, based on its nine-segmented antennae, the fossil cannot be assigned to *Adelphydraena* Perkins, 1989, the other extant genus of Hydraenini found in northern South America (Perkins 1989). Compared with the sole Kachin amber hydraenid, *Archaeodraena cretacea* Jäch & Yamamoto, 2017 (in Yamamoto *et al.* 2017b), the new specimen is easily distinguishable by several features. First, the third palpomere of the maxillary palpus is substantially shorter than the terminal (fourth) palpomere. Second, the labrum lacks a pair of acute anterior admedian projections. Third, the epipleural gutter along the outer margin is widely explanate. Fourth, the metatarsus is devoid of a fringe of long, thin ventral setae (potentially natatorial setae) (cf. Yamamoto *et al*. 2017b). Given these differences, it is plausible that the specimen represents an undescribed genus, rather than either a member of *Hydraena* or *Archaeodraena*.

Remarks. Hydraenidae is a cosmopolitan family comprising 2,083 species worldwide (Newton 2022). Most species in this family are aquatic or semiaquatic, commonly inhabiting riparian environments such as stream margins, ponds, or areas near marshes (Perkins 2000). Therefore, the discovery of the first hydraenid fossil from Hkamti amber is particularly noteworthy because it provides new insights into the paleoenvironments of the Lower Cretaceous Hkamti forests that produced the amber deposits. The finding stands for the oldest fossil record of Hydraenidae as an amber inclusion. Last but not least, it updates the definitive oldest fossil record of the crown group of the family, since the specimen reported here is placed in Hydraenini with *Archaeodraena* (see Villastrigo *et al*. 2019).

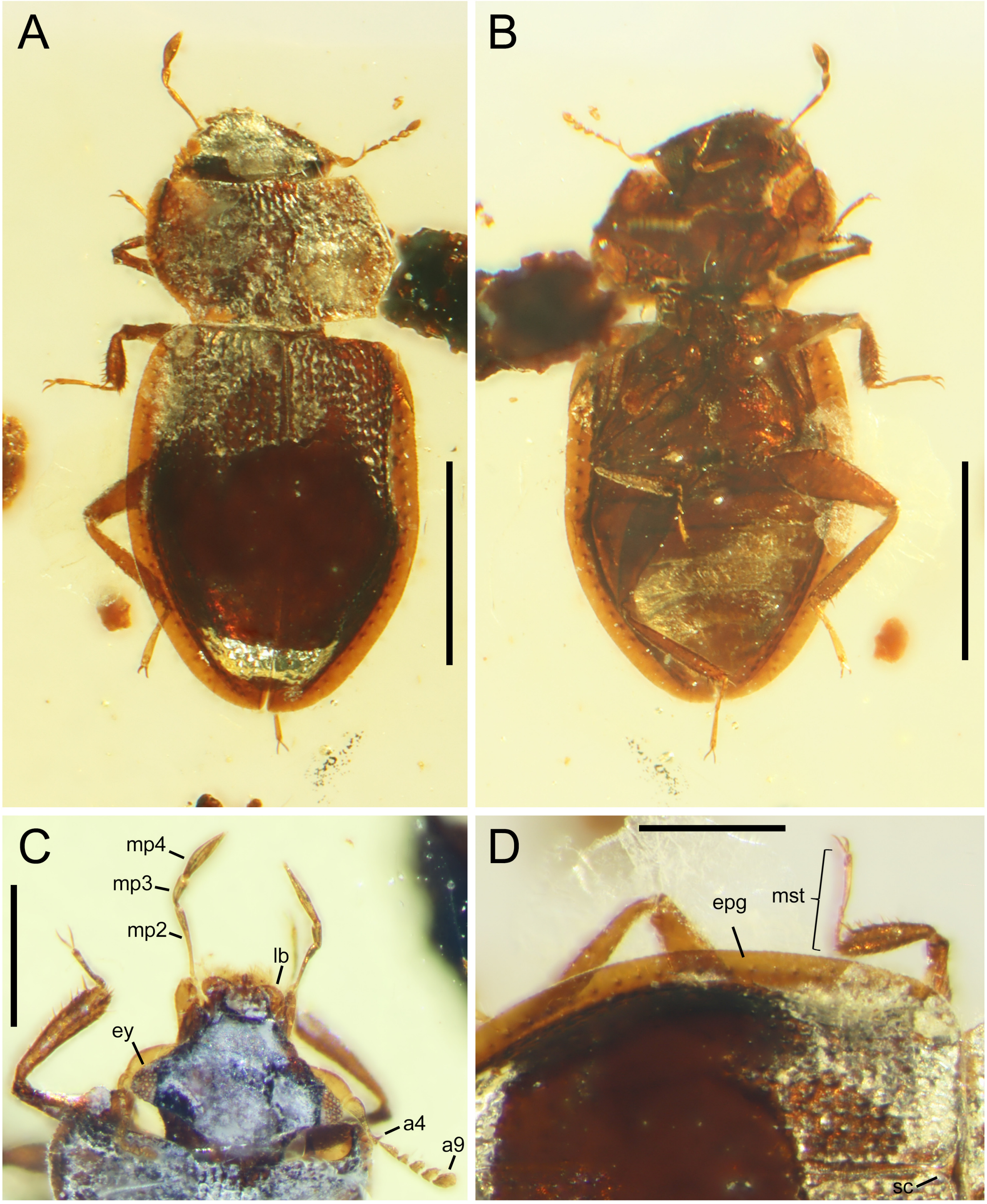

FIGURE 1. Hydraenini gen. et. sp. indet., SEHU-0000121240. A. Habitus, dorsal view; B. habitus, ventral view; C. head, frontal view; D. elytra and midleg, dorsal view. Abbreviations: a4, 9, antennomeres 4, 9; epg, explanate epipleural gutter along outer margin of elytron; ey, compound eye; lb, labrum; mp2–4, maxillary palpomeres 2–4; mst, mesotarsus; sc, scutellar shield. Scale bars: 0.5 mm (A, B); 0.2 mm (C, D).

Family Colonidae G.H. Horn, 1880 (1859)

Genus *Colonellus* Szymczakowski, 1964

Subgenus *Colonellus* Szymczakowski, 1964

(Type species: *Colonellus fleischeri* Szymczakowski, 1964)

Colonellus (*Colonellus*) *hkamtiensis* sp. nov.

(Figs 2, 3)

Etymology. The specific epithet *hkamtiensis* is derived from the Hkamti site, the amber deposit from which the type specimen originates.

Material examined. Holotype, SEHU-0000121241, female, a complete adult (Fig. 2), preserved in a pale yellow, flattened subtriangular piece of amber measuring 15.1 × 15.2 × 4.2 mm, housed in the Systematic Entomology collection (SEHU), Hokkaido University Museum, Hokkaido University, Sapporo, Japan. The holotype is relatively well-preserved, although the left antenna is entirely deformed (flattened), and an opaque air bubble is attached to the dorsal surface of the head, hindering detailed observation of this region. Syninclusion: a tiny spider (Araneae).

Locality and horizon. Hkamti site, Hkamti District, Sagaing Region, northern Myanmar; Early Albian (*ca.* 110 Ma), Early Cretaceous.

Diagnosis. Body comparatively small (*ca.* 1.9 mm long); antenna with four-segmented apical club, with evidently elongate antennomeres 8, 9 (but only weakly), and 11; legs simple, without modifications on femora and tibiae, protarsi with basal three tarsomeres strongly dilated and densely pubescent in females.

Description. Female. Body (Fig. 2) comparatively small, elongate-oval, moderately dorsally convexed, 1.90 mm long (from apex of head capsule visible dorsally to elytral apex), widest at middle of elytra with 0.91 mm body width (elytra slightly opened, as preserved). Color uniformly dark brown. Dorsal surface granulate, with dense, short, and recumbent hairs, lacking erect setae.

Head (Fig. 2) small, sub-triangular, wider than long (0.25 mm long, 0.36 mm wide), anteriorly produced, widest at base, much smaller and narrower than pronotum; neck constriction barely visible; surface even, smooth, without apparent punctures. Compound eyes small, not protruding laterally, located posteriorly, finely faceted. Antennae (Figs 2, 3A, B) eleven-segmented, comparatively long (0.69 mm, right), with last four antennomeres (*a8–11*) forming a loose and pubescent club; antennomeres 1 (scape) and 2 (pedicel) narrowly elongate, cylindrical, elongate, scape slightly wider than pedicel, slightly longer than pedicel; antennomere 3 elongate, weakly dilated apically, moderately shorter than pedicel; antennomere 4 slightly longer than wide, moderately broader than antennomere 3, somewhat strongly dilated apically; antennomere 5 as long as wide, spherical; antennomeres 6–7 transverse, gradually enlarged, broader than antennomere 5; antennomeres 8–10 distinctly enlarged, barrel-shaped, gradually shortened, weakly dilated apically, much longer and wider than preceding antennomeres; antennomere 8 elongate, apparently longer than wide; antennomere 9 weakly elongate, slightly longer than wide; antennomere 10 as long as wide or very slightly wider than long; antennomere 11 symmetrical, largely elongate-oval with acuminate apex, apparently elongate, about 1.46 times broader than long, slightly narrower but much longer than antennomere 10, about 1.33 times as long as preceding antennomere. Antennal periarticular gutters not visible. Mandibles small, with sharp apex. Maxillary palpus (Fig. 3A) four-segmented, rather short, setose; maxillary palpomere 1 small; palpomere 2 elongate, slightly widened toward apex; palpomere 3 (*mp3*) thick, dilated apically, much wider than preceding palpomere; palpomere 4 (*mp4*) conical, much shorter and narrower than palpomere 3, with acutely pointed apex. Labial palpus short.

Pronotum (Fig. 2A, D, E) semicircular, transverse (0.55 mm long along midline, 0.88 mm wide), widest near base; anterior margin of pronotum nearly straight, whereas that of posterior margin bisinuate; posterolateral corners roundly angulate; disc weakly convex, less so at basal portion portion, with dense, fine ground microsetae uniformly, but without noticeable punctation. Base of prothorax slightly wider than combined elytral base. Prosternnum (Fig. 2C) longitudinally well raised medially. Scutellar shield (Fig. 2A) sub-triangular. Mesoventrite not well observable. Metaventrite (Fig. 2C) small, transverse.

Elytra (Fig. 2A, D, E, F) entire, covering whole abdomen posteriorly, tapering toward apex; each strongly elongate, approximately 2.47 times as long as wide (left elytron 1.21 mm long from posterior pronotal margin to elytral apex, 0.49 mm wide); epipleural ridge developed; dorsal surface not striate, clothed with fine punctures and evenly uniformly pubescent by dense microsetae.

Legs (Figs 2B–F, 3C) moderately long, slender, without modifications on femora and tibiae. Forelegs with procoxae small, conical; profemora robust, clavate; protibiae straight, not distinctly curved or modified; protarsi five-segmented; basal three protarsomeres (*pt1–4*) strongly dilated (Fig. 3C), ventral surface covered with fine, dense, probable adhesive setae; protarsomere 4 small, sub-triangular; protarsomere 5 elongate, slender, as long as basal three protarsomeres combined. Midlegs with mesofemora robust, clavate; mesotibiae straight, slender, armed with dense large spines at external margins; mesotarsi elongate, five-segmented; mesotarsomeres 1–4 successively shortened; mesotarsomere 5 elongate. Hindlegs long, robust; metacoxae contiguous or subcontiguous; metafemora longer and wider than pro- and mesofemora, lacking projection; metatibiae simple, slender, longer than pro- and mesotibiae, bearing slender spines at external margins, with several blunt and uneven setae at apex; metatarsi elongate, slender, five-segmented; metatarsomeres 1–4 successively shortened, metatarsomere 5 long, elongate. Pretarsal claw simple.

Abdomen (Fig. 2B, C, F) with four visible abdominal ventrites, each strongly transverse; ventrite 4 generalized in shape, semicircular, slightly longer than ventrite 3. Intersegmental membranes between abdominal sternites

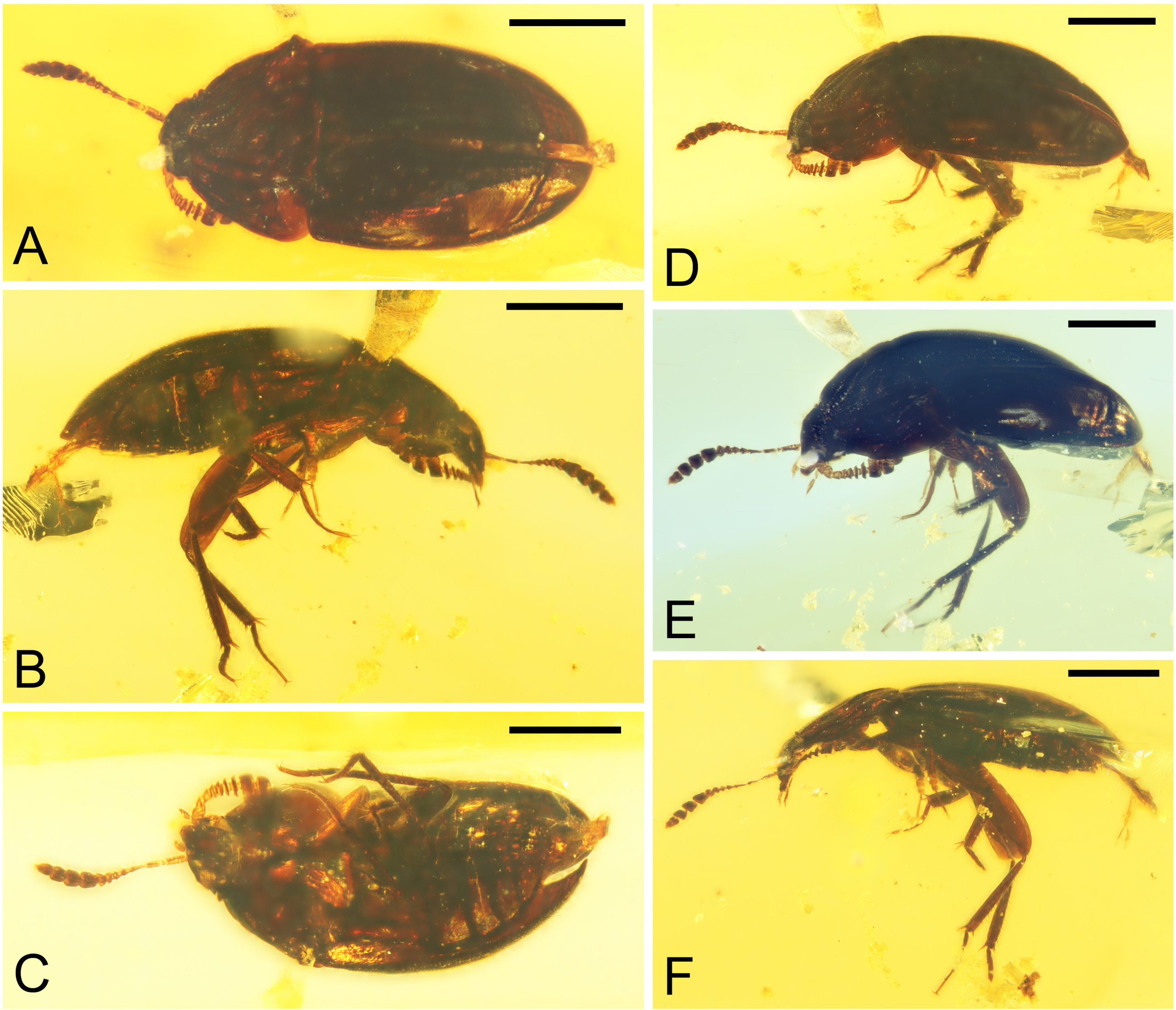

FIGURE 2. General habitus of *Colonellus* (*Colonellus*) *hkamtiensis* **sp. nov.**, holotype, SEHU-0000121241. A. Dorsal view; B. ventrolateral view, right; C. ventral view; D. dorsolateral view, left; E. dorsolateral view, left; F. lateral view, left. Scale bars: 0.5 mm (A–F).

not visible. Genitalia (Fig. 3D) with elongate gonocoxites and gonostyli.

Systematic placement. *Colonellus* (*Colonellus*) *hkamtiensis* **sp. nov.** is placed within the family Colonidae based on the combination of the following morphological features: a small, drab-brown, and elongate-elliptical body; absence of an occipital carina on the head; a tarsal formula of 5-5-5; and 11-segmented antennae, with antennomere 8 not smaller than antennomeres 7 and 9, distinguishing it from members of Leiodidae (Peck & Stephan 1996; Cai & Huang 2017a). Furthermore, the specimen is provisionally assigned to the extant genus *Colonellus* based on its elongate antennomere 11 (contrasting with *Colon* Herbst, 1797, where antennomere 11 is wider than its length; Hoshina 2009, 2016a; Cai & Huang 2017a). However, the mesoventral carina in lateral view and the apical anastomosing sensory surface of the antennal club segments are not visible in the holotype.

Comparison. The overall morphological characteristics of the new species align well with the nominotypical subgenus *Colonellus* of the genus *Colonellus*. This subgenus is readily defined by a four-segmented antennal club, in contrast to the other subgenus, *Pentacolonellus* Peck, 1998, known from India, which exhibits a distinctly developed antennal club composed of five antennomeres (Peck 1998). The new species is easily distinguished from the sole Kachin amber species of *Colonellus*, *Colonellus* (*Pentacolonellus*) *burmiticus* Cai & Huang, 2017, by its antennal club composed of four antennomeres (*versus* five in *C. burmiticus*) and its larger body size (1.90 mm *versus* 1.43 mm; Cai & Huang 2017a). Additionally, the new species can be differentiated from all four modern species of *Colonellus* recorded in Sumatra (Indonesia), Sri Lanka, and the Yaeyama Islands of Ryûkyû (southwestern Japan). It exhibits a comparatively smaller body size (1.90 mm *versus* 1.9–2.6 mm), an evidently elongate antennomere 8, and a somewhat elongate (longer than its width) antennomere 9

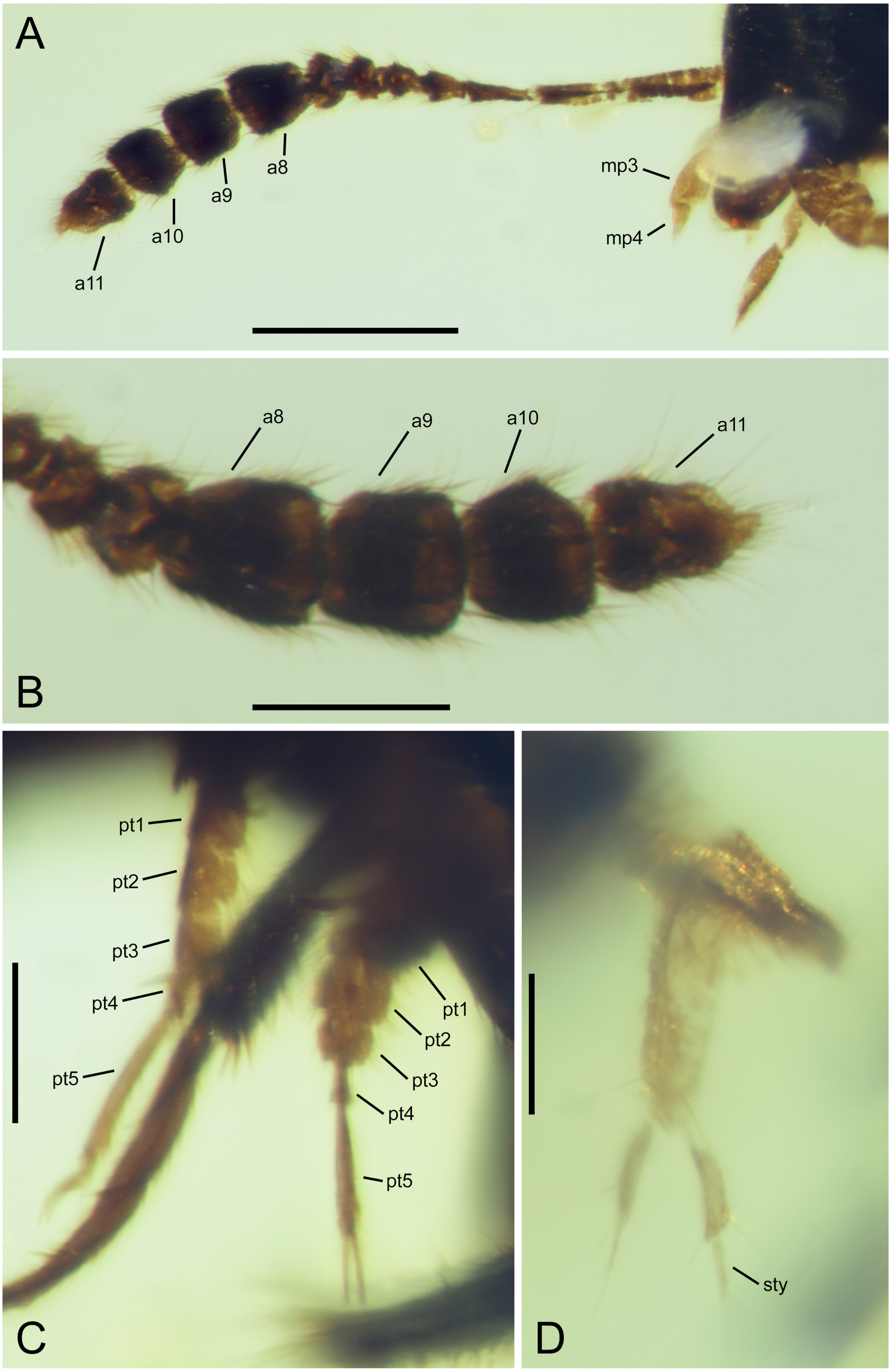

FIGURE 3. Details of *Colonellus* (*Colonellus*) *hkamtiensis* **sp. nov.**, holotype, SEHU-0000121241. A. Antenna, right, lateral view; B. enlargement of apical antennal club, right, lateral view; C. protarsi, lateral view; D. female genitalia with gonocoxites and gonostyli. Abbreviations: a8–11, antennomeres 8–11; mp3, 4, maxillary palpomeres 3, 4; pt1–5, protarsomeres 1–5; sty, gonostylus. Scale bars: 0.2 mm (A); 0.1 mm (B–D).

(Szymczakowski 1964; Hoshina 2009, 2016a). *Colonellus* (*C.*) *hkamtiensis* **sp. nov.** is also distinct from the Kachin amber colonid *Colon burmiticum* Yamamoto, 2018, in Yamamoto & Takahashi (2018). Differences include a more elongate terminal antennomere, non-striate elytra, much larger body size (1.44 mm *versus* 1.90 mm), and wider maxillary palpi.

Remarks. Cai *et al.* (2022) recently elevated the subfamily Coloninae of the family Leiodidae to Colonidae, recognizing it as a distinct family within Staphylinoidea. With 172 species across two genera (Newton 2022), Colonidae represents a relatively small family within this mega-diverse superfamily. The genus *Colon*, the nominotypical genus of the family, contributes the vast majority of its species diversity. In contrast, the genus *Colonellus* is a tiny fraction of the family, consisting of only seven species and two subspecies within two subgenera (Szymczakowski 1964; Peck 1998; Hoshina 2009; Cai & Huang 2017a; this study). This includes the fossil species *Colonellus* (*P.*) *burmiticus* from Kachin amber (Cai & Huang 2017a) and the new extinct species described in this study. All known *Colonellus* species are restricted to the Oriental region (Szymczakowski 1964; Peck 1998; Hoshina 2009). This biogeographic distributional pattern aligns with the current and previous discoveries of two *Colonellus* fossils from Myanmar amber (Cai & Huang 2017a; this study). To date, both *Colon* and *Colonellus* have been described from Kachin amber (Cai & Huang 2017a; Yamamoto & Takahashi 2018). The new species presented here represents the oldest known fossil of both the family and genus, slightly extending the earliest fossil record previously established from Kachin amber. The natural history and ecology of Colonidae remain poorly understood. However, these beetles are frequently collected using flight intercept traps (FITs) and pitfall traps (PTs) (Hoshina 2009, 2016b). Such collection suggests that Colonidae is particularly susceptible to entrapment in plant resin during flight activities, providing a plausible explanation for the relatively high abundance of *Colon* species as amber bio-inclusions in Kachin amber (Yamamoto, unpublished data).

Family Staphylinidae Latreille, 1802

Subfamily Osoriinae Erichson, 1839a

Tribe Thoracophorini Reitter, 1909

Subtribe Clavilispinina Newton & Thayer, 1992

Genus *Mesallotrochus* Cai & Huang, 2015

(Type species: *Mesallotrochus longiantennatus* Cai & Huang, 2015)

Mesallotrochus sp.

(Fig. 4)

Material examined. SEHU-0000121242, sex undetermined, a complete adult (Fig. 4), preserved in a pale yellow, elongate-oval cabochon of amber measuring 21.1 × 9.5 × 4.7 mm, housed in the Systematic Entomology collection (SEHU), Hokkaido University Museum, Hokkaido University, Sapporo, Japan. The specimen is well-preserved; however, fine details of the ventral surface of the beetle and the dorsum of the pronotum are obscured due to several large cracks in the amber piece.

Locality and horizon. Hkamti site, Hkamti District, Sagaing Region, northern Myanmar; Early Albian (*ca.* 110 Ma), Early Cretaceous.

Systematic placement. The specimen is readily assigned to the staphylinid subfamily Osoriinae based on its general habitus, which includes a parallel and elongate body shape; antennae inserted in front of the eyes beneath the shelf-like corners of the frons; short, truncate elytra exposing most of the abdomen; absence of abdominal paratergites; and short mandibles barely visible in dorsal view when closed (Newton *et al.* 2000; Cai & Huang 2015a; Yamamoto *et al.* 2024). Within Osoriinae, the specimen is confidently placed in the tribe Thoracophorini, supported by the general habitus, cephalic characters, protibia with an inner edge that is neither concave nor bearing a ctenidium, and abdominal structure lacking sutures between the tergites and sternites (Newton *et al.* 2000; Cai & Huang 2015a). The fossil is further attributed to the Kachin-amber endemic genus *Mesallotrochus* Cai & Huang, 2015, based on the following combination of diagnostic characteristics (Cai & Huang 2015a): similar small-sized habitus; transverse, rectangular pronotum with well-developed anterolateral angles; long antennae exceeding the combined length of the head and pronotum; elytra longer than the pronotum, partially covering abdominal tergite III; and slender tibiae without strong spines along the external edges.

Comparison. The Hkamti osoriine fossil bears a striking resemblance to *Mesallotrochus longiantennatus* Cai & Huang, 2015, the type species and sole representative of the extinct genus *Mesallotrochus*, described from mid-Cretaceous Kachin amber. The specimen's major morphological features align well with the holotype of *M. longiantennatus*, as highlighted earlier. However, there are notable differences: the fossil beetle appears to possess a more transverse and shorter pronotum, along with a comparatively smaller body size (2.24 mm *versus* 2.86 mm). These distinctions suggest that the new specimen represents an undescribed species of *Mesallotrochus*. Unfortunately, due to the limitations of preservation, many critical diagnostic features, including the tarsi and mouthparts, are not discernible in the Hkamti amber specimen, preventing further comparisons.

Remarks. Osoriinae, or un-margined rove beetles, is a moderately large subfamily within the mega-diverse family Staphylinidae, encompassing nearly 2,400 described species (Newton *et al.* 2022). Numerous osoriine species are commonly associated with forest habitats and are typically found in decaying wood, beneath bark, or within forest leaf litter. From Myanmar (Kachin) amber, five species representing four genera across three tribes have been described to date, marking the oldest fossil

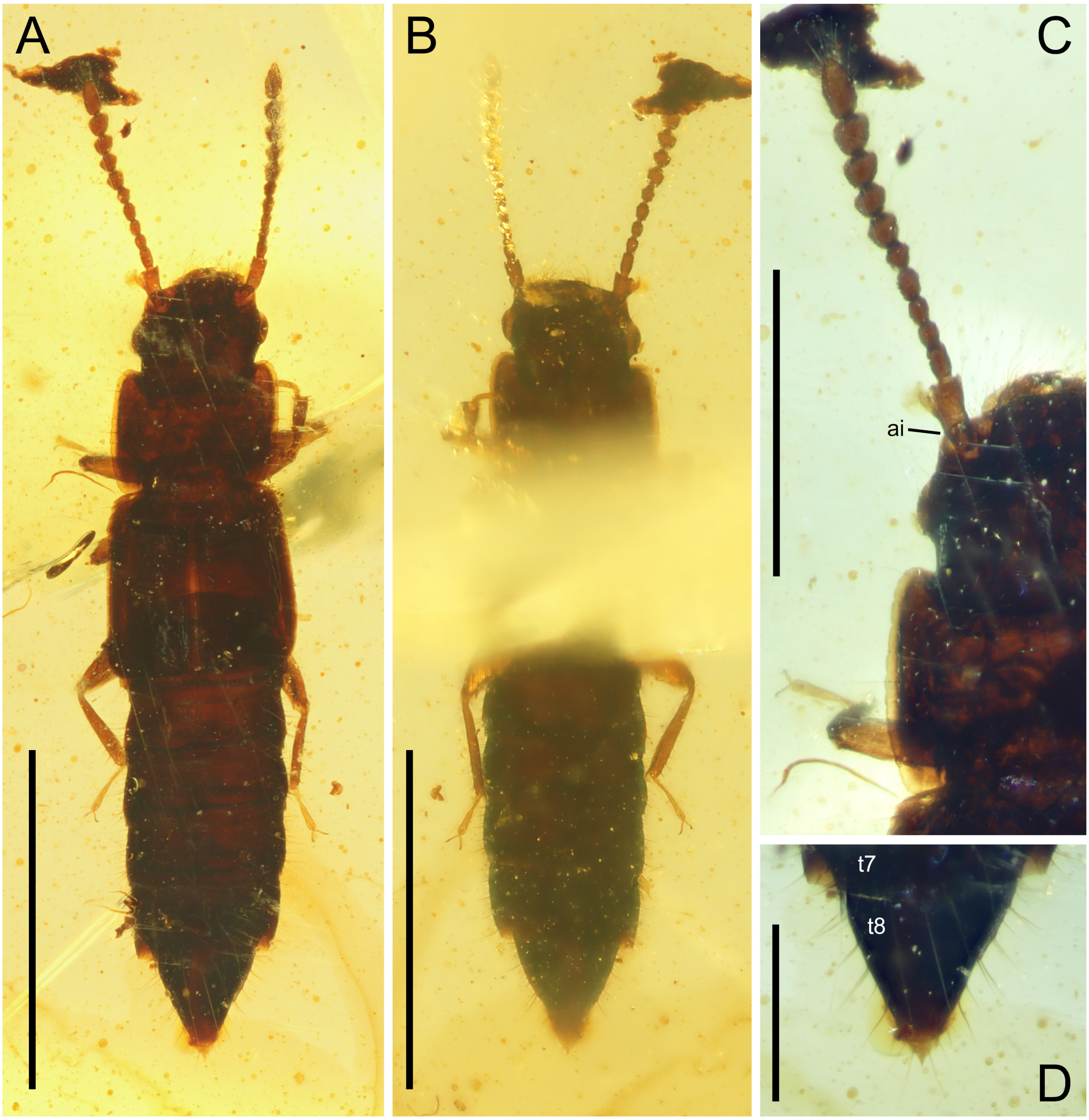

FIGURE 4. *Mesallotrochus* sp., SEHU-0000121242. A. General habitus, dorsal view; B. general habitus, ventral view; C. details of lateral half (left) of forebody, dorsal view; D. details of apex of abdomen, dorsal view. Abbreviations: ai, antennal insertion; t7, 8, tergites VII, VIII. Scale bars: 1.0 mm (A, B); 0.5 mm (C); 0.3 mm (D).

record for this subfamily (Cai & Huang 2015a; Yamamoto & Takahashi 2019; Peng *et al*. 2022; Yamamoto 2024b):

Tribe Thoracophorini: *Mesallotrochus longiantennatus* Cai & Huang, 2015.

