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First fossil trichophyine rove beetle from mid-Cretaceous amber of northern Myanmar (Coleoptera: Staphylinidae: Trichophyinae)

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Abstract.

Trichophyinae is one of the smallest subfamilies of the megadiverse rove-beetle family Staphylinidae, with only 18 species in the single extant genus *Trichophya* Mannerheim. Here we describe the first fossil representative of Trichophyinae in mid-Cretaceous amber from Kachin, northern Myanmar. †*Trichophya minor* **sp. nov.** is unusual in having non-filiform thick antennae, similar to *T. antennalis* Cameron, 1932 from India, but this new species can readily be distinguished from the latter by having much smaller and smoother body. Our finding indicates that the subfamily had been originated by the Albian–Cenomanian boundary, also showing a potential Gondwanan distribution at that time. We also briefly discuss a miniaturization trend in the Burmese amber beetles.

Key words: Staphylinidae; Trichophyinae; *Trichophya*; Kachin amber; Cenomanian; new species

1. Introduction

With over 65,000 species in one extinct and 33 extant subfamilies (Bouchard et al., 2011; Tihelka et al., 2020; Yamamoto, 2021), the rove beetles (Staphylinidae) are the largest animal and metazoan family, showing amazing morphological and ecological diversity in terrestrial ecosystems (Grebennikov and Newton, 2009; Thayer, 2016). Fossil records are vital information for understanding the origin and evolutionary history of each taxonomic category. In rove beetles, fossils are known for most subfamilies, with only a few exceptions.

Trichophyinae and its presumably sister subfamily Habrocerinae are among the few subfamilies without any fossil record until now (Ashe and Newton, 1993; Ashe, 2005; Cai et al., 2017: supplemental information; Yamamoto and Maruyama, 2018; Orlov et al., 2020). The trichophyines are one of the smallest subfamilies in the mega-diverse Staphylinidae. In fact, it contains only a single genus *Trichophya* Mannerheim with 18 extant species native to the Northern Hemisphere. Although the biology and ecology are largely unknown in Trichophyinae, they are found in various forest environments, e.g., in forest leaf litter, under bark and in squirrel middens (Legner and Moore, 1977; Newton et al., 2000; Shibata, 2001), or on fungi (Newton, 1984; Miyashita, 1997). They are typically small beetles, usually 2–3 millimetres in body length. Among the rove beetles, one of the morphological characters which define adult Trichophyinae is the presence of extremely slender, filiform, and verticillate antennae (Newton et al., 2000). This feature is known only in or within a very limited number of other staphylinid groups, namely: Dasycerinae, Habrocerinae, and Scaphidiinae (tribe Scaphisomatini only). Further notable adult characters include the presence of a strong neck constriction, five-segmented maxillary palpus including a minute and aciculate pseudosegment mounted on the spindle-shaped fourth maxillary palpomere, elytral epipleural keel or ridge absent, protrochantin exposed, mesothoracic spiracle in large well-sclerotized triangular peritreme, and two pairs of abdominal paratergites present on most segments (Ashe and Newton, 1993; Newton et al., 2000; Ashe, 2005).

The mid-Cretaceous amber Kachin amber, previously known as Burmese amber, from northern Myanmar is well known for exceptionally diverse and abundant inclusions of organisms. In fact, it currently encompasses the richest biota in Mesozoic amber by far, with nearly 1,900 named taxa (Ross, 2019, 2020, 2021), despite the fact that most studies have only been made in the last decade. In Staphylinidae, a total of 19 subfamilies have currently been recorded including recently reported subfamilies such as Piestinae (Yamamoto et al., 2019), Paederinae (Żyła et al., 2019), Pseudopsinae (Liu et al., 2020c), and Protopselaphinae (Liu et al., 2020a, d). Here we report the first fossil occurrence of Trichophyinae from Kachin amber. Our finding sheds new light on the Mesozoic origin and morphological evolution of the subfamily, and this discovery eliminates a huge gap in the fossil record of rove beetles.

