Baltic J. Coleopterol. 22(2) 2022
ISSN 1407 - 8619

Fossil Cantharidae from the Cretaceous Burmese (Kachin) amber of the Patrick Müller collection, and taxonomic information

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Fanti F., Müller P. 2022. Fossil Cantharidae from the Cretaceous Burmese (Kachin) amber of the Patrick Müller collection, and taxonomic information. *Baltic J. Coleopterol., 22(2): 331–380.*

We describe a new genus of soldier beetle, *Vitalfranzius* gen. nov., and 24 new fossil species from Cretaceous Burmese (Kachin) amber: *Burmomiles parisii* sp. nov., *Burmomiles volpei* sp. nov., *Elektrokleinia thiloi* sp. nov., *Elektrokleinia zahradniki* sp. nov., *Hukawngichthyurus barsevskisi* sp. nov., *Hukawngichthyurus ditaddeoi* sp. nov., *Sanaungulus dominikiweissbachi* sp. nov., *Sanaungulus dunlopi* sp. nov., *Sanaungulus electrum* sp. nov., *Sanaungulus franziskaeweissbachae* sp. nov., *Sanaungulus havai* sp. nov., *Sanaungulus kachinensis* sp. nov., *Sanaungulus kirstenaeweissbachae* sp. nov., *Sanaungulus leniae* sp. nov., *Sanaungulus myanmaricus* sp. nov., *Sanaungulus myitkyinaensis* sp. nov., *Sanaungulus nalae* sp. nov., *Sanaungulus nilsi* sp. nov., *Sanaungulus perkovskyi* sp. nov., *Sanaungulus peteriruedeli* sp. nov., *Sanaungulus temporiscapsula* sp. nov., *Sanaungulus ypogaeum* sp. nov., *Vitalfranzius burmiticus* sp. nov., and *Vitalfranzius cretaceus* sp. nov.

The evolution, characteristics and pecularities of fossil soldier beetles embedded in Burmese amber are also discussed. The original attribution of soldier beetles in Burmese amber to the subfamily Cantharinae is confirmed, so the attribution to the subfamily Silinae is definitively rejected. Other taxonomic acts present in this document are: *Palaeocantharis* Hsiao, Y. Li, Ren & Pang, 2021 = *Elektrokleinia* Ellenberger & Fanti, 2019 syn. nov.; *Elektrokleinia panna* (Hsiao, Y. Li, Ren & Pang, 2021) comb. nov.; *Elektrokleinia oblongoculus* (Y. Yang, Bai & W. Zhang, 2021) comb. nov.; *Elektrokleinia bilineatimaculata* (Y. Yang, Geiser & H. Liu, 2021) comb. et decl. nov.

Furthermore, we document that *Sanaungulus dominikiweissbachi* is the first Burmese fossil soldier beetles preserved during mating. We also note that the red coloration of the pronotum of *Sanaungulus ruficollis* Y. Yang, H. Liu & W. Zhao in Yang et al., 2022 is due to the amber and is not a real and natural color of the specimen.

Key words: soldier beetles, amber, paleoentomology, taxonomy, new taxa.

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INTRODUCTION

The vast amber collection of Patrick Müller, which currently includes approximately 15000 pieces of which include 100000 inclusions, is studied here. The object of this research concerns the family Cantharidae (soldier beetles), and we describe 24 new species and a new genus, while three other specimens (probably of the genus *Sanaungulus*) present in the Müller's collection (BUB3881, BUB3916, and BUB4232) are not described due to the lack of sufficient visibility. These pieces come from Burmese amber.

Today, the family Cantharidae Imhoff, 1856 is abundantly widespread all over the world except Antarctica, with over 5100 species (Delkeskamp 1977; Zhang et al. 2018). The family appears to have evolved from the Jurassic-Cretaceous boundary (Zhang et al. 2018), with inclusions embedded in Burmese amber (Fanti 2017; Ross 2019a, 2019b, 2020, 2021a, 2021b), Spanish amber: 110 mya (Peris & Fanti 2018), and Agdzhakend amber: ca. 98 mya (Kazantsev & Perkovsky 2019), plus an adpression/compression fossil of the Lower Cretaceous–Late/Upper Aptian: 122.5–112.0 mya, from the Koonwarra Fossil Bed, Australia (Jell & Duncan 1986; Fanti 2017). The extraordinary abundance of soldier beetles in Burmese amber is confirmed by the species described here. Featuring various peculiarities, rarely present in the panorama of this family, these Burmese specimens are very important for phylogenitic and evolutionary reconstructions.

MATERIALS AND METHODS

Burmese amber comes from Kachin in the Hukawng Valley in Northern Myanmar, and is currently dated to the Cretaceous: 98.79 ± 0.62 mya (Shi et al. 2012). The amber pieces, which came from Patrick Müller's collection, were donated to the "Bayerische Staatssammlung für Paläontologie und Geologie in München, Germany, or to the "Staatliches Naturhistorisches Museum Braunschweig" in Braunschweig, Germany. They were cut using a Dremel 3000 and polished with Sidol. Photographs were taken using a Nikon Lobophot microscope with Zeiss and Nikon objectives. The plates were made using the Ulead PhotoImpact Viewer SE program. Subfamilies, tribe, genera and species are listed in systematic-alphabetical order.

SYSTEMATIC PALEOENTOMOLOGY

Order Coleoptera Linnaeus, 1758
Suborder Polyphaga Emery, 1886
Infraorder Elateriformia Crowson, 1960
Superfamily Elateroidea Leach, 1815
Family Cantharidae Imhoff, 1856
Subfamily Cantharinae Imhoff, 1856
Tribe Cantharini Imhoff, 1856
Genus *Burmomiles* Fanti, Damgaard & Ellenberger, 2018

***Burmomiles parisii* sp. nov.**
(Fig. 1)

Holotype. Female, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNHM-6004 in the Staatliches Naturhistorisches Museum Braunschweig (ex Müller's collection number: BUB4457).

Type locality. Myanmar: Kachin state, Myitkyina District, Hukawng Valley.

Type horizon. Lowermost Cenomanian (98.79 ± 0.62 Ma), mid-Cretaceous.

Differential diagnosis. The genus *Burmomiles* is characterized by short elytra that do not reach the last abdominal segments, tarsal formula 5-5-5, elytra with shallow but dense punctuation arranged in striae, a pronotum enlarged and rounded at sides, the head rounded, and the unequal maxillary palpomeres with the last segment securiform (Fanti et al. 2018), all features present in the new species described here. The new taxon differs from other *Burmomiles* by its much more transverse pronotum. Furthermore, the other *Burmomiles* have pectinate antennae. *Burmomiles laticollis* Yang, Geiser & Liu, 2021 has a similar pronotum, but it has shorter elytra (less punctated) and pectinate antennae (Yang et al. 2021).

Description. Adult, alate, robust. Female, for the shape of last sternite and short antennae. Entirely dark brown. Body length: 3.0 mm.

Head rounded behind the eyes, partially covered by the pronotum, surface with shallow punctation. Eyes prominent, subelliptical, inserted laterally to the head. Mandibles falciform. Maxillary palps 4-segmented, with the last palpomere securiform. Labial palps 3-segmented with the last palpomere securiform. Antennae 11-segmented, filiform, inserted in the upper part of

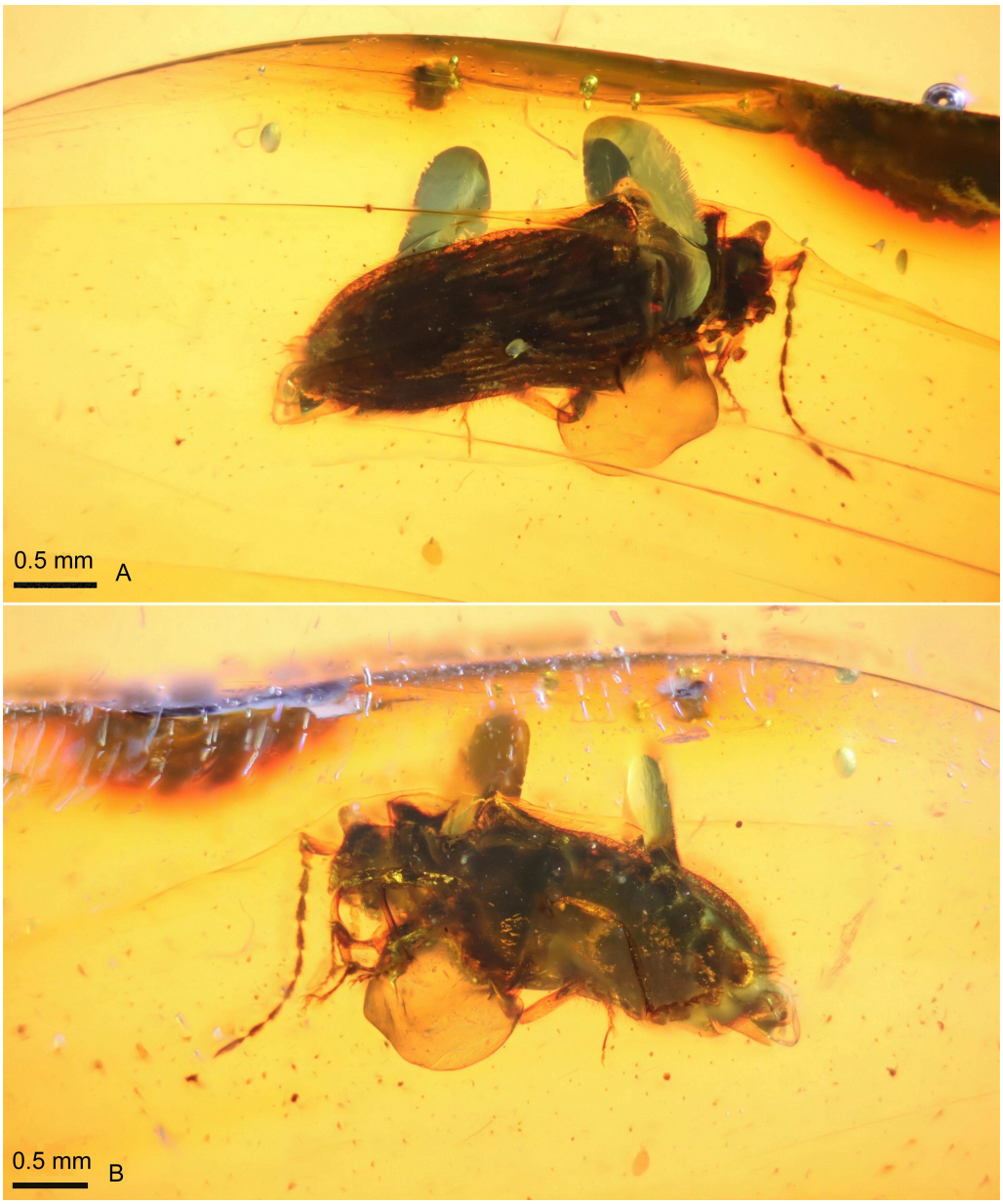

Fig. 1. *Burmomiles parisii* sp. nov. in Burmese amber. A: Holotype, dorsal view; B: Holotype, ventral view.

the head and not particularly close to the eyes, short, slightly surpassing the humeral zone of the elytra; scape club-shaped, very robust; antennomere II short, very wide and globular; antennomere III narrower than previous one and globular; antennomeres IV–X subequal, robust, swollen, longer than antennomeres II–III together; antennomere XI elongate, pointed apically; all antennomeres with setae. Pronotum very transverse, wider than head, anterior margin straight and slightly bordered, posterior margin almost straight, sides slightly curved and slightly bordered, surface completely flat with pubescence (just perceptible). Scutellum triangular-shaped with rounded apex. Elytra wider than pronotum, robust and wide, rounded at apex, not covering the last abdominal segment, wider at humeri, surface presenting a coarse and wide punctation gathered in evident striae visible for the entire elytral length. Metathoracic wings covered by elytra, and not visible. Sternum subquadrate with almost straight posterior margin. Sternites transverse and wide, last two tergites as a caudal large appendage, last sternite rounded presenting two slender and divergent lobes (oviduct). Legs very robust and with short and fitted pubescence; coxae short, robust; trochanters elongated with rounded apex; femora slightly curved, sturdier than tibiae; tibiae thin, elongate, cylindrical and slightly flat apically, pro- and mesotibiae as long as pro- and mesofemora, metatibiae longer than metafemora, with a robust spur at apex. Tarsal formula 5-5-5; first tarsomere about 1.3 times longer than second; second tarsomere elongated; third tarsomere triangular, very slightly enlarged at corners; fourth tarsomere flat, wide, very slightly lobated at corners; fifth tarsomere very elongated, thin, slightly curved, slightly enlarged apically; claws simple, very long, apparently without tooth at the base (with the base slightly wider).

Etymology. Named in honor of Francesco Parisi (University of Florence, Italy), friend of the first author (Fanti).

Syninclusions. Air bubbles, detritus, Hymenoptera (0.7 mm).

Remarks. Piece of clear, golden amber that measures 11x10x4.5 mm. The inclusion is complete, but the pronotum and ventral side are not clearly visible.

***Burmomiles volpei* sp. nov.**
(Fig. 2)

Holotype. Male, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNSB-BSPG 2021 XII 74 in the Bayerische Staatssammlung für Paläontologie und Geologie (ex Müller's collection number: BUB4027).

Type locality. Myanmar: Kachin state, Myitkyina District, Hukawng Valley.

Type horizon. Lowermost Cenomanian (98.79 ± 0.62 Ma), mid-Cretaceous.

Differential diagnosis. Head rounded behind the eyes, short elytra that do not reach the last abdominal segments and which are equipped with punctuation gathered in striae, plus a pronotum rounded at the sides, make this new species belong to the genus *Burmomiles* (Cantharidae). *Burmomiles volpei* sp. nov. is very similar to *Burmomiles willerslevorum* Fanti, Damgaard & Ellenberger, 2018, but it differs based on the slightly longer elytra, and by its pronotum less protruded at the sides and less protruded in the middle of the anterior margin (Fanti et al. 2018). Instead, *Burmomiles blixenae* Fanti & Damgaard, 2019 has a pronotum that is more bordered and shorter elytra with a different sculpture (Fanti & Damgaard 2019).

Description. Adult, alate, rather robust. Male, for the shape of last sternite. Entirely dark brown. Body length: 3.5 mm.

Head rounded behind the eyes, partially covered by the pronotum, surface with sparce punctation. Eyes very prominent, rounded, inserted laterally to the head. Mandibles falciform. Maxillary palps 4-segmented, with the last palpomere securiform. Labial palps 3-segmented with the last palpomere securiform. Antennae 11-segmented, pectinate, inserted in the frons, relatively long, surpassing the half of the elytra;

scape club-shaped, not particularly robust, slightly enlarged apically; antennomere II very short, globular; antennomere III short, slightly longer than second, triangular-shaped; antennomeres IV–IX subequal, robust, swollen, over two times longer than antennomeres II–III together, each antennomere with a long process inserted near the base; antennomere X leaner than previous ones but subequal in length, with a long process near the base; antennomere XI elongate, sturdier, squadrate apically; all antennomeres with setae. Pronotum transverse, wider than head,

Fig. 2. *Burmomiles volpei* sp. nov. in Burmese amber. A: Holotype, dorsal view; B: Holotype, ventral view.

anterior margin rounded and slightly bordered, posterior margin almost straight and bordered, sides rather curved, surface almost flat with pubescence. Scutellum triangular-shaped, elongated, with a subtruncate apex. Elytra wider than pronotum, robust, rounded at apex, not covering the last abdominal segment (and very slightly the penultimate), slightly wider at humeri, surface presenting a coarse and very wide punctation gathered in evident striae visible for the entire elytral length. Metathoracic wings slightly infuscate, longer than elytra. Sternum elongate and robust. Sternites transverse, last tergite as a caudal appendage which is relative short and rounded apically, last sternite narrower than last tergite. Legs long and slender with short and fitted pubescence; coxae short, robust; trochanters elongated with rounded apex; femora curved, sturdier than tibiae; tibiae thin, elongated, cylindrical, longer than femora, with a long spur at apex. Tarsal formula 5-5-5; first tarsomere elongated, about 1.4 times longer than second; second tarsomere elongated (pro- and mesotarsomere triangular-shaped); third tarsomere triangular, shorter than previous one; fourth tarsomere lobated at corners; fifth tarsomere very elongated, thin, curved, slightly enlarged apically; claws simple, very long, apparently without tooth at the base (with the base not enlarged).

Etymology. Named in honor of Felice Volpe (Montella, Avellino, Italy), dear friend of the first author.

Syninclusions. Air bubbles, detritus.

Remarks. Piece of rounded, clear, golden amber that measures 12x12x3 mm. To the inclusion lacks almost completely the legs of the right side.

Genus *Elektrokleinia* Ellenberger & Fanti, 2019

= *Palaeocantharis* Hsiao, Y. Li, Ren & Pang, 2021 (syn. nov.)

***Elektrokleinia thiloi* sp. nov.**
(Fig. 3)

Holotype. Probable male, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNSB-BSPG 2021 XII 20 in the Bayerische Staatssammlung für Paläontologie und Geologie (ex Müller's collection number: BUB4392).

Type locality. Myanmar: Kachin state, Myitkyina District, Hukawng Valley.

Type horizon. Lowermost Cenomanian (98.79 ± 0.62 Ma), mid-Cretaceous.

Differential diagnosis. Head restricted behind the eyes, short elytra that do not reach the last abdominal segments and equipped with punctuation gathered in striae, plus a pronotum that is little rounded at the sides, make this new species belong to the genus *Elektrokleinia* (Cantharidae). *Elektrokleinia picta* Ellenberger & Fanti, 2019 is the *Elektrokleinia* most similar to *Elektrokleinia thiloi* sp. nov., but differs by its pronotum that is less rounded anteriorly and with a less deep concavity in the first basal third of the sides (Ellenberger & Fanti 2019). *Elektrokleinia panna* (Hsiao, Y. Li, Ren & Pang, 2021) has the pronotum narrowest anteriorly.

Description. Adult, alate, rather robust. Probable male, for the last sternite deeply incised. Entirely brown-testaceous. Body length: 5.1 mm.

Head transverse, triangular behind the eyes, slightly convex dorsally, partially covered by the pronotum, surface smooth. Eyes very prominent, subelliptical, inserted laterally to the head, inter-ocular dorsal distance about 2.5 times greater than eye diameter. Mandibles elongated, falciform. Maxillary palps 4-segmented, with the first palpomere thin and elongated, second palpomere robust, third palpomere almost triangular, last palpomere securiform. Labial palps 3-segmented with the last palpomere securiform. Antennae 11-segmented, filiform, inserted in the upper part of the head and not particularly close to the eyes, short, not reaching the half of elytra; scape club-shaped; antennomeres II–III subequal, shorter than first; antennomere IV as long as antennomeres II–III together; antennomeres V–X subequal, shorter than antennomere IV;

antennomere XI elongate, with rounded apex; all antennomeres with very short setae. Pronotum transverse, wider than head, anterior margin rounded and bordered, sides irregular and slightly bordered and with a concavity in the first basal third, surface flat without pubescence. Scutellum triangular-shaped with rounded apex. Elytra wider than pronotum, parallel-sided, rounded at apex, not covering the last two abdominal segments, surface slightly pubescent presenting coarse punctation gathered in striae. Metathoracic wings transparent, slightly longer than

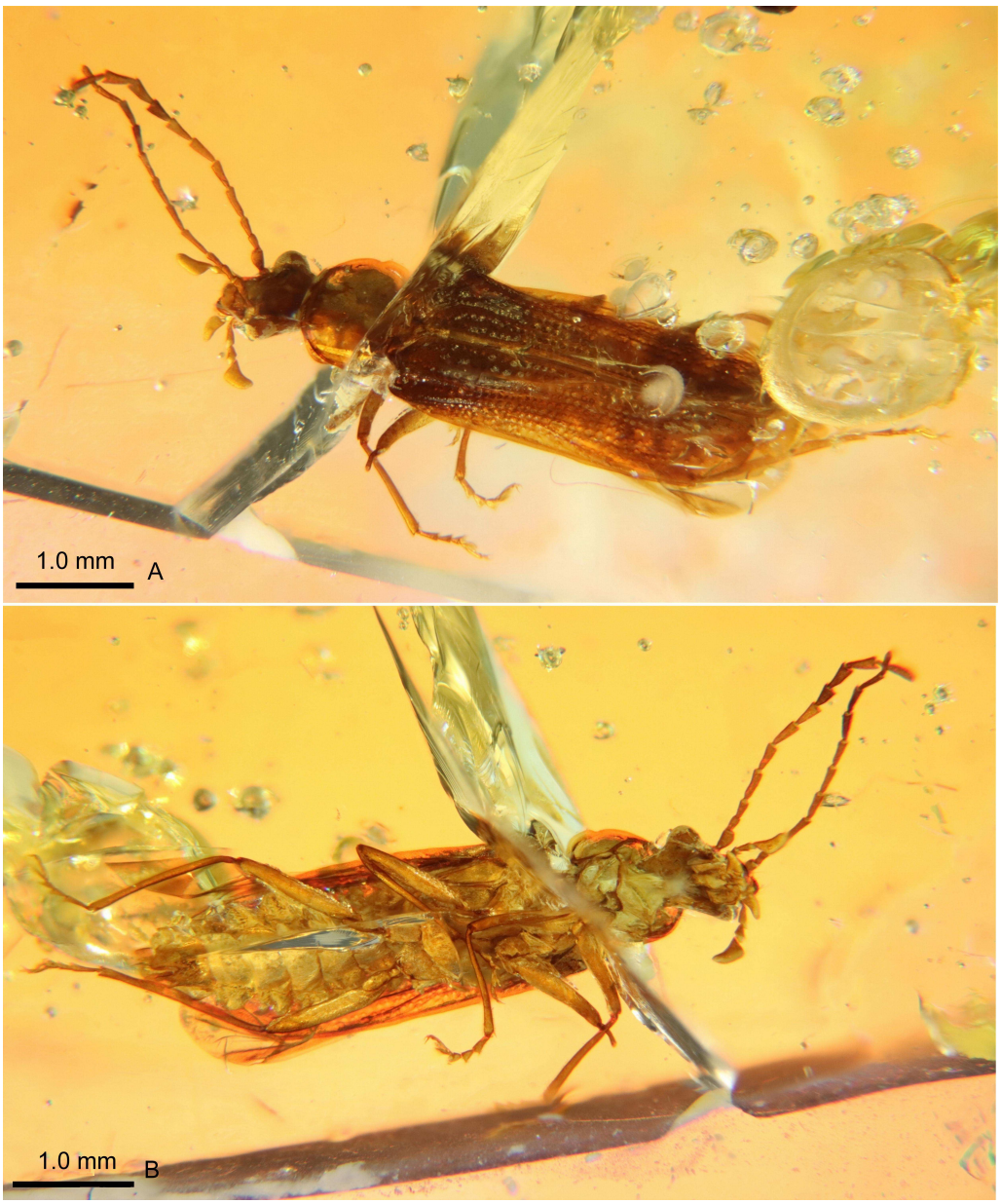

Fig. 3. *Elektrokleinia thiloi* sp. nov. in Burmese amber. A: Holotype, dorsal view; B: Holotype, ventral view.

elytra, not surpassing the last abdominal segment. Sternum subquadrate with a rounded posterior margin. Sternites transverse, last two tergites as a caudal appendage, last tergite narrower than penultimate tergite, last sternite with the posterior margin with a deep incision in the middle. Legs robust and with pubescence; coxae short, robust; trochanters elongated with rounded apex; femora almost straight; tibiae thin, elongate, cylindrical and enlarged at the apex, with a robust spur at apex, protibiae as long as profemora, mesotibiae slightly longer than mesofemora, metatibiae longer than metafemora. Tarsal formula 5-5-5; first tarsomere about 2.1 times longer than second tarsomere; third tarsomere very slightly shorter than second tarsomere and with a lobe at sides; fourth tarsomere bilobed with the lobes very elongated; fifth tarsomere elongate, thin, slightly enlarged apically; claws simple without tooth at the base.