Tribe Leptochirini: *Cretochirus newtoni* Yamamoto, 2019 in Yamamoto & Takahashi (2019); *Priochirus* (*Eopriochirus*) *thayerae* Yamamoto, 2019 in Yamamoto & Takahashi (2019); *Priochirus* (*Eopriochirus*) *trisclerite* Peng, Jiang, Chi, Long, Engel & Wang, 2022.

Tribe Eleusinini: *Eleusis sulcata* Yamamoto, 2024.

Together with the leptochirine specimen described below, the newly discovered *Mesallotrochus* specimen from Hkamti amber extends the earliest known fossil record of Osoriinae by approximately 11 million years.

Tribe Leptochirini Sharp, 1887

Genus *Cretochirus* Yamamoto, 2019 in Yamamoto & Takahashi (2019)

(Type species: *Cretochirus newtoni* Yamamoto, 2019 in Yamamoto & Takahashi (2019))

Cretochirus elongatus sp. nov.

(Figs 5–7)

Etymology. The specific epithet "*elongatus*" is derived from the Latin term *elongatus*, meaning elongated, referring to the narrowly elongate body of the new species.

Material examined. Holotype, SEHU-0000121243, sex undetermined, a complete adult (Fig. 5), preserved in a pale yellow, flattened oval piece of amber measuring 18.2 × 11.8 × 2.7 mm, housed in the Systematic Entomology collection (SEHU), Hokkaido University Museum, Hokkaido University, Sapporo, Japan. The holotype is moderately to somewhat well-preserved, although it is more or less distorted; however, the presence of air bubbles and debris prevents detailed observation of certain body parts.

Locality and horizon. Hkamti site, Hkamti District, Sagaing Region, northern Myanmar; Early Albian (*ca.* 110 Ma), Early Cretaceous.

Diagnosis. Body large (*ca*. 7.4 mm long, including mandibles), narrowly elongate, slender; head with a pair of outer lateral horns (*ohh*) apparently produced; eyes comparatively large; left mandible with ventral teeth 1 and 2 (*vt1*, *2*) very widely separated; mentum glabrous without a distinct median seta; pronotum longer than wide.

Description. Body (Fig. 5) large, elongate, sub-parallel sided, moderately flattened, 7.43 mm long with mandibles (from apex of left mandible to apex of tergite VIII), 7.09 mm long without mandibles (from clypeus to apex of tergite VIII). Color uniformly blackish brown to black; anterolateral margins of head, eyes, mandibles, and protibiae somewhat paler. Dorsal surface smooth, glossy, generally glabrous, only partially equipped with long, stout setae.

Head (Fig. 6A, B) relatively small, slightly transverse, 0.72 mm long (from clypeus to anterior margin of pronotum), 0.95 mm wide (maximum width, across compound eyes), distinctly smaller and narrower than pronotum; anterior margin between small cephalic lateral horns (Fig. 6A, *ohh*) broadly slightly emarginate, anteromedial margin depressed; vertex without longitudinal sulcus medially, well-depressed medially except raised lateral areas; tempora short; posterolateral margins of vertex without row of setae; neck (Figs 6A, B, 7A, *nc*) present, strongly constricted behind compound eyes dorsally and laterally; surface even and smooth in frons and vertex, but with well-raised lateral marginal areas (Fig. 6B; see also *le* in Yamamoto & Takahashi 2019: fig. 3C), without apparent punctation and setation. Compound eyes positioned basolaterally, rather large, strongly projecting laterally, finely faceted. Antennal insertions (Fig. 6A, B) not visible dorsally, fully concealed under shelf-like corners of frons, inserted anterior to line drawn between anterior margins of compound eyes. Antennae (Figs 5, 6) with 11 antennomeres (Fig. 6C, D, *a1*, *a9–11*), fili-moniliform, not reaching to middle of elytra, sub-parallel sided nearly in entire length, gradually densely setose apically; antennomere 1 (scape) widest, broad, narrowly elongate, robust, strongly dilated apically; antennomere 2 (pedicel) elongate, distinctly shorter and narrower than scape, 2/3 as long as antennomere 3; antennomere 3 narrowly elongate, strongly dilated apically; antennomeres 4 and 5 similar length and size, elongate, sub-parallel sided, cylindrical; antennomeres 6–10 evidently longer than wide; antennomere 11 narrowly elongate, somewhat spindle-shaped, more than twice as long as wide, with conical apex. Mandibles (Fig. 6A, B) short, small, less than half length of head capsule, produced anteriorly; right mandible with one dorsal tooth (Fig. 6B, *dt*) and at least one ventral tooth (Fig. 6B, *vt1*); left mandible with one dorsal tooth (Fig. 6B, *dt*) and two widely separated ventral teeth visible (Fig. 6B, *vt1*, *2*). Maxillary palpus (Fig. 7B) four-segmented, rather short, inconspicuous, with scattered several setae (without ground setation); maxillary palpomere 1 small, not visible from above; palpomere 2 narrowly elongate, slightly widened toward apex; palpomere 3 small, short, slightly wider than long, narrower than preceding palpomere; palpomere 4 (*mp4*) narrowly elongate, more or less fusiform, gradually tapering anteriorly from near basal quarter, much longer than palpomere 3, with conical apex. Labial palpus (Fig. 7B) three-segmented, short; labial palpomere 2 small, short; palpomere 3 narrowly elongate, weakly curved, with obliquely truncate apex. Mentum (Fig. 7B, *mtm*) trapezoidal, moderately transverse; surface slightly roughened, lacking carinae or ridges; anterior margin truncate or seemingly weakly concaved, without pointed denticle(s); central disc glabrous, probably lacking distinct median seta (*msmt* in Yamamoto & Takahashi 2019: fig. 3D). Gular sutures (Fig. 7B) narrowly separated, sub-parallel sided in anterior half, not sinuate, weakly gradually widened posteriorly.

Pronotum (Figs 5A, 6A, 7A) rectangular, slightly longer than wide (1.31 mm long along midline, 1.19 mm wide; length/width = 1.10), widest at apical quarter and slightly narrower posteriorly, distinctly broader than elytra; anterior margin of pronotum emarginate medially, whereas that of posterior margin moderately produced; each pronotal margin with row of short, thin, very sparse bristles; all pronotal angles smooth, pronotal anterolateral angles obtusely rounded, whereas pronotal posterolateral angles closer to orthogonal; dorsal surface glabrous without ground microsetae, disc slightly convex dorsally; median longitudinal sulcus present on pronotal disc (Fig. 6A, *msp*), moderately developed, only weakly expanding posteriorly, its posterior end lacking distinct rounded fovea. Prosternum (Fig. 7B) large, transverse, with medially projecting anterior margin. Pronotal hypomeron (Fig. 7B) rather wide, relatively strongly folded inwards, with moderately fine and straight inferior marginal lines (*iml* in Yamamoto & Takahashi 2019: fig. 4E). Procoxal cavities closed behind and laterally. Prosternal process between procoxae small and short, depressed between procoxae. Mesonotum well developed. Scutellar shield seemingly subtriangular (thin air layer prevents further observation of details). Mesoventrite not well observable. Metaventrite elongate, convexed ventrally.

Elytra (Fig. 5A) elongate, rectangular, subparallel-

FIGURE 5. General habitus of *Cretochirus elongatus* **sp. nov.**, holotype, SEHU-0000121243. A. Dorsal view; B. ventral view. Scale bars: 2.0 mm (A, B).

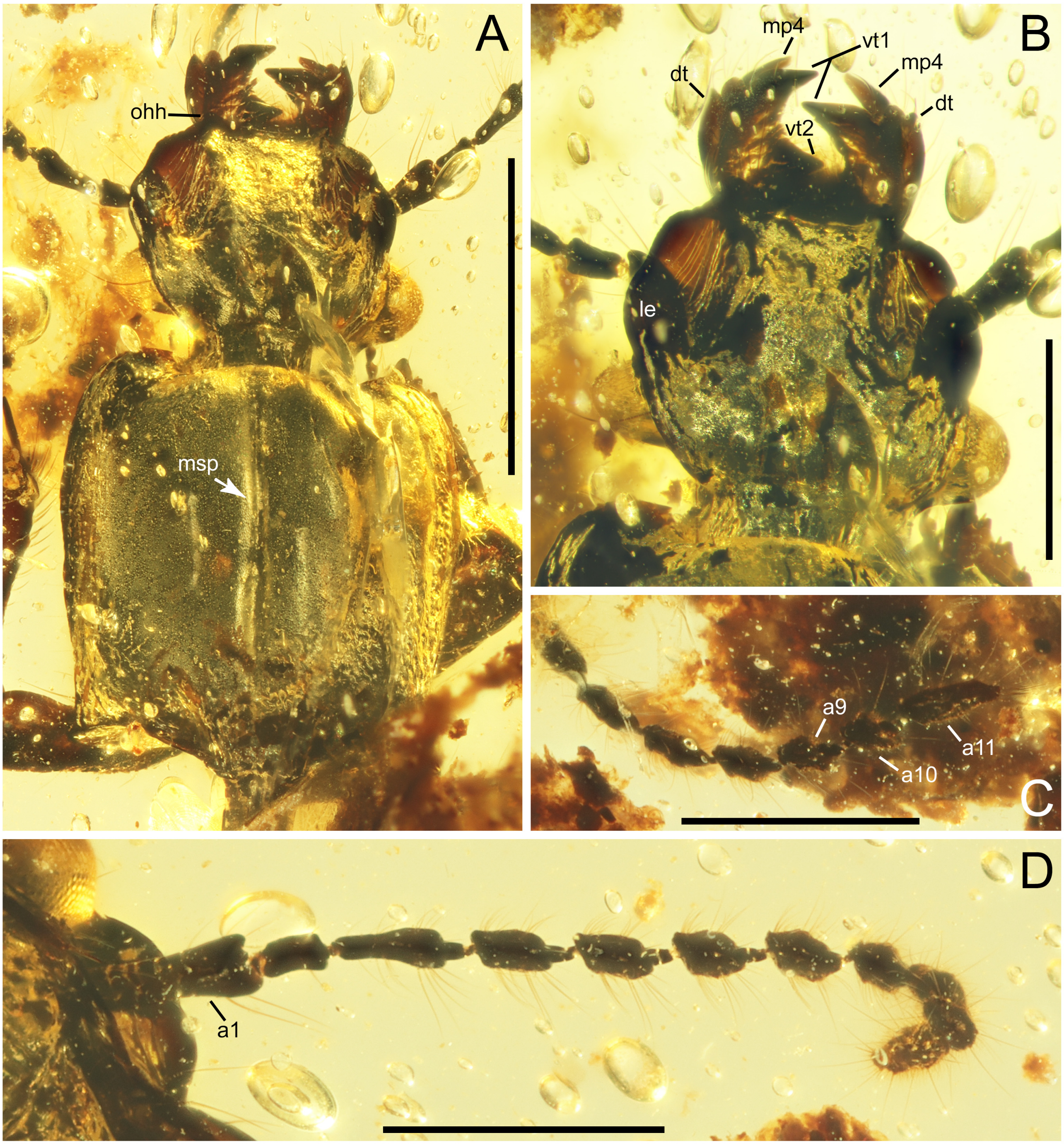

FIGURE 6. Details of *Cretochirus elongatus* **sp. nov.**, holotype, SEHU-0000121243. A. Head and pronotum, dorsal view; B. head, dorsal view; C. enlargement of apical half of antenna, left, ventral view; D. antenna, right, ventral view. Abbreviations: a1, 9–11, antennomeres 1, 9–11; dt, dorsal teeth of mandibles; le, lateral elevation of head capsule; mp4, maxillary palpomere 4; msp, median longitudinal sulcus on pronotum; ohh, outer lateral horns along anterior margin of head; vt1, 2, ventral teeth 1, 2 of mandibles. Scale bars: 1.0 mm (A); 0.5 mm (B–D).

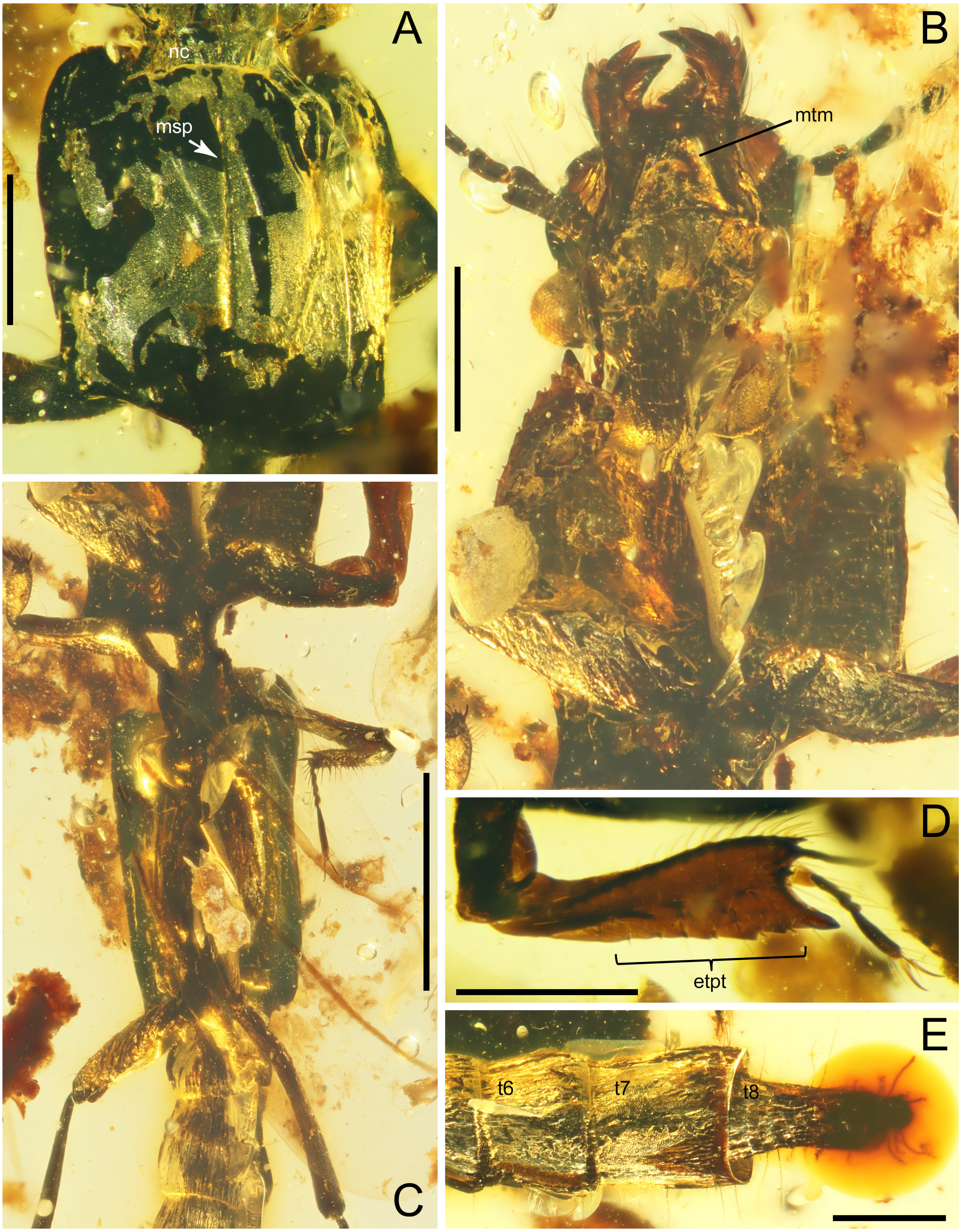

FIGURE 7. Details of *Cretochirus elongatus* **sp. nov.**, holotype, SEHU-0000121243. A. Pronotum, dorsal view; B. head and prothorax, ventral view; C. meso- and metathoraxes, ventral view; D. protibia, left, ventral view; E. abdominal apex, dorsal view. Abbreviations: etpt, external teeth along protibial edge; msp, median longitudinal sulcus on pronotum; mtm, mentum; nc, neck constriction; t6–8, tergites VI–VIII. Scale bars: 0.5 mm (A, B, D, E); 1.0 mm (C).

sided, weakly tapering posteriorly; each elytron strongly elongate, approximately 3.39 times as long as wide (left elytron 1.56 mm long from elytral shoulder to posterolateral elytral corner, 0.46 mm wide), moderately longer but narrower than pronotum; lateral margins each with row of sparse, short, stiff setae; elytral anterolateral angles (shoulders) broadly rounded, whereas elytral posterolateral angles acutely angulate; epipleural ridge present; dorsal surface without striae, carinae, or ground microsetae.

Legs (Figs 5, 7C, D) long, slender, with developed protibiae. Forelegs large, robust, conspicuous. Procoxae small, contiguous; protrochanters irregularly conical. Profemora clavate, robust. Protibiae (Figs 5, 7D) flattened, robust, strongly widened apically, only weakly crenulate along outer edges; protibial surface without ground microsetae dorsally and ventrally; outer margins with row of short setae (spine-like) between crenulae or denticles, inner margins with tufts of long setae in anterior half of protibiae; protibial apical spur long, conspicuous. Protarsi five-segmented, slender, not laterally expanded, much shorter than protibiae; protarsomere 1 elongate, protarsomeres 2–4 subequl in length, slightly shorter than protarsomere 1, protarsomere 5 longest, nearly as long as preceding four tarsomeres combined. Midlegs slightly shorter than forelegs. Mesocoxae narrowly separated, elongate oval, ventrally expanded. Mesotrochanters conical, small. Mesofemora slender, rod-like. Mesotibiae slender, rod-like; with numerous small spines and short setae, with paired spurs at posterior apex. Mesotarsi five-segmented, slender; mesotarsomeres 2–4 subequl in length, each slightly shorter than mesotarsomere 1; mesotarsomere 5 longest, nearly as long as preceding four tarsomeres combined. Hindlegs long, slender. Metacoxae subcontiguous. Metatrochanters small, nearly conical. Metafemora long, clavate. Metatibiae simple, slender, rod-like, moderately covered with setae on lateral edges. Metatarsi five-segmented, very short, slender, less than half length of metatibiae; metatarsomeres 1 elongate, metatarsomeres 2–4 subequl in length, slightly shorter than metatarsomere 1; metatarsomere 5 longest, nearly as long as preceding four tarsomeres combined. Pretarsal claws simple, moderately curved, with paired empodial setae as long as claws.

Abdomen (Figs 5, 7C, E) narrowly elongate, slender, cylindrical, progressively slightly broadened from base to tergite VIII, with six exposed sternites excluding genital segments, narrower than pterothorax; genital segments barely exposed but details not visible; all observable abdominal segments without paratergites, tergites and sternites IV–VI each fused into a continuous ring; abdominal segments IV–VI subequal in length, but that of segment VII much longer and larger, about 1.23 times as long as preceding segment (tergite), with truncate posterior margin; segment VIII elongate, partially retracted into segment VII, strongly narrowing apically, covered with dense, long setae. Surfaces of both dorsal and ventral sides generally glabrous, with only sparsely scattered suberect setae along near lateral and posterior margins. Tergite III as long as wide; tergites IV–VI each slightly wider than long, progressively broadened, dilated posteriorly; tergite VII longer than wide, sub-parallel sided. Intersegmental membranes present, well developed, conspicuous, with distinct ‘brick-wall’ like patterns. Sternite III with strong longitudinal intercoxal carina (keel) and postcoxal ridges. Genitalia not visible.

Systematic placement. The new species is easily ascribed to the staphylinid subfamily Osoriinae based on the combination of its general habitus, ring-like abdominal segments (lacking paratergites) with six visible sterna, antennal insertions fully concealed under the shelf-like corners of the frons, and several other features (Newton *et al*. 2000; Cai & Huang 2015b; Yamamoto *et al*. 2025). Among the five osoriine tribes (Moreno *et al*. 2025), the new fossil specimen can be further placed in the tribe Leptochirini based on its distinct general habitus; cephalic modifications with anterior teeth; mandibles with developed dorsal and ventral teeth; narrowly separated gular sutures; a 5-5-5 tarsal formula; small, globose procoxae without a transverse groove and carina on the mesal surface; and posteriorly closed procoxal cavities (Blackwelder 1942; Wu & Zhou 2007; Irmler 2010; Yamamoto & Takahashi 2019). Among the six genera of Leptochirini, the new taxon is assigned to the Kachin-amber endemic genus *Cretochirus* Yamamoto, 2019, based on the following combination of characteristics (Yamamoto & Takahashi 2019): protibiae with very weakly crenulated external edges; head without distinct anterior teeth; head dorsum broadly and medially impressed, encircled by moderately elevated lateral projections, lacking a longitudinal median sulcus; and mandibles short, only weakly developed, less than half length of head capsule.

Comparison. As previously noted, the specimen can be unambiguously assigned to *Cretochirus*, a genus thus far confined to Kachin amber. The second species of the genus, *Cretochirus elongatus* **sp. nov.**, is characterized by its much more elongate and larger body (7.4 mm *versus* 5.7 mm in the type species, both including mandibles), as well as differences in the mandibles and mentum. Considering these morphological features, I prefer to describe it as a new species, rather than as a variation within the type species, *C. newtoni*.

Remarks. The new species represents both the second species of the genus and the first record of *Cretochirus* outside of Kachin amber. This finding suggests the co-occurrence of *Cretochirus* in two geographically adjacent and geologically contemporaneous, but slightly differentiated, amber-producing forests, both situated on the West Burma block or Burma Terrane during the Cretaceous. Additionally, together with Thoracophorini, the discovery of Leptochirini from Hkamti amber is important because it indicates that two distinct osoriine tribes had already appeared in the Early Cretaceous. These findings imply a much older origin of the subfamily based on the presence of Thoracophorini and Leptochirini in Hkamti amber.

Subfamily Tachyporinae W.S. MacLeay, 1825

Tribe Vatesini Seevers, 1958

Genus *Procileoporus* Yamamoto, 2016

(Type species: *Procileoporus burmiticus* Yamamoto, 2016)

Procileoporus sp.

(Fig. 8)

Material examined. SEHU-0000121244, sex undetermined, an adult with partially missing left side of the body due to overpolishing (Fig. 8), preserved in a dark yellow, flattened, broadly half-moon shaped piece of amber measuring 27.1 × 22.2 × 6.8 mm, housed in the Systematic Entomology collection (SEHU), Hokkaido University Museum, Hokkaido University, Sapporo, Japan. The specimen is partially lost due to overpolishing of the amber piece. Additionally, it is difficult to observe fine details on both the dorsal and ventral sides due to the positioning of the beetle fossil. Syninclusion: a Teredidae beetle (Coleoptera: Coccinelloidea).

Locality and horizon. Hkamti site, Hkamti District, Sagaing Region, northern Myanmar; Early Albian (*ca.* 110 Ma), Early Cretaceous.

Systematic placement. The specimen can be assigned to the staphylinid subfamily Tachyporinae, specifically the Kachin amber monotypic genus *Procileoporus* Yamamoto, 2016. This assignment is based on its slender sublimuloid habitus, uniformly blackish coloration, glabrous body, small head with fourth maxillary palpomere longer than the third, spiny tibiae, and sternites IV–VII, each with a pair of long macrosetae (Yamamoto 2016a). The genus was originally established with the type species only and placed in the tribe Tachyporini. However, after a comprehensive study of Tachyporinae, it was transferred to the newly defined tachyporine tribe Vatesini (Yamamoto 2021). Although *Procileoporus* was formally reported only once with a single specimen known, it is evident that the genus is somewhat abundant in Kachin amber (Yamamoto, unpub. data).

Comparison. The *Procileoporus* specimen found in Hkamti amber closely resembles the type species of the genus, *Procileoporus burmiticus* Yamamoto, 2016, although only the lateral habitus is visible in the fossil. However, it is challenging to confirm this specimen as the type species due to its smaller body size (2.81 mm *versus* 4.22 mm, including exposed genital segments) and the poor preservation of both the holotype of *P. burmiticus* and the new material. Therefore, the Hkamti specimen is provisionally identified as *Procileoporus* sp., rather than *P. burmiticus*.

Remarks. The taxonomy of Tachyporinae, commonly referred to as crab-like rove beetles, has undergone substantial revision in recent years, particularly through the work of Yamamoto (2021). Tachyporinae was previously classified into five tribes; Yamamoto's study redefined the subfamily into four tribes, incorporating updated subfamilial and tribal concepts. Notably, the

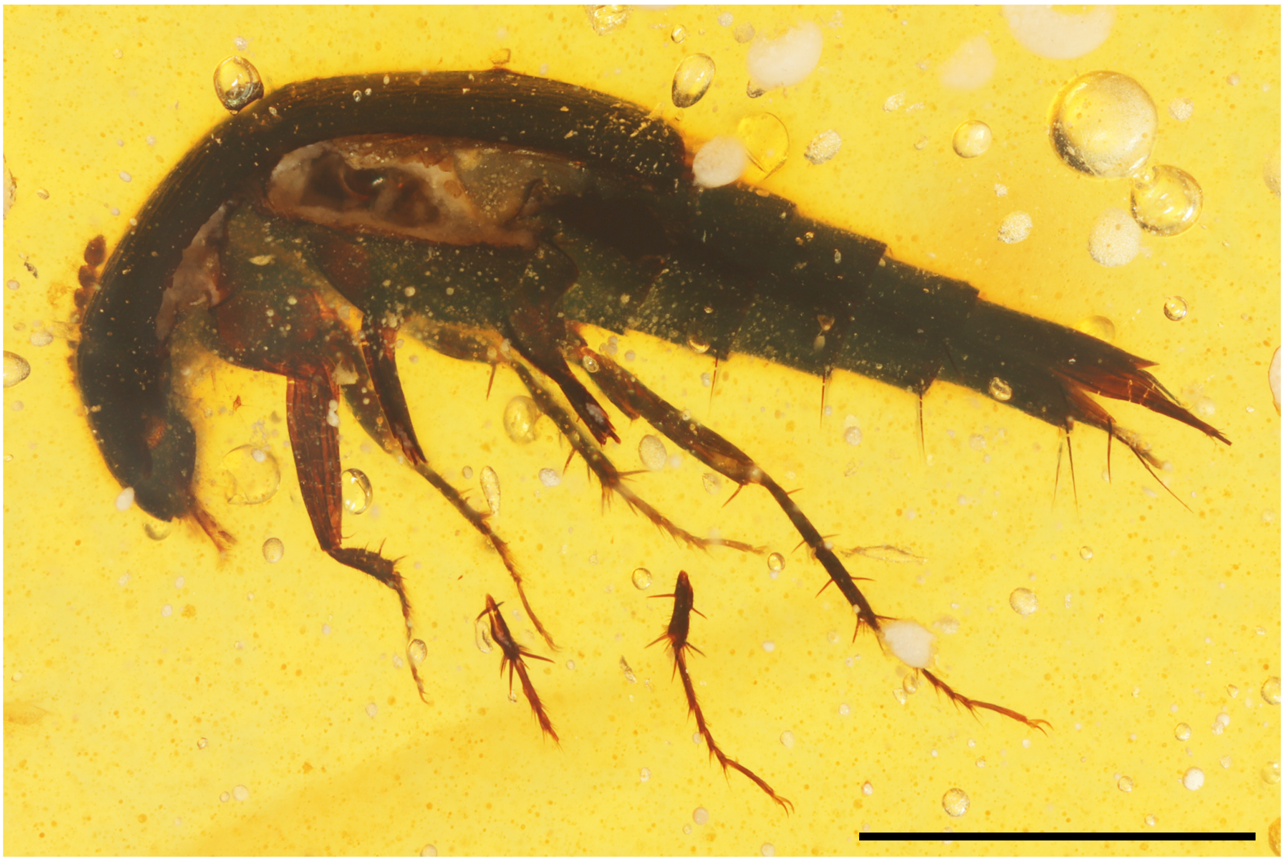

FIGURE 8. General habitus of *Procileoporus* sp., SEHU-0000121244, lateral view, left. Scale bar: 1.0 mm.

former tachyporine tribe Mycetoporini was elevated to the rank of a distinct subfamily, Mycetoporinae (Yamamoto 2021). Additionally, a *Parabolitobius* staphylinid fossil discovered in Kachin amber was assigned to Mycetoporinae, rather than the newly defined Tachyporinae (Yamamoto 2023a). Tachyporinae, comprising approximately 1,205 species worldwide (Newton *et al.* 2022), represents a moderately diverse subfamily within Staphylinidae. However, only two fossil occurrences from Myanmar (Kachin) amber had been documented prior to this study:

Tribe Tachyporini: *Tachyporus burmiticus* Yamamoto, 2024;

Tribe Vatesini: *Procileoporus burmiticus* Yamamoto, 2016.

The current discovery of a tachyporine specimen in Hkamti amber pushes back the origins of both *Procileoporus* and the tribe Vatesini by approximately 11 million years. This finding also represents the third definitive fossil record of Vatesini, following the descriptions by Yamamoto (2016) from Kachin amber and by Yamamoto & Takahashi (2016) of the genus *Coproporus* Kraatz, 1857 from Miocene Dominican amber. Moreover, the *Procileoporus* specimen from Hkamti amber constitutes the earliest amber inclusion of Tachyporinae to date.

Subfamily Aleocharinae Fleming, 1821

Tribe Mesoporini Cameron, 1959

Mesoporini gen. et. sp. indet.

(Fig. 9)

Material examined. SEHU-0000121245, male, a complete adult (Fig. 9A, B), preserved in a pale yellow, flattened, elongate-oval piece of amber measuring 20.7 × 12.7 × 2.7 mm, housed in the Systematic Entomology collection (SEHU), Hokkaido University Museum, Hokkaido University, Sapporo, Japan. The specimen is well-preserved, although a few air bubbles are attached to the underside of the body.

Locality and horizon. Hkamti site, Hkamti District, Sagaing Region, northern Myanmar; Early Albian (*ca.* 110 Ma), Early Cretaceous.