2. Material and methods

Amber material here studied was obtained from mines at the summit of Noije Bum Hill (26°20′N 96°36′E) in the Hukawng Valley, Kachin State, northern Myanmar (mapped in Cruickshank and Ko 2003). The amber-bearing horizon has been dated with 98.8 ± 0.6 Ma (earliest Cenomanian) as the minimum age based on the Uranium–lead dating of zircon crystals in the volcanic sedimentary matrix (Shi et al., 2012). A slightly older age for Kachin amber has been implied by Mao et al. (2018) and Balashov (2021). Based on these studies and the discovery of an ammonite fossil in Kachin amber (Yu et al., 2019), a mid-Cretaceous age is adopted here. The fossil resin was most likely formed by *Metasequoia* trees (Cupressaceae) in a tropical forest located near a seashore (Grimaldi and Ross 2017; Mao et al., 2018; Yu et al., 2019).

The amber specimen was cut using a hand saw, ground with emery papers of different grain sizes, and finally polished with a polishing cloth. Observation was conducted with a Leica MZ16 stereomicroscope. Photographs (Figs 1–4, Supplementary Figs 1–3) were taken with three different methods. The habitus and body parts of the fossil and extant material (Figs 1, 2F, 4, Supplementary Figs 1–2) were photographed using a Canon EOS 80D digital camera, mounted on a Canon MP-E 65 mm macro lens (F2.8, 1–5X), and with an attached Canon MT-24EX twin flash as a light source. In addition, the images of several body parts of the fossil and slide specimen of the extant material (Figs 2B, E, 3, Supplementary Fig. 3) were acquired with an Olympus DP26 digital camera mounted on an Olympus BX50 stereomicroscope. Finally, a few images of the enlarged body parts of the fossil (Fig. 2A, C, D) were obtained using a Dun Ink BK PLUS Lab System, mounted on a Canon EOS 6D digital camera with a 10× lens. During the imaging sessions, the amber specimen was completely submerged in clove oil to enhance the quality of the outputs. The software Helicon Focus 7.5.4 was used for focus stacking based on the acquired images. All images were edited, arranged, and assembled with Adobe Photoshop Elements 15 software. The sole specimen is deposited in the entomological collection of the Gantz Family Collections Center, Field Museum of Natural History (FMNH), Chicago, IL, USA, under the registered number FMNHINS-4357787. All the examined extant specimens are deposited in FMNH, and listed in Appendix 1. The Appendix 2 includes the supplementary figures used in the texts cited as Supplementary Figs 1–3. The supplementary data comprised of Appendices 1 and 2 have been deposited in the Zenodo repository (https://doi.org/10.5281/zenodo.4784783; accessed on 25 May 2021). This published work and the nomenclatural acts it contains have been registered in ZooBank, the proposed online registration system for the International Code of Zoological Nomenclature (ICZN). The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix ‘http://zoobank.org/’. The LSIDs for this publication are: urn:lsid:zoobank.org:pub:5C59F363-D3DD-450C-BDC6-14A56A492865; urn:lsid:zoobank.org:act:C375811E-115A-4D84-9647-E504799A8DB2.

3. Systematic paleontology

Order Coleoptera Linnaeus, 1758.
Superfamily Staphylinoidea Latreille, 1802.
Family Staphylinidae Latreille, 1802.
Subfamily Trichophyinae Thomson, 1858.

Genus *Trichophya* Mannerheim, 1830: 73.
Type species: *Aleochara pilicornis* Gyllenhal, 1810.

Remarks. The native distribution of *Trichophya* seems to be the Palearctic, Oriental and Nearctic regions, but several more undescribed species are known from Mexico through Nicaragua (Newton et al., 2000).

†***Trichophya minor*** sp. nov.
(Figs 1–3)
LSID: urn:lsid:zoobank.org:act:C375811E-115A-4D84-9647-E504799A8DB2.

Type material. Holotype, FMNHINS-4357787, a complete, well-preserved female adult; deposited in FMNH. The fossil specimen is embedded in an irregularly flattened, rectangular piece of transparent yellowish amber (10.5 × 3.9 × 1.9 mm).

Etymology. Latin adjective *minor* meaning small, referring to the minute body of this extinct species.

Locality and horizon. Burmese (Kachin) amber from the Hukawng Valley (26°20′N 96°36′E), Kachin State, northern Myanmar; upper Albian to lower Cenomanian (mid-Cretaceous).

Differential diagnosis. †*Trichophya minor* sp. nov. is morphologically closely similar to *T. antennalis* Cameron, 1932 (Fig. 4B, Supplementary Fig. 1B), known from northern India (Shimla Hills), in having relatively short and thick antennae, in contrast to the very long and slender, verticillate antennae of all other extant species of the genus, but it can be distinguished from *T. antennalis* by the much smaller body (ca. 1.3 mm versus 2.2 mm), shorter elytra, more strongly tapered abdomen, and smoother body surface (cf. Figs 1A and 4B).