Etymology. Named in honor of Thilo Müller, son of the second author (Patrick).

Syninclusions. Air bubbles, detritus.

Remarks. Piece of clear, golden amber that measures 20x11x5 mm. The inclusion is complete, except for the left mesothoracic leg preserved until part of the tibia.

***Elektrokleinia zahradniki* sp. nov.**
(Fig. 4)

Holotype. Probable female, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNSB-BSPG 2021 XII 18 in the Bayerische Staatssammlung für Paläontologie und Geologie (ex Müller's collection number: BUB4327).

Type locality. Myanmar: Kachin state, Myitkyina District, Hukawng Valley.

Type horizon. Lowermost Cenomanian (98.79 ± 0.62 Ma), mid-Cretaceous.

Differential diagnosis. Head restricted behind the eyes makes this new species belong to the genus *Elektrokleinia* and not to the similar genus *Burmomiles*, which has a head rounded behind the eyes. *Elektrokleinia zahradniki* sp. nov. is distinguishable from other *Elektrokleinia* by its last maxillary palpomere very elongated and not particularly securiform (strongly securiform in the already known species). It also differs by the antennomeral lengths and pronotal shape, and the sculpture of the elytra is less prominent and much smoother.

Description. Adult, alate, rather robust. Probable female, for the short antennae. Head and pronotum testaceous-brown, elytra dark brown, antennae and legs brown. Body length: 5.2 mm.

Head slightly transverse, rounded and narrower (restricted) behind the eyes, slightly convex dorsally, partially covered by the pronotum, surface smooth and pubescent equipped with short and not erected setae. Eyes little prominent, subelliptical, inserted laterally to the head. Mandibles elongated, falciform. Maxillary palps 4-segmented, last palpomere very elongated and not particularly securiform with the external side convex. Labial palps 3-segmented, with the last palpomere securiform, very curved and with pointed apex. Antennae 11-segmented, filiform, inserted in frons and far to the eyes, short, reaching the humeral zone of elytra; scape elongated, slightly club-shaped; antennomere II about 1.3-1.4 times shorter than first; antennomeres III–X subequal, robust, enlarged and slightly longer than second antennomere; antennomere XI thinner than previous ones, with squared-irregular apex; all antennomeres with very short setae. Pronotum very slightly transverse, wider than head, anterior margin rounded and very slightly bordered, posterior margin straight and strongly bordered, sides irregular and slightly bordered and enlarged in the first basal third, surface flat without pubescence and with shallow punctaction. Scutellum triangular-shaped, elongated, with rounded apex. Elytra wider than pronotum, parallel-sided with humeral zone enlarged, rounded at apex, not covering the last abdominal segment, surface very slightly pubescent presenting small coarse punctation gathered in striae little noticeable. Metathoracic wings covered by elytra. Sternum subquadrate. Sternites transverse. Legs rather robust, short; coxae short, robust; trochanters

elongated with rounded apex; femora almost straight and flat; tibiae thin, elongate, cylindrical and slightly enlarged at the apex, protibiae shorter than profemora, mesotibiae nearly as long as mesofemora, metatibiae longer than metafemora. Tarsal formula 5-5-5; first tarsomere elongated; second tarsomere slightly shorter than first; third tarsomere triangular-shaped, fourth tarsomere strongly bilobed with the lobes very elongated; fifth tarsomere elongate, thin, curved; claws simple apparently without tooth at the base.

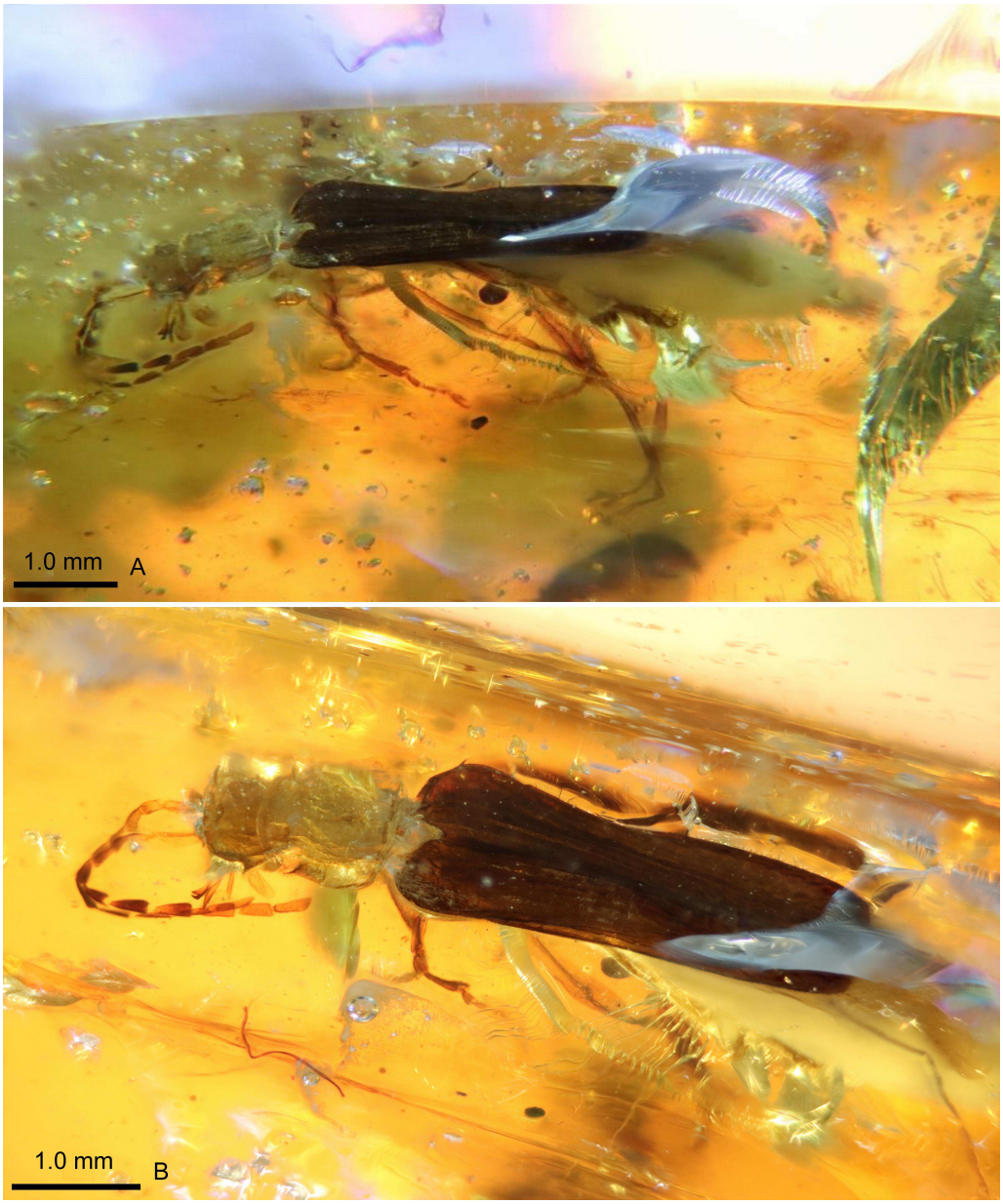

Fig. 4. *Elektrokleinia zahradniki* sp. nov. in Burmese amber. A: Holotype, dorso-lateral view; B: Holotype, dorsal view.

Etymology. Named in honor of Petr Zahradník (Czech Republic), a well-known specialist of the family Ptinidae.

Syninclusions. Air bubbles, detritus, little ant beetle.

Remarks. Piece of clear, golden amber that measures 17x10x8 mm. The inclusion is complete. The ventral part is little visible and part of the abdomen is covered by emulsion like white-cotton.

Genus *Hukawngichthyurus* Fanti & Ellenberger, 2018

***Hukawngichthyurus barsevskisi* sp. nov.**
(Fig. 5)

Holotype. Male, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNSB-BSPG 2021 XII 19 in the Bayerische Staatssammlung für Paläontologie und Geologie (ex Müller's collection number: BUB4328).

Type locality. Myanmar: Kachin state, Myitkyina District, Hukawng Valley.

Type horizon. Lowermost Cenomanian (98.79 ± 0.62 Ma), mid-Cretaceous.

Differential diagnosis. The new species is distinguishable from other *Hukawngichthyurus* by its pectinate antennae. We attribute this new species to this genus on the basis of the very short and irregular antennomeres II–III, for the pronotum with depressions and for the last abdominal segments in a kind of "fish tail." The antennae are often a variable character. For example, in the fossil genus *Sanaungulus*, there are species with pectinate or filiform antennae. Unlike what Yang et al. (2021) say about *Sanaungulus ruicheni* (Hsiao & Huang, 2018), this is not a distinguishing character, being extremely variable even in living genera.

Description. Adult, alate, slender. Male, for the shape of the last abdominal segment. Entirely dark brown. Body length: 3.4 mm.

Head rounded, convex, slightly restricted behind the eyes, surface with shallow punctation and short setae. Eyes large and prominent, subelliptical, inserted laterally to the head. Rostrum elongated. Mandibles falciform. Maxillary palps 4-segmented, last palpomere securiform with rounded apex. Labial palps 3-segmented, last palpomere stout and slightly securiform. Antennae 11-segmented, relatively short, pectinate, surpassing the half of elytra and reaching the half of abdomen, insertion of the antennae close to the eyes and in their lower part; scape robust, elongated, club-shaped; antennomere II very short, moniliform-globular, asymmetrical; antennomere III short, sturdier and longer than second, slightly irregular-distorted; antennomeres IV–X pectinate, equipped with a lobe which is very long (longer than antennomeres), rounded at apex and inserted in the basal part of antennomeres; antennomere XI filiform, rounded at apex; all antennomeres punctate with not erected and very short setae. Pronotum transverse, slightly wider than head, anterior margin undulate, posterior margin undulate and bordered, sides irregular (almost straight), surface irregular with draft and depressions (particularly near the anterior margin) and equipped with short setae. Scutellum triangular. Elytra wider than pronotum, parallel-sided, rounded and slightly dehiscent at apex, rather short and revealing the last three abdominal segments, surface smooth without punctation, equipped with few little and thin striae. Metathoracic wings transparent, folded, very slightly surpassing the elytra. Metasternum sub-quadrate; sternites transverse. Last urite with an apical lobe in each side, which is extremely long, thin, with rounded apex. Legs slender, rather long, with pubescence; coxae elongated and robust; trochanters globular-shaped, irregular, with apex rounded; femora robust and not curved, almost flat, sturdier and longer than tibiae; tibiae cylindrical, thin, without spurs at apex. Tarsal formula 5-5-5; first tarsomere elongated, about 1.2 times longer than second; second tarsomere thin at base and slightly enlarged apically; third tarsomere triangular and shorter than second; fourth tarsomere bilobed with the lobes very long and not particularly

wide; fifth tarsomere very long; claws simple without denticles or lobes.

Etymology. Named in honor of Arvīds Barševskis (Daugavpils University, Latvia), dear friend of the first author.

Syninclusions. Remains of another soldier beetle, air bubbles, detritus.

Remarks. Piece of clear, golden amber that measures 11x9x3 mm. The inclusion is complete except for the left anterior leg preserved until the tibia.

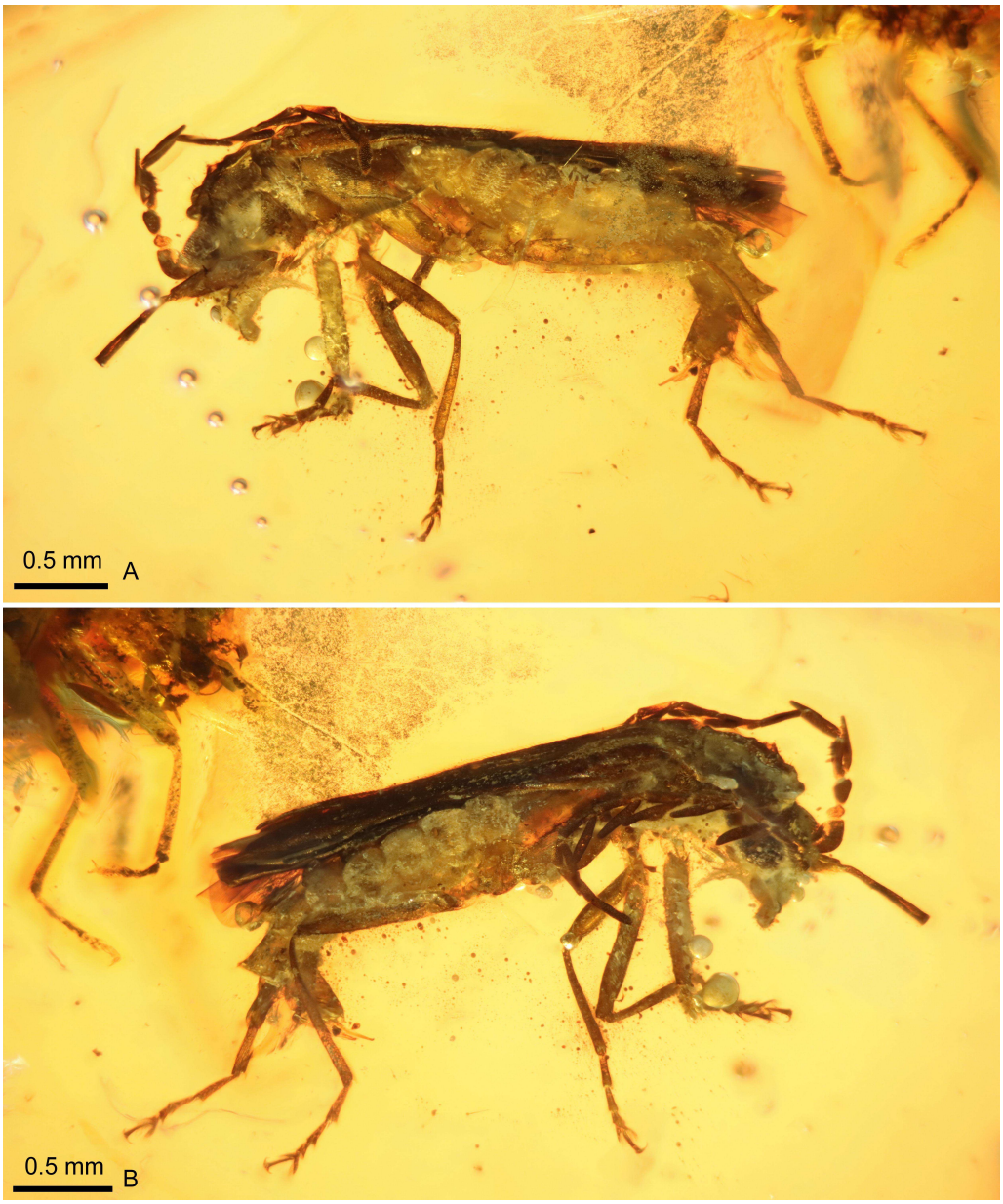

Fig. 5. *Hukawngichthyurus barsevskisi* sp. nov. in Burmese amber. A–B: Holotype, dorso-lateral views.

***Hukawngichthyurus ditaddeoi* sp. nov.**
(Fig. 6)

Holotype. Probable female, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNSB-BSPG 2021 XII 17 in the Bayerische Staatssammlung für Paläontologie und Geologie (ex Müller's collection number: BUB 4326).

Type locality. Myanmar: Kachin state, Myitkyina District, Hukawng Valley.

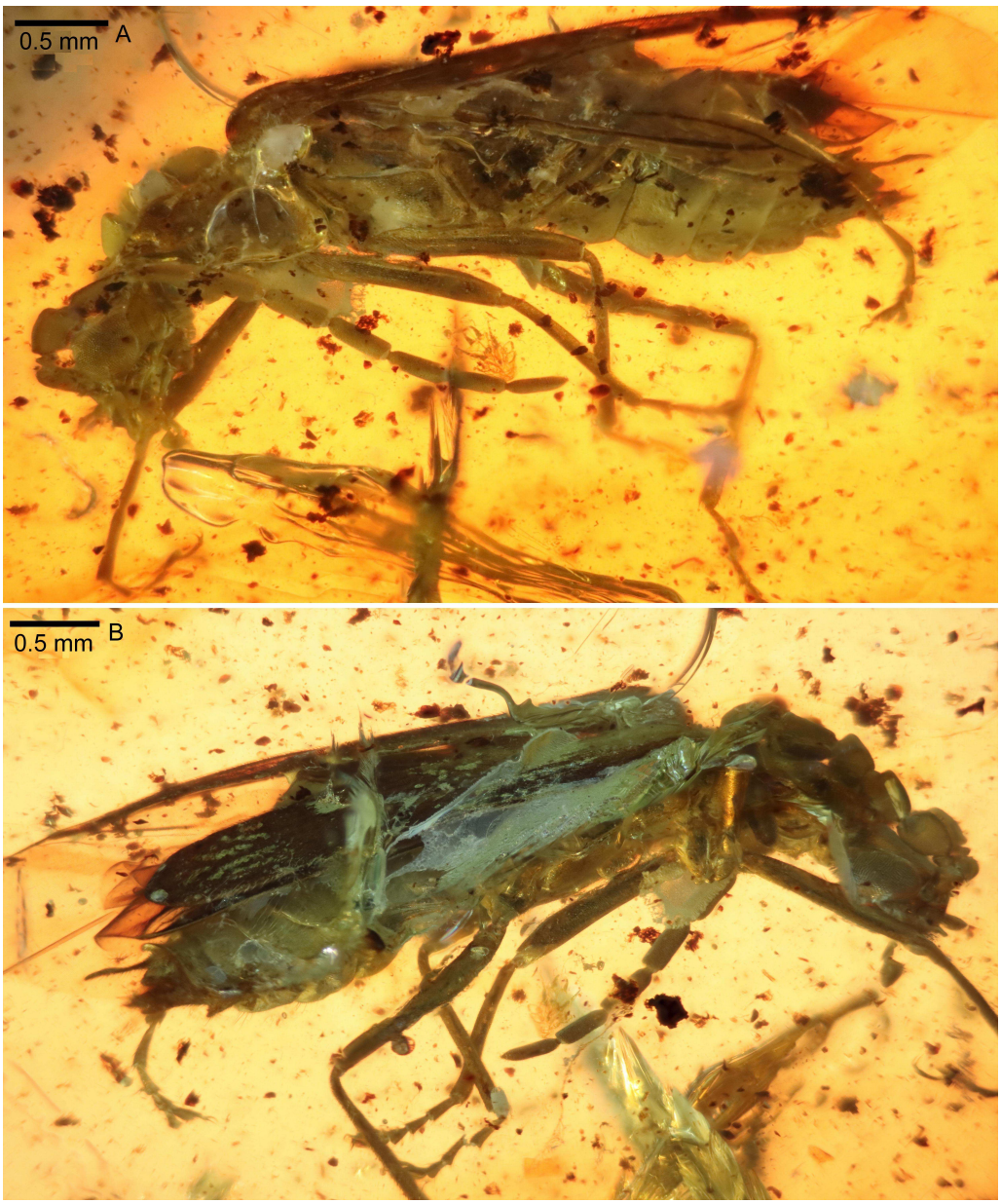

Fig. 6. *Hukawngichthyurus ditaddeoi* sp. nov. in Burmese amber. A: Holotype, ventro-lateral view; B: Holotype, dorso-lateral view.