Systematic placement. The fossil can be assigned to the subfamily Aleocharinae within Staphylinidae based on its small, sublimuloid habitus with dense ground setae; non-bulging eyes; thick, strongly clavate antennae with transverse antennomeres forming a robust club-like shape; antennal insertions located on the vertex between the eyes (behind the anterior margin of the eye); short elytra with distinctly sinuate posterolateral margins; and tibiae lacking prominent spines along the outer edges (Newton *et al.* 2000; Yamamoto & Maruyama 2018). Among the 64 aleocharine tribes, the specimen can be further classified under the tribe Mesoporini Cameron, 1959, as evidenced by its limuloid, spindle-shaped habitus; distinctly small body size (*ca.* 1.5 mm); clavate (clubbed) antennae with eleven antennomeres; four-segmented maxillary palpi (maxillary palpomere 3 large and dilated apically, whereas that of palpomere 4 short and aciculate); dorsally sculptured elytra and abdomen with dense reticulation; metacoxae with developed ventral lamellae (*sensu* Yamamoto 2021: fig. S2B); and a 5-5-5 tarsal formula (Newton *et al.* 2000; Naomi & Iwata 1996; Kim *et al.* 2011; Yamamoto *et al.* 2016; Yamamoto & Maruyama 2017).

Comparison. Unlike the 12 mesoporin genera (Newton 2022), except the Kachin amber-endemic genus *Mesosymbion* Yamamoto, Maruyama & Parker, 2016, the Hkamti aleocharine has peculiar antennae that are mostly clavate (lacking an eminent apical club); antennomeres 5–10 are strongly transverse (Fig. 9C). However, it cannot be definitively assigned to the generic concept of *Mesosymbion* (see Yamamoto *et al.* 2016, 2017c), a genus hypothesized to be termitophilous or much less likely myrmecophilous, because certain important characteristics differ from the holotype of the type species, *Mesosymbion compactus* Yamamoto, Maruyama & Parker, 2016. These differences include a narrower and less flattened body, but apparently larger (1.51 mm *versus* 1.04 mm); a non-opisthognathous head which is visible dorsally; and an apical four antennal segments of flagellum composed of rather flattened antennomeres (non-saucer shaped as in *M. compactus*), each with clearly visible (= not completely concealed) antennal stem, in lateral view (in contrast, the base of each antennal segment nested inside the segment preceding it to protect fragile antennal stem, or base, in *M. compactus*). Additionally, the mandibles and mesosternal intercoxal process of the mesocoxae were not observed in the Hkamti specimen. Based on its general similarity, the specimen may be closely related to *Mesosymbion*. Considering the insufficient morphological evidence for generic identification, I have tentatively assigned the specimen as "Mesoporini gen. et. sp. indet.", rather than associating it with *Mesosymbion*.

Remarks. With nearly 17,000 species worldwide (Newton 2022), Aleocharinae is the most species-rich subfamily in Metazoa. It is also abundant in the wild and and commonly encountered during biodiversity surveys and environmental assessments. Members of this subfamily are typically found in forest-related microhabitats such as leaf litter, rotten wood, decayed plant material, or fungi, as well as in light traps and flight interception traps (FITs).

Aleocharinae is divided into two informal groups: the "higher" group, characterized by the presence of abdominal gland, and the glandless "basal" or "lower" group (Ashe 2005; Orlov *et al.* 2021a, 2021b). The latter, representing the early-branching lineages (Yamamoto & Maruyama 2018), comprises only three tribes: Gymnusini (including former members of "Deinopsini"), Mesoporini, and Trichopseniini. This "lower" group is relatively small, containing 144 species (Newton 2022); the vast majority of Aleocharinae diversity resides in the "higher" group. Until now, the oldest fossil records of Aleocharinae were from mid-Cretaceous Kachin

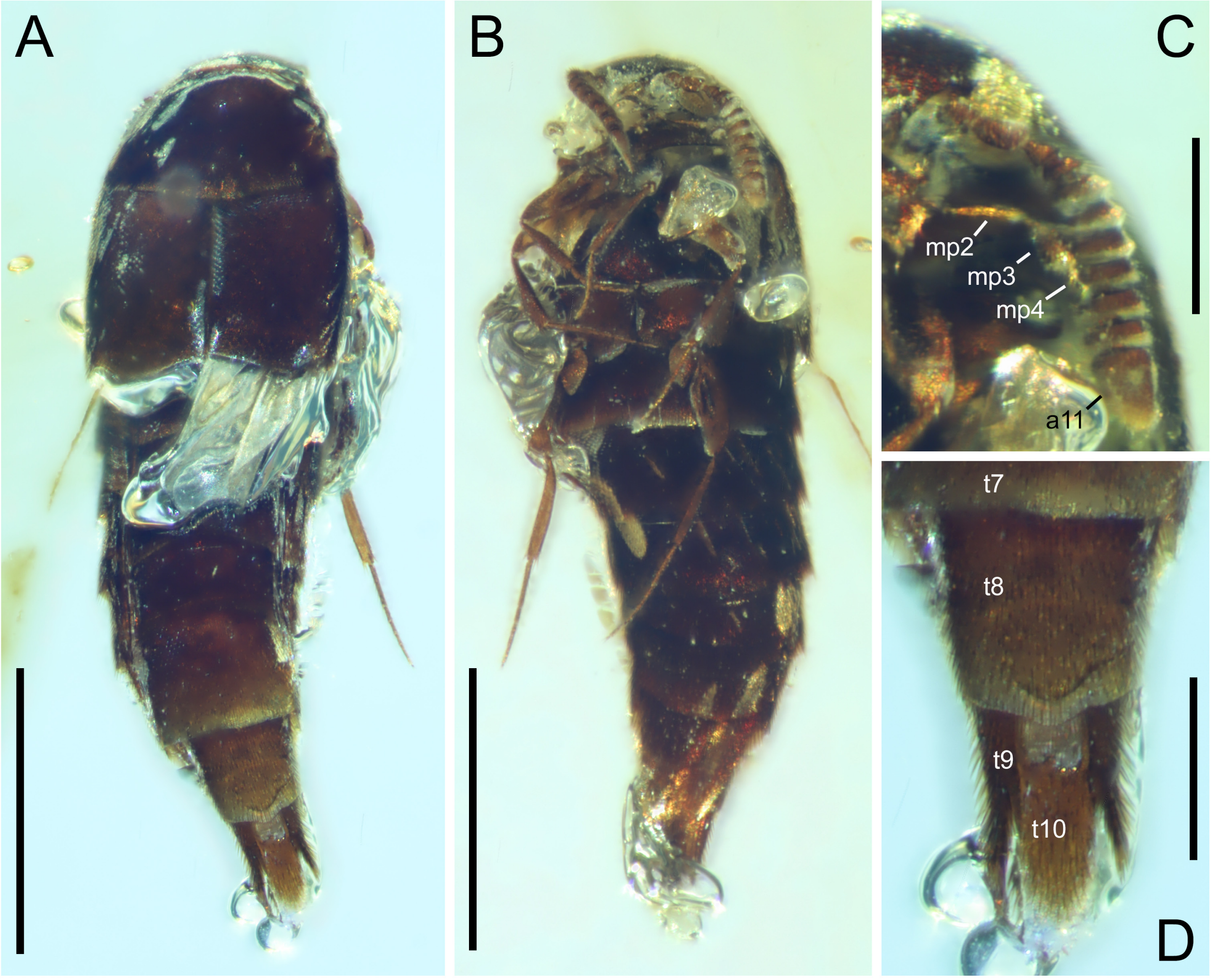

FIGURE 9. Mesoporini gen. et. sp. indet., SEHU-0000121245. A. General habitus, dorsal view; B. general habitus, ventral view; C. details of maxillary palpus and antenna, left, ventral view; D. details of apex of abdomen, dorsal view. Abbreviations: a11, antennomere 11; mp2–4, maxillary palpomeres 2–4; t7–10, tergites VII–X. Scale bars: 0.5 mm (A, B); 0.15 mm (C, D).

amber, the sole Mesozoic deposit known to preserve this subfamily (Cai & Huang 2015b; Yamamoto *et al*. 2016; Cai *et al*. 2017a; Yamamoto & Maruyama 2018).

The present discovery of Mesoporini from Hkamti amber is particularly important because it represents the earliest known fossil of this hyper-diverse subfamily, providing direct evidence of Aleocharinae presence during the Early Cretaceous. Notably, all Cretaceous aleocharine fossils discovered thus far belong to one of the three tribes of the "lower" group, with no fossil records of the "higher" group during the Mesozoic. A similar dominance of primitive aleocharine tribes and genera is observed in Eocene Baltic and Bitterfeld amber deposits (Yamamoto & Newton 2024). Recent molecular dating analyses independently suggest that Aleocharinae originated during the Early Cretaceous (Lü *et al*. 2020) or possibly as far back as the Early Jurassic (Kitchen *et al*. 2024). Therefore, this finding aligns with molecular evidence supporting the evolutionary timeline of this subfamily.

Subfamily Steninae W.S. MacLeay, 1825

Genus *Festenus* Żyła, Yamamoto, Wolf-Schwenninger & Solodovnikov, 2017

(Type species: *Festenus robustus* Żyła, Yamamoto, Wolf-Schwenninger & Solodovnikov, 2017)

Festenus sp.

(Fig. 10)

Material examined. SEHU-0000121246, female, a complete, but damaged adult (Fig. 10), preserved in a pale yellow, flattened, elongate-oval cabochon of amber measuring 20.3 × 12.3 × 4.0 mm, housed in the Systematic Entomology collection (SEHU), Hokkaido University Museum, Hokkaido University, Sapporo, Japan. The specimen is poorly preserved, with the dorsal side of the body heavily compressed and partially crushed, including the pronotum, elytra, and abdomen. Additionally, a maxillary palpus has detached from the body (Fig. 10C). The dorsal surface of the head is partially obscured by a large crack containing an air layer in the amber piece.

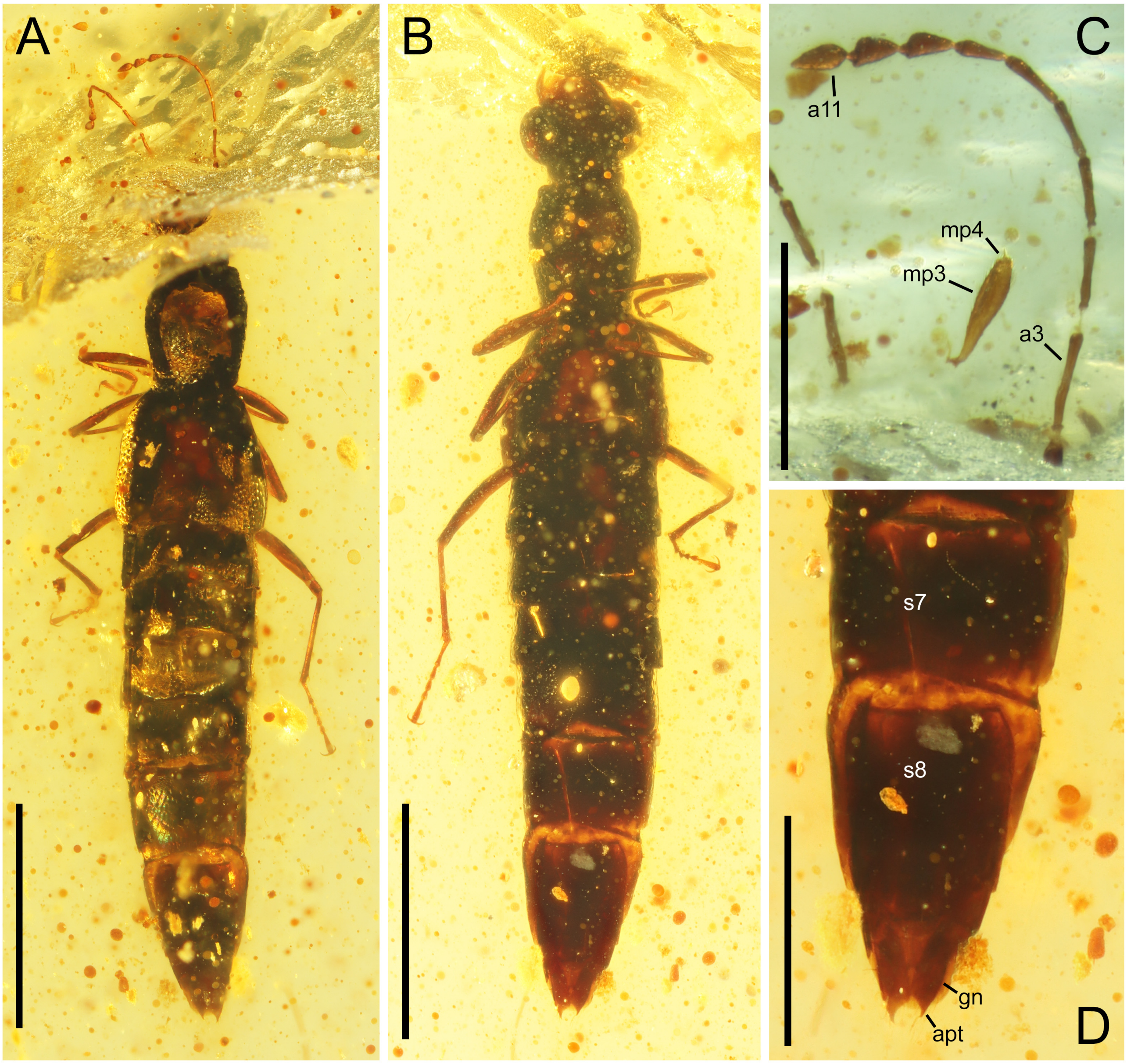

FIGURE 10. *Festenus* sp., SEHU-0000121246. A. General habitus, dorsal view; B. general habitus, ventral view; C. details of antenna and maxillary palpomeres, right, dorsal view; D. details of apex of abdomen, ventral view. Abbreviations: a3, 11, antennomeres 3, 11; apt, apicolateral tooth of gonocoxite (*sensu* Naomi *et al.* 2017: fig. 4F); gn, gonocoxite; mp3, 4, maxillary palpomeres 3, 4; s7, 8, sternites VII, VIII. Scale bars: 1.0 mm (A, B); 0.3 mm (C); 0.5 mm (D).

However, observations remain possible after immersing the amber piece in a suitable liquid. Syninclusions: poorly preserved fragments of several arthropods.

Locality and horizon. Hkamti site, Hkamti District, Sagaing Region, northern Myanmar; Early Albian (*ca.* 110 Ma), Early Cretaceous.

Systematic placement. The specimen can be confidently attributed to the staphylinid subfamily Steninae based on a combination of distinctive morphological traits, including its characteristic habitus, globular and exceptionally large eyes, slender antennae lacking a prominent apical club (but forming a loose club), cylindrical pronotum, and separated metacoxae (Newton *et al.* 2000; Brunke *et al.* 2011). The Hkamti fossil is readily attributed to the Myanmar-amber endemic genus *Festenus* Żyła, Yamamoto, Wolf-Schwenninger & Solodovnikov, 2017, based on the following combination of character states (Żyła *et al.* 2017): antennal insertions located anterior to the eyes, near the frontal margin of the head; pronotal marginal carina extending to the anterolateral prothoracic margin; and the presence of pronotosternal suture.

Comparison. The genus *Festenus* consists of four described species and one undescribed species (Żyła *et al.* 2017; Cai *et al.* 2019a; Mainda 2023, 2024). These include three species, along with the type species and an undescribed species from Kachin amber (Żyła *et al.* 2017; Cai *et al.* 2019a), as well as two species from Hkamti amber (Mainda 2023, 2024). The new material from Hkamti amber appears closely related to the

Hkamti species *Festenus annodutt* Mainda, 2023, based on its slender habitus and the coloration of the elytra. However, it is uncertain whether the specimen possesses the cap-like elevation on the frons of the head—an important synapomorphic feature of *F. annodutt*—due to observational challenges. Consequently, the specimen cannot be reliably identified as *F. annodutt*. Another Hkamti species, *Festenus microraptor* Mainda, 2024, substantially differs from the new specimen presented here in its smaller body size (approximately 1.64 mm), less elongate antennomeres (particularly the three terminal ones), slightly larger eyes, and more arcuate lateral margins of the pronotum. Notably, the new specimen is heavily damaged, which limits detailed observations and conclusive identification. Considering the fossil's poor condition, I tentatively assigned it as *Festenus* sp. in this study.

Remarks. Steninae is a moderately large subfamily of Staphylinidae, encompassing nearly 3,400 species worldwide (Newton *et al.* 2022). The genus *Stenus* Latreille, 1797, comprising over 3,100 species, is recognized as the second-largest animal genus. Notably, this species's count is close to that of the jewel-beetle genus *Agrilus* (Coleoptera: Buprestidae), which is the most species-rich genus in the animal kingdom with 3,341 species (Jendek & Grebennikov 2023). Members of this subfamily inhabit diverse environments, including forest leaf litter and debris, but are predominantly found in riparian habitats near streams, ponds, or marshes. Stenines are notable for their specialized prey-capture structures used to hunt other arthropods: a harpoon-like apparatus formed by an elongated, protrusible labium with terminal sticky cushions called paraglossae (Betz *et al.* 2018; Cai *et al.* 2019a). This unique morphology is also confirmed in the extinct genus *Festenus* (Żyła *et al.* 2017; Cai *et al.* 2019a), although the present study could not observe this structure in the fossil due to preservation limitations. The oldest definitive fossil records of Steninae are *Festenus annodutt* and *F. microraptor* from Hkamti amber. Notably, *F. microraptor* represents the smallest body size among more than 3,000 species in the subfamily. A trend toward miniaturization has been identified in several phylogenetically unrelated beetle lineages from Kachin amber (*e.g.* Yamamoto 2019, 2023b; Żyła *et al.* 2019; Li Y-D *et al.* 2020; Liu Y *et al.* 2021; Tokareva *et al.* 2023). The discovery of another example from Hkamti amber suggests a similar or convergent phenomenon in this amber source, which differs in age and locality. Together with these two species, the new material from Hkamti amber represents the earliest fossils of Steninae, indicating a potentially older origin of the subfamily, as well as a likely diverse and abundant paleofauna of Steninae in the Early Cretaceous.

Subfamily Solieriinae Newton & Tayer, 1992

Genus *Prosolierius* Thayer, Newton & Chatzimanolis, 2012

(Type species: *Prosolierius crassicornis* Thayer, Newton & Chatzimanolis, 2012)

Prosolierius antennatus sp. nov.

(Figs 11–13)

Etymology. The specific epithet *antennatus* is derived from the Latin word "antenna" and refers to the modified antennomere 3 characteristic of the new species.

Material examined. Holotype, SEHU-0000121247, sex undetermined (putative male?), a complete adult (Figs 11, 12), preserved in a pale yellow, elongate-oval, sliced piece of amber measuring 23.5 × 13.2 × 1.1 mm, housed in the Systematic Entomology collection (SEHU), Hokkaido University Museum, Hokkaido University, Sapporo, Japan. The holotype is generally well-preserved, although the presence of air bubbles and pigmentation (debris) within the amber makes it challenging to observe some fine details. Syninclusions: *Prosolierius* sp. (Figs 11, 14, see below) and partial fragments of Blattodea.

Locality and horizon. Hkamti site, Hkamti District, Sagaing Region, northern Myanmar; Early Albian (*ca.* 110 Ma), Early Cretaceous.

Diagnosis. Body relatively large (*ca.* 2.5 mm long, including abdominal apex); head shorter than pronotum; antenna somewhat long and slender, as long as combined head through elytra, with enlarged antennomere 3 (*a3*) and narrowly elongate antennomere 10.

Description. Body (Figs 11, 12) somewhat large within *Prosolierius*, narrowly elongate, fusiform, moderately dorso-ventrally flattened, 2.48 mm long (from anterior margin of head to apex of tergite VIII), 0.65 mm wide. Color uniformly pale brown to dark reddish brown; mouth parts including maxillary palpi and tarsi somewhat paler; compound eyes whitish. Dorsal surface appearing densely weakly punctured, heavily pubescent with ground microsetae.

Head (Fig. 13D) prognathous, small, weakly transverse, 0.36 mm wide (maximum width, across projecting compound eyes), much shorter and narrower than pronotum; posterior part concealed by extended pronotal apical margin; frontoclypeal groove present, probably conspicuous, but not clearly seen; vertex flattened; neck-like distinct nuchal groove on lateral and dorsal sides probably absent (posterior part of head not well visible due to extended pronotum). Compound eyes (Fig. 13C, D, *ey*) rather large, strongly projecting laterally, very coarsely faceted with large ommatidia. Antennal insertions (Fig. 13C, D) not visible dorsally, concealed under shelf-like corners of frons, distantly inserted anterior to line drawn between anterior margins of compound eyes. Antennae (Figs 12, 13A–C) with 11 antennomeres (Fig. 13A–C, *a3*, *a10*), slender, filiform, as long as combined head through elytra, almost sub-parallel sided nearly in entire length (except a3), each antennomere with very densely covered ground microsetae; antennomere 1 (scape) narrowly elongate, robust, cyrindrical, subparallel-sided, about 1.5 times longer than antennomere 2; antennomere 2 (pedicel) narrowly elongate, slender, subparallel-sided, narrower than scape, as long as antennomere 3;

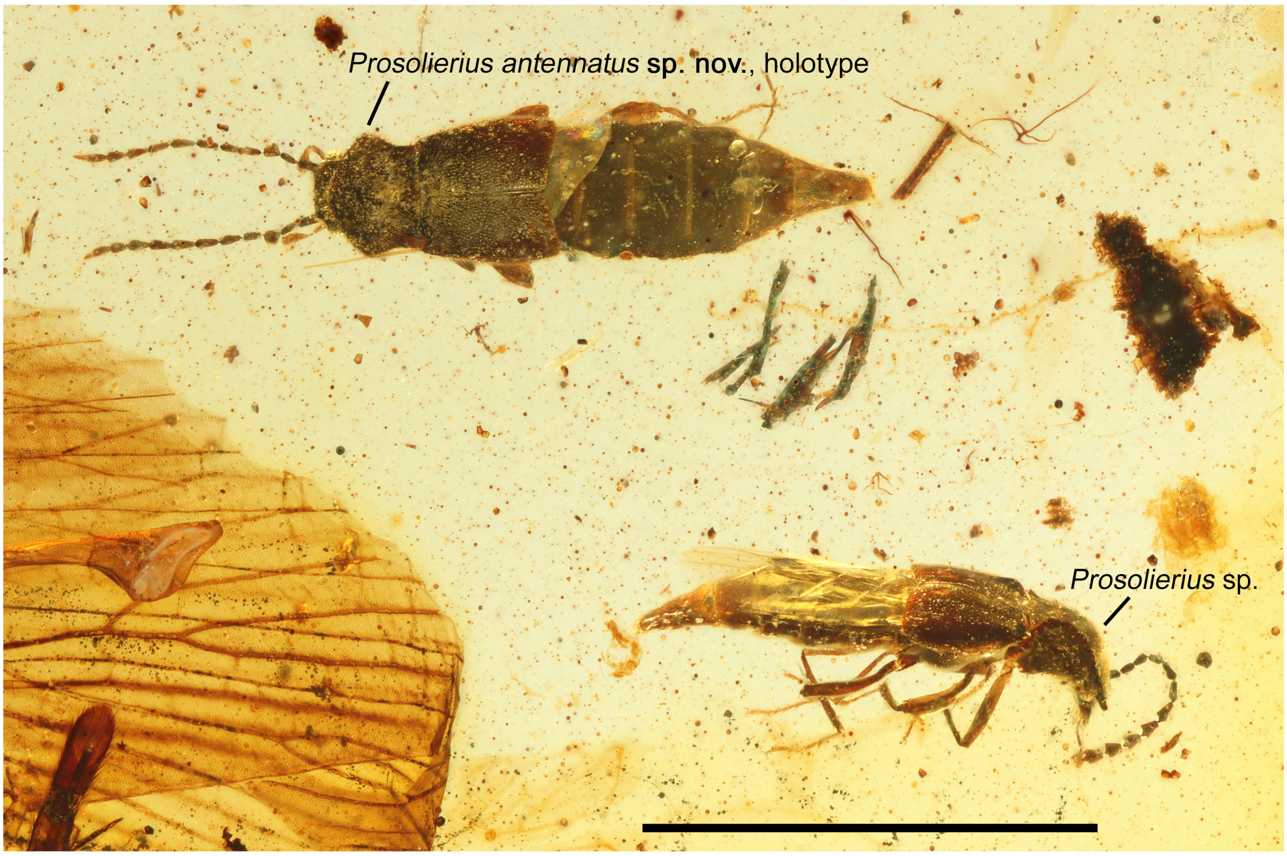

FIGURE 11. Specimens of *Prosolierius* spp. in the same amber piece, *in situ*, SEHU-0000121247: general habitus of *Prosolierius antennatus* **sp. nov.**, holotype, dorsal view; general habitus of *Prosolierius* sp., dorsolateral view, right. Scale bar: 2.0 mm.

antennomere 3 (Fig. 13A–C, *a3*), wide, distinctly modified with outer margin greatly extended outward, asymmetrical, irregularly oblong, with probable sensory invagination along outer margin (see Fig. 13B, *inv*); antennomeres 4–7 each narrowly elongate, slender, weakly dilated apically, successively increasing length, distinctly narrower than antennomere 3, but slightly thicker than antennomere 2; antennomeres 8–10 each narrowly elongate (antennomere 10 twice as long as wide), slender, moderately to somewhat strongly dilated apically, successively decreasing length, shorter than antennomere 7, as wide as preceding four antennomeres; antennomere 11 narrowly elongate, somewhat spindle-shaped, about three times as long as wide, with conical, acuminate apex. Maxillary palpus (Fig. 13C) four-segmented, long and slender, appearing densely setose with microsetae; maxillary palpomere 1 small, short; palpomere 2 (*mp2*) very long and slender, bar-like, moderately curved, gradually slightly dilated apically; palpomere 3 (*mp3*) very long, fusiform, subequal in length to preceding palpomere, strongly dilated apically and its apex truncate, with maximum width at near apex, distinctly wider than preceding palpomere; palpomere 4 minute, conical, inconspicuous. Labial palpi short, small; other details not clearly discernable. Mentum trapezoidal, moderately transverse. Further ventral structures not well visible due to large air bubble attached to surface of body.

Pronotum (Figs 12A, 13D) pentagonal, slightly wider than long (0.42 mm long along midline, 0.53 mm wide; length/width = 0.79), widest at slightly above middle, somewhat narrower than elytra; anterior margin of pronotum produced medially, whereas that of posterior margin nearly truncate; pronotal anterolateral angles arcuate to obtusely rounded, whereas pronotal posterolateral angles closer to orthogonal; dorsal surface pubescent, with dense ground microsetae uniformly, disc almost flat dorsally, but with subbasal-longitudinal grooves near basolateral margins. Pronotal hypomeron rather wide, relatively strongly folded inwards, separated from disk of pronotum by complete lateral carina. Protrochantins concealed. Scutellar shield (Fig. 13D, *sc*) small, barely visible dorsally, broardly subtriangular, with rounded apex. Mesoventrite not well visible. Metaventrite large, with discrimen (median longitudinal sulcus in posterior area).

Elytra (Figs 12A, 13D) elongate, rectangular, more or less subparallel-sided, lateral margins weakly arcuate, widest at basal 2/5; each modelately elongate, approximately 1.72 times as long as wide (right elytron 0.55 mm long from anterior margin of pronotum to posterior margin of elytral along suture, 0.32 mm wide), moderately longer and slightly wider than pronotum, with nearly truncate posterior margins; elytral anterolateral angles (shoulders) obtusely angulate, whereas elytral posterolateral angles acutely angulate or angulately rounded; epipleural ridge probably absent; dorsal surface even and smooth, with dense ground microsetae uniformly.

FIGURE 12. General habitus of *Prosolierius antennatus* **sp. nov.**, holotype, SEHU-0000121247. A. Dorsal view; B. ventral view. Scale bars: 1.0 mm (A, B).

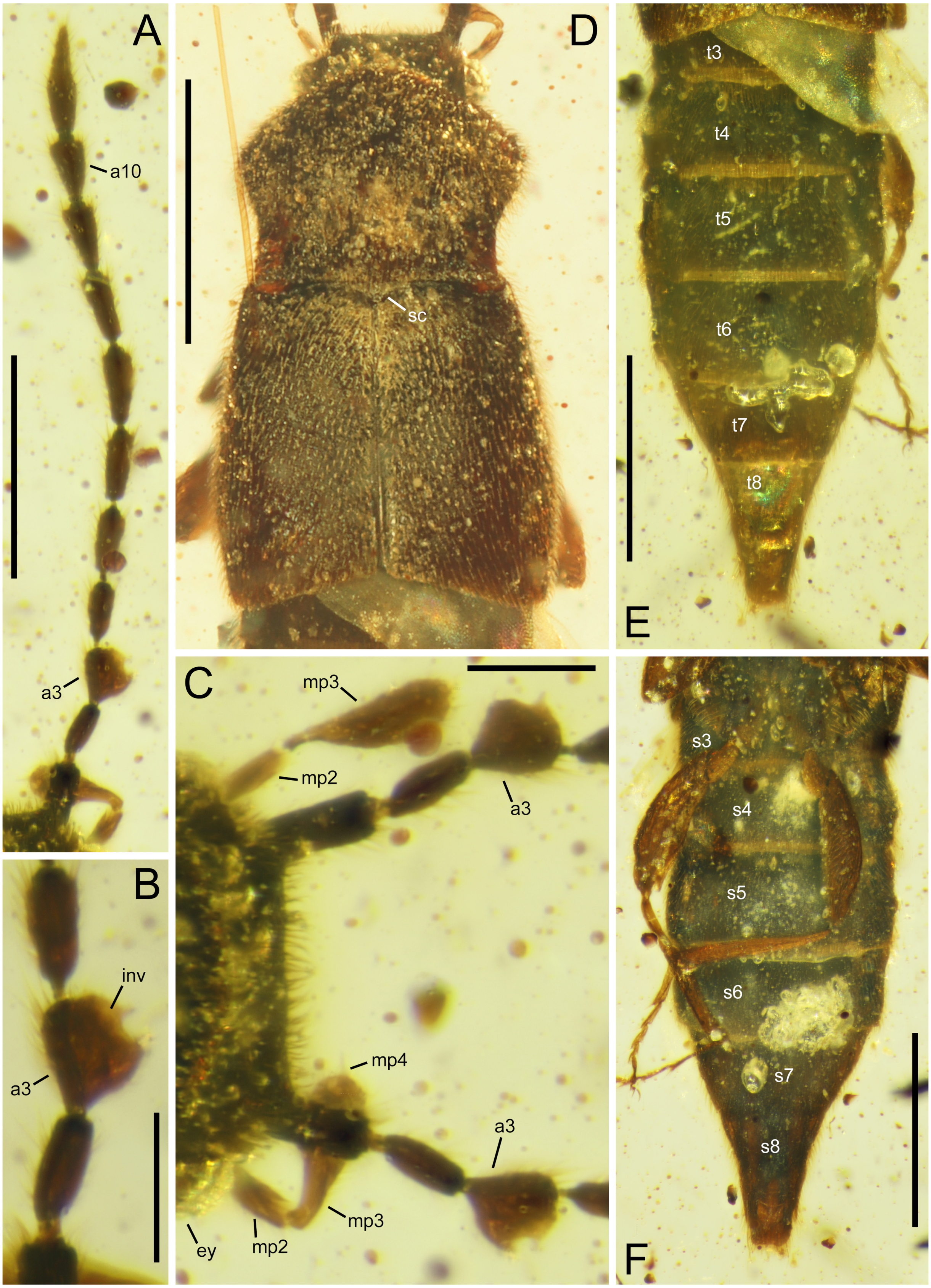

FIGURE 13. Details of *Prosolierius antennatus* **sp. nov.**, holotype, SEHU-0000121247. A. Antenna, right, dorsal view; B. enlargement of basal antennomeres, right, dorsal view, showing extended and modified antennomere 3; C. anterior part of head and basal part of antennae, dorsal view; D. forebody, dorsal view; E. abdomen, dorsal view; F. abdomen and hindlegs, ventral view. Abbreviations: a3, 10, antennomeres 3, 10; ey, compound eye; inv, invagination along outer margin of antennomere 3; mp2–4, maxillary palpomeres 2–4; s3–8, sternites III–VIII; sc, scutellar shield; t3–8, tergites III–VIII. Scale bars: 0.5 mm (A, D–F); 0.1 mm (B, C).