Description. Female. Body small (1.28 mm, measured from dorsal view), narrowly elongate, tachyporine-like. Color uniformly dark reddish brown; mouthparts, legs, and gonocoxites slightly paler. Surface uniformly weakly punctate, densely pubescent with inconspicuous microsetae.

Head (Figs 1, 2A, B) moderately deflexed, large (0.19 mm long, 0.23 mm wide), slightly smaller than pronotum, widest across eyes, moderately produced anteriorly; clypeus narrow, less than half width of maximum width of head; frontoclypeal suture (Fig. 2A, *fcs*) gently arcuate, lacking midcranial suture; neck constriction (see Supplementary Fig. 2B, C) slightly visible, with basal carina (Fig. 2A, *ch*). Labrum entire, transverse. Eyes (Figs 1, 2A, B) large, bulging, strongly projecting laterally (Fig. 2A). Antennal insertions (Fig. 2A, B, *ai*) partly exposed, distant from anterior margins of eyes (Fig. 2A). Antennae (Figs 1, 2A, B, 3A) with 11 antennomeres, slender, fili-moniliform, slightly longer than head and pronotum combined, each antennomere moderately setose with microsetae: antennomere 1 (*a1*) robust, nearly subparallel sided, only weakly dilated apically, slightly curved, about 1.4 times longer than a2; a2 strongly dilated apically, thicker than a1; a3 elongate, rather slender, much narrower than a2, less wide than a1; a4–9 small, spherical, each antennomere similar in shape and size; a10 very slightly elongate, slightly longer than a9; a11 elongate, nearly twice as long as wide, widest near middle, much larger than a10. Mandibles inconspicuous, details not visible. Maxillary palpi (Figs 2A, B, 3D) five-segmented including pseudosegment, moderate in size and length; palpomere 1 (*mp1*) small; mp2 narrowly elongate, slightly curved; mp3 robust, much shorter than mp2, strongly dilated apically; mp4 spindle-shaped, much longer than mp3, densely covered with microsetae (Fig. 3D); mp5 (pseudosegment) minute, aciculate, hyaline (Fig. 3D). Mentum trapezoidal, moderately transverse, with truncate anterior margin. Labial palpi (Fig. 2A) inconspicuous, not well visible. Gular sutures complete, widely separated, rather strongly widened toward base, each forming straight line.

Pronotum (Fig. 1A) small (0.22 mm long, 0.33 mm wide), slightly larger than head, strongly transverse (width/length = 1.5), widest slightly before base; sides arcuate, relatively strongly narrowed anteriorly; anterior margin nearly truncate; posterior margin gently rounded; anterolateral angles obtusely rounded; posterolateral angles rounded; surface with dense and fine microsetae. Prosternum (Fig. 2B, E, *ps*) small, transverse; prosternal process short, sharply pointed. Pronotal hypomeron narrow (Fig. 2B, E), relatively weakly folded inward; postcoxal process absent. Procoxal cavities opened behind. Mesoscutellum (Fig. 2C, *sc*) sub-triangular, longer than wide, with pointed apex. Elytra (Figs 1A, 2C, D) short (right elytron 0.32 mm long, 0.20 mm wide), but moderately longer than pronotum; each elytron moderately elongate (width/length = 1.6), with sinuate posterior margin (Fig. 2D, *spe*), along with a row of posteriorly directed setae (Fig. 2D). Elytral epipleural keel or ridge absent. Hindwings (Figs 1, 2F) fully developed, probably functional, with setae forming fringe along margin. Mesoventrite (Fig. 2E, *msv*) very short, strongly transverse; mesoventral process (Fig. 2E) short, sharply pointed. Metaventrite (Fig. 2E, *mtv*) large, weakly transverse; metaventral process between mesocoxae (Fig. 2E) short, seemingly pointed.