Type horizon. Lowermost Cenomanian (98.79 ± 0.62 Ma), mid-Cretaceous.

Differential diagnosis. The relatively small body size, the pronotum irregular with a convex draft, and the last urites in a kind of "fish tail" make this new species belong to the genus *Hukawngichthyurus*. The new species is distinguishable from other *Hukawngichthyurus* by its longer pronotum and elytra.

Description. Adult, alate, robust. Probable female, for the wide abdomen. Entirely brown with darker elytra. Body length: 4.9 mm.

Head elongated, convex in the anterior part and almost flat posteriorly, slightly restricted behind the eyes, surface finely punctated. Eyes large and prominent, subelliptical, inserted laterally to the head. Rostrum elongated and robust. Mandibles falciform. Maxillary palps 4-segmented, last palpomere securiform with rounded apex. Labial palps 3-segmented, last palpomere stout and slightly securiform. Antennae 11-segmented, short, filiform with the central antennomeres enlarged, reaching almost the half of elytra, insertion of the antennae close to the eyes and in their lower part; scape robust, elongated, club-shaped; antennomere II very short, moniliform-triangular; antennomere III moniliform-globular, slightly irregular; antennomeres IV–V elongated, robust; antennomeres VI–X filiform, less sturdier than previous ones; antennomere XI filiform, rounded at apex; all antennomeres with not erected and very short setae. Pronotum elongated, slightly narrower than head, anterior margin slightly undulated, posterior margin strongly undulated and slightly bordered, sides straight, surface irregular with a central convex draft. Scutellum triangular. Elytra wider than pronotum, parallel-sided, rounded at apex, rather elongated and revealing the last two abdominal segments, surface without punctation, equipped with few little and thin striae. Metathoracic wings transparent, folded, very long, surpassing the elytra and the last tergites. Metasternum large, stout, sub-quadrate; sternites wide, transverse. Last urite with two asymmetrical apical lobes in a kind of fish tail, one of which is curved and very long with the base slightly enlarged and the center thinner and newly enlarged at apex, while the other one is very short and sturdier. Legs robust, long, with pubescence; coxae elongated and robust; trochanters slightly elongated, globular-shaped with apex rounded; femora robust and slightly curved, sturdier and longer than tibiae; tibiae cylindrical, thin, without spurs at apex. Tarsal formula 5-5-5; first tarsomere elongated, about 1.2 times longer than second; second tarsomere thin at base and enlarged apically; third tarsomere triangular and shorter than second; fourth tarsomere bilobed with the lobes very long and wide; fifth tarsomere elongated with wider sides; claws simple without denticles or lobes.

Etymology. Named in honor of Vincenzo Di Taddeo (Avigliana, Italy), dear friend of the first author.

Syninclusions. Air bubbles (few), detritus (many botanical remains).

Remarks. Piece of clear amber that measures 13x12x3 mm. The inclusion is complete except for the missing right metathoracic leg. Furthermore, the right antenna is preserved until the eighth antennomere.

Genus *Sanaungulus* Fanti, Damgaard & Ellenberger, 2018

***Sanaungulus dominikiweissbachi* sp. nov.**
(Fig. 7)

Holotype and Paratype. Male and female, adult specimens in a single Burmese (Kachin) amber piece: Catalog number SNSB-BSPG 2021 XII 75 in the Bayerische Staatssammlung für Paläontologie und Geologie (ex Müller's collection number: BUB4059).

Type locality. Myanmar: Kachin state, Myitkyina District, Hukawng Valley.

Type horizon. Lowermost Cenomanian (98.79 ± 0.62 Ma), mid-Cretaceous.

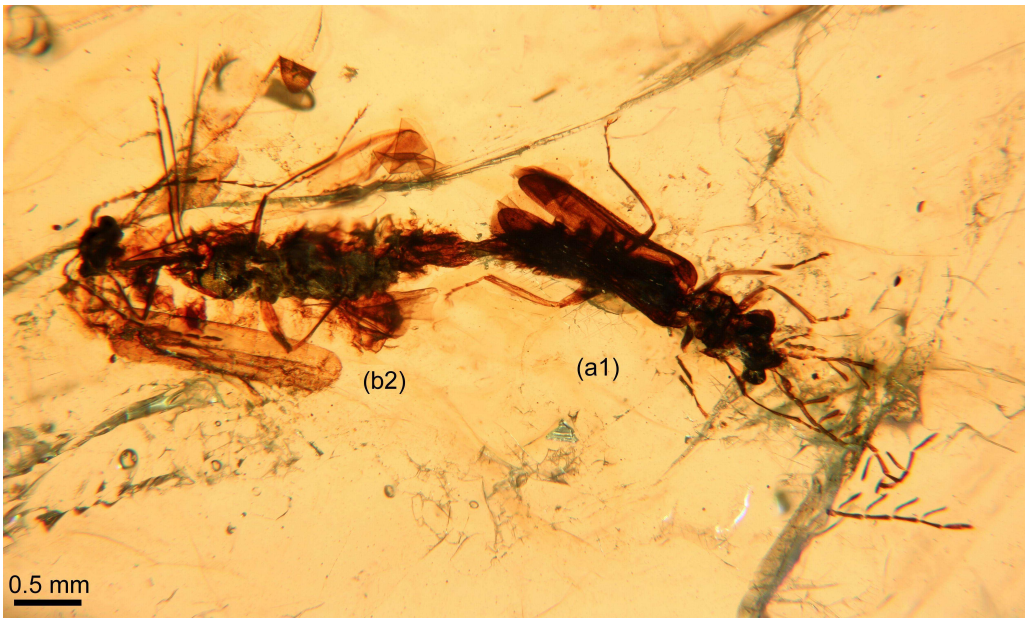

Fig. 7. *Sanaungulus dominikiweissbachi* sp. nov. in Burmese amber. Holotype and Paratype (a1: dorsal view; b2: ventral view).

Differential diagnosis. The specimen of *Sanaungulus dominikiweissbachi* sp. nov. features a male and female, the first Burmese fossil soldier beetles documented preserved during mating. The species is characterized by long (usually only one abdominal segment remains uncovered) and smooth elytra.

Description. Male and female in mating.

MALE (Holotype – A1): adult, winged, slender. Male, defined on the basis of the slender abdomen and visible aedeagus. Body length 2.7 mm. Entirely reddish-brown.

Head slightly transverse, constricted (triangular-shaped) behind the eyes, surface with shallow punctation. Eyes prominent, very large, roundish, inserted in the upper and lateral part of the head. Mandibles elongated, falciform. Maxillary palps 4-segmented with the last palpomere strongly elongated and securiform. Labial palps 3-segmented, with the last palpomere securiform. Antennae 11-segmented, pectinate, relatively long, reaching the half of elytra, antennal insertion very far from the eyes; scape strongly elongated, strongly restricted in the middle and globular at apex; antennomeres II–III short, subequal in length, globular-elongated, antennomere III at apex with a long and robust antennal process; antennomeres IV–VII very long, rather robust, each with an antennal process at apex which is very long and emarginated at apex; antennomeres VIII–IX shorter than previous ones, each with the same antennal process at apex; antennomere X as long as the previous ones, without the antennal process; antennomere XI robust, with rounded apex; all the antennomeres slightly pubescent. Pronotum elongated, almost spherical, slightly wider than head, anterior margin rounded, posterior margin almost straight, sides curved with a small and rounded tooth near the middle, corners obtuse, pronotum disc irregular. Scutellum triangular-shaped. Elytra elongated that do not cover the last abdominal segment, wider than pronotum, parallel-sided, rounded apexes, surface completely smooth with pubescence. Metathoracic wings transparent, very slightly longer than elytra. Last tergite elongated. Aedeagus trilobated with the lobes irregular, long and not plate-like. Legs thin, not particu-

larly long, slightly pubescent; coxae massive; trochanters elongated, robust, rounded apex; femora almost straight, cylindrical, very sturdier than tibiae; tibiae, thin, sub-cylindrical, long, with a thin and long spur near the apex, pro- and mesotibiae longer than pro- and mesofemora, metatibiae very longer than metafemora. Tarsal formula 5-5-5; first tarsomere long, about 1.5 times longer than second; third tarsomere short, about 1.5 times shorter than second; fourth strongly bilobed with lobes very long and pointed apically; fifth tarsomere extremely elongated, thin, slightly flat, curved; claws simple, long, pointed, without denticle at the base.

FEMALE (Paratype – B2): adult, winged, slender. Body length 2.9 mm. Entirely reddish-brown. Morphologically very similar to the Holotype.

Head transverse, constricted behind the eyes. Eyes prominent and large. Mandibles falciform. Last maxillary palpomere securiform. Antennae 11-segmented, filiform, rather long, reaching the half of abdomen, antennal insertion very far from the eyes; scape strongly elongated, restricted in the middle and globular at apex; antennomeres II–III short, subequal in length, globular-elongated; antennomeres IV–V long, rather robust; antennomeres VI–X slightly shorter and less sturdier than previous ones; antennomere XI filiform, elongated, with rounded apex; all the antennomeres slightly pubescent and without antennal process. Pronotum almost spherical. Elytra elongated that do not cover the last abdominal segment and partially the penultimate, completely smooth. Metathoracic wings transparent, very slightly longer than elytra. Sternum elongated with rounded apex. Sternites transverse and pubescent, last sternite wide.

Etymology. Named in honor of Dominik Weißbach, dear friend of the second author (Patrick).

Syninclusions. Air bubbles, detritus.

Remarks. Piece of clear, golden amber that measures 18x13x3 mm. The inclusion is complete, but the male (A1) has the left antenna detached approximately from the end of the antennomere VI and the mesothoracic legs detached from the tibia or femur but with all these parts still present and preserved in the amber piece near the body. While, the female (B2) is complete with only the elytra detached and move upwards. It is not possible to take a proper picture of the other side of specimens as there is a resin layer covering most of this part.

***Sanaungulus dunlopi* sp. nov.**
(Fig. 8)

Holotype. Female, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNSB-BSPG 2021 XII 68 in the Bayerische Staatssammlung für Paläontologie und Geologie (ex Müller's collection number: BUB3886).

Type locality. Myanmar: Kachin state, Myitkyina District, Hukawng Valley.

Type horizon. Lowermost Cenomanian (98.79 ± 0.62 Ma), mid-Cretaceous.

Differential diagnosis. The new species is characterized by an elongated pronotum with a strongly rounded anterior margin, and it is equipped with robust antennomeres. The genus *Sanaungulus* is characterized by very short elytra often with deep punctuation arranged in striae, and by a head restricted behind eyes.

Description. Adult, winged, slender. Female, defined on the shape of the last abdominal segments, and on the basis of short antennae. Body length about 3.2 mm (the body is curled). Entirely brown.

Head short, constricted (triangular-shaped) behind the eyes, smooth, without punctuation, fitted with few long setae. Eyes very prominent, large, roundish, inserted in the lateral part of the head, inter-ocular dorsal distance about 1.3 times greater than eye diameter. Mandibles elongated, falciform. Maxillary palps 4-segmented, with the last palpomere securiform. Antennae 11-segmented, filiform, robust, short, slightly surpassing the middle of the elytra; scape very elongated and club-shaped; antennomere II short; antenno-

meres III–VIII subequal in length, very robust, without antennal process, enlarged at the external corner which is rounded; antennomere IX approximately as long as previous ones, slightly narrower; antennomere X narrower than previous one, slightly enlarged at the external corner; antennomere XI eleongated, strongly squared apically; antennomeres pubescent. Pronotum very elongated, very slightly narrower than head, anterior margin strongly rounded and bordered, posterior margin rather straight and slightly bordered, corners rather acute, sides straight and

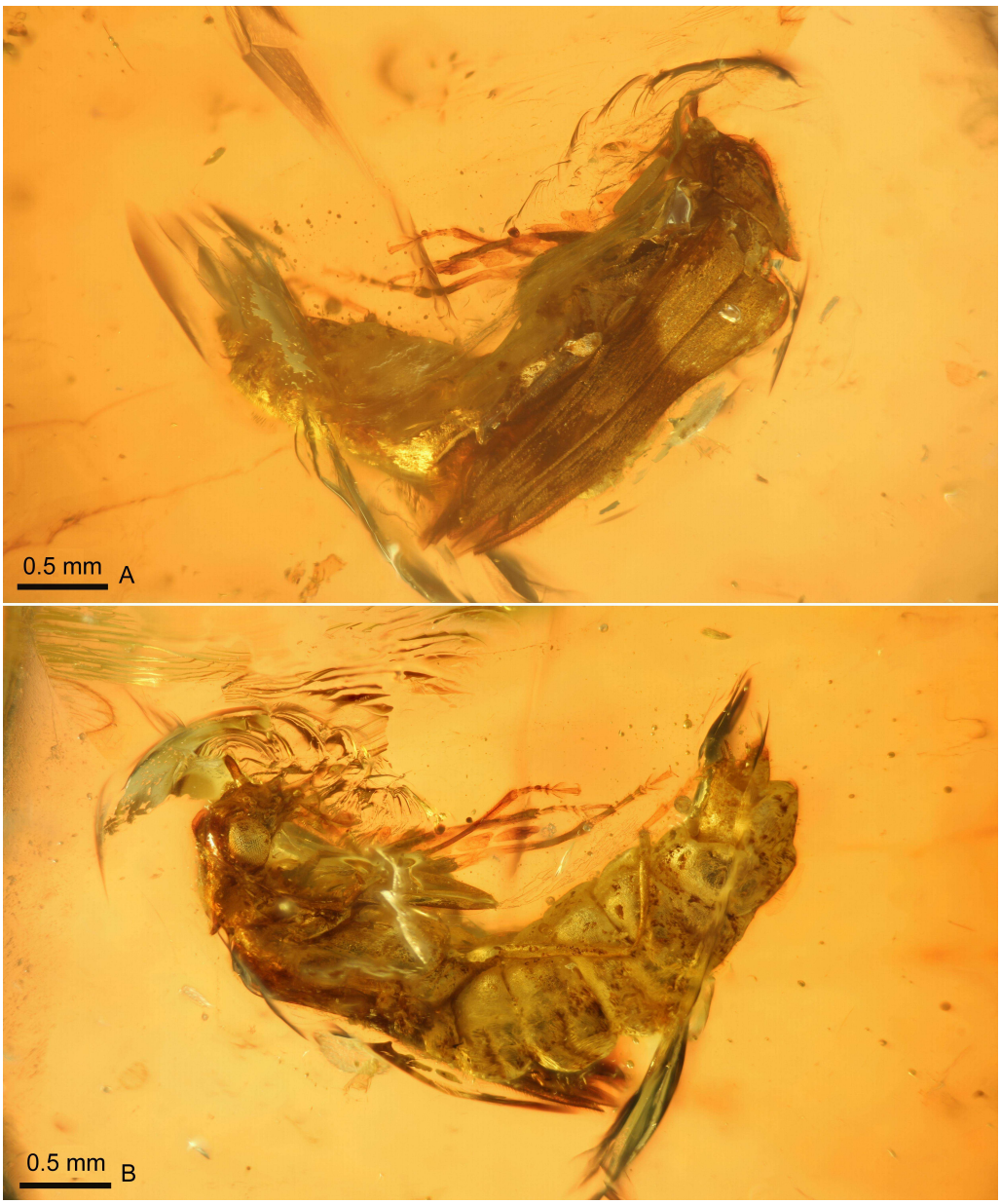

Fig. 8. *Sanaungulus dunlopi* sp. nov. in Burmese amber. A: Holotype, dorsal view; B: Holotype, ventro-lateral view.

slightly bordered, pronotum disc not flat and very slightly wrinkled with shallow punctuation. Scutellum triangular-shaped with pointed apex. Elytra very short which reveals many abdominal segments, wider than pronotum at humery, strongly dehiscent posteriorly, rounded apexes, surface strongly ruguose equipped with several short setae. Metathoracic wings transparent, very short, very slightly surpassing the elytra. Sternum elongated with posterior margin rounded, sternites strongly transverse, robust, equipped with short setae; last tergite short, wide, emarginate at apex; last sternite transverse, robust, short, as long as last tergite, with the posterior margin straight. Legs thin, pro- and mesolegs short, metalegs elongated and slender, pubescent; coxae massive; trochanters elongated and rounded apically; femora nearly straight, slightly sturdier than tibiae (expecially the metafemora); tibiae cylindrical, thin, without spurs near the apex, shorter than femora. Tarsal formula 5-5-5; first tarsomere elongated and thin; second tarsomere slightly shorter than first; third tarsomere slightly elongated and triangular-shaped; fourth strongly bilobed with the lobes very long; fifth tarsomere elongated, flat and enlarged apically; claws simple, without denticle at the base.

Etymology. Named in honor of Jason A. Dunlop (Museum für Naturkunde, Berlin), a well-known specialist of fossil arachnids and their relatives.

Syninclusions. Air bubbles, detritus.

Remarks. Piece of clear, golden amber that measures 10x9x3.5 mm. In the inclusion the right antenna and a leg are not visible.

***Sanaungulus electrum* sp. nov.**
(Fig. 9)

Holotype. Male, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNHM-6005 in the Staatliches Naturhistorisches Museum Braunschweig (ex Müller's collection number: BUB4325).

Type locality. Myanmar: Kachin state, Myitkyina District, Hukawng Valley.

Type horizon. Lowermost Cenomanian (98.79 ± 0.62 Ma), mid-Cretaceous.

Differential diagnosis. The new species is easily distinguishable by the pronotal shape, with the sides concave at the center and with an expansion/tooth near the first apical third. These features are not present in other species of the genus *Sanaungulus*.

Description. Adult, winged, slender. Male, defined on the shape of the last tergite that is very elongated, and on the basis of the rounded last sternite. Body length about 2.9–3.1 mm (head is folded). Entirely brown.

Head elongated, strongly constricted (triangular-shaped) behind the eyes, fitted with rugosity and punctuation. Eyes prominent, large, roundish, inserted in the upper and dorsolateral part of the head. Mandibles elongated, robust, falciform. Antennae 11-segmented, filiform, slender, very short and slightly surpassing the humeral zone of the elytra; scape club-shaped; antennomere II very short, globular; antennomeres III–V, thin, very long, over 2 times longer than second; antennomeres VI–X subequal in length, about 2.0 times shorter than previous ones; antennomere XI filiform, slightly longer than previous ones, rounded at apex; all the antennomeres with short pubescence. Pronotum subquadrate, slightly transverse, anterior margin straight and not bordered, posterior margin rather straight, corners obtuse, sides concave at the center and slightly expanded posteriorly and with an expansion/tooth near the first apical third, pronotum disc smooth. Scutellum triangular-shaped. Elytra short which reveals various abdominal segments, wider than pronotum, at humery enlarged and slightly dehiscent posteriorly, rounded apexes, surface smooth without rugosity and only sligthly pubescent. Metathoracic wings transparent, long, surpassing the elytra and reaching the last abdominal segments. Sternum elongated with posterior margin irregular with an expansion at the center that is very small and forked apically, sternites wide and transverse equipped with short setae; penultimate tergite with a long and thin lobe at sides that is curved; last tergite very elongated,

initially wide and flat, deeply folded apically, with the apical margin forked and globular at sides; last sternite smaller than last tergite and rounded. Legs thin, relatively short, pubescent; coxae massive, large; trochanters short, globular with rounded apex; femora nearly straight, more robust than tibiae, cylindrical; tibiae cylindrical, thin, without spurs near the apex, metatibiae very longer than metafemora. Tarsal formula 5-5-5; first tarsomere long, second tarsomere similar in size to previous one; third tarsomere short and triangular-shaped; fourth strongly bilobed

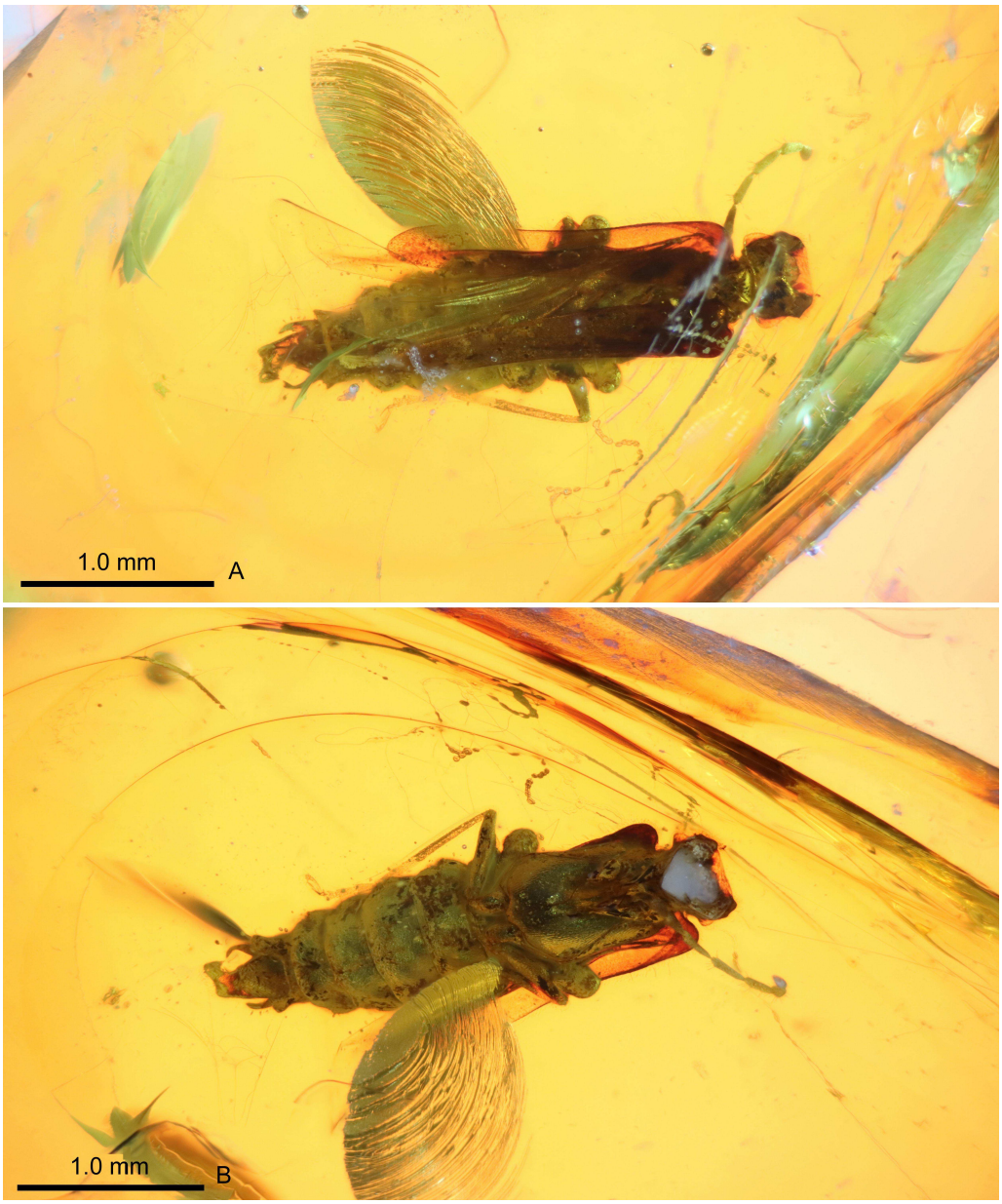

Fig. 9. *Sanaungulus electrum* sp. nov. in Burmese amber. A: Holotype, dorsal view; B: Holotype, ventral view.

and very long; fifth tarsomere elongated, thin, slightly flat and curved; claws simple, apparently without denticle at the base.