Hind wings partially exposed, appearing functional and fully developed.

Legs (Figs 12B, 13F) moderately long, slender; surface very densely setose with ground microsetae. Forelegs partially not well visible due to large air bubble. Protrochantins concealed, not ventrally visible. Procoxae and protrochanters not well observable. Profemora weakly clavate, rather flattened. Protibiae (Fig. 12B) slender, rod-like, moderately widened apically, lacking tibial spines along outer edges; protibial apical spur absent. Protarsi five-segmented, filiform, not laterally expanded, slightly shorter than protibiae; protarsomere 1 elongate, protarsomeres 2–4 progressively shortened, protarsomere 5 longest, about twice as long as preceding protarsomere. Midlegs slightly longer than forelegs. Mesocoxae appearing narrowly separated. Mesotrochanters elongate oval, small. Mesofemora weakly clavate, rather flattened. Mesotibiae slender, rod-like, moderately widened apically. Mesotarsi five-segmented, filiform, shorter than protibiae; mesotarsomere 1 elongate (basally not visible), mesotarsomeres 2–4 progressively shortened, mesotarsomere 5 seemingly longest (or as long as mesotarsomere 1), about twice as long as preceding mesotarsomere. Hindlegs moderately long, rather thick in basal half. Metacoxae subcontiguous, lacking developed ventral lamellae (*sensu* Yamamoto 2021: fig. S2B). Metatrochanters elongate oval, small. Metafemora wide, clavate, weakly curved, rather flattened. Metatibiae slender, rod-like, moderately widened apically. Metatarsi five-segmented, filiform, slightly shorter than protibiae; metatarsomeres 1–4 ventro-apically lobed; metatarsomere 1 narrowly elongate, longest, metatarsomeres 2–4 progressively shortened, metatarsomere 5 long, narrowly elongate, about twice as long as preceding metatarsomere. Pretarsal claws simple, moderately curved, with paired empodial setae as long as (or slightly longer than) claws.

Abdomen (Figs 12, 13E, F) narrowly elongate, fusiform, rather flattened, widest at middle of segment 5, strongly tapering posteriad from that point, with six exposed tergites and sternites excluding genital segments, very slightly narrower than elytra in maximum width; genital segments slightly exposed but details not visible, apparently much narrower than segment 7; abdominal segments with paratergites, composed of two pairs. Tergite III transverse, partially concealed by elytra; tergites IV–VI each somewhat strongly wider than long, subequal in length; tergite VII short, strongly transverse, moderately tapering posteriorly; tergite VIII subtriangular, with rounded posterior margin. Surfaces of both dorsal and ventral sides densely pubescent by ground microsetae, without scattered suberect macrosetae. Intersegmental membranes long, conspicuous, with distinct 'brick-wall' like patterns. Sternite III small, transverse, with weakly developed longitudinal intercoxal carina (keel); sternites IV–VII each strongly wider than long; sternite V large, longer than either sternite IV or sternite VI; sternite VII as long as preceding segment, moderately tapering posteriorly; sternite VIII subtriangular, as long as wide (visible part), with rounded posterior margin. Genitalia not visible.

Systematic placement. The new species, *Prosolierius antennatus* **sp. nov.**, can be unambiguously assigned to the staphylinid subfamily Solieriinae based on the following combination of character states (Thayer *et al.* 2012; Yamamoto 2023c): general habitus with a body length of approximately 2.5 mm; head with antennal insertions concealed by a frontal shelf; eyes bulging and extremely coarsely faceted; long and slender antennae lacking an apical club; long and slender maxillary palpi, with elongate palpomeres 2 and 3 and a distinctly shorter and narrower palpomere 4; concealed protrochantins; legs lacking external protibial spines, with a tarsal formula of 5-5-5; and abdomen with six visible sterna (sternites III–VIII) and two pairs of paratergites. The morphological traits of the new species closely fit well with the extinct genus *Prosolierius*, which includes five species previously described from mid-Cretaceous Kachin amber, with additional species from Lower Cretaceous Spanish and Lebanese ambers (Thayer *et al.* 2012; Peris *et al.* 2014; Yamamoto 2023c; Liu *et al.* 2025). These traits, such as the presence of a complete lateral carina on the pronotum (*sensu* Thayer *et al.* 2012), distinguish it from the monospecific extant genus *Solierius* Bernhauer, 1921 from southern South America. Therefore, the new species is placed within *Prosolierius*, rather than *Solierius* or a new genus.

Comparison. *Prosolierius antennatus* **sp. nov.** is readily distinguished by its unique antennal structures, as indicated by its name. The antenna is filiform and slender, and antennomere 3 is distinctly modified: prominently extended outward and somewhat quadrilateral in shape. Additionally, antennomere 10 is noticeably elongated, clearly much longer than its width. These characteristics bear similarity to those of *Prosolierius thayerae* Yamamoto, 2023, a recently described species from Kachin amber (Yamamoto 2023c). Both species share the elongated antennomere 10 and, more notably, the highly modified antennomere 3. However, the nature of these modifications substantially differs between the two species. In *P. thayerae*, both antennomeres 3 and 4 are modified, whereas in the new species, only antennomere 3 is modified. Moreover, the modification in *P. thayerae* exhibits a narrower and longer projection compared with the broader and shorter modification evident in *P. antennatus* **sp. nov.** These differences preclude conspecificity between the two species. After the submission of the present paper, Liu *et al.* (2025) described an additional *Prosolierius* species from Kachin amber, *Prosolierius qizhihaoi* Liu, Gao, Huang & Cai, 2025, which also has some modifications on the antennomeres 3 and 4. However, this species has apparently simplified ones in comparison with *P. thayerae* or even *P. antennatus* **sp. nov.** Indeed, the third antennomere of *P. qizhihaoi* is unusually markedly long, which is only slightly shorter than the terminal antennomere, whereas the fourth one is small and oval shaped (Liu *et al.* 2025). Furthermore, the new species also exhibits some resemblance to *Prosolierius tenuicornis* Thayer, Newton & Chatzimanolis, 2012, another species from Kachin amber, due to its relatively large body size and elongated antennomere 10 (Thayer *et al.* 2012). However, *P. tenuicornis* lacks such distinct antennal modifications observed in the new species and has longer antennae compared with both *P. thayerae* and *P. antennatus* **sp. nov.** In summary, *P. antennatus* **sp. nov.** is a distinct species, probably closely related to *P. thayerae* from Kachin amber.

Remarks. The modern distribution of Solieriinae is confined to a small region in South America, specifically the temperate forests of southern Chile and Argentina (Thayer *et al.* 2012). In contrast, a relatively diverse paleofauna of this subfamily has been documented in Cretaceous amber deposits from Lebanon, Spain, and Myanmar, each with distinct geological and paleobiogeographic contexts (Thayer *et al.* 2012; Peris *et al.* 2014; Yamamoto 2023c). This is important because the extant Solieriinae is represented by a single species with a highly restricted geographic range. It suggests that extinct members of this subfamily had a much broader distribution across Pangea prior to its breakup. In Burmese Kachin amber, Solieriinae, represented by *Prosolierius*, are frequently found as bioinclusions along with Hapsomelitae scydmaenine staphylinids (Yamamoto 2023c). Five of the seven fossil species of Solieriinae—all within the extinct genus *Prosolierius*—have been described from Kachin amber. Thus, the discovery of *Prosolierius* in the nearby Burmese Hkamti amber is unsurprising. It may indicate a close paleobiogeographic, geological, or paleoenvironmental relationship between the two amber deposits, particularly given the presence of *P. thayerae*, which shares the distinctive antennal modifications. Such modified antennae are rare in the 'typical' body type of Staphylinidae (excluding Scydmaeninae and Pselaphinae), making *P. antennatus* **sp. nov.** and *P. thayerae* from Kachin amber exceptional cases. Intriguingly, similar antennal modifications are relatively common in Scydmaeninae, a group that molecular analyses suggest is closely related to Solieriinae forming a sister-group relationship with it, although based on few genetic loci (McKenna *et al.* 2015). The function of these antennal modifications is also unclear. It is plausible that they serve sensory roles, such as chemical detection, or are involved in pheromone release. Notably, *P. antennatus* **sp. nov.** possesses a large pocket-like invagination along the lateral outer margins of antennomere 3 (Fig. 13A–C, *inv*), which could support such hypotheses. Since the Lebanese amber fossil reported by Thayer *et al.* (2012) was not formally named, *P. antennatus* **sp. nov.** represents the oldest described species of the genus and subfamily. Below is a checklist of all described *Prosolierius* species, including the new species:

1. *Prosolierius antennatus* **sp. nov.** (Hkamti amber);
2. *Prosolierius crassicornis* Thayer, Newton & Chatzimanolis, 2012 (Kachin amber);
3. *Prosolierius mixticornis* Thayer, Newton & Chatzimanolis, 2012 (Kachin amber);
4. *Prosolierius parvus* Peris, Chatzimanolis & Delclòs, 2014 (Spanish amber);
5. *Prosolierius tenuicornis* Thayer, Newton & Chatzimanolis, 2012 (Kachin amber);
6. *Prosolierius thayerae* Yamamoto, 2023 (Kachin amber);
7. *Prosolierius qizhihaoi* Liu, Gao, Huang & Cai, 2025 (Kachin amber).

See further details on the species' identification in "Key to species of *Prosolierius*" after the "*Prosolierius* sp." section below.

***Prosolierius* sp.**

(Figs 11, 14)

Material examined. SEHU-0000121247, sex undetermined, a complete adult (Figs 11, 14A), preserved in a pale yellow, elongate-oval, sliced piece of amber measuring 23.5 × 13.2 × 1.1 mm, housed in the Systematic Entomology collection (SEHU), Hokkaido University Museum, Hokkaido University, Sapporo, Japan. The specimen is relatively well-preserved; however, only the left ventrolateral side is visible. Syninclusions: the holotype of *Prosolierius antennatus* **sp. nov.** (Figs 11–13, see above) and partial fragments of Blattodea.

Locality and horizon. Hkamti site, Hkamti District, Sagaing Region, northern Myanmar; Early Albian (*ca.* 110 Ma), Early Cretaceous.

Systematic placement. The fossil specimen can be confidently assigned to the staphylinid subfamily Solieriinae based on its various morphological features, including a general habitus with a body length of approximately 2.1 mm; a head with likely concealed antennal insertions covered by a frontal shelf; bulging, extremely coarsely faceted eyes; long and slender antennae lacking an apical club; and long, slender maxillary palpi with very elongated palpomeres 2 and 3, and a distinctly shorter and narrower palpomere 4; legs lacking external protibial spines with a tarsal formula of 5-5-5; and abdomen composed of six visible sterna (sternites III–VIII). The specimen can further be placed in the extinct solieriine genus *Prosolierius* due to the presence of a complete lateral carina on the pronotum, which distinctly separates the pronotal disc from the pronotal hypomeron (*sensu* Thayer *et al.* 2012). Additionally, it lacks the curled laminar gular projection characteristic of other related taxa (*sensu* Thayer *et al.* 2012). Based on these diagnostic traits, the systematic placement of this fossil within *Prosolierius* is well-supported.

Comparison. As previously noted, a relatively diverse fauna of *Prosolierius* is known from Cretaceous amber deposits, making accurate species-level identification of this material somewhat challenging. The antennal shape of the specimen is simplified within the genus, lacking any special modifications. Consequently, it does not correspond to neither *P. thayerae*, *P. qizhihaoi* (both from Kachin amber: Yamamoto 2023c; Liu *et al.* 2025), nor *P. antennatus* **sp. nov.**, described above. The specimen's head is noticeably shorter than its pronotum, which excludes it from being identified as *P. crassicornis* from Kachin amber (Thayer *et al.* 2012). Additionally, the specimen exhibits a larger body size, with a scape substantially longer than the pedicel, distinguishing it from *P. parvus* in Spanish amber (Peris *et al.* 2014). The antennomere 10 is not elongate (approximately as long as

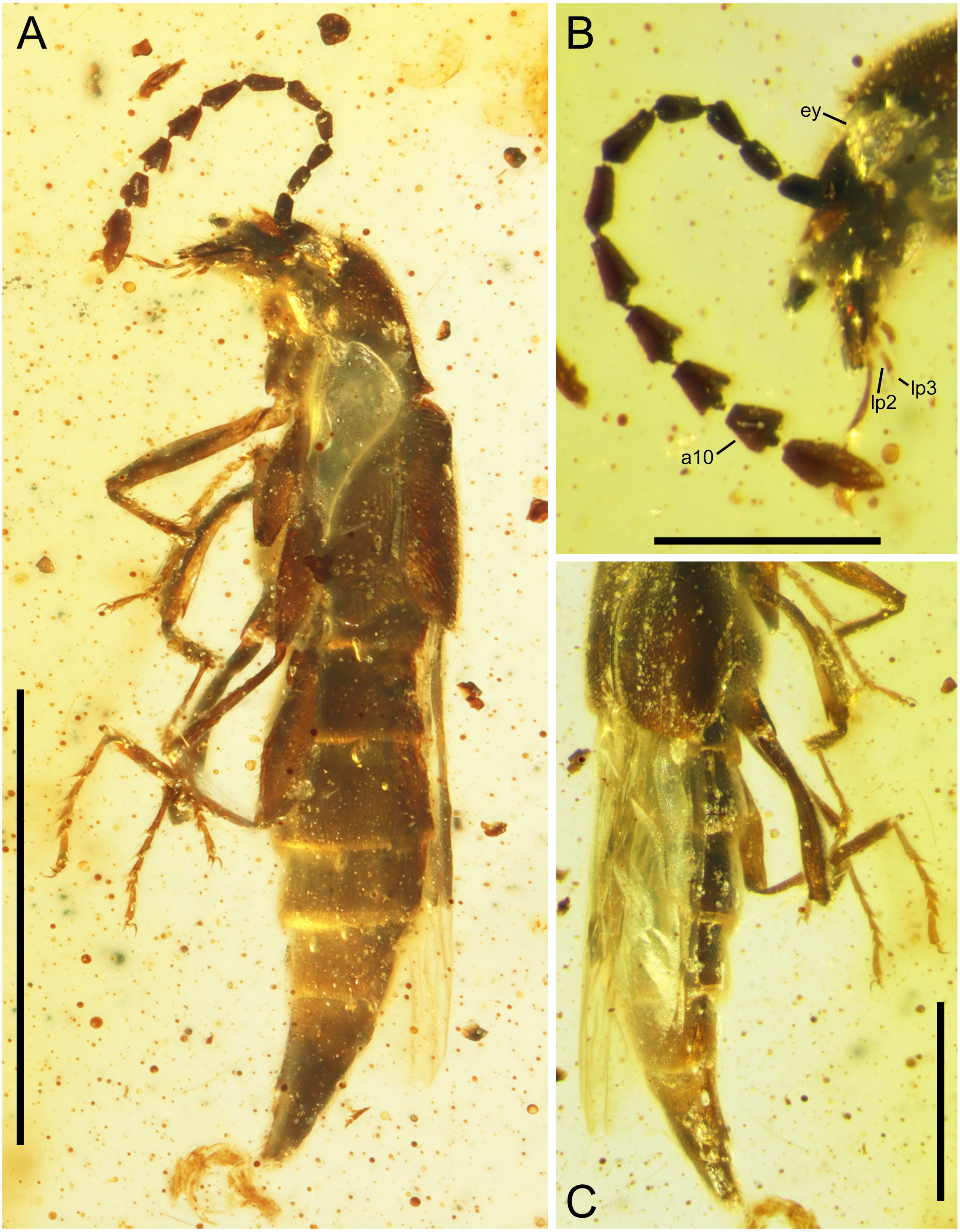

FIGURE 14. *Prosolierius* sp., SEHU-0000121247. A. General habitus, left, ventrolateral view; B. details of head and antenna, left, lateral view; C. details of elytra and abdomen, right, dorsolateral view. Abbreviations: a10, antennomere 10; ey, compound eye; lp2, 3, labial palpomeres 2, 3. Scale bars: 1.0 mm (A); 0.3 mm (B); 0.5 mm (C).

its width); it was not possible to measure and compare the antennal length with the combined length of the head and pronotum. Therefore, it cannot be definitively assigned to *P. tenuicornis* or *P. mixticornis*, both from Kachin amber (Thayer *et al.* 2012). Given these limitations and the ambiguous features, the specimen is provisionally identified as "*Prosolierius* sp."

Remarks. Along with *P. antennatus* **sp. nov.**, the new specimen represents the first discovery of Solieriinae from Hkamti amber. Intriguingly, both specimens (species) are enclosed in the same amber piece, suggesting that they coexisted in the same biome, likely sharing an ecological niche. This paper highlights two distinct antennal morphotypes in *Prosolierius* from Hkamti amber, similar to those found in Kachin amber (Yamamoto 2023c; Liu *et al*. 2025): normal unmodified antennae and partially modified antennae. Given the diverse and abundant fauna of the genus in Kachin amber and the occurrence of two specimens in a single amber piece, it is likely that more specimens of *Prosolierius*, including undescribed species, will be discovered in the Hkamti amber deposits in the future.

Key to species of *Prosolierius*

The following taxonomic identification key is largely based on Yamamoto (2023c), which is a modified version of Thayer *et al*. (2012) and Peris *et al*. (2014). Also, *Prosolierius qizhihaoi* Liu, Gao, Huang & Cai, 2025 has been added to it based on Liu *et al*. (2025).

1. Antennomeres 3 and/or 4 modified 2
- Antennomeres 3–4 simple, normal 4
2. Both antennomeres 3 and 4 modified 3
- Only antennomere 3 highly modified, enlarged, greatly extended laterally (Fig. 13A–C, *a3*) ....*P. antennatus* **sp. nov.**
3. Both antennomeres 3 and 4 highly modified, both similar shape and size, each with lobe-like distinctive projection (Yamamoto 2023c: fig. 3D, E, G)...................................... ....*P. thayerae* Yamamoto, 2023
- Both antennomeres 3 and 4 weakly simply modified, but lacking specialized modification as seen in *P. thayerae* and *P. antennatus* **sp. nov.**; antennomere 3 unusually very long, nearly as long as antennomere 11 (terminal antennomere); antennomere 4 unusually small and short, apparently shorter than either antennomere 3 or antennomere 5 (Liu *et al*. 2025: fig. 3I).. .... *P. qizhihaoi* Liu, Gao, Huang & Cai, 2025
4. Antenna long and slender, longer than combined head through elytra, all antennomeres distinctly elongate (Thayer *et al*. 2012: fig. 2E); frontoclypeal groove deeply impressed (Thayer *et al*. 2012: fig. 4A); body length *ca*. 2.6 mm....... .....*P. tenuicornis* Thayer, Newton & Chatzimanolis, 2012
- Antenna more robust, shorter than combined head through elytra, at least antennomere 10 transverse (Thayer *et al.* 2012: figs. 1B, D, 3A); frontoclypeal groove shallowly impressed or indistinct; body length *ca*. 1.0–2.6 mm....... 5
5. Head as long as pronotum .... *P. crassicornis* Thayer, Newton & Chatzimanolis, 2012
- Head shorter than pronotum 6
6. Body length *ca*. 2.3–2.6 mm; scape twice as long as pedicel; antennomeres 3–8 longer than wide; known only from Burmese (Kachin) amber.. .....*P. mixticornis* Thayer, Newton & Chatzimanolis, 2012
- Body length *ca*. 1.04–1.4 mm; scape slightly longer than pedicel; antennomeres 3–8 subquadrate; known only from Spanish amber ....*P. parvus* Peris, Chatzimanolis & Delclòs, 2014

Subfamily Scydmaeninae Leach, 1815

Supertribe Hapsomelitae Poinar & Brown, 2004

Genus *Hapsomela* Poinar & Brown, 2004

(Type species: *Hapsomela burmitis* Poinar & Brown, 2004)

Hapsomela cf. *burmitis* Poinar & Brown, 2004

(Fig. 15)

Material examined. SEHU-0000121248, male, an apparently damaged adult (Fig. 15A, B), preserved in a yellowish, rather flattened, elongate-oval cabochon of amber measuring 20.0 × 8.8 × 4.1 mm, housed in the Systematic Entomology collection (SEHU), Hokkaido University Museum, Hokkaido University, Sapporo, Japan. The specimen is heavily damaged, with most of the antennomeres and the pterothorax missing. The right elytron is widely opened, and a portion of the abdomen is evidently damaged. Notably, the male genitalia is well-exposed and can be used for species identification. Syninclusions: a poorly preserved Trichoptera and some stellate hairs of plants.

Locality and horizon. Hkamti site, Hkamti District, Sagaing Region, northern Myanmar; Early Albian (*ca*. 110 Ma), Early Cretaceous.

Systematic placement. The specimen can be confidently assigned to the extinct scydmaenine supertribe Hapsomelitae based on the combination of its distinctive general habitus, well-exposed abdominal segments (or greatly elongated abdominal segments V and VI), and a ventral hook-like structure on the protibiae (previously misinterpreted as "patella" by Poinar & Brown 2004 and Poinar 2012) (see also Chatzimanolis *et al.* 2010 and Yin 2020). Among the three genera of Hapsomelitae from Kachin amber, it can be unambiguously placed in the type genus *Hapsomela* Poinar & Brown, 2004, based on its general habitus, the structure of the protibiae, and the male genitalia (Poinar & Brown 2004; Chatzimanolis *et al.* 2010; Yin *et al.* 2020).

Comparison. The genus *Hapsomela* was described in 2004, long before the considerable increase in research concerning Myanmar amber bioinclusions. For approximately 16 years, the genus solely comprised its type species, until Yin (2020) described two additional species. Among these three *Hapsomela* species, the

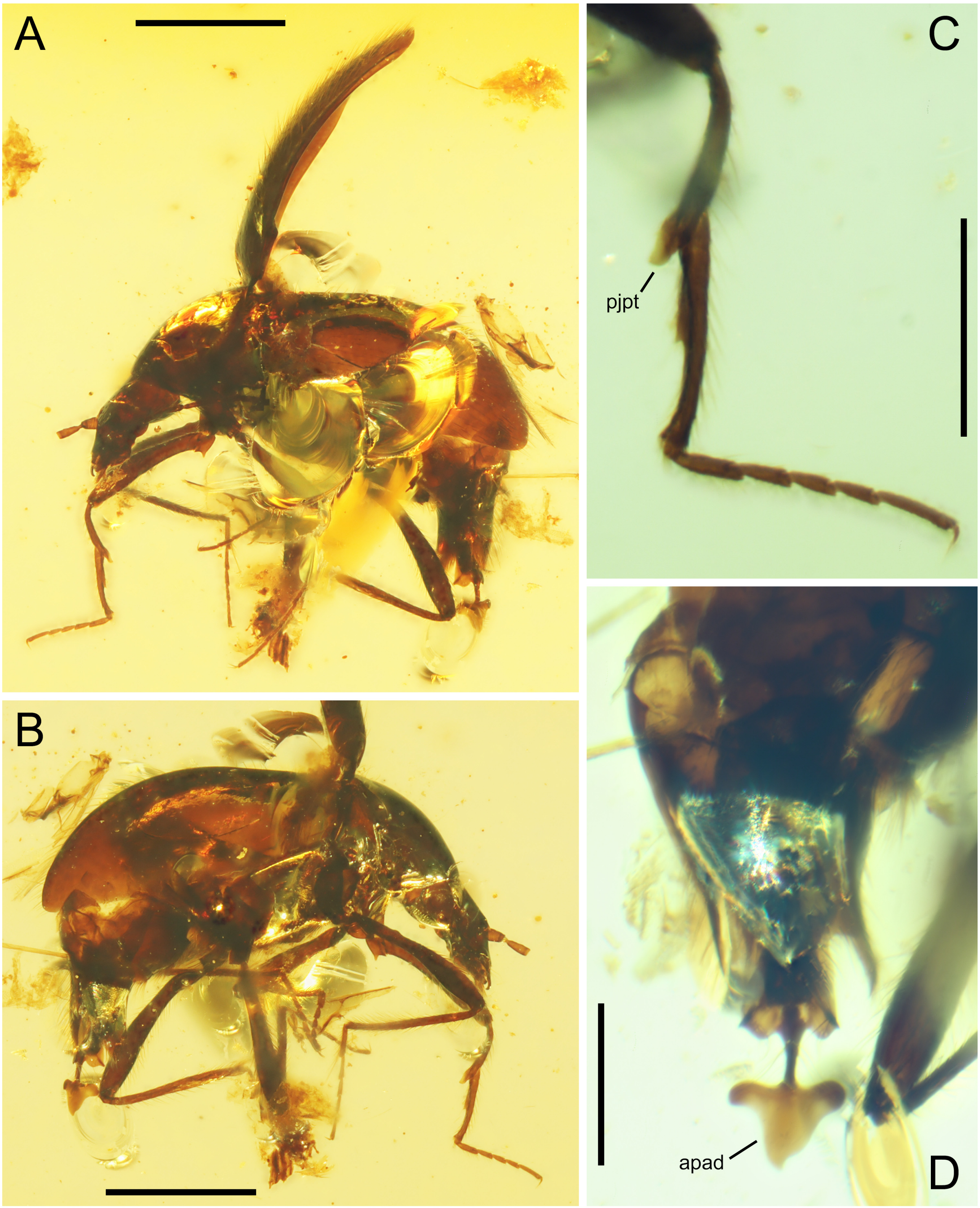

FIGURE 15. *Hapsomela* cf. *burmitis* Poinar & Brown, 2004, SEHU-0000121248. A. General habitus, left, lateral view; B. general habitus, right, lateral view; C. details of foreleg, left, lateral view, showing a projection in middle of protibia; D, details of abdominal apex with exposed male genitalia. Abbreviations: apad, apical part of aedeagus; pjpt, projection on protibia. Scale bars: 0.5 mm (A, B); 0.2 mm (C, D).

Hkamti fossil can be considered a close relative of the type species, *Hapsomela burmitis*, or even conspecific. This conclusion is supported by the detailed structure of the male genitalia (cf. Yin 2020). Additionally, the structures of the protibiae and the unmodified, simple metatibiae allow easy differentiation from the other two species of *Hapsomela* (Yin 2020). However, it may not be entirely appropriate to identify the fossil as *H. burmitis* due to the geological and geographical differences in their localities and the difficulty of accurately comparing the male aedeagus at different angles using photos provided in the literature. For instance, the male aedeagus of the new specimen does not appear to extend beyond the posterior part of the base, unlike Figure 1B of Yin (2020). Therefore, I have provisionally identified it as *Hapsomela* cf. *burmitis*.

Remarks. Hapsomelitae (originally classified as the subfamily Hapsomelinae of the family 'Scydmaenidae') was primarily established based on the putative presence of an additional foreleg podite, termed a "patella," suggesting that the protibiae are composed of two segments (Poinar & Brown 2004). However, this structure was later reinterpreted as a ventral hook-like structure of the protibiae (Chatzimanolis *et al.* 2010), and thus the term "patella" is no longer applicable to Hapsomelitae. The greatly elongated abdominal segments V and VI observed in Hapsomelitae are key features defining the group, which appear to be unique within the Scydmaeninae (Chatzimanolis *et al.* 2010; Yin 2020). It is noteworthy, however, that Chatzimanolis *et al.* (2010) suggested Hapsomelitae to be an artificial group; Jałoszyński (2014) also regarded it as a heterogeneous assemblage. The monophyly of Hapsomelitae has not yet been rigorously tested, and its systematic position within Scydmaeninae remains uncertain, pending future studies (*e.g.* phylogenetic analyses). Based on the exposed male genitalia and the available leg morphology, the new material presented here has been identified as *Hapsomela*, more specifically *H.* cf. *burmitis*, providing direct evidence of the similarity between the Kachin and Hkamti amber faunas.

Genus *Ektatotricha* Chatzimanolis, Engel & Newton, 2010

(Type species: *Ektatotricha paradoxa* Chatzimanolis, Engel & Newton, 2010)

FIGURE 16. *Ektatotricha* sp., SEHU-0000121249. A. General habitus, dorsal view; B. general habitus, ventral view; C. details of antenna and maxillary palpus, left, ventral view; D, details of abdominal apex, dorsal view. Abbreviations: exab, dorsally exposed part of abdomen; el, elytron; mp3, 4, maxillary palpomeres 3, 4. Scale bars: 0.5 mm (A, B); 0.2 mm (C, D).

***Ektatotricha* sp.**
(Fig. 16)

Material examined. SEHU-0000121249, putative female (based on its simple forelegs), a complete, well-preserved adult (Fig. 16), preserved in a pale yellowish, elongate-oval, sliced piece of amber measuring 18.5 × 11.1 × 1.9 mm, housed in the Systematic Entomology collection (SEHU), Hokkaido University Museum, Hokkaido University, Sapporo, Japan. Syninclusions: two small springtails (Collembola), a tiny mite (Acaria), a bivalve boring (Mollusca: Bivalvia: Myida: Pholadidae) and some stellate hairs of plants.

Locality and horizon. Hkamti site, Hkamti District, Sagaing Region, northern Myanmar; Early Albian (*ca.* 110 Ma), Early Cretaceous.

Systematic placement. The fossil can be confidently assigned to the extinct scydmaenine supertribe Hapsomelitae based on its distinctive general habitus with well-exposed abdominal segments, particularly the greatly elongated abdominal segments V and VI (Chatzimanolis *et al.* 2010). Hapsomelitae includes three genera, all described from Kachin amber: *Ektatotricha* Chatzimanolis, Engel & Newton, 2010; *Electroatopos* Chatzimanolis, Engel & Newton, 2010; and *Hapsomela*. The Hkamti fossil cannot be assigned to *Hapsomela* due to its relatively flattened body, non-filiform antennae, and the structure of the maxillary palpus (Chatzimanolis *et al*. 2010). Similarly, it can be excluded from *Electroatopos* because of its slender, non-clubbed antennae (Chatzimanolis *et al.* 2010). As a result, the fossil specimen is placed in *Ektatotricha*. The overall morphological features agreed well with this genus.