Legs (Figs 1B, 2B, E) relatively short, slender, lacking spines on tibiae. Protrochantins (Fig. 2B, E, *pt*) large, well exposed; procoxae (Fig. 2B, E, *pc*) conical, small, and contiguous; protrochanters small; profemora clavate, robust; protibiae (Fig. 1B) rod-like, very slender; protarsi 5-segmented, less than half length of protibiae, basal four protarsomeres small and short, together as long as protarsomere 5. Mesocoxae (Fig. 2E, *msc*) obliquely oval, short, at least partially contiguous with each other; mesofemora and mesotibiae similar to those of forelegs in shape, but slightly longer; mesotarsi (Fig. 3C) 5-segmented, about half length of mesotibiae, basal four mesotarsomeres combined moderately longer than mesotarsomere 5, tarsomere 1 (Fig. 3C, *mst1*) much longer than mesotarsomere 2. Metacoxae (Fig. 2E, *mtc*) transverse, sub-triangular, and contiguous; metacoxal lamella not developed; metatrochanters (Fig. 2E) fusiform, large; metafemora clavate, longer than mesofemora; metatibiae rod-like, very slender; metatarsi (Fig. 3E, *mtt*) 5-segmented, more than half length of metatibiae, metatarsomere 1 (Fig. 3E, *mtt1*) longest and about twice as long as tarsomere 2, and therefore, basal four metatarsomeres combined much longer than metatarsomere 5. Claws (Fig. 3C, E) simple, lacking conspicuous basal teeth.

Abdomen (Figs 1, 2F) triangular, widest in segment 4, with six visible sterna; sides evenly strongly tapering from segment 4 to apex. Tergites (Figs. 1A, 2F) lacking both pruinose spots and basolateral ridges; tergite III (Fig. 2F, *t3*) partly visible; tergites IV–VI of almost same length, each markedly transverse; tergite VII (Fig. 2F, *t7*) longest; tergite VIII

(Fig. 2F, *t8*) largely exposed, elongate, narrowing apically, with rounded posterior margin. Abdominal segments III–VII each with paratergites (one or two pairs, undetermined). Sternites III–VI (Fig. 1B) subequal in length; sternite VII slightly longer; sternite VIII (Fig. 3B, *s8*) elongate, narrowing apically, with narrowly rounded apex. Gonocoxites (Figs 1, 2F, 3B, *gc*) present, large, cylindrical; surface covered with scattered macrosetae. Styli minute, inconspicuous, much smaller than gonocoxites.

Male. Unknown.

4. Discussion

Among one extinct and 33 extant subfamilies (Bouchard et al., 2011; Tihelka et al., 2020; Yamamoto, 2021), †*Trichophya minor* sp. nov. can unambiguously be placed in the subfamily Trichophyinae based on the following criteria (Newton et al., 2000): body compact and fusiform, anteriorly located antennal insertion which is partly visible dorsally, head with well-developed neck constriction, maxillary palpus 5-segmented (fourth maxillary palpomere is large and spindle-shaped, whereas the fifth one is minute and hyaline), pronotum without postcoxal processes, protrochantin well exposed, tarsal formula 5-5-5, and abdomen with six visible sterna. One of the most distinctive morphological features is the presence of a specialized antenna, i.e., extremely slender, filiform, and verticillate antennae (Figs 4A, Supplementary Figs 1A, 3C; Newton et al., 2000). However, †*T. minor* sp. nov. lacks such a peculiar antenna as figured (Figs 1, 2A, B, 3A). Interestingly, a single extant *Trichophya* species, namely *T. antennalis* from northwestern India, is known to have a morphologically similar antenna (Fig. 4B, Supplementary Fig. 1B; Ashe and Newton, 1993). In addition, this species shares several important characters with †*T. minor* sp. nov. such as a smaller body, shorter antennae, and somewhat strongly transverse pronotum. Despite their similarities in morphology, †*T. minor* sp. nov. can be clearly differenciated from *T. antennalis* by having the much smaller body and smoother body surface. In this study, we refrain from establishing a new genus which contains these two species because of the general morphological similarities with the other extant *Trichophya* members. The only notable difference between these two species and the rest of others are the structure of the antennae, but it is considered here merely a primitive and ancestral character state, rather than a distinctive derived generic feature. Another remarkable feature of †*T. minor* sp. nov. is its markedly small body size; it is about 1.28 mm, whereas the remaining congeners range from 1.7 mm to 3.4 mm, with the exception of *T. minuta* Cameron, 1950 (1.2 mm) from Peninsular Malaysia. Several fossil occurrences have been documented that imply a miniaturization trend for the Kachin amber beetles (e.g., Yamamoto and Takahashi, 2019; Żyła et al., 2019; Liu et al., 2020d; Li et al., 2020). Although it is difficult to assume a particular reason with evidence for this phenomenon, if they are not just a taphonomic artefact, then there are two hypotheses for explanation: namely, random variation, or paleoenvironmental effect (Liu et al., 2020a). In the latter case, higher ambient temperature and/or lower atmospheric oxygen concentration could be one of the most important factors for contributing to such a miniaturization (Liu et al., 2020a). Alternatively, it could be possible to speculate that these fossils actually indicate a "maximization" trend in comparison with the Recent fauna, since (if we accept the concept of linear time) the Burmese fossils existed long before the modern fauna.

