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Fossil Cantharidae of the Patrick Müller collection from Baltic, Burmese and Chiapas amber, with taxonomic revision of the genus *Brevipterus*

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In this document we continue the study of the fossil soldier beetles (family Cantharidae) of the Patrick Müller collection. We describe twenty-one new species: *Cacomorphocerus deformis s*p. nov. from Baltic amber; *Silis* (*Silis*) *aztecimaya* sp. nov. from Chiapas amber; *Brevipterus brachypterus* sp. nov., *Brevipterus brevialatus* sp. nov., *Brevipterus dimidiatus* sp. nov., *Hukawngichthyurus monstruosus* sp. nov., *Sanaungulus ambosae* sp. nov., *Sanaungulus beeralissae* sp. nov., *Sanaungulus beerleniae* sp. nov., *Sanaungulus beernalae* sp. nov., *Sanaungulus beernilsi* sp. nov., *Sanaungulus beerthiloi* sp. nov., *Sanaungulus birmanicus* sp. nov., *Sanaungulus burgardi* sp. nov., *Sanaungulus carloi* sp. nov., *Sanaungulus elfriedeae* sp. nov., *Sanaungulus feliciaeweissbachae* sp. nov., *Sanaungulus fossilis* sp. nov., *Sanaungulus massaronei* sp. nov., *Sanaungulus rosaemariae* sp. nov., *Sanaungulus sucinus* sp. nov. from Burmese (Kachin) amber. Furthermore, the only different character, not evaluated in the original description, to have taxonomic value at the generic level of *Brevipterus* Y. Yang, H. Liu & W. Zhao, 2022 and which differentiates it from *Sanaungulus*, is exposed.

Keywords: soldier beetles, resins, paleoentomology, taxonomy, new taxa

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INTRODUCTION

Baltic, Burmese and Mexican ambers are three amber resources known since ancient times that have yielded numerous animal and plant inclusions, but while many soldier beetles are known in Baltic and Burmese amber (*e.g.,* Kazantsev 2013, 2020; Fanti 2017; Fanti & Damgaard 2019, 2020; Fanti & Müller 2022), only one Cantharidae was known for Mexican (Chiapas) amber prior to this work (Wittmer 1963). In this document we describe some new Burmese (Kachin) amber soldier beetles (family Cantharidae) and one species each from Baltic and Mexican amber. This is the second update of the specimens from the Müller's collection (Germany), which had already been recently studied (Fanti & Müller 2022).

Some amber pieces with their inclusions have not been described and studied in detail in the present paper, because they are barely visible or have part of the antennae missing (BUB4742 / SNHMB.G 8262, BUB4767 / SNHMB.G 8264, BUB4784 / SNHMB.G 8265) or we have not actually determined them (BUB4557 / SNHMB.G 8121, BUB4877 / SNHMB.G 8275), including another amber piece which presents two specimens of the genus *Sanaungulus* in copulation (BUB4873). However, all these inclusions are preserved in the Staatliches Naturhistorisches Museum Braunschweig (Germany) together with the holotypes described here.

MATERIALS AND METHODS

The Baltic amber comes from the Sambian Peninsula, Kaliningrad Region, Russia and is currently referred to the Middle Eocene climatic optimum with sedimentation in two different stages: Bartonian and Priabonian, about 47.8–33.9 Mya (Seyfullah et al. 2018; Bukejs et al. 2019).

The Mexican amber which would be better called Chiapas amber or Simojovelite - Simojovel amber (Bryant 1983; Riquelme et al. 2014), comes from mines near Simojovel de Allende, Chiapas, Mexico, and occur in alluvional grounds within beds of lignite. It is currently referred to the Miocene: between 13 million years old for the youngest sediments of the Balumtun Sandstone and 23 (or 22.8) million years old for the oldest La Quinta Formation - "basal part" (Poinar & Brown 2002; Riquelme et al. 2014; Estrada-Álvarez et al. 2023), while other similar and better calibrations refer to Serravallian-Burdigalian 13-19 mya (Seyfullah et al. 2018) or 15-20 mya (Solórzano Kraemer 2007, 2010).

The Burmese amber comes from Kachin, Hukawng Valley in Northern Myanmar, and is currently dated to the Cretaceous: 98.79 ± 0.62 mya (Shi et al. 2012).

The amber pieces containing the fossils of the Patrick Müller's collection, were donated to the "Staatliches Naturhistorisches Museum Braunschweig" at Braunschweig, Germany. They are cutted using 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.