Comparison. The Hkamti fossil aligns well with the characteristics of *Ektatotricha*. However, it lacks the mid-ventral hook on the protibiae, a distinctive morphological trait considered a male sexual characteristic in *Hapsomela* (Yin 2020). Because *Ektatotricha* and *Hapsomela* may not belong to the same clade (Chatzimanolis *et al.* 2010; Yin 2020), this absence suggests the specimen could be female, if the same sexual dimorphism found in *Hapsomela* applies to *Ektatotricha*. Another notable feature of the Hkamti specimen is its antennae. Both antennomeres 9 and 10 are elongated, each appearing longer than their width, which contrasts with the antennal proportions observed in *Ektatotricha paradoxa*, the sole species within the genus (Chatzimanolis *et al*. 2010). Given this discrepancy, it is appropriate to assign the specimen to *Ektatotricha*, but the possibility remains that it represents an undescribed species. Therefore, I have provisionally identified it as *Ektatotricha* sp.

Remarks. One of the most abundant beetle groups in mid-Cretaceous Kachin amber is Hapsomelitae, in addition to *Prosolierius* (Solieriinae) rove beetles (Yamamoto 2023c). It is therefore reasonable to assume that this group was common in the forests that produced Kachin amber. The discovery of *Hapsomela* and *Ektatotricha* in Hkamti amber demonstrates a clear connection between the faunas of Kachin and Hkamti ambers. Notably, these specimens represent the first record of Hapsomelitae outside of Kachin amber. Considering the higher abundance of *Ektatotricha* in Kachin amber, additional specimens are likely to be found in Hkamti amber. Further taxonomic efforts are needed to fully identify and classify these beetles in both Hkamti and Kachin ambers.

Discussion

General overview of the staphylinoid fauna in Hkamti amber

The insect fauna of Hkamti amber from northern Myanmar remains poorly understood. To date, only four coleopteran species have been described from this amber source (Mainda 2023, 2024; Caterino & Yamamoto 2023; Simon-Pražák *et al*. 2024). The two of them belong to Staphylinoidea, both placed within the staphylinid genus *Festenus* (Mainda 2023, 2024). In the present study, 11 staphylinoid bioinclusions were discovered across 10 pieces of Hkamti amber. This greatly enhances the broader understanding of the insect fauna of Hkamti amber compared with previous knowledge. The newly reported specimens belong to three staphylinoid families: Hydraenidae, Colonidae, and Staphylinidae. Although this familial diversity is half that of Kachin amber from northern Myanmar (which includes six families; see Table 2), it exceeds the number found in Lower–Upper Cretaceous ambers from Lebanon, Spain, France, New Jersey (USA), Taimyr (Russia), and Canada, where only one or two staphylinoid families have been recorded (*e.g.* Peris *et al.* 2016). One specimen each was identified from the families Hydraenidae and Colonidae; the remaining specimens were assigned to the rove beetle family Staphylinidae. From Cretaceous amber deposits in the world, both Hydraenidae and Colonidae represent the second finds, but they have already been known in Kachin amber. In other words, it shows the similar composition of Staphylinoidea between Hkamti amber and Kachin amber at the family level. Therefore, fossils of the staphylinoid family Leiodidae, which are relatively diverse in Kachin amber (Yamamoto & Perreau 2025), will likely be discovered in Hkamti amber in the near future.

Comprising approximately 67,000 described species globally (Newton 2022), it is not surprising that the very large family Staphylinidae represents the overwhelming majority of specimens in Hkamti amber. A similar trend has been observed in the adjacent Kachin amber (Table 2). Within Staphylinidae, six subfamilies were identified from nine specimens of Hkamti amber in this study: Osoriinae, Tachyporinae, Aleocharinae, Steninae, Solieriinae, and Scydmaeninae. All but Steninae are recorded here for the first time from Hkamti amber. Compared with the 24 staphylinid subfamilies recorded from Kachin amber, the rove beetle fauna at the subfamily level in Hkamti amber is currently much less diverse. Nevertheless, depending on the progress of future research, it is possible that more subfamilies of Staphylinidae, together with diverse Scydmaeninae and Pselaphinae taxa, will be discovered from Hkamti amber and that the number of subfamilies may even approach, if not surpass, that of Kachin amber.

TABLE 2. General overview of the paleodiversity on the staphylinoid families/subfamilies in Kachin and Hkamti ambers as of 1 June 2025. Abbreviations: AI, oldest fossil(s) of each family or subfamily as amber inclusion; fam., family (families); g., genus (genera); OC, fossil occurrence confirmed by the author and Cai *et al*. (2017: supplementary table 2); OF, oldest fossil(s) of each family or subfamily among all fossil deposits in the world; sp./spp., species; subf., subfamily (subfamilies); UT, undescribed taxon (taxa).

Family/subfamily	**Kachin amber**	**Hkamti amber**	**Oldest described fossils of each family/ subfamily from Myanmar amber**
Family Jacobsoniidae Heller, 1926	**2 g., 2 spp.**		OF****
Family Ptiliidae Erichson, 1845	**2 subf., 2 g., 3 spp.**		OF
Subfamily Nossidiinae Sörensson & Delgado, 2019	1 g., 1 sp.		OF
Subfamily Ptiliinae Erichson, 1845	1 g., 2 spp.		OF
Family Hydraenidae Mulsant, 1844	**1 subf., 1 g., 1 sp.**	**1 subf., 1 g., 1 sp.**	AI
Subfamily Orchymontiinae Perkins, 1997			
Subfamily Prosthetopinae Perkins, 1994			
Subfamily Hydraeninae Mulsant, 1844	1 g., 1 sp.	1 g., 1 sp.	AI
Subfamily Ochthebiinae C.G. Thomson, 1859			
Family Colonidae G.H. Horn, 1880 (1859)	**2 g., 2 spp.**	**1 g., 1 sp.**	OF
Family Agyrtidae C.G. Thomson, 1859			
Family Leiodidae Fleming, 1821	**3 (+1) subf., 4 g., 4 spp.**		
Subfamily Camiarinae Jeannel, 1911	1 g., 1 sp.		OF
Subfamily Catopocerinae Hatch, 1927 (1880)	1 g., 1 sp.		OF
Subfamily Leiodinae Fleming, 1821	OC		
Subfamily Cholevinae W. Kirby, 1837	2 g., 2 spp.		
Subfamily Platypsyllinae Ritsema, 1869			
Family Staphylinidae Latreille, 1802	**23 (+1) subf., 63 g., 92 spp.**	**6 subf., 8 g., 11 spp.**	
Subfamily Silphinae Latreille, 1806	1 g., 1 sp.		
Subfamily Apateticinae Fauvel, 1895			
Subfamily Trigonurinae Reiche, 1866			

......continued on the next page

TABLE 2. (Continued)

Family/subfamily	Kachin amber	Hkamti amber	Oldest described fossils of each family/ subfamily from Myanmar amber
Subfamily Scaphidiinae Latreille, 1806	OC		
Subfamily Piestinae Erichson, 1839a	1 g., 1 sp.		AI
Subfamily Osoriinae Erichson, 1839a	4 g., 5 spp.	2 g., 2 spp.	OF
Subfamily Oxytelinae Fleming, 1821	5 g., 6 spp.		AI
Subfamily Protactinae Heer, 1847†			
Subfamily Omaliinae W.S. MacLeay, 1825			
Subfamily Microsilphinae Crowson, 1950			
Subfamily Glypholomatinae Jeannel, 1962			
Subfamily Empelinae Newton & Tayer, 1992			
Subfamily Proteininae Erichson, 1839b	1 g., 1 sp.		OF
Subfamily Micropeplinae Leach, 1815	2 g., 2 spp.		OF
Subfamily Neophoninae Fauvel, 1905			
Subfamily Dasycerinae Reitter, 1887	3 g., 6 spp.		OF
Subfamily Protopselaphinae Newton & Tayer, 1995	1 g., 2 spp.		OF
Subfamily Pselaphinae Latreille, 1802	8 g., 10 spp.		
Subfamily Mycetoporinae C.G. Thomson, 1859	1 g., 1 sp.		AI
Subfamily Tachyporinae W.S. MacLeay, 1825	2 g., 2 spp.	1 g., 1 sp.	AI
Subfamily Phloeocharinae Erichson, 1839b	3 g., 3 spp.		OF
Subfamily Trichophyinae C.G. Thomson, 1858	1 g., 1 sp.		OF
Subfamily Habrocerinae Mulsant & Rey, 1876			
Subfamily Aleocharinae Fleming, 1821	3 g., 3 spp.	1 g., 1 sp.	OF
Subfamily Leptotyphlinae Fauvel, 1874			
Subfamily Oxyporinae Fleming, 1821	1 g., 1 sp. + UT**		AI

......continued on the next page

TABLE 2. (Continued)

Family/subfamily	**Kachin amber**	**Hkamti amber**	**Oldest described fossils of each family/ subfamily from Myanmar amber**
Subfamily Megalopsidiinae Leng, 1920	1 g., 1 sp.		OF
Subfamily Steninae W.S. MacLeay, 1825	1 g., 2 spp. + UT***	1 g., 3 spp.	OF
Subfamily Euaesthetinae C.G. Thomson, 1859	1 g., 1 sp.		
Subfamily Solieriinae Newton & Tayer, 1992	1 g., 5 spp.	1 g., 2 spp.	OF
Subfamily Scydmaeninae Leach, 1815	14 g., 25 spp.	2 g., 2 spp.	OF
Subfamily Pseudopsinae Ganglbauer, 1895	1 g., 1 sp.		AI
Subfamily Olisthaerinae C.G. Thomson, 1858			
Subfamily Paederinae Fleming, 1821	4 g., 6 spp.		AI
Subfamily Staphylininae Latreille, 1802	2 g., 4 spp.		AI
Subfamily, *incertae sedis*[*]	1 g., 2 spp.		
TOTAL:	**6 fam., 29 (+2) subf., 74 g., 104 spp.**	**3 fam., 7 subf., 10 g., 13 spp.**	

†, extinct taxon.

*The Kachin-amber staphylinid genus *Vetatrecus* Kypke, Solodovnikov & Żyła, 2018 was originally described as a member of the tribe Othiini in the subfamily Staphylininae (Kypke *et al*., 2019). However, it has been recently considered as "subfamily incertae sedis" by Reyes-Hernández *et al*. (2025). The accurate systematic placement of *Vetatrecus* awaits further investigation, but Reyes-Hernández *et al*. (2025) suggested that it likely belongs to Paederinae or to a separate subfamily-level stem group related to Staphylininae.

**Cai *et al*. (2017b) reported three oxyporine species from Kachin amber: an undescribed genus with one species and two species of *Oxyporus*. However, these taxa were not formally described and were instead assigned to "Taxon 1–3" in Cai *et al*. (2017b). Due to these uncertainties, I have excluded them from Table 2.

***An undescribed species of *Festenus* has been known from Kachin amber (Cai *et al*. 2019a).

****A jacobsoniid fossil is also known from a similar-aged French amber (Tihelka *et al*. 2022).

Notably, most staphylinid genera identified from Hkamti amber were also assigned to genera found in Kachin amber, namely *Mesallotrochus*, *Cretochirus*, *Procileoporus*, *Festenus*, *Prosolierius*, *Hapsomela*, and *Ektatotricha* (all but *Prosolierius* are unique to Myanmar amber). Although the aleocharine specimen was tentatively identified as "Mesoporini gen. et sp. indet.", this taxon appears closely related to the extinct genus *Mesosymbion*, which is solely known from Kachin amber. Based on the evidence presented above, the composition of the staphylinid genera in Hkamti amber is almost identical to that of Kachin amber. When the other two families of the Staphylinoidea superfamily are considered together, it can be concluded that the staphylinoid paleofauna of Hkamti amber closely resembles that of Kachin amber. As a matter of fact, both hydraenid and colonid genera found in Hkamti amber have also been recorded in Kachin amber, belonging to the same or closely related genera. These genera listed above are morphologically well-defined and characterized. As such, it is not appropriate to determine all or most of these generic examples are placed in the same genera because of convergent evolution.

The close faunal similarity between Kachin and Hkamti ambers has been previously noted and discussed by Balashov (2021) on the basis of land snail fossils from Hkamti amber. In Balashov (2021), the following two Kachin-amber endemic genera were confirmed in the paleofauna of Hkamti amber (Yu *et al*., 2018; Hirano *et al*. 2019): *Euthema* Yu, Wang & Pan, 2018 and *Archaeocyclotus* Asato & Hirano, 2019 in Hirano *et al*. (2019). Such generic simiralities between two amber deposits have been shown in a few previous studies on Coleoptera as well (Caterino & Yamamoto 2023; Mainda 2023, 2024). Furthermore, Simon-Pražák *et al*. (2024) recently reported a single specimen of clown beetles (Coleoptera: Histeridae: Onthophilinae), *Phasmister hkamticus* Caterino & Yamamoto, 2023 from Kachin amber. This onthophiline species, however, had originally been described and hitherto known from Hkamti amber only (Caterino & Yamamoto 2023), until the work of Simon-Pražák *et al*. (2024). More importantly, the present study found a scydmaenine specimen from Hkamti amber, which is very similar to the Kachin-amber endemic species, *Hapsomela burmitis* Poinar & Brown, 2004. Indeed, there are some morphological differences without the robust evidence that it truly belongs to the species. Nonetheless, the discovery is significant because the male genitalia of the Hkamti specimen is well exposed and can be comparable to that of the Kachin amber *H. burmitis* (Fig. 15D *versus* Yin 2020: fig. 1B). Simon-Pražák *et al*. (2024) and the present work indicate that the same species, or its very close relative, were present in both areas where the two different amber mines are currently located. Thus, not only similarities between the genera of both Kachin amber and Hkamti amber, but also similarities at the species level were being recognized.

The present discovery of more genera endemic to Kachin amber, such as *Procileoporus* and *Ektatotricha*, may further downplay the uniqueness of Hkamti amber. As discussed above, it can be suggested that these genera are truly shared in two different amber localities rather than explaining their morphological similarities as a result of convergent evolution by several different studies including the present findings. As Balashov (2021) concluded, these ambers might had been formed in very similar paleoenvironments, with very similar conditions of forests existed throughout the entire Albian to the early Cenomanian. Another hypothesis that Balashov (2021) noted is that the dating of at least one of these amber deposits is incorrect; in this case, it would mean that Kachin amber is at least 110 Ma or oldert. Either way, the presence of various shared staphylinoid genera is probably due to the reflection of similar paleoenvironments and geological age, and perhaps also indicating the true biogeographic affinities. In summary, the faunal similarities between the two amber deposits found in the present work are not unexpected, considering their shared geological background and geographic proximity, as well as the previous paleontological studies (Balashov 2021; Caterino & Yamamoto 2023; Mainda 2023, 2024; Simon-Pražák *et al*. 2024).

Burmese amber Staphylinoidea

Burmese amber is here limited to two deposits in northern Myanmar, namely the Kachin and Hkamti sites, because no staphylinoid fossils have been found in Tilin amber from central Myanmar. The Kachin site, located in Kachin State, is known for its exceptionally rich paleobiota, particularly its very diverse insect fossils (Ross 2019, 2024). Kachin amber has become an indispensable resource for studying the Mesozoic insect fauna and ecosystems of that era. Over 2,000 species from 28 insect orders have been recorded from this amber (Ross 2024). To date, 104 species from 74 genera of the superfamily Staphylinoidea have been documented in Kachin amber (Table 1; Appendix A), providing a comprehensive understanding of the fauna and offering a detailed picture of the biodiversity of that time.

As shown in Table 2, Agyrtidae is the only staphylinoid family not yet recorded from Kachin amber, indicating that Staphylinoidea is nearly comprehensively represented in the region. Furthermore, several fossils from other families and genera within Staphylinoidea have been found exclusively in Myanmar amber to date. For example, fossils of Colonidae have been discovered only in Kachin and Hkamti amber, with no other known occurrences worldwide (Cai & Huang 2017a; Yamamoto & Takahashi 2018; this study). The other family, Jacobsoniidae, is rare in the fossil record, and Kachin amber is the only source in the world where fossils of two genera have been discovered (Yamamoto *et al.* 2017a; Cai *et al.* 2018a). Additionally, aquatic Hydraenidae, found exclusively in Myanmar amber (from both Kachin and Hkamti sites), are represented as the unique souce of amber bioinclusions in the worldwide fossil deposits (Yamamoto *et al.* 2017b; this study). Until now, only the single hydraenid species has formally been named from Kachin amber (Yamamoto *et al.* 2017b), which belongs to the very diverse extant subfamily Hydraeninae. The definitive fossils of Ptiliidae are very rare in the fossil record globally, probably due to their minute body size and taxonomic difficulty, but three species in two extinct genera were found in Kachin amber (Yamamoto *et al.* 2018; Li Y-D *et al.* 2022, 2023). It is quite possible that the ptiliids will also be discovered in Hkamti amber in the near future. Although only a few Leiodidae fossils have been formally described (viz. 4 species in 4 extinct genera: Cai & Huang 2017b; Perreau 2019; Bao & Antunes-Carvalho 2020; Yamamoto & Perreau 2025), a more diverse and abundant assemblage exists in Kachin amber (Yamamoto & Perreau, unpublished data).

A closer look on Burmese (Kachin) amber reveals an unexpectedly large number of 24 subfamilies among the 35 subfamilies (both extant and extinct) of the family Staphylinidae. This is remarkable because it is comparable to the number of subfamilies found on a national scale. For comparison, the following numbers represent the staphylinid subfamilies in various countries or regions (including Scydmaeninae, Mycetoporinae, and Silphinae): 11 (Egypt); 16 (Papua New Guinea, Cuba); 17 (Brazil, New Zealand); 18 (Peru); 19 (Colombia, Myanmar); 20 (Denmark, excluding Greenland); 21 (Australia, UK, Lithuania); 22 (Korean Peninsula); 23 (Mexico, Japan); 24 (China, including Taiwan); and 25 (Canada) (*e.g.* Klimaszewski *et al.* 1996; Herman 2001; Navarette-Heredia *et al.* 2002; Newton *et al.* 2005; Peck 2005; Tamutis *et al.* 2011; Brunke *et al.* 2012; Asenjo *et al.* 2013; Shibata *et al.* 2013; Newton *et al.* 2015; Schülke & Smetana 2015; Ahn *et al.* 2017; Koszela *et al.* 2018; Li *et al.* 2019; Newton 2022; Park & Ahn 2024). Although the size of the forests that produced Myanmar amber remains unknown, it is evident that they were smaller than those of present-day China or Australia due to the island-like configuration of the West Burma block, or Burma Terrane, during that time period (see Fig. 17; Heine & Müller 2005; Poinar 2019; Westerweel *et al.* 2019). Nevertheless, as many as 24 subfamilies of Staphylinidae were distributed across what was then an island. Additionally, taxa from the entire Staphylinoidea superfamily coexisted within this region. It is noteworthy that such a large number of staphylinid subfamilies, along with five other staphylinoid families, have been discovered in the Hukawng Valley (Kachin State, northern Myanmar), an amber-producing region covering only approximately 14,000 square kilometers. Given the similar trend found in the present work, Hkamti amber may hold the closely associated staphylinid fauna with Kachin amber, along with potentially much more diverse subfamilies of Staphylinidae. Notably, even the current number of staphylinid subfamilies from Hkamti amber (= 6) has already surpassed most of the amber deposits worldwide, except mega-fossil deposits such as Baltic, Dominican, and surely Kachin ambers. Further researches on Burmese amber from both sites are essential to uncover more about this fascinating and scientifically important topic. Finally, I would also like to see the advancement of research on the Upper Cretaceous Tilin amber from central Myanmar, which has been little studied in paleontological contexts.

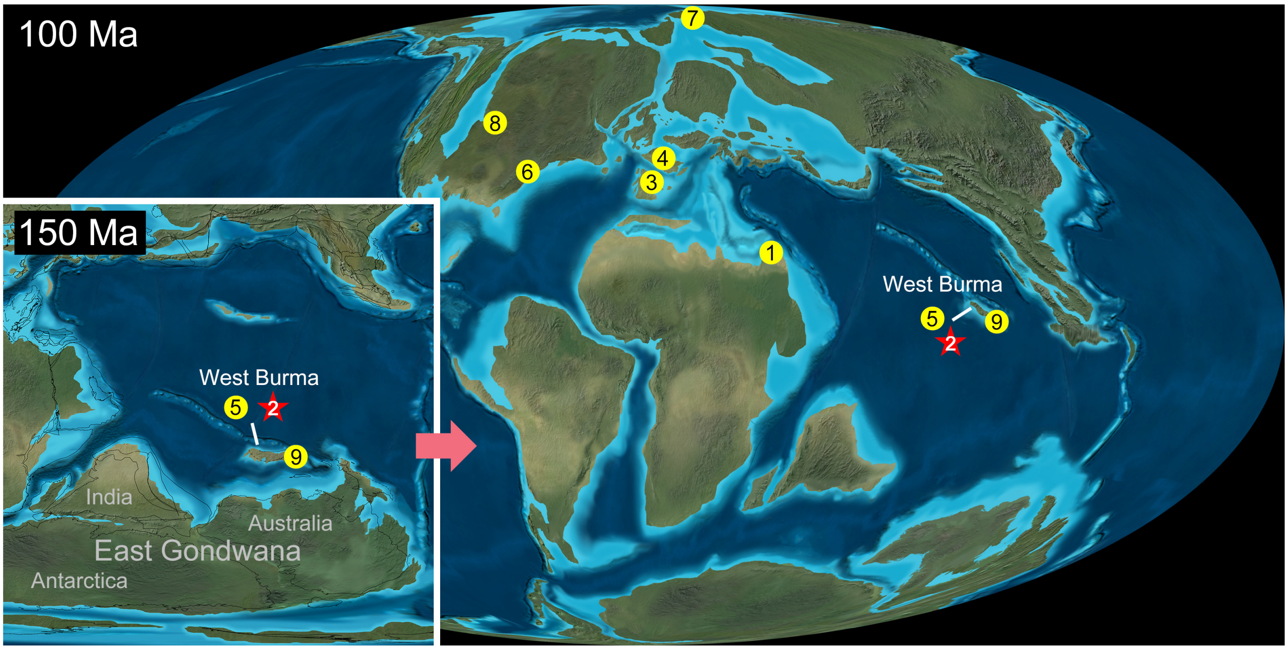

FIGURE 17. Paleogeographic distributions of major Cretaceous amber deposits in the world mapped on a plate-tectonic reconstruction at the time of mid-Cretaceous (100 Ma), also showing the location of West Burma block (Burma Terrane), with Myanmar amber deposits, at the boundary of Lower Cretaceous and Upper Jurassic (150 Ma). Paleogeographic reconstructions (maps) were modified from Global Paleogeography and Tectonics in Deep Time Maps ©2016 Colorado Plateau Geosystems Inc. The localities of amber-producing forests are based on Peris & Rust (2020): (1) Lebanon (late Barremian); (2) Hkamti, Myanmar (early Albian); (3) Spain (late Albian); (4) France (late Albian/early Cenomanian–Santonian); (5) Kachin, Myanmar (early Cenomanian); (6) New Jersey, USA (late Turonian); (7) Taimyr, Russia (middle Santonian); (8) Canada (late Campanian); and (9) Tilin, Myanmar (uppermost Campanian).

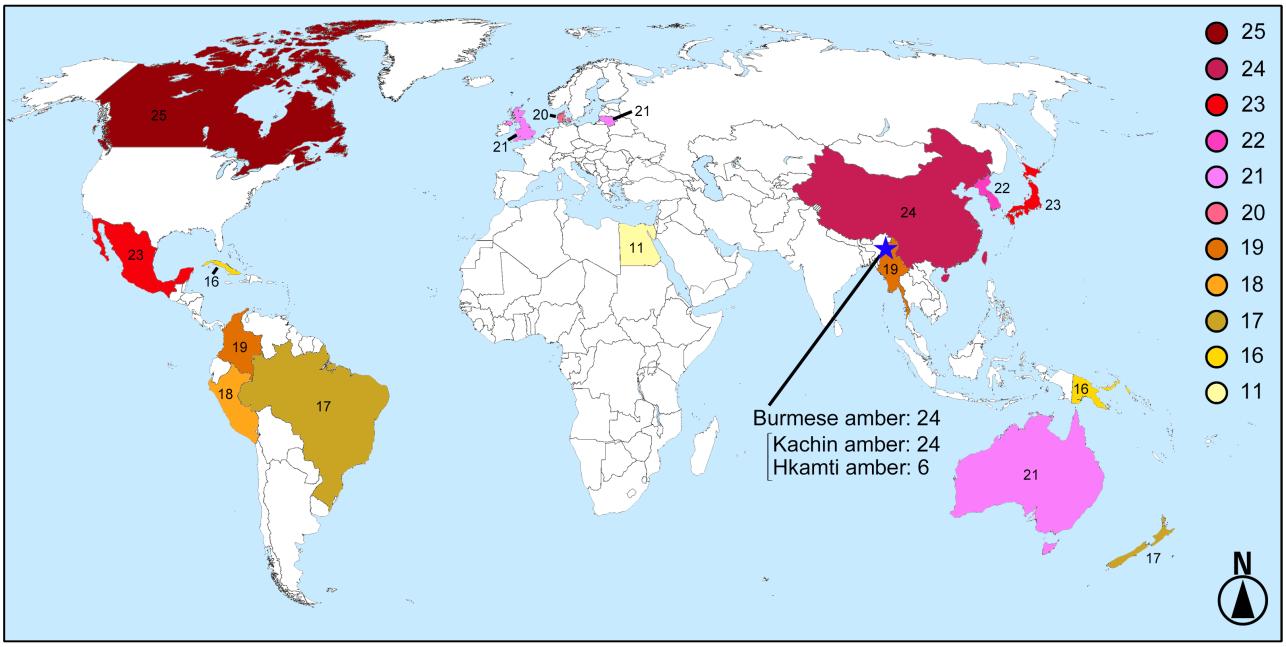

FIGURE 18. Exact counts of subfamilies of Staphylinidae in selected countries or regions, with amber deposits in Myanmar (Kachin and Hkamti sites). Note that Staphylinidae includes the newly added subfamily Mycetoporinae and the following two former familial members: Scydmaeninae and Silphinae, previously treated as 'Scydmaenidae' and 'Silphidae', respectively. The selected countries or regions (highlighted in color) with the following numbers represent the counts of staphylinid subfamilies recorded based on various literature so far, some of which were compiled by multiple sources (*e.g.* Klimaszewski *et al.* 1996; Herman 2001; Navarette-Heredia *et al.* 2002; Newton *et al.* 2005; Peck 2005; Tamutis *et al.* 2011; Brunke *et al.* 2012; Asenjo *et al.* 2013; Shibata *et al.* 2013; Newton *et al.* 2015; Schülke & Smetana 2015; Ahn *et al.* 2017; Koszela *et al.* 2018; Li *et al.* 2019; Newton 2022; Park & Ahn 2024): 11 (Egypt); 16 (Papua New Guinea, Cuba); 17 (Brazil, New Zealand); 18 (Peru); 19 (Colombia, Myanmar); 20 (Denmark, excluding Greenland); 21 (Australia, UK, Lithuania); 22 (Korean Peninsula); 23 (Mexico, Japan); 24 (China, including Taiwan); and 25 (Canada). Credit of the original blank world map: Free Software Foundation, licensed under the Creative Commons Attribution-Share Alike 3.0 Unported license (CC BY-SA 3.0, https://commons.wikimedia.org/wiki/File:World_map_blank_black_lines_4500px_monochrome.png), derived from Wikimedia Commons.

Origin and early evolution of certain staphylinoid taxa

This study of the staphylinoid fossils from Hkamti amber has yielded several valuable discoveries. Although the staphylinoid assemblage presented here is smaller in terms of genera and species compared with the previously reported Kachin amber paleofauna, Hkamti amber is approximately 11 million years older than Kachin amber (Xing & Qiu 2020). This age difference provides a unique opportunity to study the origin and early evolution of various phylogenetic lineages. As a result, these new fossils from Hkamti amber offer useful insights that extend the known origin of certain Staphylinoidea taxonomic units based on direct fossil evidence.

One of the most striking discoveries in this study was the identification of the oldest fossil in the family Colonidae. Previously, the oldest known fossils of this family were found in Kachin amber, but the new discovery in Hkamti amber updates this record. Additionally, this study revealed the oldest fossil of the hydraenid subfamily Hydraeninae, which predates the Kachin amber fossil reported by Yamamoto *et al.* (2017b). This finding also marks the earliest fossil record of the tribe Hydraenini and is the oldest known amber fossil of the family. Within the rove beetle family Staphylinidae, fossils from three subfamilies—Osoriinae, Aleocharinae, and Steninae—constitute the oldest known fossil records worldwide. Of particular note is the fossil from the subfamily Aleocharinae, the largest of all staphylinid subfamilies, encompassing nearly 17,000 species across 1,337 genera (Newton 2022). The overwhelming diversity of this subfamily has extensive implications for evolutionary biology (*e.g.* Kitchen *et al.* 2024). The fossil aleocharine staphylinid found in this study, as well as those from Kachin amber, belong to the primitive, glandless group of Aleocharinae, specifically the tribes Gymnusini, Trichopseniini, and Mesoporini. Although these "lower" Aleocharinae do not represent the majority of the "higher" group, their discovery is important for efforts to trace the origin of this subfamily, which likely dates back even further, according to molecular dating analyses (Lü *et al.* 2020; Kitchen *et al.* 2024). Therefore, the present direct fossil evidence of mesoporin is becoming closer to the estimated origin of Aleocharinae by DNA data (Lü *et al.* 2020). Regarding Osoriinae, the two fossil taxa reported in this study extend the oldest known fossil record for this subfamily, which was previously represented by fossils from Kachin amber. These Hkamti fossils also provide the oldest records for their respective tribes, *viz.*

Thoracophorini and Leptochirini. Intriguingly, the two genera found in Hkamti amber, *i.e. Mesallotrochus* and *Cretochirus*, were previously known only from Kachin amber, making this the second fossil record of these genera. The findings of two different osoriine tribes indicate that the origin of Osoriinae should be much older based on the fossil record. Although not the oldest fossil in the subfamily, the fossil from Tachyporinae identified as *Procileoporus* sp. is the earliest definitive fossil of this subfamily in amber. It also represents the oldest known member of the Vatesini tribe.

As mentioned above, the overall composition of the staphylinoids in Hkamti amber is strikingly similar to that of the tribes and genera found in Kachin amber. However, because Hkamti amber is older, several discoveries have been made that substantially reshape the evolutionary history of each taxon.

Unexpected absence of some staphylinoid lineages in Burmese amber

As indicated in Table 2, Burmese amber contains an extensive representation of subfamilial and tribal taxa within Staphylinoidea, with apparently high survey accuracy. This is particularly true for the family Staphylinidae, where it will be challenging to add more taxa at the subfamily level in the future. Such difficulty arises because the undocumented subfamilies of Staphylinidae are generally known only from a small number of genera and species or are geographically restricted to modern terrestrial ecosystems, such as Olisthaerinae, Empelinae, Neophoninae, Microsilphinae, or Glypholomatinae. Nevertheless, the discovery of rare subfamilies such as Protopselaphinae (Liu Y *et al*. 2020, 2021) and Trichophyinae (Yamamoto & Newton 2021) in Kachin amber suggests potential for the discoveries of these undocumented subfamilies in future studies on amber deposits in Myanmar.