The paleofauna of the Kachin amber is considered to have an affinity with Gondwana. Indeed, the West Burma Block where the amber producing forests in Kachin once located was actually connected to a marginal area of the ancient Australian landmass and was gradually uplifted northwards during the Late Triassic to Late Jurassic (Heine and Müller, 2005; Poinar, 2019; Westerweel et al. 2019). At the time of the mid-Cretaceous, when the amber was formed, the Block was an isolated island in the Tethys Sea (Westerweel et al. 2019), resulting in the presence of a rich Gondwanan fauna that is currently endemic to the Southern Hemisphere, specifically Australasia or South America (e.g., Cai et al., 2019; Liu et al., 2020b). Of note, the Indian endemic leiodid subgenus *Pentacolonellus* Peck, 1997 of the genus *Colonellus* Szymczakowski (Peck, 1997) has been found from Kachin amber (Cai and Huang, 2017). Thus, our finding of a *Trichophya* species with a possible affinity to India is significant when considering such a Gondwanan association. The current distribution of Trichophyinae, or *Trichophya*, is rather cosmopolitan, known from the Nearctic, northern Neotropical, Palaearctic, Oriental, and Australian regions (Ashe and Newton, 1993; Thayer, 2016). However, the native range of this group is narrower and confined to the northern hemisphere; the distribution in Australia should be considered as a result of human introduction (Thayer, 2016). Our discovery shows that *Trichophya* was indigenous to the northern part of Myanmar during the mid-Cretaceous, providing implications for the native distribution of Trichophyinae. Finally, the extant members of *Trichophya* have usually been found from mountaneous areas, whereas the Kachin amber species inhabited in a tropical forest very close to a seashore (Mao et al., 2018; Yu et al., 2019). This may suggest a different ecological strategy of *Trichophya* beetles at that time in comparison with the Recent ones.

5. Conclusions

A new species, †*Trichophya minor* sp. nov., is herein described from mid-Cretaceous Burmese (Kachin) amber based on a well-preserved adult female. It represents the first fossil record of the subfamily Trichophyinae and increases the total number of staphylinid subfamilies known from Kachin amber from 19 to 20. Our finding also indicates that the extant genus *Trichophya* had originated by the mid-Cretaceous. This new fossil species provides insights into several trends known in Kachin amber, i.e., a long-term morphological stability, Gondwanan affinity, and miniaturization (see Liu et al., 2020a), together with evolutionary insight into a certain specialized body part, namely antennae in our case. The discovery of †*T. minor* sp. nov. may be important as a key fossil calibration point for future dating of molecular phylogenetic trees as there is no fossil record from the presumed sister subfamily Habrocerinae (Cai et al., 2017: supplementary table 2).

Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/

Figures

Fig. 1. Habitus photographs of holotype (FMNHINS-4357787) of †*Trichophya minor* sp. nov. in mid-Cretaceous Kachin amber from northern Myanmar. A. dorsal view; B. ventral view. Scale bars: 0.5 mm.