Etymology. Derived from the Latin noun "*ēlectrum*" = yellow amber, succinite. Specific epithet is to be treated as noun in apposition.

Syninclusions. Air bubbles, detritus.

Remarks. Piece of clear, golden amber that measures 12x6x2 mm. The inclusion lacks four legs and there is only one antenna that is completely detached from the body. Furthermore, the head (and its frons) in the ventral part is covered by an emulsion like white-cotton.

***Sanaungulus franziskaeweissbachae* sp. nov.** (Fig. 10)

Holotype. Probably male, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNSB-BSPG 2021 XII 72 in the Bayerische Staatssammlung für Paläontologie und Geologie (ex Müller's collection number: BUB 3899).

Type locality. Myanmar: Kachin state, Myitkyina District, Hukawng Valley.

Type horizon. Lowermost Cenomanian (98.79 ± 0.62 Ma), mid-Cretaceous.

Differential diagnosis. *Sanaungulus franziskaeweissbachae* sp. nov. is very similar to *Sanaungulus nilsi* (described in the present work), but the new species differs based on its more robost second antennomere and much longer metathoracic wings. Based on these characters and others of lesser importance, the two specimens are not considered here as male and female of the same species.

Description. Adult, winged, slender. Probably male, defined on the basis of the last abdominal segment triangular shaped. Body length 2.8 mm. Entirely brown.

Head elongated, slightly constricted (triangular-shaped) behind the eyes, equipped with pubescence and shallow punctation. Eyes prominent, extremely large, elongated, inserted in the lateral part of the head. Mandibles elongated, very robust, strongly curved, falciform, pointed apicallly,

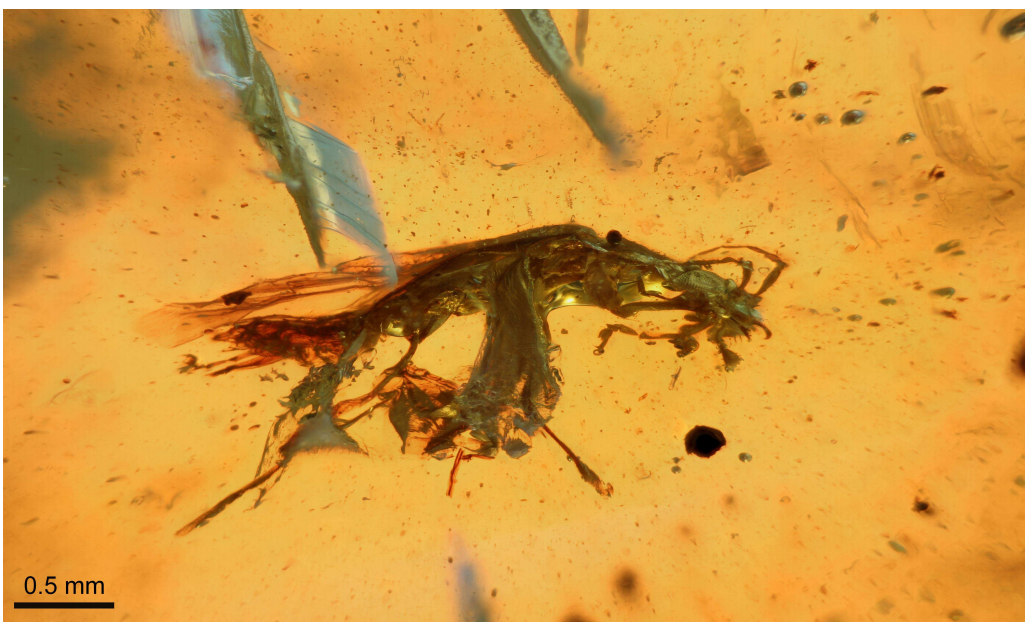

Fig. 10. *Sanaungulus franziskaeweissbachae* sp. nov. in Burmese amber. Holotype, lateral view.

without teeth. Maxillary palps 4-segmented with the last palpomere very elongated and securiform. Labial palps 3-segmented, with the last palpomere elongated and securiform. Antennae 11-segmented, filiform, rather robust, short, approximately reaching the half of elytra, antennal insertion far from the eyes; scape robust, very elongated, slightly club-shaped; antennomeres II–III short, thinner than first, antennomere II suboval and more robust than antennomere III; antennomeres IV–IX subequal, filiform, very elongated; antennomere X slightly shorter than previous ones; antennomere XI filiform, rounded at apex; all the antennomeres with short pubescence. Pronotum very elongated, slightly narrower than head, anterior margin slightly roundish, posterior margin slightly undulated and slightly bordered, sides straight and bordered, corners obtuse, pronotum disc pubescent and slighlty convex near the posterior margin. Scutellum triangular-shaped. Elytra short which reveals various abdominal segments, at humeri slightly wider than pronotum, posteriorly parallel-sided and rather dehiscent apically, rounded apexes, surface pubescent and with a very small rugosity. Metathoracic wings transparent, very long, longer than elytra and surpassing the last abdominal segments. Sternum elongated with posterior margin rounded, sternites narrow and transverse, last tergite elongated with pointed apex which has the margin rounded, last sternite shorter and narrower than last tergite with pointed apex. Legs thin, extremely long, pubescent; coxae extraordinary massive, elongated, very enlarged; trochanters elongated, with rounded apex; femora slightly curved, more robust than tibiae, subcylindrical; tibiae flattened, thin, with a small and obtuse spur near the apex, protibiae very shorter than profemora, meso- and metatibiae very longer than meso- and metafemora. Tarsal formula 5-5-5; first protarsomere long, about 3.0 times longer than second; second protarsomere robust, enlarged apically; third protarsomere short, bilobed with pointed apex; fourth protarsomere strongly bilobed with a pointed and short lobe at each corners; fifth protarsomere elongated, thin, flat and curved; claws simple, without denticle at the base.

Etymology. Named in honor of Franziska Weißbach, dear friend of the second author (Patrick).

Syninclusions. Air bubbles, detritus.

Remarks. Piece of clear, golden amber that measures 11x10x2 mm.The inclusion is complete, but well visible only in the lateral view.

***Sanaungulus havai* sp. nov.**
(Fig. 11)

Holotype. Male, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNHM-6006 in the Staatliches Naturhistorisches Museum Braunschweig (ex Müller's collection number: BUB4453).

Type locality. Myanmar: Kachin state, Myitkyina District, Hukawng Valley.

Type horizon. Lowermost Cenomanian (98.79 ± 0.62 Ma), mid-Cretaceous.

Differential diagnosis. The new species is characterized by antennae equipped with an antennal process near the base of antennomeres IV–X, a feature not present in other *Sanaungulus* except for the species described below (see differential diagnosis below).

Description. Adult, winged, slender. Male, defined on the shape of the last abdominal segments. Body length about 3.2 mm. Testaceous-brown with black head behind the eyes.

Head elongated, strongly constricted (triangular-shaped) behind the eyes, fitted with small rugosity and shallow punctuation. Eyes very prominent, roundish, inserted in the upper and dorsolateral part of the head, inter-ocular dorsal distance about 4.1 times greater than eye diameter. Mandibles elongated, falciform. Maxillary palps 4-segmented, with the last palpomere securiform. Antennae 11-segmented, pectinate, slender, long, almost reaching the apex of the elytra; scape very elongated and enlarged apically; antennomere II short, globular; antennomere III thin, filiform, about 2.1 times longer than second; antennomeres IV–VII subequal in length, each

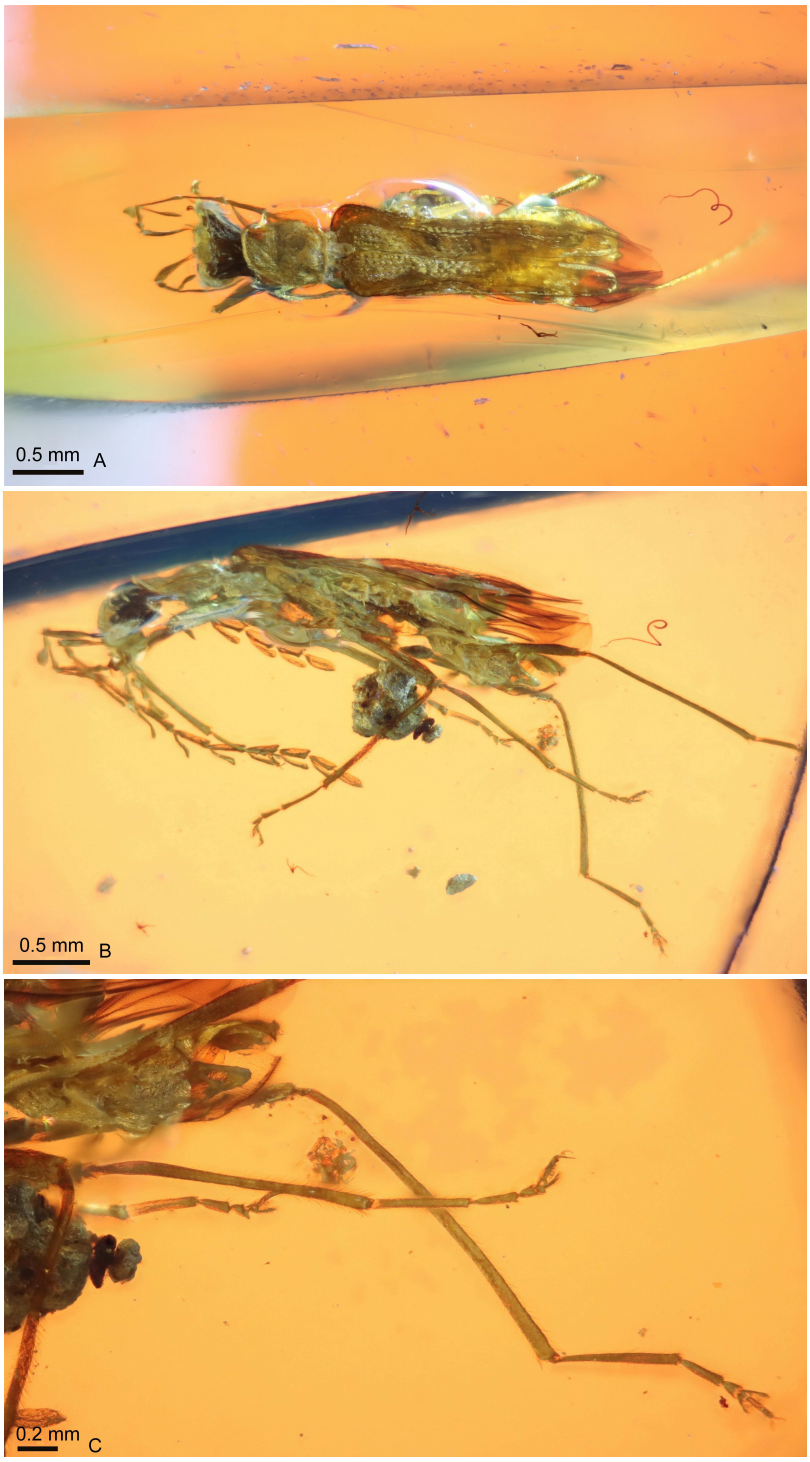

Fig. 11. *Sanaungulus havai* sp. nov. in Burmese amber. A: Holotype, dorsal view; B: Holotype, lateral view; C: Holotype, detail of legs.

equipped near their base with a long, thin and curved antennal process, squared apically; antennomeres VIII–X, slightly shorter and stouter than previous ones, each equipped near their base with a long antennal process (stouter than previous ones), almost rounded apically; antennomere XI filiform and robust; antennomeres pubescent. Pronotum longer than wide, slightly wider than head, anterior margin rounded and bordered, posterior margin rather straight, corners obtuse, sides narrower anteriorly, pronotum disc irregular and slightly wrinkled with impressed punctuation. Scutellum triangular-shaped with rounded apex. Elytra short which reveals two abdominal segments, wider than pronotum, at humery enlarged and very slightly dehiscent posteriorly, rounded apexes, surface with strongly impressed punctuation gathered in striae. Metathoracic wings transparent, long, surpassing the elytra and the last abdominal segments. Sternum elongated with posterior margin irregular, sternites transverse equipped with short setae; last tergite elongated, wide and curved and very slightly folded at the apical sides; penultimate sternite with an urophysis at sides wich is rather robust and evident and rounded at apex; last sternite very elongated, curved and thin. Legs thin, very long, pubescent; coxae massive; trochanters elongated; femora nearly straight, more robust than tibiae, cylindrical; tibiae cylindrical, thin, without spurs near the apex, very longer than femora. Tarsal formula 5-5-5; first tarsomere extremely long and thin; second tarsomere about 2.0 times shorter than first; third tarsomere short and triangular-shaped; fourth strongly bilobed with the lobes very long; fifth tarsomere elongated, thin, slightly flat and curved; claws simple, without denticle at the base.

Etymology. Named in honor of Jiří Háva (Czech Republic), a well-known specialist of the family Dermestidae.

Syninclusions. Air bubbles, detritus, stellate hairs.

Remarks. Piece of clear, golden amber that measures 8x7x3 mm. The inclusion is complete except for the left posterior leg preserved until the first tarsomere.

***Sanaungulus kachinensis* sp. nov.**
(Fig. 12)

Holotype. Male, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNSB-BSPG 2021 XII 14 in the Bayerische Staatssammlung für Paläontologie und Geologie (ex Müller's collection number: BUB4312).

Type locality. Myanmar: Kachin state, Myitkyina District, Hukawng Valley.

Type horizon. Lowermost Cenomanian (98.79 ± 0.62 Ma), mid-Cretaceous.

Differential diagnosis. The new species is characterized by antennae equipped with an antennal process near the base of antennomeres IV–X. It differs from *Sanaungulus havai* sp. nov. based on the head that is less triangular behind the eyes, the pronotum with a median incision, and by antennae with longer rami. It differs from *Sanaungulus ruficollis* Y. Yang, Liu & Zhao in Y. Yang, Zhao, Geiser, W. Zhang, Ren, Bai & Liu, 2022 based on the antennal processes, the pronotum incised, and by longer metathoracic wings (Yang et al. 2022).

Description. Adult, winged, slender. Male, defined on the shape of the last abdominal segments. Body length about 2.8 mm. Entirely brown.

Head elongated, slightly constricted behind the eyes, fitted with small rugosity. Eyes very prominent, roundish, inserted in the upper and dorsolateral part of the head. Mandibles elongated, very robust, falciform. Maxillary palps 4-segmented, with the last palpomere strongly securiform. Labial palps 3-segmented, with the last palpomere securiform. Antennae 11-segmented, pectinate, slender, long, surpassing the apex of the elytra; scape elongated, robust; antennomere II short; antennomere III filiform, about 1.9 times longer than second; antennomeres IV–X subequal in length, each equipped near their base with a very long, robust, almost straight antennal process (longer than antennomere), almost rounded apically; antennomere XI filiform, extremely long, rounded apically; all the antennomeres with short pubescence. Pronotum longer

than wide, as wide as head, anterior margin rounded and bordered, posterior margin rather straight, corners obtuse, sides almost straight, pronotum disc with a transversal median and deep incision, equipped with short setae. Scutellum triangular-shaped. Elytra short which reveals various abdominal segments, as wide as pronotum, sub-parallel, rounded apexes, surface with shallow punctuation and several short setae. Metathoracic wings transparent, long, surpassing the elytra and reaching the last abdominal segments. Sternum elongated, almost straight posteriorly, sternites transverse equipped with short setae; last tergite elongated, wide and strongly

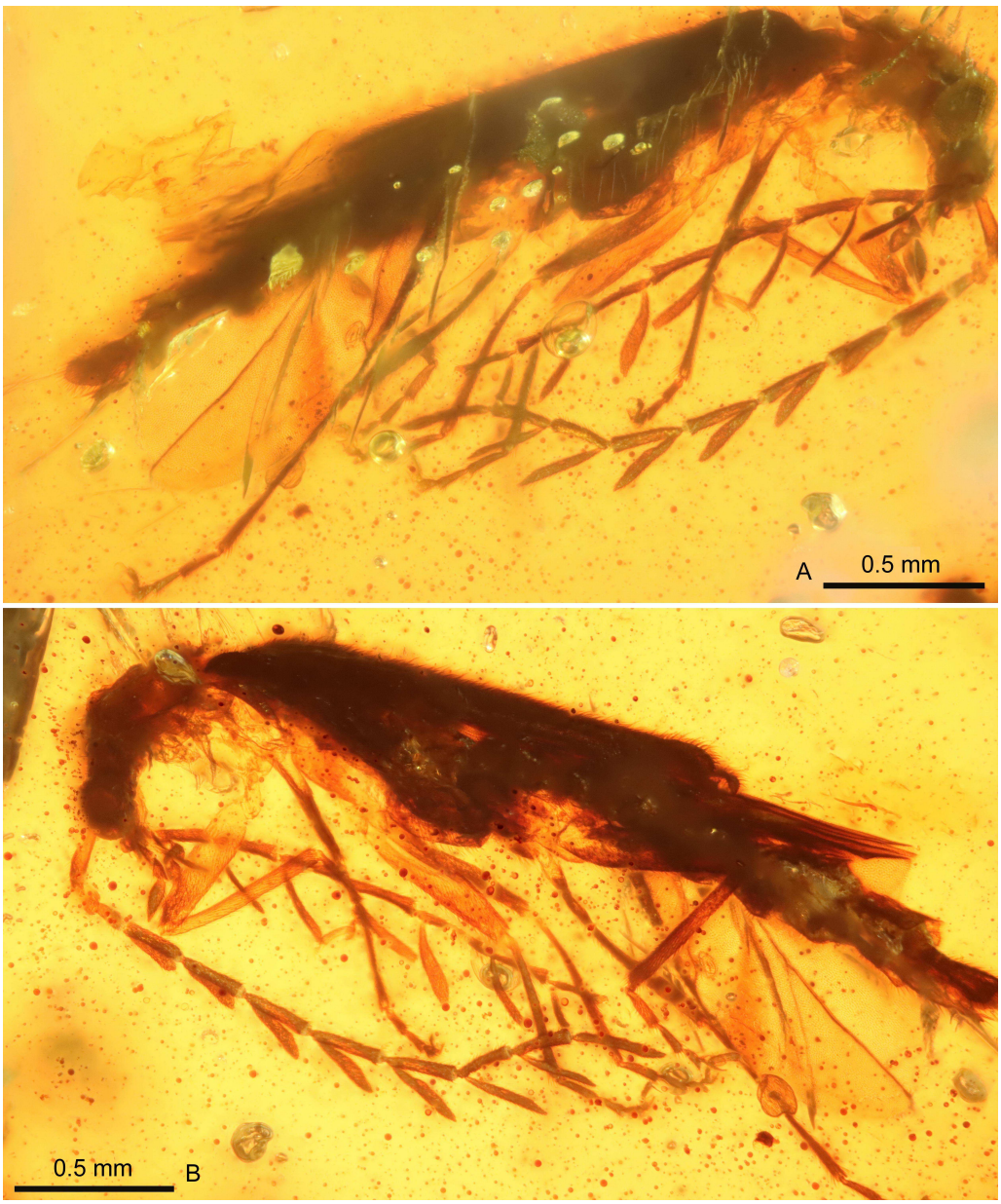

Fig. 12. *Sanaungulus kachinensis* sp. nov. in Burmese amber. A–B: Holotype, lateral views.

globular (spatuliform); last sternite elongated, very thin. Legs thin, long, pubescent; coxae massive, elongated, with rounded apex; trochanters elongated, robust, with rounded apex; femora slightly curved, more robust than tibiae; tibiae cylindrical, thin, without spurs near the apex, pro- and mesotibiae slightly shorter than pro- and mesofemora, metatibiae slightly longer than metafemora. Tarsal formula 5-5-5; first tarsomere long; second tarsomere about 1.2 times shorter than first; third tarsomere triangular-shaped, short, straight apically; fourth tarsomere short, strongly bilobed; fifth tarsomere elongated, thin, flat and strongly curved; claws simple, apparently without denticle at the base.