Although broad research efforts are progressively uncovering the full scope of Myanmar's amber paleofauna, a few staphylinoid taxa remain absent from the remarkably diverse assemblage. For instance, at the family level, Agyrtidae is the only family that has not been recorded in Myanmar amber. While the fossil record of Agyrtidae is sparse in the world, reliable records exist from Eocene Baltic/Bitterfeld amber and even the Jurassic Period (Newton 1997; summarized in Chatzimanolis 2018). Additionally, the subfamily Leiodinae within the family Leiodidae has not yet been formally recorded from Myanmar amber, but it has been identified in Kachin amber (Yamamoto & Perreau, unpublished data). With respect to Hydraenidae, only the subfamily Hydraeninae has been found in Myanmar amber (both Kachin and Hkamti; Yamamoto *et al*. 2017b; this study). Other subfamilies within Hydraenidae may also be present, although their discovery may be challenging because these are, after all, primarily aquatic insects.

The most notable absence in the Staphylinidae family from Myanmar amber is the subfamily Omaliinae. Despite its high species's diversity and richness, comprising 120 genera and over 1,700 species across all zoogeographical regions (Thayer 2016; Newton 2022), Omaliinae has not been recorded in either Kachin or Hkamti amber. This absence is particularly intriguing considering that the subfamily is quite prevalent in Eocene Baltic amber (Zanetti *et al.* 2016; Shavrin & Yamamoto 2019, 2020). Although the lack of records may be due to insufficient research, it is possible that Omaliinae was originally absent from the amber-producing forests of Myanmar. One potential explanation could be that many members of Omaliinae are associated with riparian habitats and therefore may not have been preserved in amber. However, aquatic beetles from families such as Gyrinidae, Dytiscidae, Elmidae, and Hydraenidae have been constantly found in Myanmar amber (Cai *et al*. 2018b; Yang *et al*. 2019; Liang *et al*. 2020; Yamamoto *et al*. 2017b; this study). In this context, the absence of Omaliinae remains somewhat unusual. Furthermore, although the present preliminary study of Hkamti amber did not yield any omaliine fossils, trends in Kachin amber suggest that it is unlikely to be found in this amber source either. In addition to Omaliinae, the relatively large subfamily Leptotyphlinae is also absent. Members of this subfamily live deep underground, making them less likely to be trapped in amber, even if they were present in the forests that produced Burmese amber.

Despite the emerging comprehensive picture of the Staphylinoidea fauna in Myanmar amber, notable gaps and uncertainties remain, particularly regarding these missing subfamilies. These issues warrant further exploration and resolution in future research.

Morphological stasis *versus* character evolution

The phenomenon of long-term morphological stasis, or bradytely, refers to remarkably slow or minimal morphological change over deep evolutionary time (Simpson 1944). This phenomenon has been observed in various unrelated lineages of fossil beetles found in Kachin amber, showing the antiquity of some Recent genera. Dozens of species of extant beetle genera have hitherto been recorded in Kachin amber, probably reflecting this stasis. These examples of extant genera recorded from Kachin amber are found from all four coleopteran suborders. Of note, Staphylinoidea holds by far the highest number of examples of such cases (*Derolathrus* and *Sarothrias* in Jacobsoniidae, *Colon* and *Colonellus* in Colonidae, and various staphylinid genera of 14 subfamilies including *Nicrophorus*, *Eleusis*, *Priochirus*, *Ochthephilus*, *Micropeplus*, *Protopselaphus*, *Parabolitobius*, *Tachyporus*, *Phloeocharis*, *Vicelva*, *Trichophya*, *Oxyporus*, *Megalopinus*, *Octavius*, *Scydmaenus*, *Clidicus*, and *Coomania*: Clarke & Chatzimanolis 2009; Cai *et al.* 2014; Yamamoto & Solodovnikov 2016; Yamamoto 2017, 2024a, 2024b; Yamamoto *et al.* 2017a; Cai & Huang 2017a; Jałoszyński *et al.* 2018; Cai *et al.* 2018a; Yamamoto & Takahashi 2018, 2019; Yin & Cai 2019; Jiang *et al.* 2020; Liu Y *et al.* 2020, 2021; Yamamoto & Newton 2021, 2023; Peng *et al.* 2022;

Jenkins Shaw *et al.* 2022; Li Y-D *et al*. 2024a; Chen *et al*. 2025). This phenomenon, wherein 100-million-year-old fossils are considered as extant genera, is prevalent throughout beetles, particularly in Staphylinoidea and, more specifically, Staphylinidae. Please note, however, that there is a possibility that we observe the convergency in external characters for those fossil species, although they are identified in extant genera. Nevertheless, it is noteworthy that many different researches had made such conclusions. As several previous studies and my present work indicated, it can be considered they (at least most) belong truly to extant genera, rather than the superficial similarity based on convergent evolution, due to the presence or absence of distinct diagnostic features found by various authors. In contrast, this morphological stasis is not observed in the beetle superfamily Curculionoidea, a very large and diverse group of weevils. Such difference may be considered by a habitat preference of beetles; most staphylinoids are inhabited in cryptic microhabitats such as leaf litter, in soil, decayed wood, fungi, rotten fruit, animal feces, or under bark. Clarke & Chatzimanolis (2009) proposed a hypothesis that "the continuous presence of mesic habitats over geological time" had contributed to the bradytely in staphylinoid genera, although the "mesic habitat" hypothesis has not been statistically tested (Chatzimanolis 2018), awaiting rigorous verification. Interestingly, most taxa of the other insect orders from Myanmar amber are placed in extinct genera, tribes, subfamilies, or even families, as represented by large orders of Odonata, Hymenoptera, Diptera, Hemiptera, Orthoptera, Neuroptera, and Dictyoptera (including †Aethiocarenodea, †Alienoptera, Blattodea, Isoptera, and Mantodea).

From Hkamti amber, a single fossil of the colonid genus *Colonellus* was discovered, representing an extant genus and subgenus. It is interesting to note that both modern subgenera, *i.e. Colonellus* and *Pentacolonellus*, are now found in Myanmar amber (Cai & Huang 2017a; this study). The remaining Hkamti fossils are primarily from extinct genera, some of which are also known from Kachin amber. Although the staphylinoid fauna of Hkamti amber is not yet fully understood, its strong similarity to Kachin amber suggests that additional fossils from modern genera could be uncovered in the future.

Gondwanan faunal elements of Hkamti amber

In recent years, the association between Kachin amber and Gondwanan faunal elements has received increased special attention (Poinar 2019). According to the recent hypothesis (Zheng *et al*. 2018; Westerweel *et al*. 2019; Xing & Qiu 2020), the resin-producing forests of Myanmar, which include both Hukwang Valley (Kachin) and Hkamti mining sites, were located on the West Burma block or also called Burma Terrane (Fig. 17). The West Burma block has experienced a tumultuous geological history, with a long migration journey drifting northward from Gondwana (Fig. 17), resulting in having at least partly Gondwanan affinities (Westerweel *et al*. 2019; Jouault *et al*. 2022). The unique biota of Myanmar amber is believed to have been formed during a period at the time of amber deposition when West Burma block was an isolated island as part of a Trans-Tethyan island arc that existed for over 20 million years in the Tethys Ocean (Westerweel *et al*. 2019; Jouault *et al*. 2022). Before the separation from Gondwana, this island-like West Burma block had been located near the Australian block in East Gondwana and been separated from the northeastern margin of Gondwana; subsequently, it had been gradually uplifted northward during the Late Jurassic to Early Cretaceous (Heine & Müller 2005; Seton *et al*., 2012; Westerweel *et al*. 2019; Jouault *et al*. 2021, 2022).

Multiple beetles with Gondwanan associations have been discovered in Kachin amber, such as the southern hemisphere-endemic extant clambid genus *Sphaerothorax* (Cai *et al*. 2019b), as well as the New Zealand-endemic extant monotomid genus *Lenax* (Liu Z *et al*. 2020). Moreover, the Lepiceridae, a myxophagan beetle family currently restricted to Central America and north South America, has continuously been found from Kachin amber (Jałoszyński *et al*. 2017b, 2020; Poinar 2019). However, no fossil beetles with a clear Gondwanan association, such as extant Gondwanan genera, have been identified in Hkamti amber, including this study. Nonetheless, some intriguing examples remain to be explored. For instance, the extant colonid genus *Colonellus*, found in this study, is currently distributed in the Oriental region, including India and Sri Lanka, and extends to the Yaeyama Islands in southwestern Japan (Szymczakowski 1964; Peck 1998; Hoshina 2009). Additionally, the modern osoriine staphylinid *Allotrochus*, closely related to the extinct genus *Mesallotrochus* found in both Hkamti and Kachin ambers, is known from subtropical and tropical regions of Australia, the Ethiopian region, and Madagascar (Herman 2001; Newton 1990, 2022). It is also recorded from the Yaeyama Islands in the Oriental region, close to the border with the Palearctic region (Naomi & Irmler 2012). Furthermore, the staphylinid subfamily Solieriinae is currently restricted to specific parts of southern South America (Thayer *et al.* 2012). The discovery of this subfamily in Myanmar amber, including Hkamti amber, initially may suggest a connection between Gondwana and the amber source. However, given that fossils of Solieriinae has also been found in Spanish amber from the Early Cretaceous (Peris *et al*. 2014), its current distribution is more prudently interpreted as a relict, or complicated formation process of Spanish amber, rather than based on strong evidence of a Gondwanan origin.

As discussed above, the faunal relationship between Hkamti amber and Gondwanan elements remains unclear; further research is required to gather additional information. Interestingly, several extant beetle genera with apparent Laurasian origins have also been discovered in Kachin amber. For instance, the Palearctic-endemic *Parabolitobius*, a staphylinid beetle found in Kachin amber, highlights a potential Laurasian connection to the amber deposit or suggests a broader past Pangean distribution of this genus (Yamamoto 2023a). Similarly, two Holarctic genera, *Phloeocharis* and *Vicelva*, both belonging to the staphylinid subfamily Phloeocharinae, have recently been identified in Kachin amber (Yamamoto & Newton 2023; Li Y-D *et al.* 2024a). These discoveries suggest that the formation and evolution of the Myanmar amber biota are more complex than previously understood, warranting further investigation.

Conclusion

Prior to this study, as the member of Staphylinoidea, only two species of the staphylinid genus *Festenus* in the subfamily Steninae were known from Lower Cretaceous Hkamti (Khamti) amber (*ca.* 110 Ma), Sagaing Region, northern Myanmar (Mainda 2023, 2024). This study, however, reports the discovery of 11 staphylinoid taxa from Hkamti amber, representing three staphylinoid families; nine belong to the family Staphylinidae, and the remaining two were classified as Hydraenidae and Colonidae, respectively. As a result, this work represents the first comprehensive report of the paleofauna of Staphylinoidea with Hkamti amber, providing an initial glimpse into the past diversity of this hyper-diverse superfamily within this amber deposit. Most taxa identified in this study are also previously found in Kachin amber, which is geographically and geologically associated with Hkamti amber, again suggesting a close faunal similarity between these two biotas as demonstrated by a few previous studies (Balashov 2021; Caterino & Yamamoto 2023; Simon-Pražák *et al*. 2024). Although the detailed formation process of Hkamti amber remains uncertain, the high similarity to Kachin amber suggests that Hkamti amber was formed in a tropical resiniferous forest near the sea coast (see also Balashov 2021). The discovery of these morphologically informative fossils, some of which represent the oldest known fossils or the earliest fossil records of amber bioinclusions, is noteworthy because they provide insights into the origin and early evolution of staphylinoid beetles. Additionally, the fossils reported here provide valuable calibration points for future molecular dating analyses. For instance, the oldest fossil evidence for the mega-diverse Aleocharinae staphylinids (~ 17,000 species) found in my study is particularly significant, because it does not belong to the earliest diverged clade within the subfamily, viz. the tribe Gymnusini (Ashe 2005; Yamamoto & Maruyama 2018; Orlov *et al.* 2021a; Kitchen *et al.* 2024). Hence, the use of the new specimen "Mesoporini gen. et. sp. indet." as an additional molecular calibration point will refine divergence estimates of Aleocharinae, and probably will reshape the estimation of origin and divergence time of the entire subfamily and each aleocharine tribe shown by Lü *et al*. (2020). Similarly, the usage of fossil information from the new hydraenid specimen for molecular dating may be important for inferring the origin and early diversification of the modern giant reparian genus *Hydraena* (> 1000 species). Despite these important discoveries, much remains to be uncovered, and further research is essential. Based on the findings of this study, it is plausible that more staphylinoid taxa, as well as related groups known from Kachin amber, will be found in Hkamti amber in the future. Notably, genera such as *Colon* (Colonidae) and *Protodasycerus* Yamamoto, 2016 (Staphylinidae: Dasycerinae), along with diverse Scydmaeninae staphylinids including *Scydmobisetia* Jałoszyński & Yamamoto 2016 and *Cenomaniola* Jałoszyński & Yamamoto, 2017, which are abundant in Kachin amber (Yamamoto 2016b; Jałoszyński *et al.* 2016, 2017a), were not encountered in this study but are likely to be discovered in Hkamti amber. It is almost certain that additional subfamilies of Staphylinidae will be identified in the future.

Data Availability

The higher-resolution figures are available through the Zenodo repository (https://doi.org/10.5281/zenodo.15526248).

Declaration of competing interest

The author declares that I have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Ethical statement

All of the amber-fossil specimens used in the present study originated from the Hkamti (Khamti) excavation site, a non-conflict zone in Myanmar (Peretti 2020, 2021). The amber from this site, namely so-called 'Hkamti (Khamti) amber', have been legally mined and traded under governmental permits (Haug *et al*. 2020). Therefore, it is considered that each piece of amber used in this work is not related to the recent armed conflicts and humanitarian problems in Myanmar.

Funding

This study was supported partly by the Grant-in-Aid for JSPS Fellows (JP20J00159) given to SY from the Japan Society for the Promotion of Science (JSPS), Tokyo, Japan.

Acknowledgments

SY thanks Dr. Masahiro Ôhara (HUM) and members of Systematic Entomology, Hokkaido University, Sapporo, Japan, particularly Dr. Kazunori Yoshizawa, for their kind support and the provision of equipment during the study. Additionally, SY is deeply indebted to Dr. Manfred A. Jäch (Naturhistorisches Museum Wien, Vienna, Austria) and Dr. Paweł Jałoszyński (University of Wrocław, Wrocław, Poland) for their valuable insights regarding the identification of hydraenid and

Scydmaeninae staphylinid specimens, respectively. SY is also grateful to Mr. Junnosuke Shimonaka (Graduate School of Agriculture, Hokkaido University), Dr. Alfred F. Newton (Field Museum of Natural History, Chicago, USA), and to Dr. Vasily V. Grebennikov (Canadian Food Inspection Agency, Ottawa, Canada) for literature. Two anonymous reviewers and the chief editor (Dr. Zhi-Qiang Zhang) contributed to significant improvements in the manuscript.

References

Ahn, K.J., Cho, Y.B., Kim, Y.H., Yoo, I.S. & Newton, A.F. (2017) Checklist of the Staphylinidae (Coleoptera) in Korea. *Journal of Asia-Pacific Biodiversity*, 10 (3), 279–336. https://doi.org/10.1016/j.japb.2017.06.006

Asenjo, A., Irmler, U., Klimaszewski, J., Herman, L.H. & Chandler, D.S. (2013) A complete checklist with new records and geographical distribution of the rove beetles (Coleoptera, Staphylinidae) of Brazil. *Insecta Mundi*, 0277, 1–419.

Ashe, J.S. (2005) Phylogeny of the tachyporine group subfamilies and 'basal' lineages of the Aleocharinae (Coleoptera: Staphylinidae) based on larval and adult characteristics. *Systematic Entomology*, 30 (1), 3–37. https://doi.org/10.1111/j.1365-3113.2004.00258.x

Balashov, I. (2021) The first records of mollusks from mid-Cretaceous Hkamti amber (Myanmar), with the description of a land snail, *Euthema myanmarica* n. sp. (Caenogastropoda, Cyclophoroidea, Diplommatinidae). *Journal of Paleontology*, 95 (5), 994–1003. https://doi.org/10.1017/jpa.2021.26

Bao, T. & Antunes-Carvalho, C. (2020) Two new polyphagan beetles (Tenebrionidae, Leiodidae) from lower Cenomanian amber of Myanmar. *Cretaceous Research*, 116, 104599. https://doi.org/10.1016/j.cretres.2020.104599

Bernhauer, M. (1921) Zur Staphylinidenfauna von Südamerika (24. Beitrag). *Deutsche Entomologische Zeitschrift*, 1921, 65–77.

Blackwelder, R.E. (1942) Notes on the classification of the staphylinid beetles of the groups Lispini and Osoriinae. *Proceedings of the United States National Museum*, 92 (3140), 75–90.

Betz, O., Koerner, L. & Dettner, K. (2018) The biology of Steninae. *In*: Betz, O., Irmler, U. & Klimaszewski, J. (Eds.), *Biology of Rove Beetles (Staphylinidae): Life History, Evolution, Ecology and Distribution*. Springer, Cham, pp. 229–283. https://doi.org/10.1007/978-3-319-70257-5_11

Bouchard, P., Bousquet, Y., Davies, A.E. & Cai, C. (2024) On the nomenclatural status of type genera in Coleoptera (Insecta). *ZooKeys*, 1194, 1–981. https://doi.org/10.3897/zookeys.1194.106440

Brunke, A., Klimaszewski, J. & Anderson, R.S. (2012) Present taxonomic work on Staphylinidae (Coleoptera) in Canada: progress against all odds. *In*: Klimaszewski, J. & Anderson, R. (Eds.), *Biosystematics and Ecology of Canadian Staphylinidae (Coleoptera) II*. *ZooKeys*, 186, 1–5. https://doi.org/10.3897/zookeys.186.3252

Brunke, A., Newton, A., Klimaszewski, J., Majka, C. & Marshall, S. (2011) Staphylinidae of eastern Canada and adjacent United States. Key to subfamilies; Staphylininae: tribes and subtribes, and species of Staphylinina. *Canadian Journal of Arthropod Identification*, 12, 1–110. https://doi.org/10.3752/cjai.2010.09

Cai, C., Clarke, D.J., Yin, Z., Fu, Y. & Huang, D. (2019a) A specialized prey-capture apparatus in mid-Cretaceous rove beetles. *Current Biology*, 29 (4), R116–R117. https://doi.org/10.1016/j.cub.2019.01.002

Cai, C. & Huang, D. (2015a) The oldest osoriine rove beetle from Cretaceous Burmese amber (Coleoptera: Staphylinidae). *Cretaceous Research*, 52, 495–500. https://doi.org/10.1016/j.cretres.2014.03.020

Cai, C. & Huang, D. (2015b) 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. *Gondwana Research*, 28 (4), 1579–1584. https://doi.org/10.1016/j.gr.2014.09.016

Cai, C. & Huang, D. (2017a) First fossil Coloninae from Upper Cretaceous Burmese amber (Coleoptera: Staphylinoidea: Leiodidae). *Cretaceous Research*, 77, 69–74. https://doi.org/10.1016/j.cretres.2017.05.005

Cai, C. & Huang, D. (2017b) First definitive fossil agyrtodine beetles: an extant southern hemisphere group recorded from Upper Cretaceous Burmese amber (Coleoptera: Staphylinoidea: Leiodidae). *Cretaceous Research*, 78, 161–165. https://doi.org/10.1016/j.cretres.2017.06.017

Cai, C., Huang, D., Newton, A.F., Eldredge, K.T. & Engel, M.S. (2017) Early evolution of specialized termitophily in Cretaceous rove beetles. *Current Biology*, 27 (8), 1229–1235. https://doi.org/10.1016/j.cub.2017.03.009

Cai, C., Lawrence, J.F., Yamamoto, S., Leschen, R.A.B., Newton, A.F., Ślipiński, A., Yin, Z., Huang, D. & Engel, M.S. (2019b) Basal polyphagan beetles in mid-Cretaceous amber from Myanmar: biogeographic implications and long-term morphological stasis. *Proceedings of the Royal Society B: Biological Sciences*, 286 (1894), 20182175. https://doi.org/10.1098/rspb.2018.2175

Cai, C., Leschen, R.A.B., Hibbett, D.S., Xia, F. & Huang, D. (2017) Mycophagous rove beetles highlight diverse mushrooms in the Cretaceous. *Nature Communications*, 8 (1), 14894. https://doi.org/10.1038/ncomms14894

Cai, C., Maier, C.A. & Huang, D. (2018b) A new riffle beetle in Upper Cretaceous amber from northern Myanmar (Coleoptera: Elmidae). *Cretaceous Research*, 89, 154–159. https://doi.org/10.1016/j.cretres.2018.03.022

Cai, C., Newton, A.F., Thayer, M.K., Leschen, R.A. & Huang, D. (2016) Specialized proteinine rove beetles shed light on insect–fungal associations in the Cretaceous. *Proceedings of the Royal Society B: Biological Sciences*, 283 (1845), 20161439. https://doi.org/10.1098/rspb.2016.1439

Cai, C., Ślipiński, A., Leschen, R.A.B., Yin, Z., Zhuo, D. & Huang, D. (2018a) The first Mesozoic Jacobson's beetle (Coleoptera: Jacobsoniidae) in Cretaceous Burmese amber and biogeographical stasis. *Journal of Systematic Palaeontology*, 16 (7), 543–550. https://doi.org/10.1080/14772019.2017.1314388

Cai, C.-Y., Thayer, M.K., Engel, M.S., Newton, A.F., Ortega-Blanco, J., Wang, B., Wang, X.-D. & Huang, D.-Y. (2014)

Early origin of parental care in Mesozoic carrion beetles. *Proceedings of the National Academy of Sciences of the United States of America*, 111 (39), 14170–14174. https://doi.org/10.1073/pnas.1412280111

Cai, C., Tihelka, E., Giacomelli, M., Lawrence, J.F., Ślipiński, A., Kundrata, R., Yamamoto, S., Thayer, M.K., Newton, A.F., Leschen, R.A.B., Gimmel, M.L., Lü, L., Engel, M.S., Bouchard, P., Huang, D., Pisani, D. & Donoghue, P.C.J. (2022) Integrated phylogenomics and fossil data illuminate the evolution of beetles. *Royal Society Open Science*, 9 (3), 211771. https://doi.org/10.1098/rsos.211771

Cameron, M. (1959) New species of Staphylinidae (Col.) from Angola (IV). *Publicações Culturais da Companhia de Diamantes de Angola*, 48, 113–120.

Caterino, M.S. & Yamamoto, S. (2023) New onthophiline fossil species (Coleoptera: Histeridae: Onthophilinae) from mid-Cretaceous Burmese amber. *The Coleopterists Bulletin*, 77 (3), 432–438. https://doi.org/10.1649/0010-065X-77.3.432

Chatzimanolis, S. (2018) A review of the fossil history of Staphylinoidea. *In*: Betz, O., Irmler, U. & Klimaszewski, J. (Eds.), *Biology of Rove Beetles (Staphylinidae): Life History, Evolution, Ecology and Distribution*. Springer, Cham, pp. 27–45. https://doi.org/10.1007/978-3-319-70257-5_3

Chatzimanolis, S., Engel, M.S., Newton, A.F. & Grimaldi, D.A. (2010) New ant-like stone beetles in mid-Cretaceous amber from Myanmar (Coleoptera: Staphylinidae: Scydmaeninae). *Cretaceous Research*, 31 (1), 77–84. https://doi.org/10.1016/j.cretres.2009.09.009

Chatzimanolis, S., Grimaldi, D.A., Engel, M.S. & Fraser, N.C. (2012) *Leehermania prorova*, the earliest staphyliniform beetle, from the Late Triassic of Virginia (Coleoptera: Staphylinidae). *American Museum Novitates*, 3761, 1–28. https://doi.org/10.1206/3761.2

Chatzimanolis, S., Newton, A.F., Soriano, C. & Engel, M.S. (2013) Remarkable stasis in a phloeocharine rove beetle from the Late Cretaceous of New Jersey (Coleoptera, Staphylinidae). *Journal of Paleontology*, 87 (2), 177–182. https://doi.org/10.1666/12-114.1

Chen, X.-H., Newton, A.F., Huang, D., Lü, L. & Cai, C. (2018a) The first Mesozoic record of *Ochthephilus* (Coleoptera: Staphylinidae: Oxytelinae) from mid-Cretaceous Burmese amber. *Insect Systematics & Evolution*, 1–12. https://doi.org/10.1163/1876312X-bja10071

Clarke, D.J. & Chatzimanolis, S. (2009) Antiquity and long-term morphological stasis in a group of rove beetles (Coleoptera: Staphylinidae): description of the oldest *Octavius* species from Cretaceous Burmese amber and a review of the "Euaesthetine subgroup" fossil record. *Cretaceous Research*, 30 (6), 1426–1434. https://doi.org/10.1016/j.cretres.2009.09.002

Crowson, R.A. (1950) The classification of the families of British Coleoptera. *The Entomologist's Monthly Magazine*, 86, 149–171, 274–288, 327–344.

Cruickshank, R.D. & Ko, K. (2003) Geology of an amber locality in the Hukawng Valley, northern Myanmar. *Journal of Asian Earth Sciences*, 21 (5), 441–455. https://doi.org/10.1016/S1367-9120(02)00044-5

Emery, C. (1886) Über Phylogenie und Systematik der Insekten. *Biologisches Zentralblatt*, 5, 648–656.

Erichson, W.F. (1839a) *Genera et species staphylinorum insectorum Coleopterorum Familiae*. F. H. Morin, Berlin, viii + 400 pp.

Erichson, W.F. (1839b) *Die Käfer der Mark Brandenburg. Erster Band. Zweite Abtheilung*. F.H. Morin, Berlin, pp. 385–740.

Erichson, W.F. (1845) [I., II. Lieferungen]. *In*: *Naturgeschichte der Insecten Deutschlands. Erste Abtheilung. Coleoptera. Dritter Band*. Nicolai, Berlin, 1–320 pp.

Fauvel, A. (1874) *2e supplément aux staphylinides. [Faune gallo-rhénane, cont.]. Tome troisième. [livraison 5]*. Le Blanc-Hardel, Caen, pp. 25–46.

Fauvel, A. (1895) Staphylinides nouveaux de l'Inde et de la Malaisie. *Revue d'Entomologie*, 14 (6–10), 180–286.

Fauvel, A. (1905) Sur une tribu nouvelle de staphylinides. *Revue d'Entomologie*, 24 (5/6), 98–100.

Fikáček, M., Beutel, R.G., Cai, C., Lawrence, J.F., Newton, A.F., Solodovnikov, A., Ślipiński, A., Thayer, M.K. & Yamamoto, S. (2020) Reliable placement of beetle fossils via phylogenetic analyses – Triassic *Leehermania* as a case study (Staphylinidae or Myxophaga?). *Systematic Entomology*, 45 (1), 175–187. https://doi.org/10.1111/syen.12386

Fleming, J. (1821) *Insecta. Supplement to the Fourth, Fifth and Sixth Editions of the Encyclopaedia Britannica Volume Fifth [Part 1]*. A. Constable and Company, Edinburgh, pp. 41–56 + pl. 85.

Ganglbauer, L. (1895) *Die Käfer von Mitteleuropa. Die Käfer der österreichisch-ungarischen Monarchie, Deutschlands, der Schweiz, sowie des französischen und italienischen Alpengebietes. Zweiter Band. Familienreihe Staphylinoidea. 1. Theil: Staphylinidae, Pselaphidae*. Carl Gerold's Sohn, Vienna, vi + 880 + [1] pp.

Gautam, S., McKenzie, S., Katzke, J., Hita Garcia, F., Yamamoto, S. & Economo, E.P. (2024) Evolution of odorant receptor repertoires across Hymenoptera is not linked to the evolution of eusociality. *Proceedings of the Royal Society B: Biological Sciences*, 291 (2031), 20241280. https://doi.org/10.1098/rspb.2024.1280

Grimaldi, D.A. & Ross, A.J. (2017) Extraordinary Lagerstätten in amber, with particular reference to the Cretaceous of Burma. *In*: Fraser, N.C. & Sues, H.-D. (Eds.), *Terrestrial Conservation Lagerstätten: Windows into the Evolution of Life on Land*. Dunedin Academic Press, Edinburgh, pp. 287–342.

Heine, C. & Müller, R.D. (2005) Late Jurassic rifting along the Australian North West Shelf: margin geometry and spreading ridge configuration. *Australian Journal of Earth Sciences*, 52 (1), 27–39. https://doi.org/10.1080/08120090500100077

Hatch, M.H. (1927) Studies on the carrion beetles of Minnesota, including new species. *Technical Bulletin, University of Minnesota Agricultural Experiment Station*, 48, 1–19.

Haug, J.T., Azar, D., Ross, A., Szwedo, J., Wang, B., Arillo, A., Baranov, V., Bechteler, J., Beutel, R., Blagoderov, V., Delclòs, X., Dunlop, J., Feldberg, K., Feldmann, R., Foth, C., Fraaije, R.H.B., Gehler, A., Harms, D., Hedenäs, L., Hyžný, M., Jagt, J.W.M., Jagt-Yazykova, E.A., Jarzembowski, E., Kerp, H., Khine, P.K., Kirejtshuk, A.G., Klug, C., Kopylov, D.S., Kotthoff, U., Kriwet, J., McKellar, R.C., Nel, A., Neumann, C., Nützel, A., Peñalver, E., Perrichot, V., Pint, A., Ragazzi, E., Regalado, L., Reich, M., Rikkinen, J., Sadowski, E.-M., Schmidt, A.R., Schneider, H., Schram, F.R., Schweigert, G., Selden, P., Seyfullah, L.J., Solórzano-Kraemer, M.M., Stilwell, J.D., van Bakel, B.W.M., Vega, F.J., Wang, Y. & Haug, C. (2020) Comment on the letter of the Society of Vertebrate Paleontology (SVP) dated April 21,2020 regarding "Fossils from conflict zones and reproducibility of fossil-based scientific data": Myanmar amber. *PalZ*, 94, 431–437. https://doi.org/10.1007/s12542-020-00522-x

Heer, O. (1847) Die Insektenfauna der Tertiärgebilde von Oeningen und von Radoboj in Croatien. Erste Abtheilung: Käfer. *Neue Denkschriften der Allgemeinen Schweizerischen Gesellschaft für die Gesammten Naturwissenschaften*, 8 (5), 1–229 + (1), pls. 1–8.

Heller, K.M. (1926) Fauna sumatrensis (Beitrag Nr. 29). Rhysodidae et familia nova Jacobsoniidae (prope Rhysodidae? Col.). *Supplementa Entomologica*, 14, 126–128.

Herbst, J.F.W. (1797) *Natursystem aller bekannten in- und ausländischen Insekten, als eine Fortsetzung der von Buffonschen Naturgeschichte. Der Käfer, siebenter Theil*. J. Pauli, Berlin, xi + 346 pp., 26 pls.