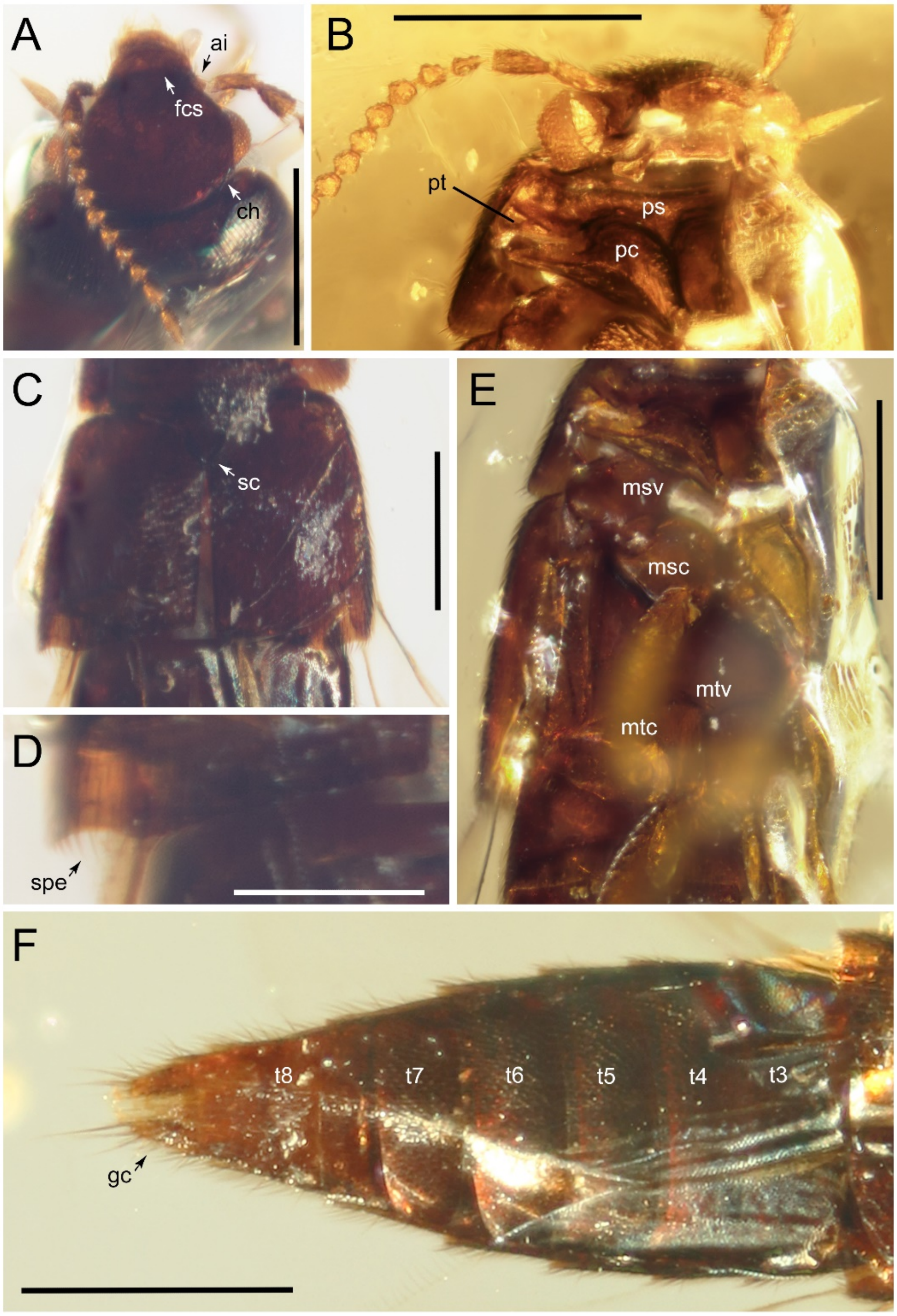

Fig. 2. Morphological details of holotype (FMNHINS-4357787) of †*Trichophya minor* sp. nov. in mid-Cretaceous Kachin amber from northern Myanmar. A. head and left antenna, dorsal view; B. head, prothorax, and procoxae, ventral view; C. Elytra and mesoscutellum, dorsal view; D. posterior margin of left elytron, dorsal view; E. Meso- and metathorax, ventral view; F. Abdomen, dorsal view. Abbreviations: ai, antennal insertion; ch, basal carina on head; fcs, frontoclypeal suture; gc, gonocoxite; msc, mesocoxa; msv, mesoventrite; mtc, metacoxa; mtv, metaventrite; pc, procoxa; ps, prosternum; pt, protrochantin; sc, mesoscutellum; spe, sinuate posterior margin of elytron; t3–8, tergites 3–8. Scale bars: 0.2 mm (A–C, E), 0.1 mm (D), 0.3 mm (F).