Etymology. Derived from the toponym Kachin (the locality where the amber mines are located) + the Latin suffix *-ēnsis*.

Syninclusions. Air bubbles, detritus, one Diptera.

Remarks. Piece of clear (surface is slightly blurred), golden amber that measures 11x9x2.5 mm. The inclusion is complete except for the right antenna preserved until the tenth antennomere.

***Sanaungulus kirstenaeweissbachae* sp. nov.**
(Fig. 13)

Holotype. Female, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNHM-6007 in the Staatliches Naturhistorisches Museum Braunschweig (ex Müller's collection number: BUB4483).

Type locality. Myanmar: Kachin state, Myitkyina District, Hukawng Valley.

Type horizon. Lowermost Cenomanian (98.79 ± 0.62 Ma), mid-Cretaceous.

Differential diagnosis. *Sanaungulus kirstenaeweissbachae* sp. nov. differs from *Sanaungulus troelsikloevedali* Fanti & Damgaard, 2019 based on its head that is slightly more transverse and a wider pronotum (Fanti & Damgaard 2019). *Sanaungulus ghitaenoerbyae* Fanti, Damgaard & Ellenberger, 2018 has the last antennomeres more robust and shorter than *Sanaungulus kirstenaeweissbachae* sp. nov. (Fanti et al. 2018). *Sanaungulus kirstenaeweissbachae* sp. nov. differs from *Sanaungulus emarginaticollis* Y. Yang, Liu & Bai in Y. Yang, Zhao, Geiser, W. Zhang, Ren, Bai & Liu, 2022 by its more transverse and different shape of the pronotum (Yang et al. 2022).

Description. Adult, winged, rather robust. Female, defined on the basis of the large last sternite. Body length 3.0 mm. Entirely brown.

Head very transverse, constricted (triangular-shaped) behind the eyes, surface irregular with shallow punctation. Eyes prominent, very large, sub-elliptical, inserted in the lateral part of the head. Mandibles elongated, falciform. Maxillary palps 4-segmented with the last palpomere elongated and securiform. Labial palps 3-segmented, with the last palpomere securiform. Antennae 11-segmented, pectinate, long, slightly surpassing the apex of elytra, antennal insertion far from the eyes; scape club-shaped, elongated, very robust; antennomeres II–III short, subequal in length, swollen apically; antennomeres IV–VII extremely long, each equipped at apex with an antennal process which is very long and thin with an emarginate apex; antennomeres VIII–X shorter than previous ones, not enlarged and robust, without the antennal process at apex; antennomere XI filiform, not enlarged and robust, long, with rounded apex; all the antennomeres slightly pubescent. Pronotum very transverse, approximately as wide as head, anterior margin undulate and slightly bordered, posterior margin almost straight and feebly bordered, sides rounded, corners obtuse, pronotum disc irregular with very shallow punctation. Scutellum narrow, triangular-shaped, pointed at apex. Elytra short which reveals some abdominal segments, at humeri wider than pronotum, posteriorly parallel-sided and very slightly dehiscent apically, rounded apexes, surface presenting a very coarse and wide punctation gathered in evident striae visible for the entire elytral length. Metathoracic wings transparent, longer than elytra, not reaching the last abdominal segment. Sternum very robust with margin almost straight; sternites transverse, wide and pubescent; last

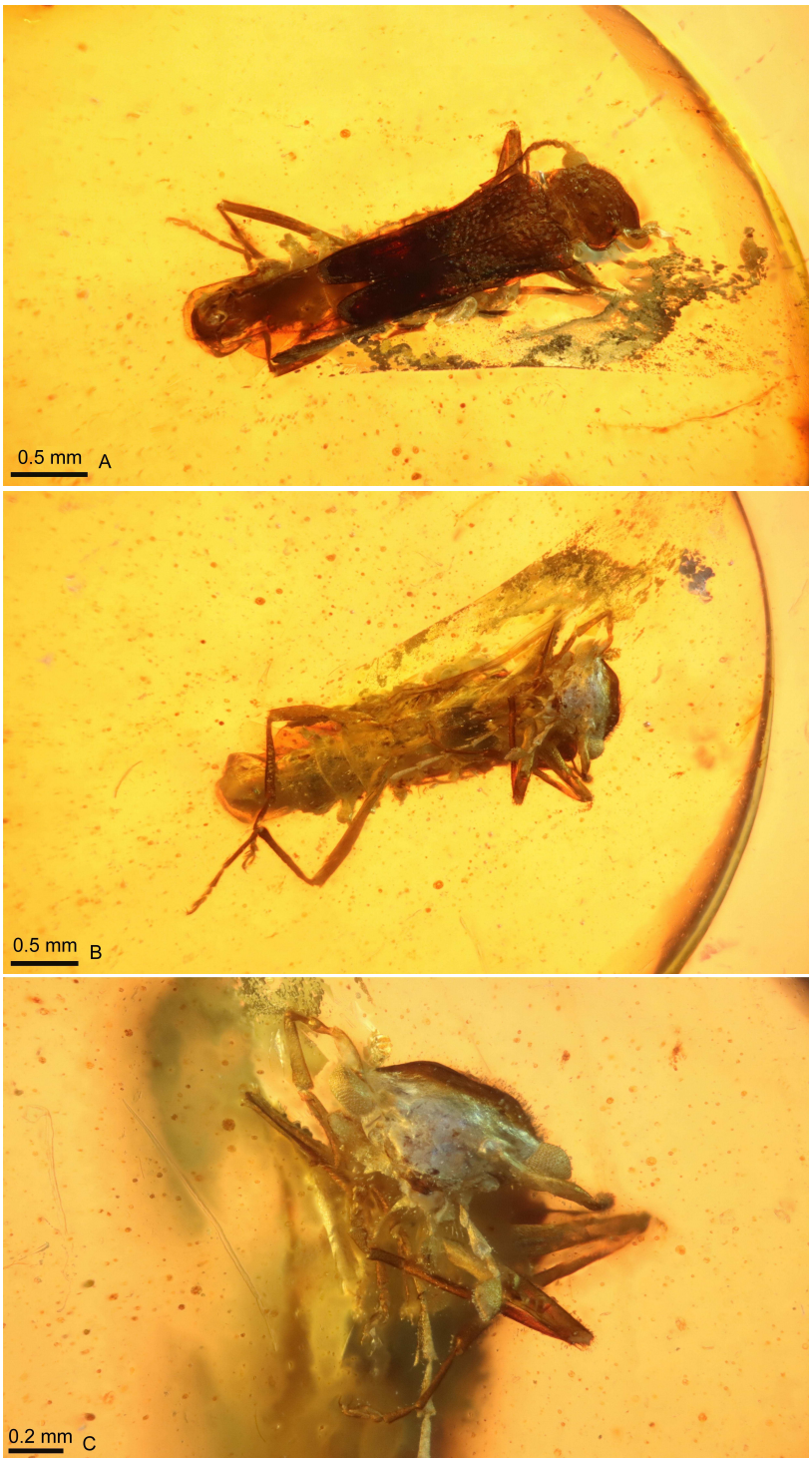

Fig. 13. *Sanaungulus kirstenaeweissbachae* sp. nov. in Burmese amber. A: Holotype, dorsal view; B: Holotype, ventral view; C: Holotype, detail of head.

sternite very large and robust, rounded. Legs rather robust, relatively long, slightly pubescent; coxae massive; trochanters very elongated, robust, with rounded apex; femora almost straight, sub-cylindrical, slightly sturdier than tibiae; tibiae, thin, sub-cylindrical, with a small spur near the apex, protibiae approximately as long as profemora, mesotibiae longer than mesofemora, metatibiae shorter than metafemora. Tarsal formula 5-5-5; first metatarsomere extremely long, about 2.3 times longer than second; third tarsomere short; fourth strongly bilobed; fifth tarsomere elongated, thin, cylindrical and curved; claws simple, pointed, without denticle at the base.

Etymology. Named in honor of Kirsten Weißbach, dear friend of the second author (Patrick).

Syninclusions. Air bubbles, detritus, an Alydidae.

Remarks. Piece of clear, golden amber in Cabochon that measures 14x10x4 mm. The inclusion is complete, with the head partially covered by emulsion.

***Sanaungulus leniae* sp. nov.**
(Fig. 14)

Holotype. Sex undefined, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNHM-6008 in the Staatliches Naturhistorisches Museum Braunschweig (ex Müller's collection number: BUB4315).

Type locality. Myanmar: Kachin state, Myitkyina District, Hukawng Valley.

Type horizon. Lowermost Cenomanian (98.79 ± 0.62 Ma), mid-Cretaceous.

Differential diagnosis. The non-dehiscent and wide elytra make this new species easily distinguishable from all other *Sanaungulus*. This character could easily make one think we this is a new genus; unfortunately, the specimen has a crumpled abdomen and we cannot evaluate the length of the elytra. Only the discovery of one or more similar specimens will clarify the taxon.

Description. Adult, winged, rather robust. Sex undefined. Body length 2.1 mm. Entirely reddish-brownish.

Head transverse, wide, slightly convex in the apex, constricted behind the eyes, covered by pronotum, smooth with short pubescence. Eyes prominent, large, convex, roundish-subelliptic, inserted in the lateral-upper part of the head, inter-ocular dorsal distance about 3.9 times greater than the eye diameter. Mandibles falciform, slender. Maxillary palps 4-segmented with the last palpomere securiform. Labial palps 3-segmented. Antennae 11-segmented, filiform, short, not reaching the half of elytra, antennal insertion in frons, far from eyes; scape elongated, robust, curved and distorted; antennomere II short, robust, enlarged and globular from the middle to the apex; antennomere III thinner and longer than second; antennomere IV slightly shorter than antennomere III; antennomeres V–VIII filiform and sub-equal in length; antennomeres IX–XI globular-elongated, sturdier than previous ones, with antennomere IX clavate, antennomere X shorter than previous one and antennomere XI rounded at apex; all the antennomeres with very short pubescence. Pronotum transverse, as long as head (eyes are slightly extruded), anterior margin very slightly curved and not bordered, posterior margin almost straight and not bordered, sides strongly curved, corners rounded, pronotum disc smooth and flat and pubescent. Scutellum small, triangular-shaped, with pointed apex. Elytra elongate, wider than pronotum and head, subparallel-sided with apex enlarged, strongly rounded apexes, surface smooth without punctaction, and sligthly pubescent equipped with short and not erected setae. Metathoracic wings transparent, almost completely covered by elytra, as long as elytra or very slightly longer. Sternum very elongated and subquadrate with posterior margin almost straight, sternites transverse, last tergite elongated, narrower than previous ones and rounded at apex. Legs thin, rather long, pubescent; coxae massive, elongated, curved; trochanters elongated, curved, roundish at apex; femora very sturdier than tibiae, nearly straight; tibiae cylindrical, thin, without

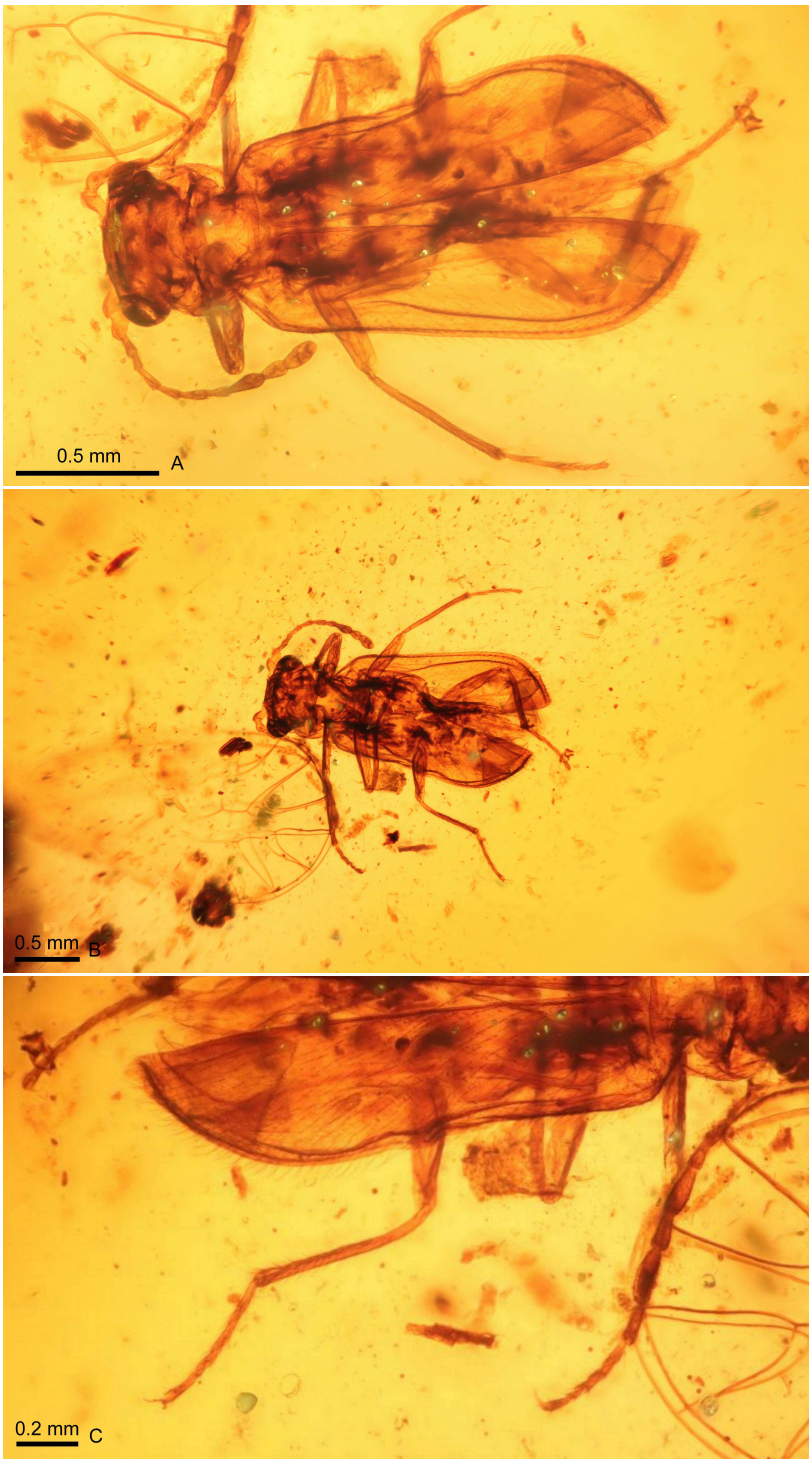

Fig. 14. *Sanaungulus leniae* sp. nov. in Burmese amber. A: Holotype, dorsal view; B: Holotype, ventral view; C: Holotype, detail of right metathoracic leg and right antenna.

spurs near the apex, metatibiae longer than metafemora. Tarsal formula 5-5-5; first tarsomere very elongated and thin; second tarsomere about 1.3 times shorter than first, third tarsomere shorter than second; fourth slightly bilobed; fifth tarsomere elongated, thin, flat and curved; claws simple, without denticle at the base.

Etymology. Named in honor of Leni Müller, daughter of the second author (Patrick).

Syninclusions. Two Psocoptera, one Diptera, air bubbles, detritus.

Remarks. Piece of clear, golden amber in Cabochon cut 27x14x5 mm. The inclusion is complete, but its abdomen is folded and crumpled.

***Sanaungulus myanmaricus* sp. nov.**
(Fig. 15)

Holotype. Probable male, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNHM-6009 in the Staatliches Naturhistorisches Museum Braunschweig (ex Müller's collection number: BUB4166).

Type locality. Myanmar: Kachin state, Myitkyina District, Hukawng Valley.

Type horizon. Lowermost Cenomanian (98.79 ± 0.62 Ma), mid-Cretaceous.

Differential diagnosis. *Sanaungulus myanmaricus* sp. nov. is characterized by a very elongated pronotum with the surface slightly undulate, a feature present only in *Sanaungulus nilsi* sp. nov. and *Sanaungulus kachinensis* sp. nov. *S. nilsi* has a pronotum more concave in the middle and more bordered at the margins (especially at the posterior margin), while *S. kachinensis* has a pronotum that is shorter and with a transversal incision.

Description. Adult, winged, slender. Probable male, defined on the basis of slender abdomen and long antennae. Body length 3.2 mm. Entirely brown.

Head transverse, constricted (triangular-shaped) behind the eyes, equipped with pubescence and punctation. Eyes prominent, large, roundish, inserted in the upper and lateral part of the head. Mandibles elongated, falciform. Maxillary palps

Fig. 15. *Sanaungulus myanmaricus* sp. nov. in Burmese amber. Holotype, lateral view.

4-segmented with the last palpomere securiform. Labial palps 3-segmented, with the last palpomere elongated and strongly securiform. Antennae 11-segmented, pectinate, surpassing half of elytra and reaching half of abdomen, antennal insertion in the eyes proximity; scape slender, elongated, slightly enlarged apically; antennomere II short, swollen apically; antennomere III elongated, filiform, about 1.8 times longer than second; antennomere IV longer and stouter than previous one; antennomeres V–IX extremely long, each equipped near the base with a long antennal process which is very long and rounded apically; antennomere X shorter than previous ones, equipped with an antennal process shorter than others and slightly squadrate at the base; antennomere XI short and robust, with rounded apex; all the antennomeres pubescent. Pronotum very elongated, narrower than head, anterior margin undulate, posterior margin extend backward in the middle and slightly bordered, sides straight and bordered, corners obtuse, pronotum disc irregular with small concavity and drafts. Scutellum triangular-shaped. Elytra short which reveals various abdominal segments, at humeri wider than pronotum, posteriorly parallel-sided and slightly dehiscent apically, rounded apexes, surface pubescent. Metathoracic wings transparent, slightly longer than elytra. Sternum elongated, sternites transverse, last abdominal segment wide and with rounded apex. Legs thin, extremely long, pubescent; coxae massive; trochanters elongated, with rounded apex; femora almost straight, cylindrical, slightly sturdier than tibiae; tibiae, thin, cylindrical, extremely long, with a spur near the apex, pro- and mesotibiae shorter than pro- and mesofemora, metatibiae as long as metafemora. Tarsal formula 5-5-5; first tarsomere long, about 2.0 times longer than second; third tarsomere short, triangular-shaped; fourth strongly bilobed; fifth tarsomere extremely elongated, thin, flat and curved; claws simple, long, pointed, without denticle at the base.

Etymology. Derived from the toponym Myanmar (nation where the amber mines are located).

Syninclusions. Air bubbles, detritus, stellate hairs, an unidentified insect.

Remarks. Piece of clear, golden amber that measures 18x11x4 mm. The inclusion is complete but well visible only laterally (one side).

***Sanaungulus myitkyinaensis* sp. nov.**
(Fig. 16)

Holotype. Probable male, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNHM-6010 in the Staatliches Naturhistorisches Museum Braunschweig (ex Müller's collection number: BUB4462).

Type locality. Myanmar: Kachin state, Myitkyina District, Hukawng Valley.

Type horizon. Lowermost Cenomanian (98.79 ± 0.62 Ma), mid-Cretaceous.

Differential diagnosis. *Sanaungulus myitkyinaensis* sp. nov. is characterized by pectinated antennae with an antennal process in antennomeres VI–X. The new species is easily distinguishable from other *Sanaungulus* by its extremely elongated head.

Description. Adult, winged, rather robust. Probable male, defined on the basis of long antennae. Body length 3.3 mm. Entirely brown.