Herman, L.H. (2001) Catalog of the Staphylinidae (Insecta: Coleoptera). 1758 to the end of the second millennium. Parts I–VII. *Bulletin of the American Museum of Natural History*, 265, 1–4218 (in 7 vols.). https://doi.org/10.1206/0003-0090.265.1.1

Hirano, T., Asato, K., Yamamoto, S., Takahashi, Y. & Chiba, S. (2019) Cretaceous amber fossils highlight the evolutionary history and morphological conservatism of land snails. *Scientific Reports*, 9, 15886. https://doi.org/10.1038/s41598-019-51840-3

Horn, G.H. (1880) Synopsis of the Silphidae of the United States with reference to the genera of other countries. *Transactions of the American Entomological Society and Proceedings of the Entomological Section of the Academy of Sciences*, 8 ([2]), 219–319, pls. 5–7.

Hoshina, H. (2009) A taxonomic revision of the subfamily Coloninae (Coleoptera: Leiodidae) from Japan and Taiwan. *Tijdschrift voor Entomologie*, 152 (2), 237–286.

Hoshina, H. (2016a) Notes on the subfamily Coloninae of Japan (II). *SAYABANE*, *New Series*, 22, 1–7. (in Japanese, with English title.)

Hoshina, H. (2016b) Notes on the subfamily Coloninae of Japan (I). *SAYABANE*, *New Series*, 21, 1–7. (in Japanese, with English title.)

Irmler, U. (2010) A new genus of Osoriinae in the Neotropical Region with a cladistic analysis of the tribe Thoracophorini (Insecta: Coleoptera: Staphylinidae). *Arthropod Systematics & Phylogeny*, 68 (2), 229–237. https://doi.org/10.3897/asp.68.e31729

Jäch, M.A., Beutel, R.G., Delgado, J.A. & Díaz, J.A. (2016) 14.1 Hydraenidae Mulsant. *In*: Beutel, R.G. & Leschen, R.A.B. (Eds.), *Handbook of Zoology, Arthropoda: Insecta Coleoptera, Beetles. Volume 1, 2nd edition*. De Gruyter, Berlin, pp. 316–345.

Jałoszyński, P. (2014) Phylogeny of a new supertribe Cephenniitae with generic review of Eutheiini and description of a new tribe Marcepaniini (Coleoptera: Staphylinidae: Scydmaeninae). *Systematic Entomology*, 39 (1), 159–189. https://doi.org/10.1111/syen.12044

Jałoszyński, P., Brunke, A.J., Yamamoto, S. & Takahashi, Y. (2018) Evolution of Mastigitae: Mesozoic and Cenozoic fossils crucial for reclassification of extant tribes (Coleoptera: Staphylinidae: Scydmaeninae). *Zoological Journal of the Linnean Society*, 184 (3), 623–652. https://doi.org/10.1093/zoolinnean/zly010

Jałoszyński, P., Luo, X.-Z., Hammel, J.G., Yamamoto, S. & Beutel, R.G. (2020) The mid-Cretaceous †*Lepiceratus* gen. nov. and the evolution of the relict beetle family Lepiceridae (Insecta: Coleoptera: Myxophaga). *Journal of Systematic Palaeontology*, 18 (13), 1127–1140. https://doi.org/10.1080/14772019.2020.1747561

Jałoszyńsk, P. & Szawaryn, K. (2024) Characters of a new species of the Cretaceous genus †*Loeblitoides* affirm affinities to the extant '*Syndicus* group' of Stenichnini (Coleoptera: Staphylinidae: Scydmaeninae). *Zootaxa*, 5497 (1), 123–132. https://doi.org/10.11646/zootaxa.5497.1.7

Jałoszyński, P., Yamamoto, S. & Takahashi, Y. (2016) *Scydmobisetia* gen. nov., the first definite Glandulariini from Upper Cretaceous Burmese amber (Coleoptera: Staphylinidae: Scydmaeninae). *Cretaceous Research*, 65, 59–67. https://doi.org/10.1016/j.cretres.2016.04.011

Jałoszyński, P., Yamamoto, S. & Takahashi, Y. (2017a) A new extinct genus of Glandulariini with two species from Upper Cretaceous Burmese amber (Coleoptera: Staphylinidae: Scydmaeninae). *Cretaceous Research*, 72, 142–150. https://doi.org/10.1016/j.cretres.2016.12.021

Jałoszyński, P., Yamamoto, S. & Takahashi, Y. (2017b) Discovery of a new Mesozoic species of the ancient genus *Lepicerus* (Coleoptera: Myxophaga: Lepiceridae), with implications for the systematic placement of all previously described extinct 'lepiceroids'. *Cretaceous Research*, 78, 95–102. https://doi.org/10.1016/j.cretres.2017.06.001

Janák, J. (2024) A new genus, two new species and a new record of Paederinae from Cretaceous Burmese amber (Coleoptera: Staphylinidae). *Studies and Reports Taxonomical Series*, 20 (2), 383–393.

Jeannel, R. (1911) Biospeologica XIX. Révision des Bathysciinae (Coléoptères Silphides). Morphologie, distribution géographique, systématique. *Archives de Zoologie Expérimentale et Générale*, (5) 7[47](1), 1–641, pls. 1–24.

Jeannel, R. (1962) Les Silphidae, Liodidae, Camiaridae et Catopidae de la paléantarctide occidentale. *In*: Delamare-Deboutteville, C. & Rapoport, E. (Eds.), *Biologie de l'Amérique Australe. Vol. I. Études sur la faune du sol*. Centre National de la Recherche Scientifique, Paris, pp. 481–525.

Jendek, E. & Grebennikov, V.V. (2023) Summary of native geographic distribution of all 3,341 species of the most speciose animal genus *Agrilus* (Coleoptera: Buprestidae). *Journal of Insect Biodiversity*, 39 (2), 32–78. https://doi.org/10.12976/jib/2023.39.2.1

Jenkins Shaw, J., Solodovnikov, A., Bai, M. & Żyła, D. (2022) New Burmese amber rove beetle fossils assigned to the rare extant subfamily Coomaniinae (Coleoptera: Staphylinidae). *Insects*, 13 (9), 767. https://doi.org/10.3390/insects13090767

Jiang, R., Peng, Z. & Wang, S. (2020) The oldest *Micropeplus* (Coleoptera, Staphylinidae, Micropeplinae) species from mid-Cretaceous Burmese amber. *Cretaceous Research*, 106, 104218. https://doi.org/10.1016/j.cretres.2019.104218

Jouault, C., Maréchal, A., Condamine, F.L., Wang, B., Nel, A., Legendre, F. & Perrichot, V. (2022) Including fossils in phylogeny: a glimpse into the evolution of the superfamily Evanioidea (Hymenoptera: Apocrita) under tip-dating and the fossilized birth–death process. *Zoological Journal of the Linnean Society*, 194 (4), 1396–1423. https://doi.org/10.1093/zoolinnean/zlab034

Jouault, C., Perrichot, V. & Nel, A. (2021) New flat wasps from mid-Cretaceous Burmese amber deposits highlight the bethylid antiquity and paleobiogeography (Hymenoptera: Chrysidoidea). *Cretaceous Research*, 123, 104772. https://doi.org/10.1016/j.cretres.2021.104772

Kim, Y.-H., Lee, S.-G. & Ahn, K.-J. (2011) Description of *Dictyon termitophilum* new species and a key to the species of the genus *Dictyon* Fauvel (Coleoptera: Staphylinidae: Aleocharinae). *Journal of the Kansas Entomological Society*, 84 (3), 174–178. https://doi.org/10.2317/JKES110305.1

Kirby, W. (1837) Part the fourth and last. The insects. *In*: Richardson, J. (Ed.), *Fauna boreali-Americana; or the zoology of the northern parts of British America: containing descriptions of the objects of natural history collected on the late northern land expeditions, under command of Captain Sir John Franklin, RN*. J. Fletcher, Norwich, xxxix + 325 + [2] pp., 8 pls.

Kitchen, S.A., Naragon, T.H., Brückner, A., Ladinsky, M.S., Quinodoz, S.A., Badroos, J.M., Viliunas, J.W., Kishi, Y., Wagner, J.M., Miller, D.R., Yousefelahiyeh, M., Antoshechkin, I.A., Eldredge, K.T., Pirro, S., Guttman, M., Davis, S.R., Aardema, M.L. & Parker, J. (2024) The genomic and cellular basis of biosynthetic innovation in rove beetles. *Cell*, 187 (14), P3563–3584.E26. https://doi.org/10.1016/j.cell.2024.05.012

Klimaszewski, J., Newton, A.F. Jr., A.F. & Thayer, M.K. (1996) A review of the New Zealand rove beetles (Coleoptera: Staphylinidae). *New Zealand Journal of Zoology*, 23 (2), 143–160. https://doi.org/10.1080/03014223.1996.9518074

Koszela, K., Żyła, D. & Solodovnikov, A. (2018) The interactive digital key to rove beetles (Coleoptera: Staphylinidae) of Denmark. Available from: https://www.danbiller.dk/aboutthekey (accessed 9 October 2024).

Kraatz, G. (1857) *Naturgeschichte der Insecten Deutschlands. Erste Abtheilung Coleoptera. Zweiter Band. Lieferung 3–6*. Nicolai, Berlin, pp. 377–1080.

Kugelann, J.G. (1794) Verzeichniss der in einigen Gegenden Preussens bis jetzt entdeckten Käfer-Arten, nebst kurzen Nachrichten von denselben. *Neuestes Magazin für die Liebhaber der Entomologie*, 1 (5), 513–582.

Kypke, J., Solodovnikov, A., Brunke, A.J., Yamamoto, S. & Żyła, D. (2019) The past and the present through phylogenetic analysis: the rove beetle tribe Othiini now and 99 Ma. *Systematic Entomology*, 44 (1), 1–18. https://doi.org/10.1111/syen.12305

Lameere, A. (1900) Notes pour la classification des Coléoptères. *Annales de la Société Entomologique de Belgique*, 44 (9), 355–377, 1 pl.

Latreille, P.A. (1797) *Précis des caractères génériques des insectes, disposés dans un ordre naturel*. Prévôt, Paris [&] F. Bourdeaux, Brive, xiii + [1] + 201 + [7] pp.

Latreille, P.A. (1802) *Histoire naturelle, générale et particulière, des crustacés et des insectes. Ouvrage faisant suite à l'histoire naturelle générale et particulière, composée par Leclerc de Buffon, et rédigée par C. S. Sonnini, membre de plusieurs sociétés savantes. Familles naturelles des genres. Tome troisième*. F. Dufart, Paris, i–xii, 13–467 pp.

Latreille, P.A. (1806) *Genera crustaceorum et insectorum secundum ordinem naturalem in familias disposita, iconibus exemplisque plurimis explicata. Tomus secundus*. Amand Koenig, Paris, 280 pp.

Leach, W.E. (1815) Entomology. *In*: Brewster, D. (Ed.), *The Edinburgh Encyclopaedia; or dictionary of arts, sciences, and miscellaneous literature. [Vol. IX, part I.]*. William Blackwood, Edinburgh, pp. 57–172. https://doi.org/10.5962/bhl.title.66019

Leng, C.W. (1920) *Catalogue of the Coleoptera of America, North of Mexico*. John D. Sherman, Jr., Mount Vernon, New York, x + 470 pp.

Li, L.-Z., Hu, J.-Y., Peng, Z, Tang, L., Yin, Z.-W. & Zhao, M.-J. (2019) *Catalogue of Chinese Coleoptera. Volume 3. Staphylinidae*. Science Press, Beijing, [4] + xix + 720 pp.

Li, Y.-D., Newton, A.F., Huang, D.-Y. & Cai, C.-Y. (2022) The first fossil of Nossidiinae from mid-Cretaceous amber of northern Myanmar (Coleoptera: Ptiliidae). *Frontiers in Ecology and Evolution*, 10, 911512. https://doi.org/10.3389/fevo.2022.911512

Li, Y.-D., Newton, A.F., Huang, D.-Y. & Cai, C.-Y. (2024a) A new fossil species of the extant genus *Vicelva* from mid-Cretaceous Kachin amber (Coleoptera: Staphylinidae). *Ecology and Evolution*, 14 (6), e11487. https://doi.org/10.1002/ece3.11487

Li, Y.-D., Ruta, R., Huang, D.-Y. & Cai, C.-Y. (2025) Revised phylogenomic analysis and Cretaceous fossil evidence reveal new insights into evolution of Scirtinae (Coleoptera: Scirtidae). *Journal of Systematics and Evolution*, 1–13. https://doi.org/10.1111/jse.13182

Li, Y.-D., Yamamoto, S., Huang, D.-Y. & Cai, C.-Y. (2020) A miniaturized ommatid beetle in mid-Cretaceous Burmese amber (Coleoptera: Archostemata: Ommatidae). *Papéis Avulsos de Zoologia*, 60, e20206063. https://doi.org/10.11606/1807-0205/2020.60.63

Li, Y.-D., Yamamoto, S., Huang, D.-Y. & Cai, C.-Y. (2021a) New species of *Paraodontomma* from mid-Cretaceous Burmese amber with muscle tissue preservation (Coleoptera: Archostemata: Ommatidae). *Papéis Avulsos de Zoologia*, 61, e20216153. https://doi.org/10.11606/1807-0205/2021.61.53

Li, Y.-D., Yamamoto, S., Newton, A.F. & Cai, C.-Y. (2023) *Kekveus brevisulcatus* sp. nov., a new featherwing beetle from mid-Cretaceous amber of northern Myanmar (Coleoptera: Ptiliidae). *PeerJ*, 11, e15306. https://doi.org/10.7717/peerj.15306

Liang, Z., Qi, Z., Chen, J. & Jia, F. (2020) *Cretodineutus rotundus* gen. et sp. nov., the oldest adult whirligig beetle from the Upper Cretaceous of Myanmar (Coleoptera, Gyrinidae, Gyrininae). *Cretaceous Research*, 106, 104251. https://doi.org/10.1016/j.cretres.2019.104251

Linnaeus, C. (1758) *Systema naturae per regna tria naturae, secundum classes, ordines, genera species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. Tomus*

I. Laurentii Salvii, Holmiae, iv + 824 pp.

Liu, N., Gao, L., Huang, D. & Cai, C. (2025) *Prosolierius qizhihaoi* sp. nov., a new species of solieriine rove beetles from mid-Cretaceous Kachin amber (Coleoptera: Staphylinidae). *Journal of Asia-Pacific Entomology*, 28, 102405.
https://doi.org/10.1016/j.aspen.2025.102405

Liu, Y., Tihelka, E., Huang, D., Tian, L. & Cai, C. (2021) A new fossil species of the rove beetle subfamily Protopselaphinae (Coleoptera: Staphylinidae) from mid-Cretaceous Burmese amber. *Historical Biology*, 33 (10), 2019–2024.
https://doi.org/10.1080/08912963.2020.1762594

Liu, Y., Tihelka, E., Yamamoto, S., Yin, Z., Huang, D., Tian, L. & Cai, C. (2020) The first fossil record of the rove beetle subfamily Protopselaphinae (Coleoptera: Staphylinidae) from mid-Cretaceous Burmese amber. *Cretaceous Research*, 110, 104416.
https://doi.org/10.1016/j.cretres.2020.104416

Liu, Z., Tihelka, E., McElrath, T., Yamamoto, S., Ślipiński, A., Wang, B., Ren, D. & Pang, H. (2020) New minute clubbed beetles (Coleoptera, Monotomidae, Lenacini) from mid-Cretaceous amber of northern Myanmar. *Cretaceous Research*, 107, 104255.
https://doi.org/10.1016/j.cretres.2019.104255

Lü, L., Cai, C.-Y., Zhang, X., Newton, A.-F., Thayer, M.-K. & Zhou, H.-Z. (2020) Linking evolutionary mode to palaeoclimate change reveals rapid radiations of staphylinoid beetles in low-energy conditions. *Current Zoology*, 66 (4), 435–444.
https://doi.org/10.1093/cz/zoz053

MacLeay, W.S. (1825) *Annulosa Javanica, or an attempt to illustrate the natural affinities and analogies of the insects collected in Java by Thomas Horsfield, M.D. F.L. & G.S. and deposited by him in the museum of the honourable East-India Company. Number 1*. Kingsbury, Parbury, and Allen, London, xii + 50 pp., 1 pl.

Mainda, T. (2023) *Festenus annodutt* nov. sp. from Burmese amber (Coleoptera, Staphylinidae, Steninae). *Linzer Biologische Beiträge*, 54 (2), 573–576.
https://doi.org/10.35011/lbb.54.2-38

Mainda, T. (2024) The diminutive fear of the Cretaceous edaphon: *Festenus microraptor* nov. sp. from 110 Ma old Hkamti-Burmese amber (Coleoptera, Staphylinidae, Steninae). *Linzer Biologische Beiträge*, 56 (1), 129–133.

Mao, Y., Liang, K., Su, Y., Li, J., Rao, X., Zhang, H., Xia, F., Fu, Y., Cai, C. & Huang, D. (2018) Various amber ground marine animals on Burmese amber with discussions on its age. *Palaeoentomology*, 1 (1), 91–103.
https://doi.org/10.11646/palaeoentomology.1.1.11

McKenna, D.D., Farrell, B.D., Caterino, M.S., Farnum, C.W., Hawks, D.C., Maddison, D.R., Seago, A.E., Short, A.E.Z., Newton, A.F. & Thayer, M.K. (2015) Phylogeny and evolution of Staphyliniformia and Scarabaeiformia: forest litter as a stepping stone for diversification of nonphytophagous beetles. *Systematic Entomology*, 40 (1), 35–60.
http://dx.doi.org/10.1111/syen.12093

McKenna, D.D., Shin, S., Ahrens, D., Balke, M., Beza-Beza, C., Clarke, D.J., Donath, A., Escalona, H.E., Friedrich, F., Letsch, H., Liu, S., Maddison, D., Mayere, C., Misof, B., Murina, P.J., Niehuis, O., Peters, R.S., Podsiadlowski, L., Pohl, H., Scully, E.D., Yan, E.V., Zhou, X., Ślipiński, A. & Beutel, R.G. (2019) The evolution and genomic basis of beetle diversity. *Proceedings of the National Academy of Sciences of the United States of America*, 116 (49), 24729–24737.
https://doi.org/10.1073/pnas.1909655116

Moreno, C., Newton, A.F. & Casari, S.A. (2025) The larval description of *Glyptoma denieri* (Bernhauer) from Brazil provides clarification on new status of the subtribe Glyptomina (Coleoptera, Staphylinidae, Osoriinae). *Zootaxa*, 5620 (2), 295–314.
https://doi.org/10.11646/zootaxa.5620.2.5

Mulsant, É. (1844) *Palpicornes. Histoire naturelle des Coléoptères de France. [Tome 3]*. Maison, Paris, vii + 197 + [7, errata + suppl.] pp., 1 pl.

Mulsant, É. & Rey, C. (1876) [Histoire naturelle des Coléoptères de France]. Tribu des brévipennes. [Staphyliniens.]. *Annales de la Société d'Agriculture, Histoire Naturelle et Arts Utiles de Lyon*, (4) 8[1875], 145–856, [7, explic.], pls. 1–6.

Naomi, S.-I. & Irmler, U. (2012) First record of the genus *Allotrochus* Fagel, 1955 (Coleoptera: Staphylinidae: Osoriinae) from the Oriental Region, with description of the new species *A. takahashii* from Ishigaki Is., Nansei Islands, Japan. *Biogeography*, 14, 105–110.
https://doi.org/10.11358/biogeo.14.105

Naomi, S.-I. & Iwata, R. (1996) *Kistnerium japonicum* Naomi et Iwata n. gen. et n. sp., the first representative of the tribe Mesoporini (Coleoptera, Staphylinidae, Aleocharinae) from Japan, associated with termite (Isoptera: Rhinotermitidae). *Sociobiology*, 28 (1), 73–81.

Naomi, S.-I., Nomura, S. & Puthz, V. (2017) The subfamily Steninae Macleay, 1825 (Coleoptera: Staphylinidae) of Japan Part 1. *Dianous* and *Stenus* (*S. comma* group to *S. guttalis* group). *National Museum of Nature and Science Monographs*, 46, 1–339.

Navarrete-Heredia, J.L., Newton, A.F., Thayer, M.K., Ashe, J.S. & Chandler, D.S. (2002) *GuÍA Ilustrada para los Géneros de Staphylinidae (Coleoptera) de México. Illustrated Guide to the Genera of Staphylinidae (Coleoptera) of Mexico*. Universidad de Guadalajara y Conabio, Guadalajara, Mexico, xii + 401 pp.

Newton, A.F. Jr. (1990) *Myrmelibia*, a new genus of myrmecophile from Australia, with a generic review of Australian Osoriinae (Coleoptera: Staphylinidae). *Invertebrate Taxonomy*, 4 (1), 81–94.
https://doi.org/10.1071/IT9900081

Newton, A.F. Jr. (1997) Review of Agyrtidae (Coleoptera), with a new genus and species from New Zealand. *Annales Zoologici (Warszawa)*, 47 (1/2), 111–156.

Newton, A. (2022) Staphyliniformia world catalog database (version August 2022): Staphylinoidea, Hydrophiloidea, Synteliidae, Sphaeritidae, Cretohisteridae. *In*: Bánki, O., Roskov, Y., Döring, M., Ower, G., Vandepitte, L., Hobern, D., Remsen, D., Schalk, P., DeWalt, R.E., Keping, M., Miller, J., Orrell, T., Aalbu, R., Adlard, R., Adriaenssens, E.M., Aedo, C., Aescht, E., Akkari, N., Alexander, S., *et al*. (Eds.), Catalogue of Life Checklist (Aug 2022). Available from: https://www.catalogueoflife.org/data/dataset/1204 (accessed 22 October 2024).

Newton, A.F., Gutiérrez-Chacón, C. & Chandler, D.S. (2005) Checklist of the Staphylinidae (Coleoptera) of Colombia. *Biota Colombiana*, 6 (1), 1–72.

Newton, A.F., Thayer, M.K., Ashe, J.S. & Chandler, D.S. (2000)

Staphylinidae Latreille, 1802. *In*: Arnett, R.H. Jr. & Thomas, M.C. (Eds.), *American Beetles. Volume 1. Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia*. CRC Press, Boca Raton, FL, pp. 272–418.

Newton, A.F. Jr. & Thayer, M.K. (1992) Current classification and family-group names in Staphyliniformia (Coleoptera). *Fieldiana: Zoology (New Series)*, 67, 1–92.

Newton, A.F. Jr. & Thayer, M.K. (1995) Protopselaphinae new subfamily for *Protopselaphus* new genus from Malaysia, with a phylogenetic analysis and review of the Omaliine Group of Staphylinidae including Pselaphidae (Coleoptera). *In*: Pakaluk, J. & Ślipiński, S.A. (Eds.), *Biology, phylogeny and classification of Coleoptera: Papers celebrating the 80th birthday of Roy A Crowson*. Muzeum i Instytut Zoologii PAN, Warszawa, pp. 219–320 (in 2 vols.).

Nyunt, T.T., Tay, T., Ying, L., Krishnaswamy, M., Cho, C., Kyaw, N., Aung, W. & Chanmuang, N.C. (2020) Amber from Khamti, Sagaing Region, Myanmar. *The Journal of Gemmology*, 37 (3), 314–322.
https://doi.org/10.15506/JoG.2020.37.3.314

Orlov, I., Leschen, R.A.B., Żyła, D. & Solodovnikov, A. (2021a) Total-evidence backbone phylogeny of Aleocharinae (Coleoptera: Staphylinidae). *Cladistics*, 37 (4), 343–374.
https://doi.org/10.1111/cla.12444

Orlov, I., Newton, A.F. & Solodovnikov, A. (2021b) Phylogenetic review of the tribal system of Aleocharinae, a mega-lineage of terrestrial arthropods in need of reclassification. *Journal of Zoological Systematics and Evolutionary Research*, 59 (8), 1903–1938.
https://doi.org/10.1111/jzs.12524

Park, J.-Y. & Ahn, K.-J. (2024) Two rove beetle subfamilies Phloeocharinae and Trichophyinae (Coleoptera: Staphylinidae) new to Korea. *Journal of Asia-Pacific Biodiversity*, 17 (2), 232–234.
https://doi.org/10.1016/j.japb.2023.12.006

Peck, S.B. (1998) *Colonellus* (*Pentacolonellus*) *gilli*, new subgenus and new species from India (Coleoptera: Leiodidae: Coloninae). *Elytron, Barcelona*, 11, 63–70.

Peck, S.B. (2005) A checklist of the beetles of Cuba with data on distributions and bionomics. *Arthrropods of Florida and Neighboring Land Areas*, 18, vi + 1–241 + vii.

Peck, S.B. & Stephan, K. (1996) A revision of the genus *Colon* Herbst (Coleoptera: Leiodidae: Coloninae) of North America. *The Canadian Entomologist*, 128 (4), 667–741.
https://doi.org/10.4039/Ent128667-4

Peng, Y., Jiang, R., Shi, C., Long, X., Engel, M.S. & Wang, S. (2022) A new subgenus and species of *Priochirus* from mid-Cretaceous Kachin amber (Coleoptera: Staphylinidae: Osoriinae). *Insects*, 13 (6), 513.
https://doi.org/10.3390/insects13060513

Peretti, A. (2020) Ethical guidelines for Burmese amber acquisitions. *Journal of Applied Ethical Mining of Natural Resources and Paleontology* (*PMF Journal*), 1, 4–78. Available from: https://www.pmf.org/journal (accessed 19 May 2025).

Peretti, A. (2021) An alternative perspective for acquisitions of amber from Myanmar including recommendations of the United Nations Human Rights Council. *Journal of International Humanitarian Action*, 6, 12.
https://doi.org/10.1186/s41018-021-00101-y

Peris, D., Bao, T., Mähler, B. & Philips, T.K. (2020) A morphologically unique species of Ptinidae (Coleoptera) and the first found in mid-Cretaceous Kachin amber (Myanmar). *Journal of Systematic Palaeontology*, 18 (10), 873–883.
https://doi.org/10.1080/14772019.2019.1695291

Peris, D., Chatzimanolis, S. & Delclòs, X. (2014) Diversity of rove beetles (Coleoptera: Staphylinidae) in Early Cretaceous Spanish amber. *Cretaceous Research*, 48, 85–95.
https://doi.org/10.1016/j.cretres.2013.11.008

Peris, D. & Rust, J. (2020) Cretaceous beetles (Insecta: Coleoptera) in amber: the palaeoecology of this most diverse group of insects. *Zoological Journal of the Linnean Society*, 189 (4), 1085–1104.
https://doi.org/10.1093/zoolinnean/zlz118

Peris, D., Thayer, M.K. & Néraudeau, D. (2014) Oldest Omaliini (Coleoptera: Staphylinidae: Omaliinae) discovered in the opaque Cretaceous amber of Charentes. *Annals of the Entomological Society of America*, 107 (5), 902–910.
https://doi.org/10.1603/AN14047

Peris, D., Ruzzier, E., Perrichot, V. & Delclòs, X. (2016) Evolutionary and paleobiological implications of Coleoptera (Insecta) from Tethyan-influenced Cretaceous ambers. *Geoscience Frontiers*, 7 (4), 695–706.
https://doi.org/10.1016/j.gsf.2015.12.007

Perkins, P.D. (1989) *Adelphydraena*, new genus, and two new species from Venezuela, and remarks on phylogenetic relationships within the subtribe Hydraenina (Coleoptera: Hydraenidae). *Proceedings of the Biological Society of Washington*, 102 (2), 447–457.

Perkins, P.D. (1994) [new taxa] *In*: Perkins, P.D. & Balfour-Browne, J. (Eds.), A contribution to the taxonomy of aquatic and humicolous beetles of the family Hydraenidae in southern Africa. *Fieldiana: Zoology (New Series)*, 77, viii + 1–159.

Perkins, P.D. (1997) Life on the effective bubble: exocrine secretion delivery systems (ESDS) and the evolution and classification of beetles in the family Hydraenidae (Insecta: Coleoptera). *Annals of Carnegie Museum*, 66 (2), 89–207.

Perkins, P.D. (2000) Hydraenidae Mulsant, 1844. *In*: Arnett, R.H. Jr. & Thomas, M.C. (Eds.), *American Beetles. Volume 1. Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia*. CRC Press, Boca Raton, FL, pp. 228–232.

Perreau, M. (2019) *Archaeocerus uenoi* n. gen. n. sp. (Coleoptera Leiodidae Catopocerinae) from Albian/Cenomanian age amber of Myanmar. *Zootaxa*, 4638 (4), 595–600.
https://doi.org/10.11646/zootaxa.4638.4.9

Poinar, G. Jr. (2012) Desiomorphs in amber. *American Entomologist*, 58 (4), 214–223.
https://doi.org/10.1093/ae/58.4.214

Poinar, G. Jr. (2019) Burmese amber: evidence of Gondwanan origin and Cretaceous dispersion. *Historical Biology*, 31 (10), 1304–1309.
https://doi.org/10.1080/08912963.2018.1446531

Poinar, G. Jr. & Brown, A.E. (2004) A new subfamily of Cretaceous antlike stone beetles (Coleoptera: Scydmaenidae: Hapsomelinae) with an extra leg segment. *Proceedings of the Entomological Society of Washington*, 106 (4), 789–796.

Reiche, L. (1866) Étude des espèces de mylabrides de la collection de L. Reiche, suivie d'une note sur le genre *Trigonurus* Mulsant et description d'une espèce nouvelle. *Annales de la Société Entomologique de France*, (4) 5[1865](4), 627–642.

Reitter, E. (1887) *Bestimmungs-Tabellen der Europäischen*

Coleopteren. III. Enthaltend die Familien: Scaphididae, Lathridiidae und Dermestidae. II. Auflage. E. Reitter, Mödling, 75 pp.

Reitter, E. (1909) *Fauna Germanica. Die Käfer des Deutschen Reiches. Nach der analytischen Methode bearbeitet. II. Band*. K. G. Lutz, Stuttgart, 392 pp., pls. 41–80.

Reyes-Hernández, J.L., Brunke, A., Hansen, A.K., Zhao, Q., Jenkins Shaw, J., Newton, A.F. & Solodovnikov, A. (2025) Evolutionary systematics of the Staphylininae rove beetles (Coleoptera: Staphylinidae) resolved by integration of phylogenomics, comparative morphology and historical biogeography. *Systematic Entomology*, 1–30. https://doi.org/10.1111/syen.12677

Richter, A., Boudinot, B.E., Yamamoto, S., Katzke, J. & Beutel, R.G. (2022) The first reconstruction of the head anatomy of a Cretaceous insect, †*Gerontoformica gracilis* (Hymenoptera: Formicidae), and the early evolution of ants. *Insect Systematics and Diversity*, 6 (5), 4. https://doi.org/10.1093/isd/ixac013

Ritsema, C. (1869) [untitled note on *Platypsyllus castoris*]. *Petites Nouvelles Entomologiques*, (1) 1(10), 23–38.