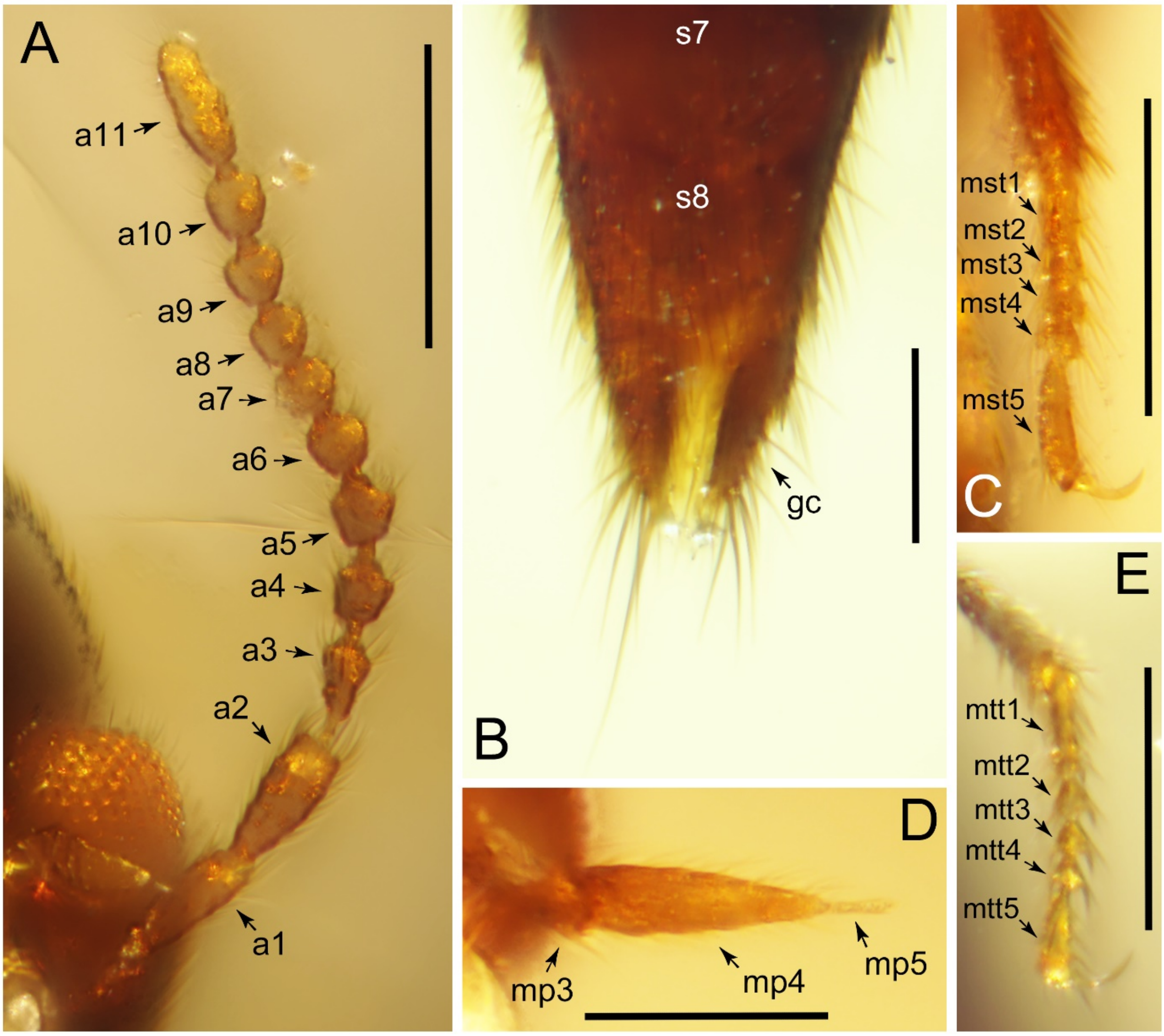

Fig. 3. Morphological details of holotype (FMNHINS-4357787) of †*Trichophya minor* sp. nov. in mid-Cretaceous Kachin amber from northern Myanmar. A. right antenna, ventral view; B. abdominal terminalia, ventral view; C. left mesotarsus, ventral view; D. left maxillary palpus; E. left metatarsus, ventral view. Abbreviations: a1–11, antennomeres 1–11; gc, gonocoxite; mp3–5, maxillary palpomeres 3–5; mst1–5, mesotarsomeres 1–5; mtt1–5, metatarsomeres 1–5; s7–8, sternites 7–8. Scale bars: 0.1 mm (A–C, E), 0.05 mm (D).