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 †Cacomorphocerini Fanti & Kupryjanowicz, 2018
Genus †*Cacomorphocerus* Schaufuss, 1892
= †*Hoffeinsensia* Kuśka & Kania, 2010

†*Cacomorphocerus deformis* sp. nov.
(Fig. 1)

Holotype. Male, adult specimen in a Baltic amber piece: Catalog number SNHMB.G 8123 in the Staatliches Naturhistorisches Museum Braunschweig (ex Müller's collection number: BALT50).

Type locality. Sambian Peninsula, Kaliningrad Region, Russia.

Type horizon. Middle Eocene (Lutetian) (47.8–41.2 Ma) to late Eocene (Priabonian) (37.8–33.9 Ma).

Fig. 1. *Cacomorphocerus deformis* sp. nov. in Baltic amber (code SNHMB.G 8123). A: Holotype, dorsal view, scale bar = 1.0 mm; B: Holotype, ventral view, scale bar = 0.5 mm; C: Holotype, detail of antennae plus head and pronotum, scale bar = 0.5 mm.

Differential diagnosis. The new species is easily recognizable by the antennomeres VI-IX modified (antennomeres VIII-IX only moderately), with in particular the antennomere VI robust, elongated and rounded, and antennomere VII asymmetric, distorted and strongly transverse. Characteristics not present in the other *Cacomorphocerus*.

Description. Adult, alate, robust. Male, based on the shape of last sternite: Small, strongly concave in the middle, and smaller than last tergite. Entirely dark brown. Body length: 4.9 mm.

Head rounded, little transverse, almost completely exposed, gradually restricted behind the eyes, covered with short setae and shallow punctation. Eyes roundish, small, convex and prominent, inserted in the later part of the head. Mandible falciform, elongated. Maxillary palps 4-segmented with the first palpomere short and globular, second palpomere elongated and robust, third palpomere about 1.4 times shorter than second, last palpomere elongated and slightly securiform. Labial palps 3-segmented with the last palpomere strongly securiform. Antennae short, reaching the half of elytra, strongly pubescent, 12-segmented, inserted in the middle and far from the eyes; scape not particularly elongated, stout; antennomere II short, small, almost globular, about 1.4 times shorter than first; antennomere III longer and sturdier than second, robust and enlarged; antennomeres IV-V subequal, robust, shorter than third (IV elongated-globular, V more triangular shaped); antennomere VI modified, the sturdier, wide, very robust, globular-elongated; antennomere VII saucer-shaped, strongly transverse, asymmetrical and distorted, with an irregular lobe at side; antennomere VIII short, globular-elongated, slightly asymmetrical; antennomere IX flat and elongated; antennomeres X–XII elongated and filiform with the last rather long and rounded at apex. Pronotum slightly narrower than head, transverse, anterior margin almost completely straight and rather bordered, posterior margin straight and less bordered than anterior margin, sides straight, corners

rounded, surface bulged in the posterior part and slightly concave near the anterior margin, surface equipped with short setae. Scutellum triangular-shaped, rather wide and rounded at apex. Elytra long, covering and surpassing the last abdominal segments, wider than pronotum and wider than head, slightly larger from middle to apex, rounded at apex, surface slightly wrinkled and equipped with long setae. Posterior wings slightly longer than elytra. Metasternum robust equipped with setae; sternites transverse and pubescent; last sternite short and smaller than last tergite and with a deep hollow / concavity at the center. Legs short, strongly pubescent; coxae elongated; trochanters elongated with rounded apex; femora cylindrical, slightly curved; tibiae slender, cylindrical, without apical spurs, pro- and mesotibiae shorter than pro- and mesofemora, metatibiae longer than metafemora. Tarsi 5-segmented; first tarsomere elongated; second tarsomere about 1.4 times shorter than first; third tarsomere triangular; fourth bilobed with lobes wide; fifth tarsomere elongated and thin; claws simple with a small and evident (obtuse) tooth at base.

Etymology. Derived from the Latin adjective "*dēformis*" = deformed. In reference to some antennomeres modified, strongly deformed.

Syninclusions. Debris.

Remarks. Piece of clear, golden amber that measures 24 x 16 x 4 mm. The inclusion is complete and clearly visible, with small white emulsions.

Tribe Cantharini Imhoff, 1856
Genus †*Brevipterus* Y. Yang, H. Liu & W. Zhao in Zhao, Liu, Geiser & Yang, 2022

†*Brevipterus brachypterus* sp. nov.
(Fig. 2)