Ross, A.J. (2019) Burmese (Myanmar) amber checklist and bibliography 2018. *Palaeoentomology*, 2 (1), 22–84. https://doi.org/10.11646/palaeoentomology.2.1.5

Ross, A.J. (2024) Complete checklist of Burmese (Myanmar) amber taxa 2023. *Mesozoic*, 1 (1), 21–57. https://doi.org/10.11646/mesozoic.1.1.4

Ross, A., Mellish, C., York, P. & Crighton, B. (2010) Burmese amber. *In*: Penney, D. (Ed.), *Biodiversity of Fossils in Amber from the Major World Deposits*. Siri Scientific Press, Manchester, pp. 208–235.

Schülke, M. & Smetana, A. (2015) Family Staphylinidae Latreille, 1802. *In*: Löbl, I. & Löbl, D. (Eds.), *Catalogue of Palaearctic Coleoptera. Volume 2. Hydrophiloidea—Staphylinoidea. Revised and Updated Edition*. Brill, Leiden/Boston, pp. 304–1134.

Seevers, C.H. (1958) A revision of the Vatesini, a tribe of Neotropical myrmecophiles (Coleoptera, Staphylinidae). *Revista Brasileira de Entomologia*, 8, 181–202.

Seton, M., Müller, R.D., Zahirovic, S., Gaina, C., Torsvik, T., Shepard, G., Talsma, A., Gurnis, M., Turner, M., Maus, S. & Chandler, M. (2012) Global continental and ocean basin reconstructions since 200 Ma. *Earth-Science Review*, 113 (3, 4), 212–270. https://doi.org/10.1016/j.earscirev.2012.03.002

Sikes, D.S., Thayer, M.K. & Newton, A.F. (2024) Large carrion and burying beetles evolved from Staphylinidae (Coleoptera, Staphylinidae, Silphinae): a review of the evidence. *ZooKeys*, 1200, 159–182. https://doi.org/10.3897/zookeys.1200.122835

Simon-Pražák, J., Yamamoto, S., Lackner, T., Fikáček, M., Prokop, J. & Caterino, M.S. (2024) A bonanza of Cretaceous fossils provides insights into the evolution of antennal protection in clown beetles (Coleoptera: Histeridae). *Zoological Journal of the Linnean Society*, 202 (3): zlae137. https://doi.org/10.1093/zoolinnean/zlae137

Simpson, G. (1944) *Tempo and Mode in Evolution*. Columbia University Press, New York, xviii + 237 pp.

Sharp, D. (1887) Fam. Staphylinidae [part]. *In*: Godman, F.D. & Salvin, O. (Eds.), *Biologia Centrali-Americana. Insecta. Coleoptera. Volume I. Part 2*. Taylor & Francis, London, pp. 673–747, 18–19 pls.

Shavrin, A.V. & Yamamoto, S. (2019) Unexpected palaeodiversity of omaliine rove beetles in Eocene Baltic amber (Coleoptera: Staphylinidae: Omaliinae). *ZooKeys*, 863, 35–83. https://doi.org/10.3897/zookeys.863.34662

Shavrin, A.V. & Yamamoto, S. (2020) A remarkable new species of the rove beetle genus *Anthobium* Leach, 1819 from Eocene Baltic amber (Coleoptera, Staphylinidae, Omaliinae). *ZooKeys*, 973, 89–101. https://doi.org/10.3897/zookeys.973.53940

Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q. & Li, X. (2012) Age constraint on Burmese amber based on U–Pb dating of zircons. *Cretaceous Research*, 37, 155–163. https://doi.org/10.1016/j.cretres.2012.03.014

Shibata, Y., Maruyama, M., Hoshina, H., Kishimoto, T., Naomi, S.-I., Nomura, S., Puthz, V., Shimada, T., Watanabe, Y. & Yamamoto, S. (2013) Catalogue of Japanese Staphylinidae (Insecta: Coleoptera). *Bulletin of the Kyushu University Museum*, 11, 69–218.

Sörensson, M. & Delgado, J.A. (2019) Unveiling the smallest – systematics, classification and a new subfamily of featherwing beetles based on larval morphology (Coleoptera: Ptiliidae). *Invertebrate Systematics*, 33 (5), 757–806. https://doi.org/10.1071/IS19007

Szymczakowski, W. (1964) Révision des Colonidae (Coleoptera) des régions orientale et australienne. *Acta Zoologica Cracoviensia*, 9, 469–527.

Tamutis, V., Tamutė, B. & Ferenca, R. (2011) A catalogue of Lithuanian beetles (Insecta, Coleoptera). *ZooKeys*, 121, 1–494. https://doi.org/10.3897/zookeys.121.732

Tihelka, E., Peris, D., Cai, C. & Perrichot, V. (2022) A Jacobson's beetle from Cretaceous Charentese amber (Coleoptera: Jacobsoniidae). *Geodiversitas*, 44 (3), 47–56. https://doi.org/10.5252/geodiversitas2022v44a3

Thayer, M.K. (2016) Staphylinidae Latreille, 1802. *In*: Beutel, R.G. & Leschen, R.A.B. (Eds.), *Handbook of Zoology, Arthropoda: Insecta, Coleoptera, Beetles, Volume 1: Morphology and Systematics (Archostemata, Adephaga, Myxophaga, Polyphaga partim), Second edition*. Walter de Gruyter, Berlin/Boston, pp. 394–442.

Thayer, M.K., Newton, A.F. & Chatzimanolis, S. (2012) *Prosolierius*, a new mid-Cretaceous genus of Solieriinae (Coleoptera: Staphylinidae) with three new species from Burmese amber. *Cretaceous Research*, 34, 124–134. https://doi.org/10.1016/j.cretres.2011.10.010

Thomson, C.G. (1858) Försök till uppställning af Sveriges Staphyliner. *Öfversigt af Kongliga Vetenskaps-Akademiens Förhandlingar*, 15 (1), 27–40.

Thomson, C.G. (1859) *Skandinaviens Coleoptera, synoptiskt bearbetade. Tom. I.* Berlingska Boktryckeriet, Lund, [3] + 290 pp.

Tokareva, A., Koszela, K., Ferreira, V.S., Yamamoto, S. & Żyła, D. (2023) The oldest case of paedomorphosis in rove beetles and description of a new genus of Paederinae from Cretaceous amber (Coleoptera: Staphylinidae). *Scientific Reports*, 7, 45904. https://doi.org/10.1038/s41598-023-32446-2

Ulitzka, M.R. (2018) A first survey of Cretaceous thrips from Burmese amber including the establishment of a new family of Tubulifera (Insecta: Thysanoptera). *Zootaxa*, 4486 (4), 548–558.
https://doi.org/10.11646/zootaxa.4486.4.8

Villastrigo, A., Jäch, M.A., Cardoso, A., Valladares, L.F. & Ribera, I. (2019) A molecular phylogeny of the tribe Ochthebiini (Coleoptera, Hydraenidae, Ochthebiinae). *Systematic Entomology*, 44 (2), 273–288.
https://doi.org/10.1111/syen.12318

Westerweel, J., Roperch, P., Licht, A., Dupont-Nivet, G., Win, Z., Poblete, F., Ruffet, G., Swe, H.H., Thi, M.K. & Aung, D.W. (2019) Burma Terrane part of the Trans-Tethyan arc during collision with India according to palaeomagnetic data. *Nature Geoscience*, 12, 863–868.
https://doi.org/10.1038/s41561-019-0443-2

Wu, J. & Zhou, H.-Z. (2007) Phylogenetic analysis and reclassification of the genus *Priochirus* Sharp (Coleoptera: Staphylinidae: Osoriinae). *Invertebrate Systematics*, 21 (1), 73–107.
https://doi.org/10.1071/IS06010

Xing, L. & Qiu, L. (2020) Zircon U–Pb age constraints on the mid-Cretaceous Hkamti amber biota in northern Myanmar. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 558, 109960.
https://doi.org/10.1016/j.palaeo.2020.109960

Yamamoto, S. (2016a) The oldest tachyporine rove beetle in amber (Coleoptera, Staphylinidae): a new genus and species from Upper Cretaceous Burmese amber. *Cretaceous Research*, 65, 163–171.
https://doi.org/10.1016/j.cretres.2016.05.001

Yamamoto, S. (2016b) The first fossil of dasycerine rove beetle (Coleoptera: Staphylinidae) from Upper Cretaceous Burmese amber: phylogenetic implications for the omaliine group subfamilies. *Cretaceous Research*, 58, 63–68.
https://doi.org/10.1016/j.cretres.2015.09.022

Yamamoto, S. (2017) Discovery of the oxyporine rove beetle in the Mesozoic amber and its evolutionary implications for mycophagy (Coleoptera: Staphylinidae). *Cretaceous Research*, 74, 198–204.
https://doi.org/10.1016/j.cretres.2017.02.018

Yamamoto, S. (2019) Fossil evidence of elytra reduction in ship-timber beetles. *Scientific Reports*, 9, 4938.
https://doi.org/10.1038/s41598-019-41310-1

Yamamoto, S. (2021) Tachyporinae revisited: phylogeny, evolution, and higher classification based on morphology, with recognition of a new rove beetle subfamily (Coleoptera: Staphylinidae). *Biology*, 10, 323.
https://doi.org/10.3390/biology10040323

Yamamoto, S. (2023a) *Parabolitobius antiquus* sp. nov., the first Mesozoic amber inclusion of mycetoporine rove beetles (Coleoptera: Staphylinidae: Mycetoporinae). *Journal of Asia-Pacific Entomology*, 26 (4), 102155.
https://doi.org/10.1016/j.aspen.2023.102155

Yamamoto, S. (2023b) The smallest stag beetles (Coleoptera, Lucanidae): hidden paleodiversity in mid-Cretaceous Kachin amber from northern Myanmar. *Evolutionary Systematics*, 7 (2), 211–235.
https://doi.org/10.3897/evolsyst.7.104597

Yamamoto, S. (2023c) A new species of *Prosolierius* rove beetle with highly modified antennae from mid-Cretaceous Kachin amber of northern Myanmar (Coleoptera, Staphylinidae, Solieriinae). *Journal of Asia-Pacific Entomology*, 26 (2), 102075.
https://doi.org/10.1016/j.aspen.2023.102075

Yamamoto, S. (2024a) Earliest fossil record of Tachyporini rove beetles in mid-Cretaceous Kachin amber from northern Myanmar (Coleoptera: Staphylinidae: Tachyporinae). *Journal of Asia-Pacific Entomology*, 27 (2), 102227.
https://doi.org/10.1016/j.aspen.2024.102227

Yamamoto, S. (2024b) First fossil eleusinin rove beetle (Coleoptera: Staphylinidae: Osoriinae: Eleusinini) from mid-Cretaceous Kachin amber of northern Myanmar and its evolutionary implications. *Palaeoworld*, 33 (1), 152–161.
https://doi.org/10.1016/j.palwor.2023.01.007

Yamamoto, S., Jäch, M.A. & Takahashi, Y. (2017b) Discovery of the first hydraenid beetle in amber, with description of a new genus and species (Coleoptera: Staphylinoidea: Hydraenidae). *Cretaceous Research*, 78, 27–33.
https://doi.org/10.1016/j.cretres.2017.05.015

Yamamoto, S. & Maruyama, M. (2017) A new genus and species of the rove beetle tribe Mesoporini from Baltic amber (Coleoptera: Staphylinidae: Aleocharinae). *Historical Biology*, 29 (2), 203–207.
https://doi.org/10.1080/08912963.2016.1144750

Yamamoto, S. & Maruyama, M. (2018) Phylogeny of the rove beetle tribe Gymnusini sensu n. (Coleoptera: Staphylinidae: Aleocharinae): implications for the early branching events of the subfamily. *Systematic Entomology*, 43 (1), 183–199.
https://doi.org/10.1111/syen.12267

Yamamoto, S., Maruyama, M. & Parker, J. (2016) Evidence for social parasitism of early insect societies by Cretaceous rove beetles. *Nature Communications*, 7, 13658.
https://doi.org/10.1038/ncomms13658

Yamamoto, S., Maruyama, M. & Parker, J. (2017c) Evidence from amber for the origins of termitophily. *Current Biology*, 27 (16), R792–R794.
https://doi.org/10.1016/j.cub.2017.06.078

Yamamoto, S. & Newton, A.F. (2021) First fossil trichophyine rove beetle from mid-Cretaceous amber of northern Myanmar (Coleoptera: Staphylinidae: Trichophyinae). *Cretaceous Research*, 127, 104951.
https://doi.org/10.1016/j.cretres.2021.104951

Yamamoto, S. & Newton, A.F. (2023) The earliest fossil record of the extant rove beetle genus *Phloeocharis* from mid-Cretaceous Kachin amber of northern Myanmar and its biogeographic implications (Coleoptera: Staphylinidae: Phloeocharinae). *Journal of Asia-Pacific Entomology*, 26, 102050.
https://doi.org/10.1016/j.aspen.2023.102050

Yamamoto, S. & Newton, A.F. (2024) The first aleocharine rove beetle fossil from mid-Eocene Bitterfeld amber of Germany (Coleoptera: Staphylinidae: Aleocharinae: Hypocyphtini). *The Coleopterists Bulletin*, 78 (2), 233–238.
https://doi.org/10.1649/0010-065X-78.2.233

Yamamoto, S., Newton, A.F., Perkovsky, E.E. & Jenkins Shaw, J. (2025) The first record of osoriine rove beetles (Coleoptera: Staphylinidae) in Eocene Baltic amber. *Historical Biology*, 37 (4), 998–1005.
https://doi.org/10.1080/08912963.2024.2349101

Yamamoto, S. & Perreau, M. (2025) *Burmaphagus yamamotoae*, a new genus and species of Ptomaphagini beetles from mid-Cretaceous Kachin amber (Coleoptera: Leiodidae: Cholevinae). *Revue suisse de Zoologie*, 132 (1), 101–107. https://doi.org/10.35929/RSZ.0142

Yamamoto, S., Shavrin, A.V. & Kairišs, K. (2022) A second fossil species of the enigmatic rove beetle genus *Charhyphus* in Eocene Baltic amber, with implications on the morphology of the female genitalia (Coleoptera: Staphylinidae: Phloeocharinae). *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 113 (1), 39–50. https://doi.org/10.1017/S1755691021000360

Yamamoto, S. & Solodovnikov, A. (2016) The first fossil Megalopsidiinae (Coleoptera: Staphylinidae) from Upper Cretaceous Burmese amber and its potential for understanding basal relationships of rove beetles. *Cretaceous Research*, 59, 140–146. https://doi.org/10.1016/j.cretres.2015.10.024

Yamamoto, S. & Takahashi, Y. (2016) *Coproporus electron* sp. nov., the first tachyporine rove beetle in Dominican amber (Coleoptera, Staphylinidae). *PalZ*, 90 (3), 629–635. https://doi.org/10.1007/s12542-016-0315-7

Yamamoto, S. & Takahashi, Y. (2018) First discovery of Coloninae fossil in Cretaceous Burmese amber (Coleoptera, Staphylinoidea, Leiodidae). *PalZ*, 92, 195–201. https://doi.org/10.1007/s12542-017-0386-0

Yamamoto, S. & Takahashi, Y. (2019) First and oldest Leptochirini rove beetles illuminate diverse cephalic structures in the Cretaceous (Coleoptera: Staphylinidae: Osoriinae). *Systematic Entomology*, 44 (3), 588–611. https://doi.org/10.1111/syen.12342

Yamamoto, S., Takahashi, Y. & Parker, J. (2017a) Evolutionary stasis in enigmatic jacobsoniid beetles. *Gondwana Research*, 45, 275–281. https://doi.org/10.1016/j.gr.2016.12.008

Yang, Q., Chen, Z.-Y. & Jia, F.-L. (2019) *Ambarticus myanmaricus* gen. et sp. nov., the first diving beetle from mid-Cretaceous amber of northern Myanmar (Coleoptera, Dytiscidae, Dytiscinae). *Cretaceous Research*, 102, 1–6. https://doi.org/10.1016/j.cretres.2019.05.005

Yu, T., Wang, B. & Pan, H. (2018) New terrestrial gastropods from mid-Cretaceous Burmese amber. *Cretaceous Research*, 90, 254–258. https://doi.org/10.1016/j.cretres.2018.04.015

Zanetti, A., Perreau, M. & Solodovnikov, A. (2016) Two new fossil species of Omaliinae from Baltic amber (Coleoptera: Staphylinidae) and their significance for understanding the Eocene-Oligocene climate. *Arthropod Systematics & Phylogeny*, 74 (1), 53–64.

Zhang, S.-Q., Che, L.-H., Li, Y., Liang, D., Pang, H., Ślipiński, A. & Zhang, P. (2018) Evolutionary history of Coleoptera revealed by extensive sampling of genes and species. *Nature Communications*, 9, 205. https://doi.org/10.1038/s41467-017-02644-4

Zheng, D., Chang, S.-C., Perrichot, V., Dutta, S., Rudra, A., Mu, L., Thomson, U., Li, S., Zhang, Q., Zhang, Q., Wong, J., Wang, J., Wang, H., Fang, Y., Zhang, H. & Wang, B. (2018) A late Cretaceous amber biota from Central Myanmar. *Nature Communications*, 9, 3170. https://doi.org/10.1038/s41467-018-05650-2

Zhuang, Y., Xu, W., Zhang, G., Mai, H., Li, X., He, H., Ran, H. & Liu, Y. (2022) Unparalleled details of soft tissues in a Cretaceous ant. *BMC Ecology and Evolution*, 22 (1), 146. https://doi.org/10.1186/s12862-022-02099-2

Yin, Z.-W. (2020) Discrimination of species of *Hapsomela* Poinar & Brown (Coleoptera: Staphylinidae: Scydmaeninae) in mid-Cretaceous Burmese amber. *Palaeoentomology*, 3 (3), 309–316. https://doi.org/10.11646/palaeoentomology.3.3.11

Yin, Z.-W. & Cai, C.-Y. (2019) A new species of minute Scydmaenini (Coleoptera: Staphylinidae: Scydmaeninae) in mid-Cretaceous amber from Myanmar. *Cretaceous Research*, 101, 70–75. https://doi.org/10.1016/j.cretres.2019.05.001

Żyła, D., Yamamoto, S. & Jenkins Shaw, J. (2019) Total-evidence approach reveals an extinct lineage of Paederinae rove beetles from the Cretaceous Burmese amber. *Palaeontology*, 62 (6), 935–949. https://doi.org/10.1111/pala.12435

Żyła, D., Yamamoto, S., Wolf-Schwenninger, K. & Solodovnikov, A. (2017) Cretaceous origin of the unique prey-capture apparatus in mega-diverse genus: stem lineage of Steninae rove beetles discovered in Burmese amber. *Scientific Reports*, 7, 45904. https://doi.org/10.1038/srep45904

Appendix A

A complete checklist of Staphylinoidea in Myanmar (Kachin & Hkamti) amber as of 1 June 2025. This checklist was compiled primarily based on Ross (2024) with some changes, including the addition of the following publications: Yamamoto (2024a, 2024b); Li Y-D *et al.* (2024a); Jałoszyński & Szawaryn (2024); Janák (2024); Liu *et al.* (2025); Chen *et al.* (2025); Reyes-Hernández *et al.* (2025); Yamamoto & Perreau (2025); and this study.

Abbreviations: fam., family (families); g., genus (genera); OC, fossil occurrence confirmed by the author and Cai *et al*. (2017: supplementary table 2); sp./spp., species; subf., subfamily (subfamilies).

KACHIN AMBER (6 fam., 29 (+2) subf., 74 g., 104 spp.)

Family Jacobsoniidae Heller, 1926 (2 g., 2 spp.)
Derolathrus abyssus Yamamoto & Parker, 2017
Sarothrias cretaceus Cai, Ślipiński, Leschen, Yin, Zhuo & Huang, 2017

Family Ptiliidae Erichson, 1845 (2 subf., 2 g., 3 spp.)
Subfamily Nossidiinae Sörensson & Delgado, 2019 (1 g., 1 sp.)
Crenossidium slipinskii Li, Newton & Cai, 2022
Subfamily Ptiliinae Erichson, 1845 (1 g., 2 spp.)
Kekveus brevisulcatus Li, Yamamoto, Newton & Cai, 2023
Kekveus jason Yamamoto, Grebennikov & Takahashi, 2018

Family Hydraenidae Mulsant, 1844 (1 subf., 1 g., 1 sp.)
Subfamily Hydraeninae Mulsant, 1844 (1 g., 1 sp.)
Archaeodraena cretacea Jäch & Yamamoto, 2017

Family Colonidae G.H. Horn, 1880 (1859) (2 g., 2 spp.)
Colon burmiticum Yamamoto, 2018
Colonellus (*Pentacolonellus*) *burmiticus* Cai & Huang, 2017

Family Leiodidae Fleming, 1821 (3+1 subf., 4 g., 4 spp.)
Subfamily Camiarinae Jeannel, 1911 (1 g., 1 sp.)
Cretagyrtodes glabratus Cai & Huang, 2017
Subfamily Catopocerinae Hatch, 1927 (1880) (1 g., 1 sp.)
Archaeocerus uenoi Perreau, 2019
Subfamily Leiodinae Fleming, 1821 (OC)
Subfamily Cholevinae W. Kirby, 1837 (2 g., 2 spp.)
Burmaphagus yamamotoae Yamamoto & Perreau, 2025
Cretoptomaphagus microsoma Bao & Antunes- Carvalho, 2020

Family Staphylinidae Latreille, 1802 (23+1 subf., 63 g., 92 spp.)
Subfamily Silphinae Latreille, 1806 (1 g., 1 sp.)
Nicrophorus sp.
Subfamily Scaphidiinae Latreille, 1806 (OC)
Subfamily Piestinae Erichson, 1839 (1 g., 1 sp.)
Propiestus archaicus Yamamoto, Caron & Bortoluzzi, 2018
Subfamily Osoriinae Erichson, 1839 (4 g., 5 spp.)
Cretochirus newtoni Yamamoto, 2019
Eleusis sulcata Yamamoto, 2023
Mesallotrochus longiantennatus Cai & Huang, 2014
Priochirus (*Eopriochirus*) *thayerae* Yamamoto, 2019
Priochirus (*Eopriochirus*) *trisclerite* Peng, Jiang, Chi, Long, Engel & Wang, 2022
Subfamily Oxytelinae Fleming, 1821 (5 g., 6 spp.)
Gollandia planata Makranczy, Yamamoto & Engel, 2018
Ochthephilus wui Chen, Newton, Huang, Lü & Cai, 2025
Kupakara luminosus Chen, Newton, Huang, Lü & Cai, 2023
Kupakara makranczyi Chen, Newton, Huang, Lü & Cai, 2023
Prajna tianmiaoae Lü, Cai & Huang, 2016
Vidya scabra Chen, Wang, Huang, Lü & Cai, 2023
Subfamily Proteininae Erichson, 1839 (1 g., 1 sp.)
Vetuproteinus cretaceus Cai, Newton & Thayer, 2016
Subfamily Micropeplinae Leach, 1815 (2 g., 2 spp.)
Micropeplus pengweii Jiang, Peng & Wang, 2019
Protopeplus cretaceus Cai & Huang, 2014
Subfamily Dasycerinae Reitter, 1887 (3 g., 6 spp.)
Cedasyrus dimorphus Yin & Cai, 2020
Protodasycerus aenigmaticus Yamamoto, 2016
Protodasycerus corpulentus Yin & Cai, 2020
Protodasycerus gigas Yin & Cai, 2020
Protodasycerus tuberculatus Yamamoto, Newton & Yin, 2020
Vetudasycerus burmiticus Cai, Thayer, Newton, Yin & Huang, 2017
Subfamily Protopselaphinae Newton & Tayer, 1995 (1 g., 2 spp.)
Protopselaphus newtoni Liu, Tihelka & Cai, 2020
Protopselaphus thayerae Liu, Tihelka & Cai, 2020
Subfamily Pselaphinae Latreille, 1802 (8 g., 10 spp.)
Archemastax divida Yin, Zhou, Cai & Newton, 2019
Boreotethys arctopteryx Parker, 2016
Boreotethys grimaldii Parker, 2016
Burmagluta rougemonti Yin & Cai, 2021
Cretobrachygluta laurasiensis Yin, Kurbatov, Cuccodora & Cai, 2019
Cretobythus excavatus Yin, Parker & Cai, 2017
Megabythinus spinitibialis Yin, Zhao & Cai, 2021
Priscaplectus carinatus Yin, Chandler & Cai, 2019
Priscaplectus grandiceps Yin, Chandler & Cai, 2019
Protrichonyx rafifrons Parker, 2016
Subfamily Mycetoporinae C.G. Thomson, 1859 (1 g., 1 sp.)
Parabolitobius antiquus Yamamoto, 2023
Subfamily Tachyporinae W.S. MacLeay, 1825 (2 g., 2 spp.)
Procileoporus burmiticus Yamamoto, 2016
Tachyporus burmiticus Yamamoto, 2024
Subfamily Phloeocharinae Erichson, 1839 (3 g., 3 spp.)
Angucharcotes thayerae Li, Newton & Cai, 2022
Phloeocharis burmana Yamamoto & Newton, 2023
Vicelva rasilis Li, Newton, Huang & Cai, 2024
Subfamily Trichophyinae C.G. Thomson, 1858 (1 g., 1 sp.)
Trichophya minor Yamamoto & Newton, 2021
Subfamily Aleocharinae Fleming, 1821 (3 g., 3 spp.)
Cretodeinopsis aenigmatica Cai & Huang, 2015
Cretotrichopsenius burmiticus Cai, Huang, Newton, Eldredge & Engel, 2017
Mesosymbion compactus Yamamoto, Maruyama & Parker, 2016
Subfamily Oxyporinae Fleming, 1821 (1 g., 1 sp.)
Oxyporus (*Oxyporus*) *cretaceous* Yamamoto, 2017
Subfamily Megalopsidiinae Leng, 1920 (1 g., 1 sp.)
Megalopinus extinctus Yamamoto & Solodovnikov, 2016
Subfamily Steninae W.S. MacLeay, 1825 (1 g., 2 spp.)
Festenus gracilis Żyła, Yamamoto, Wolf-Schwenninger &

Solodovnikov, 2017
Festenus robustus Żyła, Yamamoto, Wolf-Schwenninger & Solodovnikov, 2017
Subfamily Euaesthetinae C.G. Thomson, 1859 (1 g., 1 sp.)
Octavius electrospinosus Clarke & Chatzimanolis, 2009
Subfamily Solieriinae Newton & Tayer, 1992 (1 g., 5 spp.)
Prosolierius crassicornis Thayer, Newton & Chatzimanolis, 2012
Prosolierius mixticornis Thayer, Newton & Chatzimanolis, 2012
Prosolierius tenuicornis Thayer, Newton & Chatzimanolis, 2012
Prosolierius thayerae Yamamoto, 2023
Prosolierius qizhihaoi Liu, Gao, Huang & Cai, 2025
Subfamily Scydmaeninae Leach, 1815 (14 g., 25 spp.)
Cenomaniola carinata Jałoszyński & Yamamoto, 2017
Cenomaniola macrophthalma Jałoszyński & Yamamoto, 2017
Clidicostigus arachnipes Jałoszyński, Brunke & Bai, 2017 (=*Cascomastigus monstrabilis* Yin & Cai, 2017)
Clidicostigus minor (Yin, Cai & Huang, 2018)
Clidicus archaicus (Cai & Huang, 2016)
Clidicus burmiticus (Yin, Cai, Huang & Li, 2017)
Ektatotricha paradoxa Chatzimanolis, Engel & Newton, 2010
Electroatopos castaneus Chatzimanolis, Engel & Newton, 2010
Hapsomela burmitis Poinar & Brown, 2004
Hapsomela minor Yin, 2020
Hapsomela tibialis Yin, 2020
Kachinus antennatus Chatzimanolis, Engel & Newton, 2010
Kuafu borealis Yin, Cai & Huang, 2017
Loeblitoides separatus Jałoszyński, 2019
Loeblitoides latus Jałoszyński & Szawaryn, 2024
Nuegua elongata Yin, Cai & Newton, 2018
Pangusyndicus excavatus Yin, Zhou & Cai, 2018
Pangusyndicus longirostris Jałoszyński, 2019
Praphennium carinatum Jałoszyński, 2018
Scydmaenus linqibini Yin & Zhou, 2020
Scydmaenus minor Yin & Cai, 2019
Scydmobisetia dentipes Jałoszyński & Bai, 2020
Scydmobisetia loebli Yin, Zhou & Cai, 2018
Scydmobisetia mengjiae Yin, Zhou & Cai, 2018
Scydmobisetia vetutissima Jałoszyński & Yamamoto, 2016
Subfamily Pseudopsinae Ganglbauer, 1895 (1 g., 1 sp.)
Cretopseudopsis maweii Liu, Tihelka, Tian, Huang & Cai, 2020
Subfamily Paederinae Fleming, 1821 (4 g., 6 spp.)
Cretoprocirrus trichotos Jenkins Shaw & Żyla, 2020
Dactylonudon longitarsus Janák, 2024
Diminudon kachinensis Żyła, Yamamoto & Jenkins Shaw, 2019
Diminudon schomannae Żyła, Yamamoto & Jenkins Shaw, 2019
Midinudon elongatus Janák, 2024
Midinudon juvenis Tokareva & Żyła, 2023
Subfamily Staphylininae Latreille, 1802 (2 g., 4 spp.)
Coomania enkarsios Jenkins Shaw, Solodovnikov, Bai & Żyła, 2022
Coomania megistos Jenkins Shaw, Solodovnikov, Bai & Żyła, 2022
Coomania yini Jenkins Shaw, Solodovnikov, Bai & Żyła, 2022
Xantholinini gen. et. sp. indet.
Subfamily, *incertae sedis* (1 g., 2 spp.)
Vetatrecus adelfiae Kypke, Solodovnikov & Żyła, 2018
Vetatrecus secretum Kypke, Solodovnikov & Żyła, 2018

HKAMTI (KHAMTI) AMBER (3 fam., 7 subf., 10 g., 13 spp.)

Family Hydraenidae Mulsant, 1844 (1 subf., 1 g., 1 sp.)
Subfamily Hydraeninae Mulsant, 1844 (1 g., 1 sp.)
Hydraenini gen. et. sp. indet.

Family Colonidae G.H. Horn, 1880 (1859) (1 g., 1 sp.)
Colonellus (*Colonellus*) *hkamtiensis* **sp. nov.**

Family Staphylinidae Latreille, 1802 (6 subf., 8 g., 11 spp.)
Subfamily Osoriinae Erichson, 1839 (2 g., 2 spp.)
Mesallotrochus sp.
Cretochirus elongatus **sp. nov.**
Subfamily Tachyporinae W.S. MacLeay, 1825 (1 g., 1 sp.)
Procileoporus sp.
Subfamily Aleocharinae Fleming, 1821 (1 g., 1 sp.)
Mesoporini gen. et. sp. indet.
Subfamily Steninae W.S. MacLeay, 1825 (1 g., 3 spp.)
Festenus annodutt Mainda, 2023
Festenus microraptor Mainda, 2024
Festenus sp.
Subfamily Solieriinae Newton & Tayer, 1992 (1 g., 2 spp.)
Prosolierius antennatus **sp. nov.**
Prosolierius sp.
Subfamily Scydmaeninae Leach, 1815 (2 g., 2 spp.)
Ektatotricha sp.
Hapsomela cf. *burmitis* Poinar & Brown, 2004