Head extremely long, curved, surface smooth equipped with only some long hairs. Eyes relatively small, very slightly sub-elliptical, inserted in the upper and lateral part of the head. Mandibles elongated, falciform, slender with a pointed apex. Maxillary palps 4-segmented with the last palpomere securiform. Labial palps 3-segmented, with the last palpomere securiform. Antennae 11-segmented, pectinate, very long, almost reaching the last abdominal segment, antennal insertion in the eyes proximity; scape club-shaped; antennomere II short, slightly swollen apically; antennomere III elongated, filiform, about 1.4 times longer than second; antennomeres IV–V extremely long, without antennal process, enlarged (in a shape of a draft) apically, antennomere V the longest; antennomere VI elongated, as long as antennomere IV, equipped near the base with a long antennal process which is very long and rounded apically; antennomere VII

shorter than previous one, equipped with a long antennal process near the base; antennomeres VIII–X sub-equal, shorter and sturdier than previous one, each equipped near the base with an antennal process shorter and slightly sturdier than others; antennomere XI rather robust, with slightly squadrate and pointed apex; all the antennomeres pubescent. Pronotum elongated, slightly narrower than head, anterior margin straight and strongly bordered, posterior margin slightly undulate (expecially in the middle) and strongly bordered, sides straight and bordered,

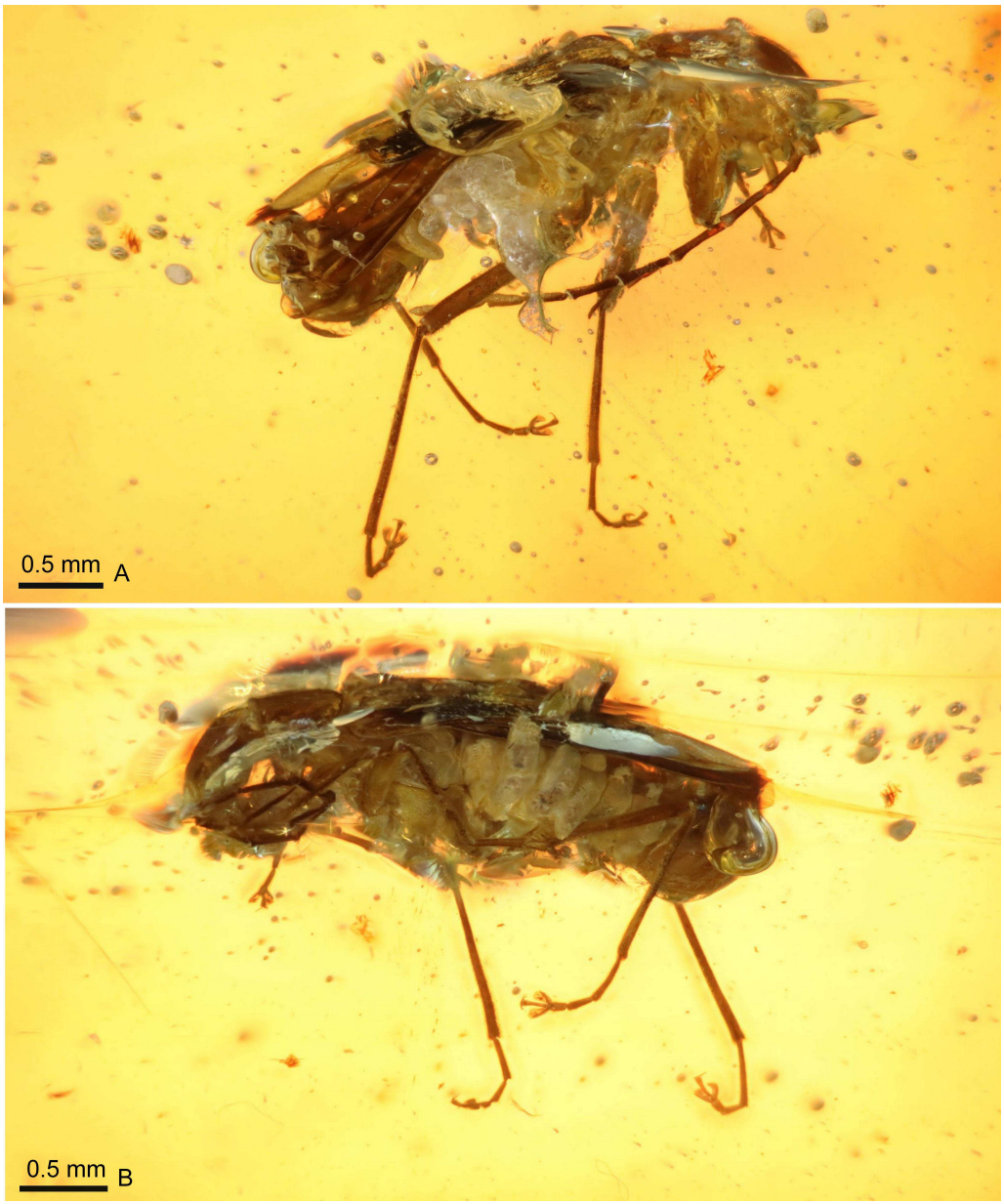

Fig. 16. *Sanaungulus myitkyinaensis* sp. nov. in Burmese amber. A: Holotype, dorso-lateral view; B: Holotype, ventro-lateral view.

corners rounded, pronotum disc almost flat with short pubescence. Elytra short which reveals various abdominal segments, wider than pronotum, gibbous at humeri, parallel-sided, rounded apexes, surface pubescent with confused and impressed punctuation. Metathoracic wings longer than elytra, reaching the last abdominal segments. Sternites transverse, last sternite very wide. Legs thin, long, pubescent; coxae massive; trochanters elongated; femora almost straight, cylindrical, sturdier than tibiae; tibiae, thin, cylindrical, long, without a spur at apex, protibiae shorter than profemora, meso- and metatibiae longer than meso- and metafemora. Tarsal formula 5-5-5; first tarsomere very long, about 2.0 times longer than second; third tarsomere robust; fourth strongly bilobed; fifth tarsomere elongated, thin, curved; claws simple, without denticle at the base.

Etymology. Derived from the toponym Myitkyina (district where the amber mines are located) + the Latin suffix *-ēnsis*.

Syninclusions. Air bubbles, detritus.

Remarks. Piece of clear, golden amber that measures 13x10x3 mm. The inclusion is complete but the head is bent and the left proleg is not well visible.

***Sanaungulus nalae* sp. nov.**
(Fig. 17)

Holotype. Male, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNHM-6011 in the Staatliches Naturhistorisches Museum Braunschweig (ex Müller's collection number: BUB4033).

Type locality. Myanmar: Kachin state, Myitkyina District, Hukawng Valley.

Type horizon. Lowermost Cenomanian (98.79 ± 0.62 Ma), mid-Cretaceous.

Differential diagnosis. *Sanaungulus nalae* sp. nov. differs from other *Sanaungulus* with filiform antennae for a combination of characters: Head partially covered by pronotum, smooth elytra, and a pronotal shape with the sides wider near the posterior margin and narrower from the anterior margin to the middle.

Description. Adult, winged, slender. Male, defined on the shape of the last sternite which is triangular, and narrower than the last tergite. Body length 5.2 mm. Entirely brown.

Head transverse, wide, slightly convex in the middle, constricted behind the eyes, smooth with short pubescence. Eyes prominent, very large, roundish and slightly subelliptic, inserted in the lateral part of the head, inter-ocular dorsal distance about 2.1 times greater than the eye diameter. Mandibles falciform. Maxillary palps 4-segmented with the last palpomere very elongated, securiform. Labial palps 3-segmented. Antennae 11-segmented, filiform, short, slightly surpassing the half of elytra and almost reaching the half of abdomen, antennal insertion in the eyes proximity; scape elongated, robust; antennomere II very short, subovate; antennomere III thinner and about 1.8 times longer than second; antennomeres IV–V subequal, slightly longer than antennomere III; antennomere VI as long as the previous ones, slightly thinner; antennomeres VII–X filiform, subequal; antennomere XI filiform, slightly sturdier than previous ones, rounded at apex; all the antennomeres with short pubescence. Pronotum transverse, wider than head, narrow anteriorly, anterior margin rounded and strongly bordered, posterior margin almost straight, sides enlarged near the posterior margin and narrower from the anterior margin to the middle, posterior corners rounded, pronotum disc smooth and pubescent. Scutellum triangular-shaped. Elytra short which reveals various abdominal segments, at humeri wider than pronotum, humeral zone slightly gibbous, posteriorly parallel-sided, rounded apexes, surface smooth and sligthly pubescent equipped with short setae. Metathoracic wings infuscate, very longer than elytra, not reaching the apex of abdomen. Sternum elongated with posterior margin rounded, sternites narrow and transverse, last tergite wide with posterior margin rounded, last sternite triangular and narrower than last tergite. Legs thin, relatively short, pubescent; coxae mas-

Fig. 17. *Sanaungulus nalae* sp. nov. in Burmese amber. A: Holotype, dorsal view; B: Holotype, ventral view; C: Holotype, detail of head and pronotum.

sive, elongated, curved; trochanters elongated, curved, roundish at apex; femora more robust than tibiae, nearly straight; tibiae cylindrical, thin, without spurs near the apex, longer than femora. Tarsal formula 5-5-5; first tarsomere long, about 2.8 times longer than second; third tarsomere short, triangular; fourth strongly bilobed; fifth tarsomere elongated, thin, flat and curved; claws simple, without denticle at the base.

Etymology. Named in honor of Nala Müller, daughter of the second author (Patrick).

Syninclusions. Diptera (partial), air bubbles, detritus.

Remarks. Piece of clear, honey colored amber that measures 10x10x4.5 mm. The inclusion is complete. The specimen is ventrally covered by a white and large cotton-like emulsion.

***Sanaungulus nilsi* sp. nov.**
(Fig. 18)

Holotype. Female, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNSB-BSPG 2021 XII 64 in the Bayerische Staatssammlung für Paläontologie und Geologie (ex Müller's collection number: BUB4393).

Type locality. Myanmar: Kachin state, Myitkyina District, Hukawng Valley.

Type horizon. Lowermost Cenomanian (98.79 ± 0.62 Ma), mid-Cretaceous.

Differential diagnosis. *Sanaungulus nilsi* sp. nov. differs from other species of *Sanaungulus* with filiform antennae by its very elongated pronotum.

Description. Adult, winged, slender. Female, defined on the basis of short antennae and large abdomen. Body length 3.3 mm. Entirely brown with testaceous abdomen.

Head rounded, slightly constricted (triangular-shaped) behind the eyes, equipped with dense pubescence and shallow punctation. Eyes prominent, large, roundish, inserted in the upper and lateral part of the head. Mandibles elongated, falciform, without teeth. Maxillary palps 4-segmented with the last palpomere very elongated and securiform. Labial palps 3-segmented, with the last palpomere elongated and securiform. Antennae 11-segmented, filiform, robust, short, reaching half of elytra and the first abdominal segment, antennal insertion in the eyes proximity; scape robust, club-shaped; antennomeres II–III short, subequal, thinner than first; antennomere IV elongated, the longest; antennomeres V–X slightly shorter than antennomere IV, subequal, with antennomeres V–VIII sturdier than others; antennomere XI filiform, longer than previous ones, enlarged in the middle, rounded at apex; all the antennomeres with short pubescence. Pronotum very elongated, subrectangular, as wide as head, concave in the middle, anterior margin straight, posterior margin slightly undulated and strongly bordered, sides straight and bordered, corners obtuse, pronotum disc concave and pubescent. Scutellum triangular-shaped. Elytra short which reveals various abdominal segments, at humeri slightly wider than pronotum, posteriorly parallel-sided and slighty dehiscent apically, rounded apexes, surface pubescent and with a very small rugosity. Metathoracic wings longer than elytra, slightly surpassing the half of abdomen. Sternum elongated with posterior margin rounded, sternites large and transverse, last tergite elongated with rounded apex and narrower than penultimate tergite which is large and transverse, last sternite wide and enlarged at sides and slightly pointed apically. Legs thin, relatively long, pubescent; coxae massive; trochanters elongated, with rounded apex; femora slightly curved, more robust than tibiae, slightly flat; tibiae flattened, thin, with spurs near the apex, protibiae as long as profemora, mesotibiae slightly longer than mesofemora, metatibiae longer than metafemora. Tarsal formula 5-5-5; first tarsomere long, about 0.4 times longer than second; third tarsomere short and slightly bilobed; fourth strongly bilobed; fifth tarsomere elongated, thin, slightly flat and curved; claws simple, without denticle at the base.

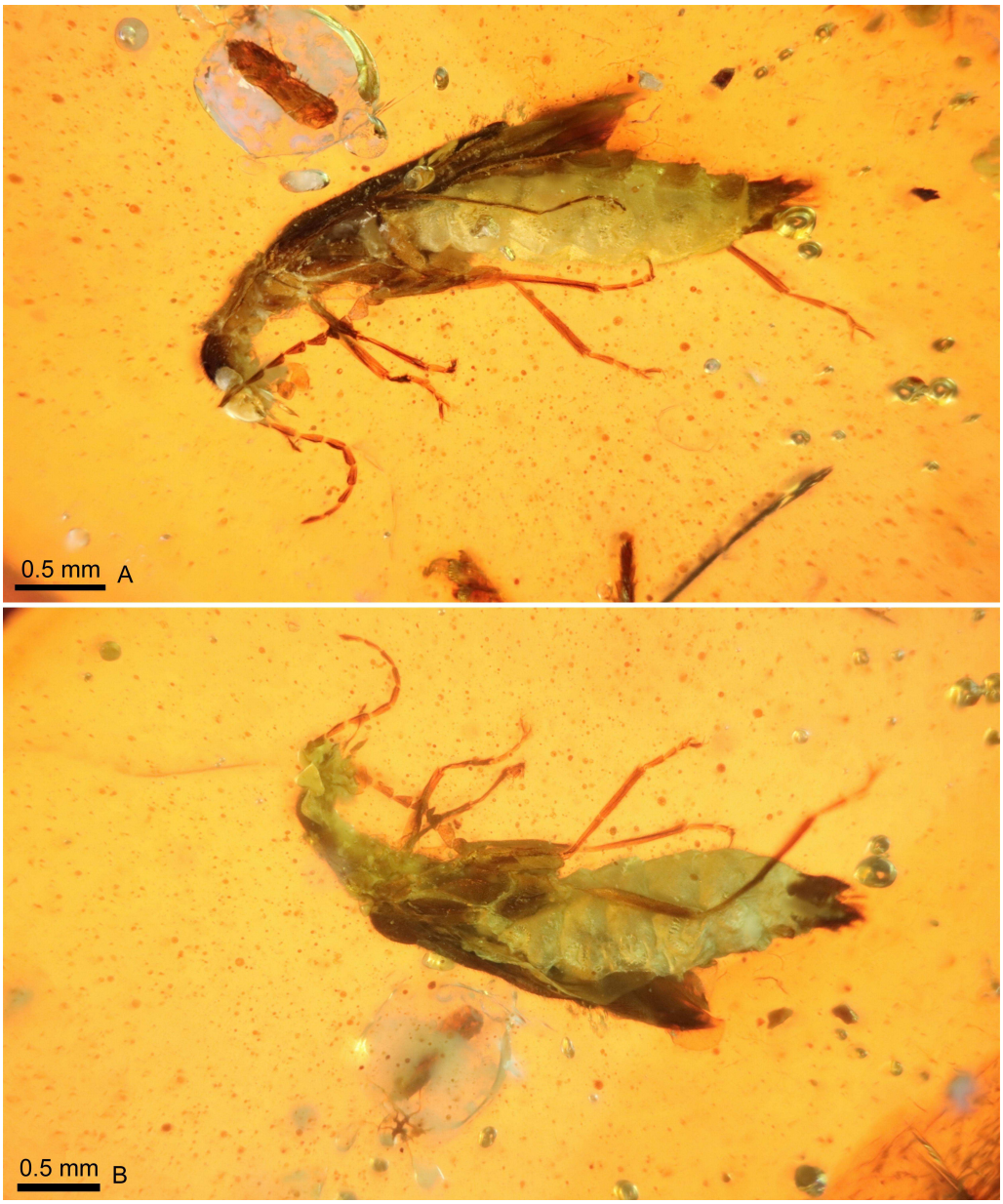

Fig. 18. *Sanaungulus nilsi* sp. nov. in Burmese amber: A: Holotype, lateral view; B: Holotype, ventral view.

Etymology. Named in honor of Nils Müller, son of the second author (Patrick).

Syninclusions. Cecidomyiidae (leg), cicada (leg), air bubbles, detritus.

Remarks. Piece of clear, golden amber that measures 19x7.5x3.3 mm. The inclusion is complete.

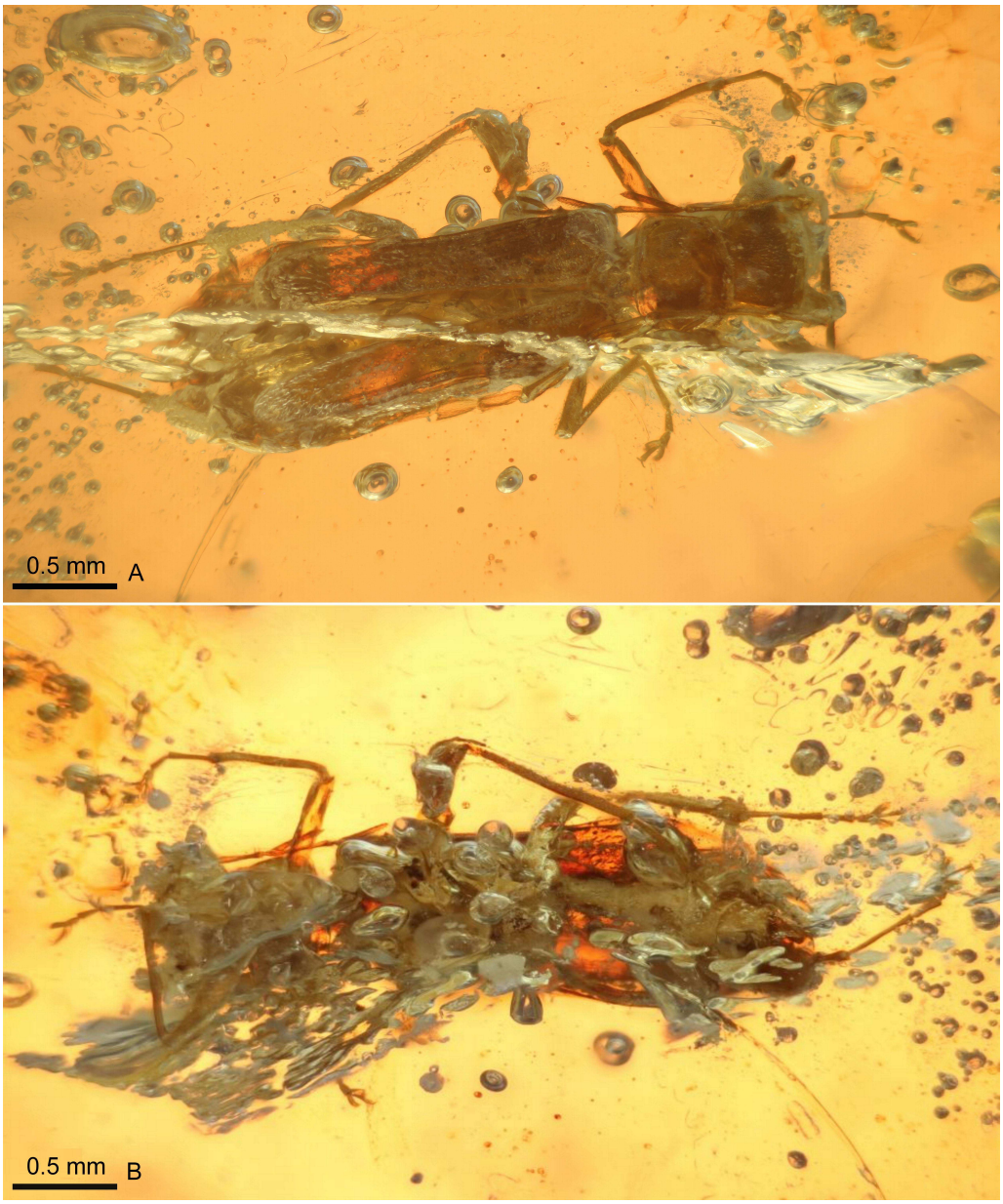

Fig. 19. *Sanaungulus perkovskyi* sp. nov. in Burmese amber. A: Holotype, dorsal view; B: Holotype, ventral view.

***Sanaungulus perkovskyi* sp. nov.**
(Fig. 19)

Holotype. Male, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNSB-BSPG 2021 XII 69 in the Bayerische Staatssammlung für Paläontologie und Geologie (ex Müller's collection number: BUB3888).

Type locality. Myanmar: Kachin state, Myitkyina District, Hukawng Valley.

Type horizon. Lowermost Cenomanian (98.79 ± 0.62 Ma), mid-Cretaceous.

Differential diagnosis. *Sanaungulus perkovskyi* sp. nov. is characterized by a strongly transverse pronotum and pectinate antennae (the antennal process in antennomeres IV–VII). *Sanaungulus ghitaenoerbyae* Fanti, Damgaard & Ellenberger, 2018 is the most similar taxon and differs from the new species because of its more transverse head and its pronotum with its sides and posterior margin not straight (Fanti et al. 2018). *Sanaungulus troelsikloevedali* Fanti & Damgaard, 2019 differs from the new species described here by its longer antennae with more slender last antennomeres (Fanti & Damgaard 2019).

Description. Adult, winged, rather robust. Male, defined on the basis of the last abdominal segment triangular shaped. Body length 3.2 mm. Entirely testaceous-brown.

Head not particularly transverse, constricted (triangular-shaped) behind the eyes, pubescent with shallow punctation. Eyes prominent, large, roundish, inserted in the upper and lateral part of the head. Mandibles elongated, falciform. Maxillary palps 4-segmented with the last palpomere securiform. Labial palps 3-segmented, with the last palpomere securiform. Antennae 11-segmented, pectinate, approximately slightly surpassing the half of elytra, antennal insertion far from the eyes; scape club-shaped, robust; antennomeres II–III short with antennomere II sturdier and swollen apically; antennomeres IV–VI extremely long, each equipped with an antennal process at apex which is very long and robust and slightly pointed apically; antennomere VII shorter than previous ones, equipped with a long antennal process; antennomere VIII sturdier and shorter than previous one and without the antennal process; antennomeres IX–X very robust, flat, enlarged at sides; antennomere XI filiform, less sturdier than previous ones, with rounded apex; all the antennomeres pubescent with setae very short. Pronotum transverse, wider than head, anterior margin undulate and strongly bordered, posterior margin straight and bordered, sides straight and bordered, corners obtuse, pronotum disc pubescent with shallow punctation. Scutellum triangular-shaped, very wide at base, with rounded apex. Elytra short which reveals some abdominal segments, robust, wider than pronotum, posteriorly parallel-sided and not dehiscent apically, rounded apexes, surface with coarse and impressed punctation gathered in striae. Metathoracic wings transparent, longer than elytra. Sternum elongated with posterior margin almost straight, sternites transverse and pubescent, last sternite small and triangular shaped. Legs thin, long, slightly pubescent; coxae massive; trochanters small, rounded; femora almost straight, slightly flat, sturdier than tibiae; tibiae, thin, cylindrical, long, without spurs near the apex, pro- and mesotibiae very slightly longer than pro- and mesofemora, metatibiae longer than metafemora. Tarsal formula 5-5-5; first tarsomere long, about 1.4 times longer than second; third tarsomere short, triangular-shaped; fourth strongly bilobed with lobes elongated and rounded apically; fifth tarsomere elongated, thin, cylindrical and curved; claws simple, long, pointed, without denticle at the base.