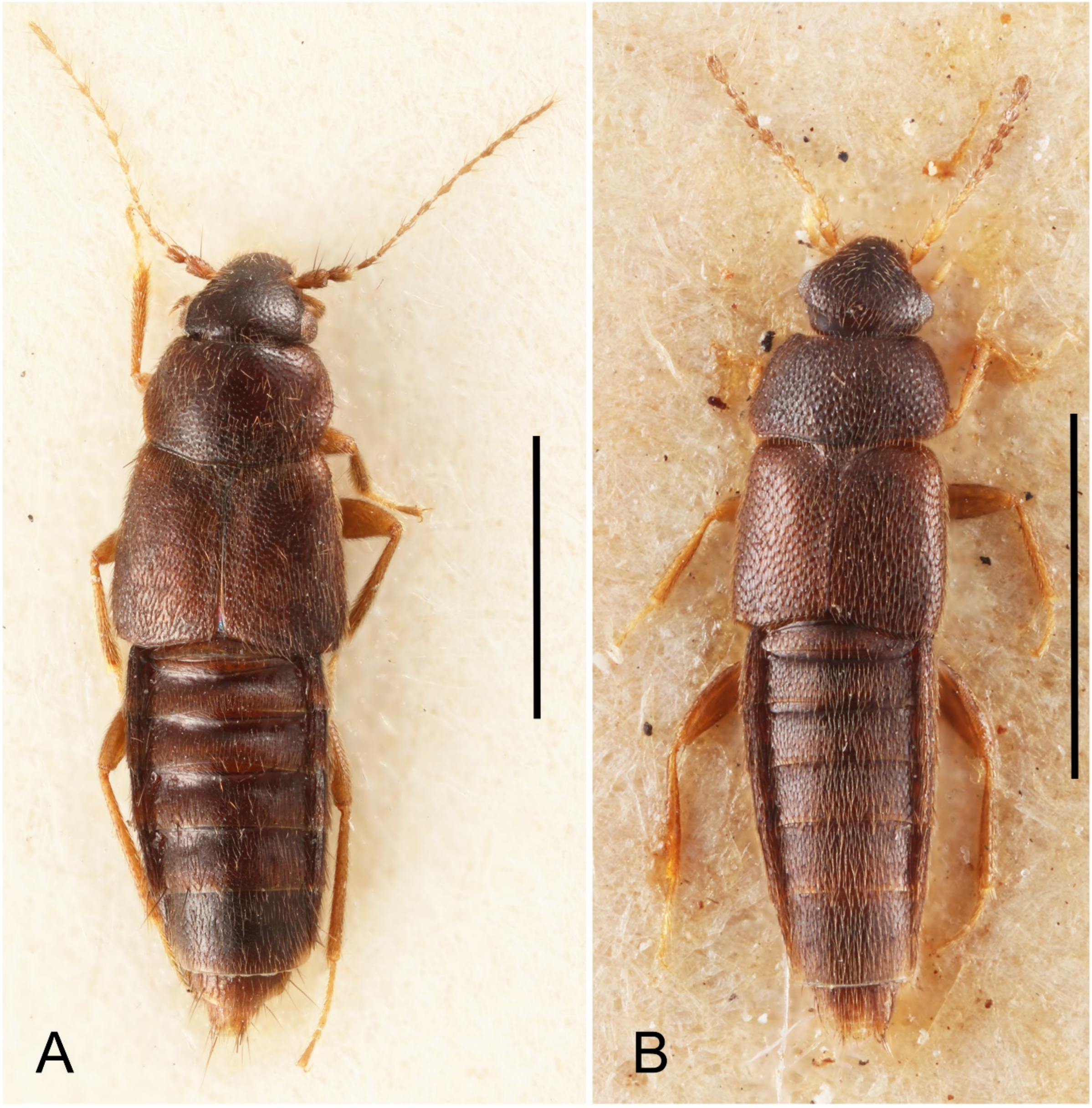

Fig. 4. Extant species of Trichophyinae. A. *Trichophya pilicornis* (Gyllenhal) from Austria; B. *T. antennalis* Cameron from northwestern India. Scale bars: 1.0 mm.

Highlights

• The first fossil Trichophyinae is described from mid-Cretaceous Burmese amber and placed in the extant genus *Trichophya*.

• †*Trichophya minor* sp. nov. is closely related to the extant species *T. antennalis* from India based on antennae and body size.

• Our finding indicates that Trichophyinae had originated by the mid-Cretaceous.

• Our discovery is also congruent with the hypothesis of the Gondwanan origin of Burmese (Kachin) amber.