Etymology. Named in honor of Evgeny E. Perkovsky (Ukraine), a well-known palaeontologist.

Syninclusions. Air bubbles (very large), detritus.

Remarks. Piece of very clear amber that measures 12x8x2 mm. The inclusion is complete, but many big bubbles in the amber cover the majority of its ventral part.

***Sanaungulus peteriruedeli* sp. nov.**
(Fig. 20)

Holotype. Sex undefined, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNHM-6012 in the Staatliches Naturhistorisches Museum Braunschweig (ex Müller's collection number: BUB4460).

Type locality. Myanmar: Kachin state, Myitkyina District, Hukawng Valley.

Type horizon. Lowermost Cenomanian (98.79 ± 0.62 Ma), mid-Cretaceous.

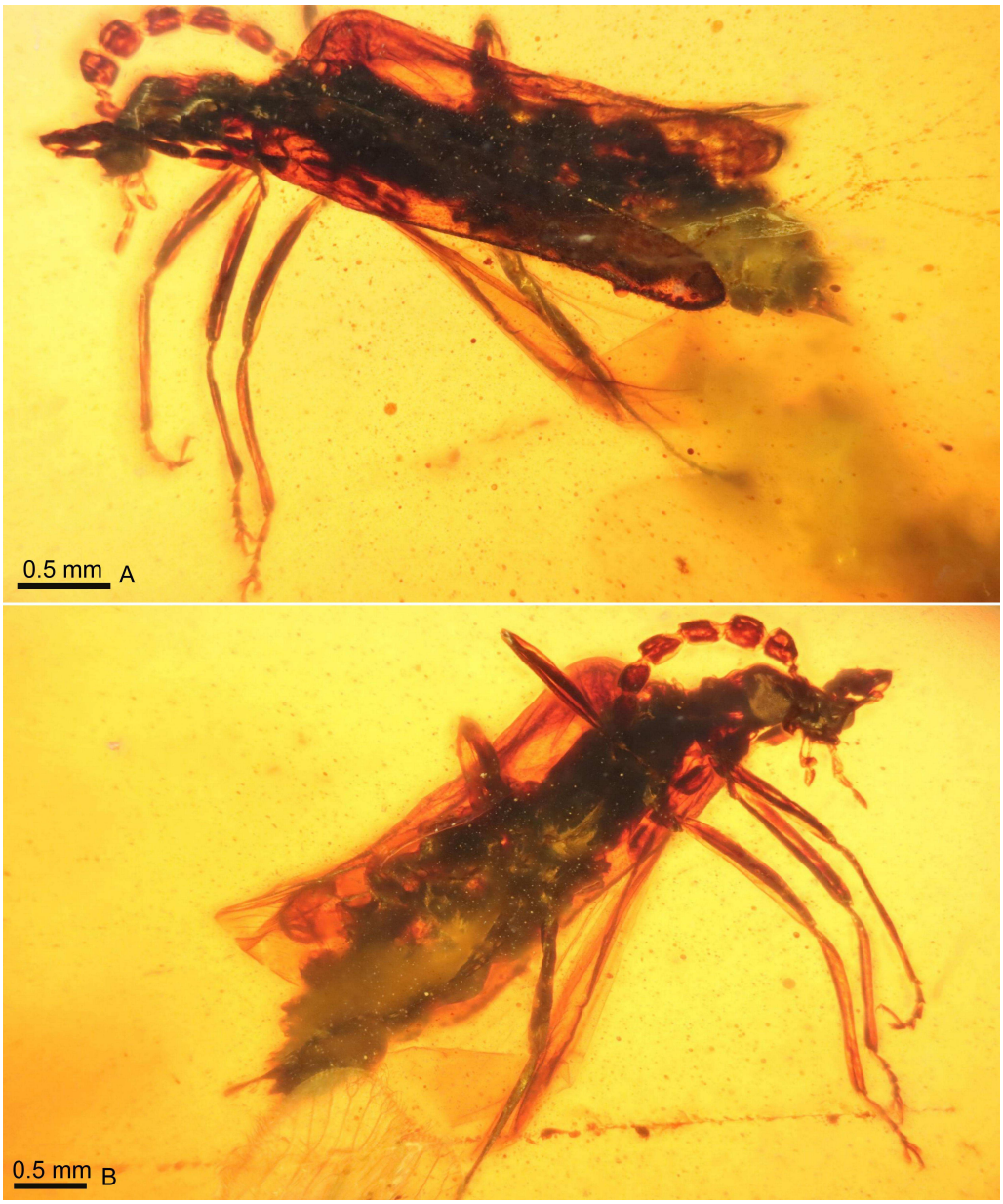

Fig. 20. *Sanaungulus peteriruedeli* sp. nov. in Burmese amber. A: Holotype, dorsal view; B: Holotype, ventral view.

Differential diagnosis. *Sanaungulus peteriruedeli* sp. nov. is characterized by its antennae with very large and robust antennomeres, in particular antennomeres III–VII.

Description. Adult, winged, rather robust. Sex undefined. Body length 4.1 mm. Entirely brown.

Head transverse, constricted (triangular-shaped) behind the eyes, surface irregular. Eyes prominent, very large, roundish, inserted in the

upper and lateral part of the head. Mandibles elongated, robust, falciform. Maxillary palps 4-segmented with the last palpomere strongly elongated and securiform. Labial palps 3-segmented, with the last palpomere securiform. Antennae 11-segmented, slightly surpassing half of elytra and not reaching half of abdomen, antennal insertion far from the eyes; scape club-shaped, elongated, robust; antennomere II very short, small, swollen apically; antennomeres III–IV extremely wide and robust, flat, stouter than scape; antennomeres V–VI robust, less wide and slightly longer than previous ones; antennomeres VII–X robust, narrower than previous ones; antennomere XI robust, with rounded apex; all the antennomeres pubescent. Pronotum very elongated, slightly narrower than head, anterior margin undulate and not bordered, posterior margin slightly curved in the middle and slightly bordered, sides straight except for a small tooth near the apex and not bordered, corners obtuse, pronotum disc irregular with large drafts. Scutellum triangular-shaped, wide basally with rounded apex. Elytra short which reveals some abdominal segments, at humeri strongly wider than pronotum, posteriorly parallel-sided and slightly dehiscent apically, rounded apexes, surface smooth (only few and very small punctuation) with pubescence. Metathoracic wings transparent, approximatively as long as elytra. Sternum very elongated and slender, sternites transverse and pubescent, last sternite small, penultimate abdominal segment with a long lobe at the apical corners. Legs thin, long, slightly pubescent; coxae massive; trochanters elongated, robust, with thin and rounded apex; femora curved, cylindrical, slightly sturdier than tibiae; tibiae, thin, subcylindrical, long, with a small spur near the apex, pro- and mesotibiae slightly longer than pro- and mesofemora, metatibiae longer than metafemora. Tarsal formula 5-5-5; first tarsomere long, about 1.1-1.2 times longer than second; third tarsomere short, triangular-shaped; fourth strongly bilobed; fifth tarsomere extremely elongated, thin, cylindrical and curved; claws simple, long, pointed, without denticle at the base.

Etymology. Named in honor of Peter Rüdel, friend of the second author (Patrick), and a great amber collector.

Syninclusions. Detritus, air bubbles (small), a specimen of Berothidae (Neuroptera).

Remarks. Piece of brownish Burmese amber that measures 14x9x4 mm. The inclusion is complete and only opacified in the last sternites due to the presence of emulsion.

***Sanaungulus temporiscapsula* sp. nov.**
(Fig. 21)

Holotype. Female, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNSB-BSPG 2021 XII 16 in the Bayerische Staatssammlung für Paläontologie und Geologie (ex Müller's collection number: BUB4314).

Type locality. Myanmar: Kachin state, Myitkyina District, Hukawng Valley.

Type horizon. Lowermost Cenomanian (98.79 ± 0.62 Ma), mid-Cretaceous.

Differential diagnosis. The species is easily distinguishable by its antennomeres II–IV that are short and subequal in length.

Description. Adult, winged, slender. Female, defined on the shape of the last urites and short antennae. Body length 3.9 mm. Entirely dark brown.

Head transverse, strongly constricted (triangular-shaped) behind the eyes, fitted with rugosity and punctuation. Eyes very prominent, very large, roundish, inserted in the upper and lateral part of the head, inter-ocular dorsal distance approximately 1.8 times greater than the eye diameter. Mandibles falciform. Maxillary palps 4-segmented with the last palpomere elongated and securiform. Antennae 11-segmented, filiform, rather robust, short, slightly surpassing the humeral zone of the elytra and not reaching the half of elytra, antennal insertion in the eyes proximity; scape elongated, slender, filiform and not enlarged apically; antennomeres II–IV very

short, almost globular, subequal in length with the fourth antennomere slightly serrate apically and slightly longer; antennomere V slightly longer than previous one, antennomeres VI–VIII about 1.5 times longer than antennomere IV; antennomeres IX–X shorter than previous ones, and slightly stouter; antennomere XI filiform, squared at apex; all the antennomeres with short pubescence. Pronotum transverse, as wide as head, slightly narrow anteriorly, anterior margin rounded and bordered, posterior margin almost straight, sides slightly restricted anteriorly and

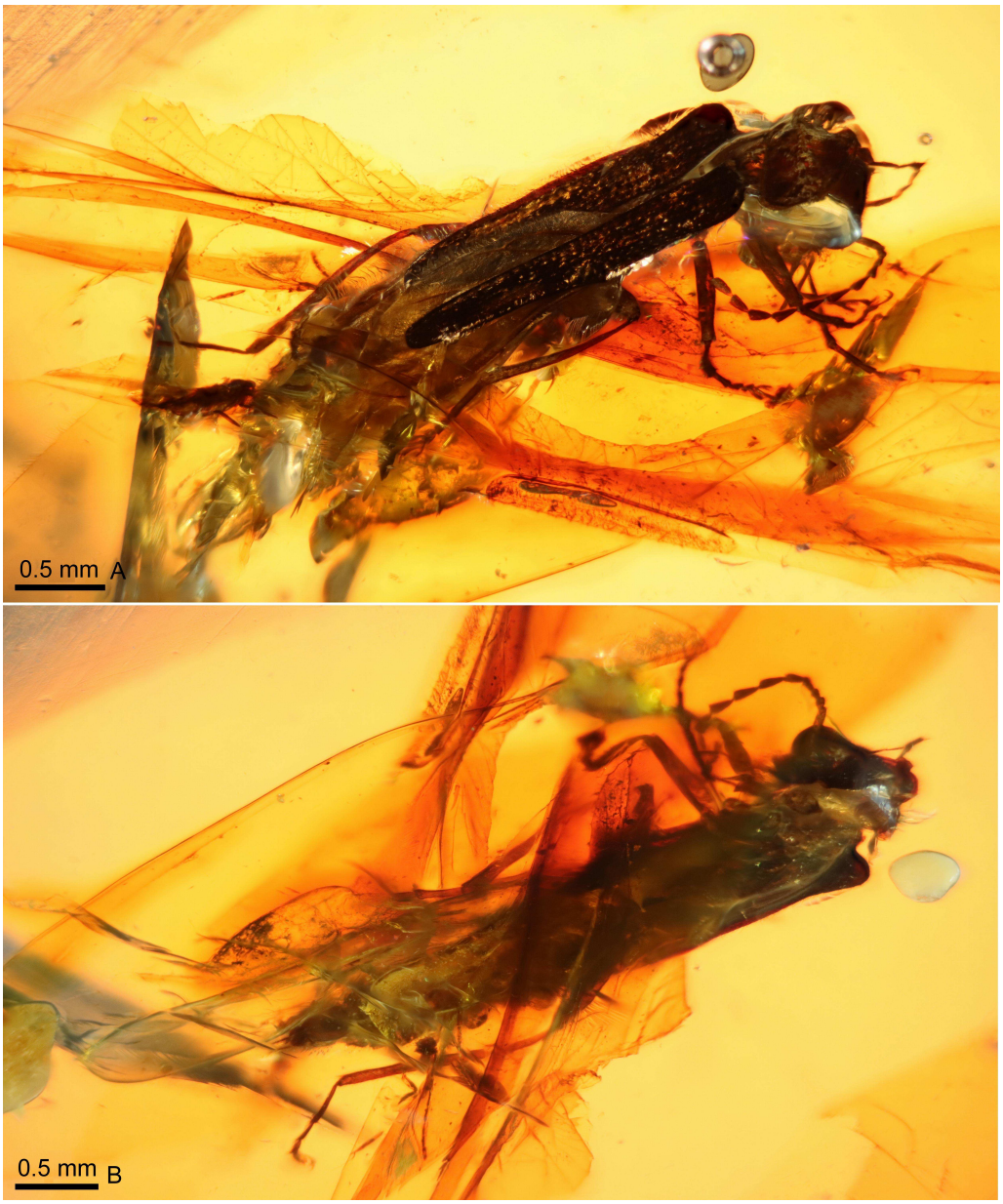

Fig. 21. *Sanaungulus temporiscapsula* sp. nov. in Burmese amber. A: Holotype, dorsal view; B: Holotype, ventral view.

expanded posteriorly, posterior corners obtuse, pronotum disc convex and slightly wrinkled. Scutellum triangular-shaped. Elytra short which reveals various abdominal segments, at humeri wider than pronotum, dehiscent posteriorly, rounded apexes, surface with impressed punctation gathered in striae, pubescent. Metathoracic wings transparent, longer than elytra. Sternum elongated, sternites wide and transverse, last tergite small with two short lobes, last sternite small and rounded. Legs thin, posterior legs long, pubescent; coxae massive; trochanters rounded; femora nearly straight, more robust than tibiae; tibiae slightly flattened, thin, enlarged apically, without spurs near the apex, pro- and mesotibiae strongly shorter than pro- and mesofemora, metatibiae very longer than metafemora. Tarsal formula 5-5-5; first tarsomere long, about 2.0 times longer than second; third tarsomere short and enlarged apically; fourth strongly bilobed; fifth tarsomere very elongated, thin; claws simple, apparently without denticle at the base.

Etymology. Derived from the Latin noun "*tempŏris*" (*tempŭs*) = time, and the Latin noun "*capsŭla*" = capsule. Thus = time capsule. In reference to the fact that the amber piece has embedded the new species making it reach us through time. Specific epithet is to be treated as noun in apposition.

Syninclusions. Air bubbles, detritus.

Remarks. Piece of clear, golden amber that measures 14x7x2.5 mm. The inclusion is complete except for the left antenna broken and almost completely missing.

***Sanaungulus ypogaeum* sp. nov.**
(Fig. 22)

Holotype. Female, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNSB-BSPG 2021 XII 67 in the Bayerische Staatssammlung für Paläontologie und Geologie (ex Müller's collection number: BUB4165).

Type locality. Myanmar: Kachin state, Myitkyina District, Hukawng Valley.

Type horizon. Lowermost Cenomanian (98.79 ± 0.62 Ma), mid-Cretaceous.

Differential diagnosis. *Sanaungulus ypogaeum* sp. nov. differs from other species of *Sanaungulus* with filiform antennae: *Sanaungulus ruicheni* (Hsiao & Huang, 2018), *Sanaungulus morellii* Fanti & Damgaard, 2020, *Sanaungulus rosenzweigi* Fanti & Damgaard, 2020, and the species described here based on its pronotum that is strongly narrow anteriorly and with a rounded anterior margin (Hsiao & Huang 2018; Fanti & Damgaard 2020).

Description. Adult, winged, slender. Female, defined on the shape of the last urites and on the basis of the short antennae. Body length 4.9 mm. Head and pronotum testaceous-brown, elytra and legs brown.

Head elongated, very narrow, strongly constricted (triangular-shaped) behind the eyes, fitted with rugosity and impressed punctuation. Eyes prominent, very large, roundish, inserted in the upper and dorsolateral part of the head, inter-ocular dorsal distance about 0.6 times greater than the eye diameter. Mandibles elongated, robust, falciform, without teeth. Maxillary palps 4-segmented with the last palpomere strongly securiform. Labial palps 3-segmented, with the last palpomere slightly securiform. Antennae 11-segmented, filiform, robust, short and slightly surpassing the humeral zone of the elytra, antennal insertion in the eyes proximity; scape elongated, robust, club-shaped; antennomere II very short, globular; antennomere III short, thinner and longer than second; antennomere IV elongated, the longest; antennomeres V–VII about 0.2 times shorter than antennomere IV; antennomeres VIII–X shorter than previous ones; antennomere XI filiform, longer than previous ones, rounded at apex; all the antennomeres with short pubescence. Pronotum transverse, wider than head, narrow anteriorly, anterior margin rounded and very slightly bordered, posterior margin almost straight, sides rounded, posterior corners obtuse, pronotum disc smooth. Scutellum triangular-shaped. Elytra short which reveals various abdominal segments, at humeri wider than pronotum

and as wide as pronotum at the apex, humeral zone enlarged, posteriorly parallel-sided, rounded apexes, surface sligthly pubescent and with a very small rugosity. Metathoracic wings almost completely covered by elytra. Sternum elongated with posterior margin rounded, sternites narrow and transverse, last tergite deeply incised apically and divided in two lobes, last sternite small and rounded. Legs thin, relatively long, pubescent; coxae massive; trochanters elongated, with rounded apex; femora nearly straight, more robust than tibiae, cylindrical; tibiae flat-

Fig. 22. *Sanaungulus ypogaeum* sp. nov. in Burmese amber. A: Holotype, dorsal view; B: Holotype, ventral view.

tened, thin, without spurs near the apex, protibiae slightly longer than profemora, metatibiae very longer than metafemora. Tarsal formula 5-5-5; first tarsomere long, about 2.0 times longer than second; third tarsomere short and bilobed; fourth strongly bilobed; fifth tarsomere elongated, thin, slightly flat and curved; claws simple, without denticle at the base.

Etymology. Derived from the Latin noun "*ўpŏgaeum* (*hўpŏgēum*)" = hypogeum, tomb. In reference to the fact that the amber that has incorporated the specimen is its tomb. Specific epithet is to be treated as noun in apposition.

Syninclusions. Air bubbles, detritus.

Remarks. Piece of clear, golden amber in Cabochon cut 18x14x2.8 mm. The inclusion is complete.

Genus *Vitalfranzius* gen. nov.

Type species. *Vitalfranzius burmiticus* Fanti & P. Müller sp. nov., by present designation. The genus currently includes two species.

Etymology. Named in honor of the great friend of the first author, Francesco Vitali (Museum of Luxembourg). Derived from his entomological nickname "vitalfranz". The gender is masculine.

Diagnosis. The maxillary palps 4-segmented with the last palpomere securiform, the tarsal formula 5-5-5, a pronotum without modified lateral margin, tarsomeres III–IV without ventral lobes, smooth elytra, and the absence of a long neck, permits to assign this new genus belonging to the family Cantharidae and its subfamily Cantharinae. The new genus is characterized by smooth and very short elytra that leave various abdominal segments uncovered, the rounded head behind the eyes, short and robust legs, and the last abdominal segment slightly forked apically. Four other genera from Burmese amber have very short elytra: *Hukawngichthyurus* Fanti & Ellenberger, 2018, *Ornatomalthinus* Poinar & Fanti, 2016, *Sanaungulus* Fanti, Damgaard & Ellenberger, 2018 and *Brevipterus* Y. Yang, H. Liu & W. Zhao (Poinar & Fanti 2016; Fanti et al. 2018; Fanti & Ellenberger 2018; Zhao et al. 2022). The most similar is *Ornatomalthinus* which has a similar rounded head, but the new genus differs for the smooth elytra (with striations provided of relief points in *Ornatomalthinus*), the smooth head and pronotum (wrinkled and rugose in *Ornatomalthinus*), and particularly by the last abdominal segment forked (rounded in *Ornatomalthinus*). *Vitalfranzius* gen. nov. is also similar to *Brevipterus* but differs for the head strongly rounded and shorter, the pronotum not subreniform, elytra completely smooth and for the antennae not pectinate.

Distribution. Currently known only from the Cretaceous Burmese (Kachin) amber.

***Vitalfranzius burmiticus* sp. nov.**
(Fig. 23)

Holotype. Female, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNSB-BSPG 2021 XII 15 in the Bayerische Staatssammlung für Paläontologie und Geologie (ex Müller's collection number: BUB4313).

Type locality. Myanmar: Kachin state, Myitkyina District, Hukawng Valley.

Type horizon. Lowermost Cenomanian (98.79 ± 0.62 Ma), mid-Cretaceous.

Differential diagnosis. Smooth and very short elytra, the rounded head behind the eyes, antennae filiform, and the last abdominal segment slightly forked apically make this new species belong to the genus *Vitalfranzius* gen. nov. The new species is characterized by filiform antennae and its transverse pronotum.

Description. Adult, winged, rather robust. Female, defined on the shape of the last abdominal segment and on the basis of the short antennae. Body length 5.0 mm. Entirely reddish-brown.

Head strongly rounded, slightly transverse, slightly convex, not constricted (triangular-shaped) behind the eyes, surface smooth. Eyes

prominent, large, roundish, inserted in the upper and dorsolateral part of the head. Mandibles elongated, falciform. Maxillary palps 4-segmented with the last palpomere securiform. Labial palps 3-segmented. Antennae 11-segmented, filiform, slender, short, almost reaching the half of elytra but not reaching the half of abdomen, antennal insertion in the eyes proximity; scape elongated, robust, club-shaped; antennomere II short, globular; antennomeres III–IX subequal in length, very elongated, longer than previous one; antennomere X slightly shorter and stouter than

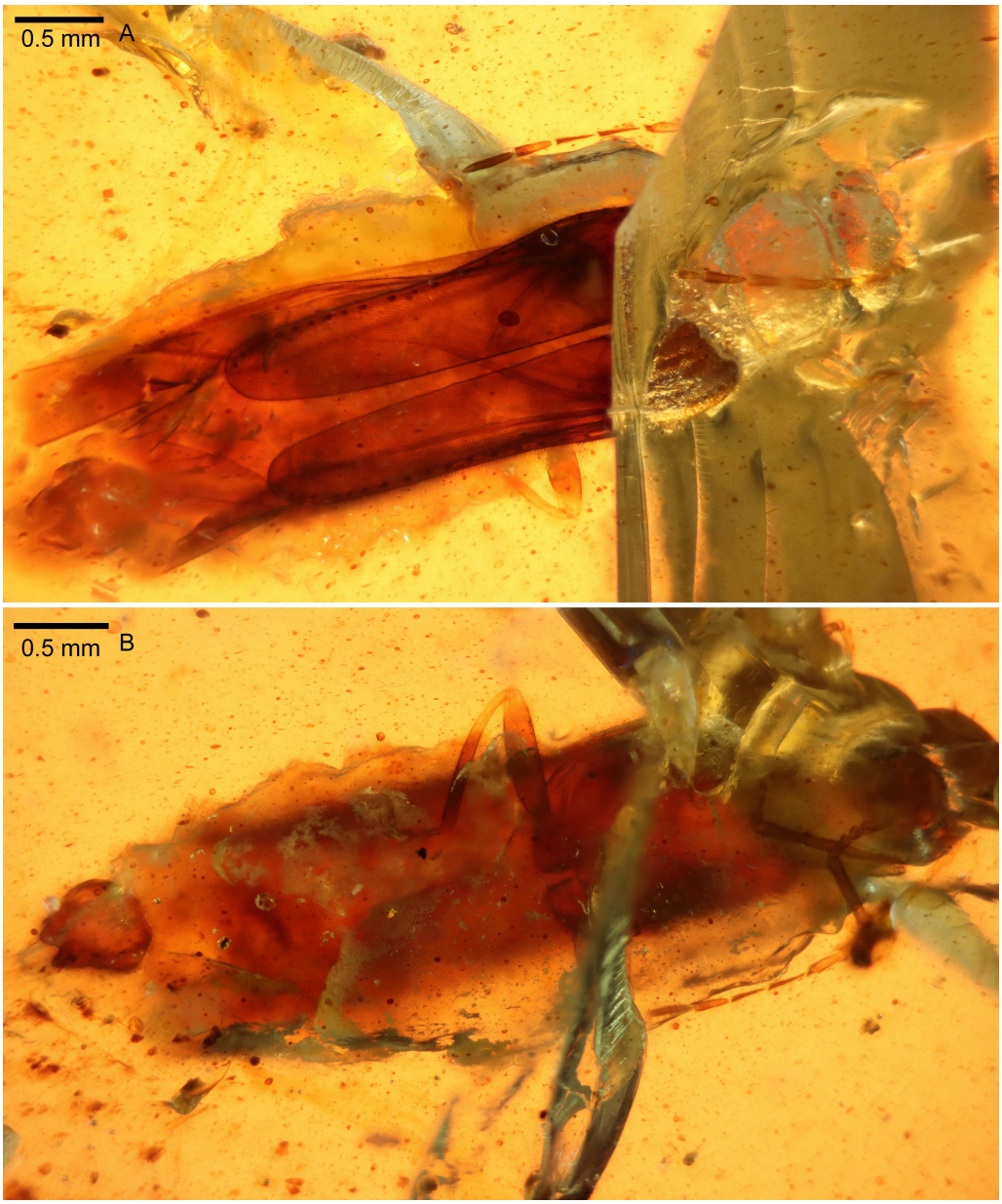

Fig. 23. *Vitalfranzius burmiticus* gen. et sp. nov. in Burmese amber. A: Holotype, dorsal view; B: Holotype, ventral view.

previous ones; antennomere XI filiform, longer than antennomere VIII, rounded at apex; antennomeres pubescent. Pronotum transverse, slightly wider than head, anterior and posterior margin almost straight and bordered, sides straight and bordered, corners obtuse, pronotum disc smooth. Scutellum robust, triangular-shaped. Elytra short which reveals various abdominal segments, at humeri wider than pronotum and as wide as pronotum at the center and apex, humeral zone rather enlarged, posteriorly parallel-sided, rounded apexes, suture robust and evident, surface completely smooth without pubescence and punctation. Metathoracic wings transparent, longer than elytra, almost reaching the apex od abdomen. Sternum elongated, subrectangular, with posterior margin slightly rounded, sternites very wide and transverse, last tergite robust with forked apex equipped with incised concavity at the center, last sternite initially robust and globular and apically forked with short and robust lobes slightly incised at the center. Legs robust, very short, pubescent with several short setae; coxae very massive and rounded; trochanters elongated and curved, with rounded apex; femora at anterior margin straight and posterior margin curved, more robust than tibiae, slightly flat; tibiae cylindrical, thin, with a spur near the apex, longer than femora, metatibiae slightly curved. Tarsal formula 5-5-5; first tarsomere long, about 1.8 times longer than second; third tarsomere short, triangular and slightly bilobed at sides; fourth globular and bilobed; fifth tarsomere elongated, thin, flat and curved; claws apparently simple without tooth.

Etymology. The specific epithet "*burmiticus*" derives from the occurrence of this fossil in "burmite", another name for Burmese amber.

Syninclusions. Air bubbles, detritus.

Remarks. Piece of clear, golden amber that measures 20x11x4 mm. Two legs of the inclusion are not present/visible, and its head and pronotum are partially covered and opacized by the amber surface as well as the ventral part (with emulsion).

***Vitalfranzius cretaceus* sp. nov.**
(Fig. 24)

Holotype. Sex undefined, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNSB-BSPG 2021 XII 66 in the Bayerische Staatssammlung für Paläontologie und Geologie (ex Müller's collection number: BUB4236).

Type locality. Myanmar: Kachin state, Myitkyina District, Hukawng Valley.

Type horizon. Lowermost Cenomanian (98.79 ± 0.62 Ma), mid-Cretaceous.

Differential diagnosis. Smooth and very short elytra, the rounded head behind the eyes, antennae serrate, and the last abdominal segment slightly forked apically make this new species belong to the genus *Vitalfranzius* gen. nov. The new species is easily distinguishable from other species of *Vitalfranzius* by its serrate antennae and a rounded pronotum at the sides and anterior margin.

Description. Adult, winged, rather robust. Sex undefined. Body length 4.0 + head 0.8 mm (detached from the body). Entirely reddish-brown.

Head strongly rounded, slightly transverse, slightly convex, not constricted (triangular-shaped) behind the eyes, surface smooth. Eyes prominent, large, convex, roundish-oblong, inserted in the upper and lateral part of the head. Mandibles very elongated and robust, falciform with pointed apex, equipped with a robust tooth inserted about at the two third of the mandible's length. Maxillary palps 4-segmented with the last palpomere elongated, securiform with apex rounded. Labial palps 3-segmented. Antennae 11-segmented, serrate, rather robust, very short, millimetrically reaches the humeral zone of the elytra, antennal insertion far from the eyes; scape elongated, robust, club-shaped; antennomere II extremely short, globular; antennomeres III–XI subequal in length, short, robust, each equipped with a short and robust antennal process slightly elongated with rounded apex, but antennomeres III–IV slightly longer than the following, and

the antennomeres IX–XI stouter than previous ones with the lobe more squared-irregulaar apically and wider (also the antennomere VIII has the antennal process squared-irregular apically). Pronotum strongly rounded, slightly wider than head, anterior margin strongly rounded, posterior margin almost straight, sides strongly rounded, anterior corners completely rounded and not visible, posterior corners small and obtuse, pronotum disc smooth. Scutellum distorted, not well visible. Elytra short, at humeri wider than pronotum and narrower than

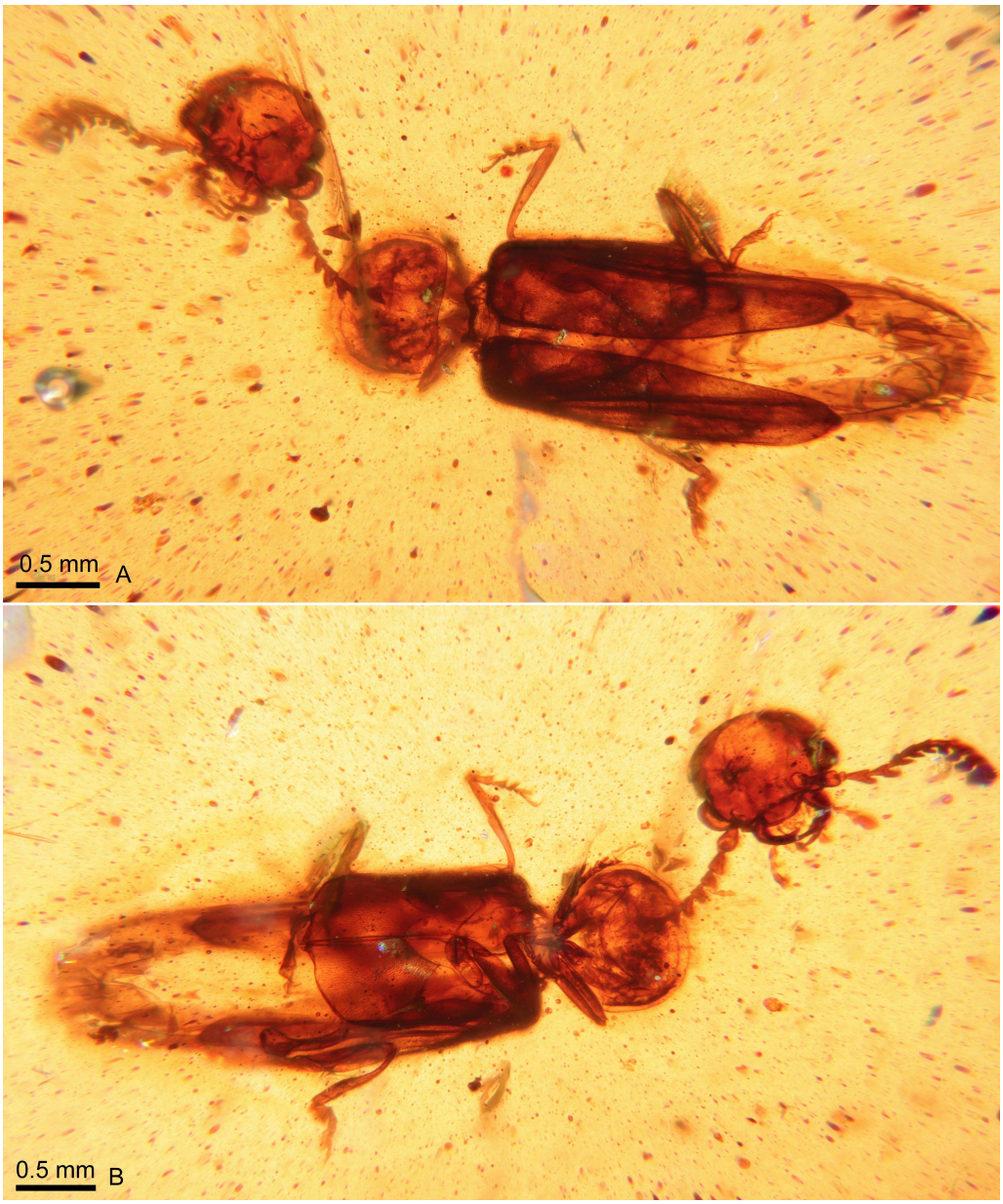

Fig. 24. *Vitalfranzius cretaceus* gen. et sp. nov. in Burmese amber. A: Holotype, dorsal view; B: Holotype, ventral view.

pronotum at the apex, posteriorly slightly dehiscent, rounded apexes, suture robust and evident, surface smooth with very short setae and without punctation. Metathoracic wings transparent, longer than elytra. Sternum elongated, rectangular, with posterior margin irregular. Legs robust, very short, pubescent with several short setae; coxae massive, very elongated, with rounded apex; trochanters elongated, with rounded apex; femora slightly curved, more robust than tibiae, cylindrical; tibiae slightly flat, thin, with a spur near the apex, shorter than femora. Tarsal formula 5-5-5; first tarsomere long, about 1.5 times longer than second; third tarsomere short, triangular; fourth strongly bilobed; fifth tarsomere elongated, thin, flat and curved; claws simple without tooth.

Etymology. From the Latin adjective "*crētācĕus*" = cretaceous. In reference to the geological period (Cretaceous, derived from the Latin "*crēta*" = chalk) in which the amber was deposited.

Syninclusions. Air bubbles, detritus.

Remarks. Piece of clear, golden amber that measures 20x12x3 mm. The inclusion lacks the whole abdomen, while the head is present but completely detached from the body. Furthermore, the left antenna is preserved until the ninth antennomere. Some debris and the surface with reddish-black spots could mistakenly suggest the presence of a fronto-clypeal suture.

DISCUSSION

Cretaceous amber resources are very important in reconstructing the evolution of the family Cantharidae. Burmese amber (Kachin amber) is very rich in biodiversity as regards to this family. The specimens show ancestral characters that are rarely present today. To date, only representatives of the subfamilies Cantharinae and Malthininae are known from this amber. Recently, Hsiao et al. (2021) moved *Archaeomalthodes rosetta* Hsiao, Ślipiński & Pang in Hsiao, Ślipiński, Deng & Pang, 2016 from Malthininae, where it was originally inserted (Hsiao et al. 2016), to Dysmorphocerinae on the exclusive basis of the deeply punctate and reticulated elytra, and the last maxillary palpomere globular pointed. This attribution retrieved by Zhao et al. (2022) has been rejected by Fanti (2021) based on the inconsistence of these characters. In fact, the presence in *Archaeomalthodes rosetta* of the last maxillary palpomere globular pointed and short elytra are in deep contrast with the typical features of Dysmorphocerinae, which have long elytra and the last maxillary palpomere securiform or globular with a flat apex, and with only one case where it is globular-pointed (Brancucci 1980; Fanti 2021). Due to these and other peculiarities Dysmorphocerinae appears paraphyletic (Brancucci 1980).

Burmite cantharids were originally included in the subfamily Cantharinae (Poinar & Fanti 2016). That taxonomic position was reiterated several times subsequently (Fanti & Ellenberger 2016; Fanti 2018; Fanti et al. 2018; Fanti & Damgaard 2019, 2020; Ellenberger & Fanti 2019), while some other authors considered them or placed them in the subfamily Silinae (Hsiao & Huang 2018; Hsiao et al. 2021; Yang et al. 2021) on the basis of abbreviated elytra, deeply punctate or striate elytra, the shape of penultimate and ultimate sternite, and for the eversible cuticular vesicles. However, the attribution of these remains to the subfamily Cantharinae has recently been reiterated, one hopes definitively by Zhao et al. (2022).

Poinar & Fanti (2016) already documented the typical characters of Cantharinae present in Burmite cantharids. However, it is clear there is a need for Burmite cantharids to be better framed phylogenetically (Hsiao et al. 2021). In fact, their combination of characters present in a few cases means it's possible that certain species could be placed. But this must be established with convincing and robust evidence that these are not simple characters at the generic level or hypothetical characters difficult to find in fossils. Even less useful is to clutter up the taxonomy by considering them *incertae sedis* (Hsiao

et al. 2021), especially if the characters are compatible with a well-known subfamily, as is the case here. Until then we will consider the Burmite Cantharidae to be included in the subfamily Cantharinae based on the securiform last palpomere, unmodified pronotum, fourth tarsomere not split trasversally in the basal part and by the shape of last sternites. While the abbreviated elytra instead occur in various subfamilies and often evolve in extreme environmental conditions and by orogenesis, as well as the eversible cuticular vesicles are also present in the fossil Malthininae and in the existing Cantharinae (Fanti & Pankowski 2018; Yang et al. 2021). These features, therefore, are not typical of Silinae trait as reported by Hsiao & Huang (2018) or Hsiao et al. (2021).

In addition, Hsiao et al. (2021) report that the lycid-mimicry proposal advanced by Poinar & Fanti (2016) and reiterated by Fanti & Ellenberger (2016) of some Cantharidae is conjecture. However, Hsiao et al. (2021) do not in the least consider the fact (well known for dozens of years) that mimicry in arthropods is not based only on coloration as they claim, but also on morphology (Biffi & Geiser 2022) and even on behavior (*e.g.*, myrmecomorphy), with the situation therefore much more complex than they want to believe. Coloration is probably the basic model for the establishment of a mimetism, while other characters such as the striated or reticulated elytra may have come later (Motyka et al. 2021). In addition, recently a similar mimicry like Cantharidae and Lycidae has been proposed between the Cretaceous genus *Prototrichalus* (Tenebrionoidea) and the family Lycidae (Motyka et al. 2021). Furthermore, other similar morphological details between different groups such as antennae or elytra widened at the apex are well known for playing a fundamental role in mimicry. In biology it is known that they bring advantages and therefore a greater perpetuation in the evolution of species. The color is not visible in fossils of Burmese Cantharidae (even if one species has preserved the original blue-metallic color) but this does not exclude the possibility that in life a lycid-mimic coloration may have been present in these taxa. Therefore, in this document the lycid mimicry of some Burmite cantharids is strongly reaffirmed again.

Unlike what was reported several times by Yang et al. (2021), their material is by no means of "superior quality" than that of Fanti et al. (2018) and Fanti & Damgaard (2019). This remains for us a subjective claim.

In addition, the triangular or rounded head shape behind the eyes, unlike what Yang et al. (2021) say, is not an "over-valuated" trait, but is extremely important even in living species or tribes (*e.g.*, *Malthinus* instead of *Malthodes*; tribe Podabrini; and many others). Therefore, *Burmomiles*, with a rounded head; and *Elektrokleinia*, with a triangular head; are well differentiable by this character, one that we believe is fundamental. Among other things, Yang et al. (2021) exclude this aspect by taking as an example *Lycocerus s.l.* Its precisely being in "*sensu lato*" indicates that the genus could be paraphyletic or at least that it is not yet well understood at a phylogenetic and evolutionary level and in its phenological expressions.

Yang et al. (2022) and Zhao et al. (2022) affirmed the association and clade *Burmomiles* + *Sanaungulus*, but the latter genus has a different pronotum, elytra shorter with different sculpture and a head that is strongly triangular behind eyes. Therefore, based on the original description (Ellenberger & Fanti 2019), the most related genus of *Burmomiles* is *Elektrokleinia*, which differs substantially in the shape of the head (Ellenberger & Fanti 2019). *Sanaungulus ruficollis* Y. Yang, H. Liu & W. Zhao in Y. Yang et al., 2022 appears to have a brown head and pronotum, and the red neck hypothesized by the authors (Yang et al. 2022) appears due to the amber, and is not a real and natural color of the specimen.

Hsiao et al. (2021) describe the genus *Palaeocantharis* Hsiao, Y. Li, Ren & Pang, 2021, however it appears identical to the genus *Elektrokleinia* Ellenberger & Fanti, 2019 for the same *habitus*, the similar pronotum and last

abdominal segments, and identical elytral sculpture, and particularly for the same shape of head which is more or less restricted behind the eyes, and also for the tarsomeres I–III very slightly dilated at sides, exactly as in *Elektrokleinia*. The pronotum with pair of shallow longitudinal grooves at basal half (Hsiao et al. 2021) is here considered a simple character of specific level, therefore *Palaeocantharis* is here considered synonymous of *Elektrokleinia* syn. nov. and its species has the new combination: *Elektrokleinia panna* (Hsiao, Y. Li, Ren & Pang, 2021) comb. nov.

Yang et al. (2021), in describing three species of the genus *Burmomiles*, do not take into account *Elektrokleinia* described two years earlier (Ellenberger & Fanti 2019). Two of the three species described have the head triangular behind the eyes, a character not present in *Burmomiles* but typical of *Elektrokleinia*, from which they differ only in the pectinate antennae instead of filiform-serrate. This is not always a diagnostic character at the genus level (Ellenberger & Fanti 2019). Therefore, these taxa are here transferred to the genus *Elektrokleinia* as: *Elektrokleinia oblongoculus* (Y. Yang, Bai & W. Zhang, 2021) comb. nov. and *Elektrokleinia bilineatimaculata* (Y. Yang, Geiser & H. Liu, 2021) comb. et decl. nov.

In conclusion, *Cretocantharis* Hsiao, Y. Li, Ren & Pang, 2021, with its rounded head, appears quite similar to *Burmomiles*, but new specimens are needed to establish a possible synonymy. Thus, additional study of fossil materials is extremely important to better understand the evolution and biogeography of these beetles.

ACKNOWLEDGEMENTS

We are very grateful to Peter Rüdel (Gröbenzell, Bavaria, Germany) for helping us donate the amber pieces to the Paleontological Museum Münich, and the State Natural History Museum in Braunschweig, as well as to these institutions for supporting us.

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Received: 02.12.2022.
Accepted: 23.12.2022.