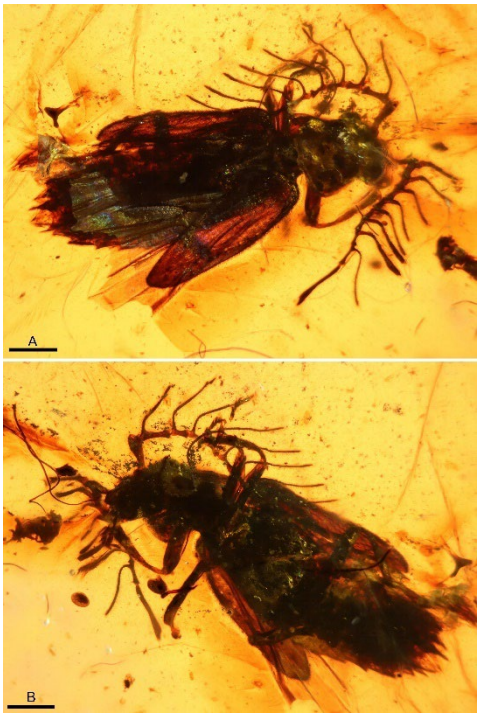

Fig. 2. *Brevipterus brachypterus* sp. nov. in Burmese amber (code SNHMB.G 8129). A: Holotype, dorsal view, scale bar = 0.5 mm; B: Holotype, ventral view, scale bar = 0.5 mm.

Holotype. Male, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNHMB.G 8129 in the Staatliches Naturhistorisches Museum Braunschweig (ex Müller's collection number: BUB3942).

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 its pronotum wider posteriorly.

Description. Adult, alate, robust. Male, based on the shape of last abdominal

segment. Body length 3.7 mm. Entirely dark brown-reddish.

Head almost completely exposed, transverse, slightly rounded dorsally, restricted posteriorly, about as wide as pronotum, surface with shallow punctation. Eyes rounded and very prominent, inter-ocular dorsal distance about 4.0 times greater than eye diameter. Mandibles falciform. Last maxillary palpomere very elongated, rather robust, securiform, with rounded apex. Antennae pectinate, 11-segmented, almost reaching the elytral apex, all antennomeres pubescent including the branches; antennomere I elongated, club-shaped, robust; antennomere II very short; antennomeres III–X robust, each with a branch (extremely long, thin, squared apically) extended from lateral side of the joint near base; antennomere XI clearly elongated, rather robust, with sides not straight, strongly squared apically. Pronotum trapezoidal, wider posteriorly, anterior margin nearly straight (only very slightly protruded at the center) and finely bordered, posterior margin straight and strongly bordered, sides restricted anteriorly, surface not completely flat and without punctation. Scutellum long, with rounded apex. Elytra very short, which do not cover some abdominal segments, wider than pronotum, dehiscent apically, rounded apexes, surface smooth and strongly pubescent (very short setae). Posterior wings transparent, well developed, longer than elytra, almost completely covering the last abdominal segment. Metasternum elongated, rounded apically; sternites transverse, wrinkled, and with punctation; last sternite narrow, triangular-shaped; last tergite narrow, lobed, with a deep concavity at the center. Aedeagus invisible. Legs robust, short, pubescent; coxae massive; trochanters short, rounded; femora almost straight, very robust; tibiae cylindrical, protibiae longer than profemora, meso- and metatibiae shorter than meso- and metafemora. Tarsal formula 5-5-5; first tarsomere long; second tarsomere slightly shorter than first; third short, triangular; fourth tarsomere strongly bilobed with lobes long and rounded apically; fifth tarsomere elongated, thin; claws simple.

Etymology. New Latin, derived from the Ancient Greek *βραχύς* (brakhús) = short, and the Ancient Greek *πτερόν* (pterón) = wing. In reference to the abbreviated wings.

Syninclusions. Air bubbles, detritus (also some soil), botanical remains.

Remarks. Piece of clear amber that measures 14 x 13 x 2 mm. The inclusion is complete except for a median leg missing from half of tibia.

†*Brevipterus brevialatus* sp. nov.
(Fig. 3)

Holotype. Male, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNHMB.G 8128 in the Staatliches Naturhistorisches Museum Braunschweig (ex Müller's collection number: BUB4311).

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 differs from the other taxa of the genus *Brevipterus* (Fanti & Damgaard 2019; Zhao et al. 2022) by its pronotum strongly transverse with sides less rounded.

Description. Adult, alate, robust. Male, based on the shape of last abdominal segment. Body length: 3.0 mm. Entirely brown-testaceous (reddish).

Fig. 3. *Brevipterus brevialatus* sp. nov. in Burmese amber (code SNHMB.G 8128). A: Holotype, dorsal view, scale bar = 0.5 mm; B: Holotype, ventral view, scale bar = 0.5 mm; C: Holotype, detail of head and pronotum, scale bar = 0.2 mm.

Head almost completely exposed, transverse, rounded dorsally, restricted posteriorly (a kind of neck), narrower than pronotum, surface with shallow punctation. Eyes rounded and very prominent (telescopic), inter-ocular dorsal distance about 3.8 times greater than eye diameter. Mandibles falciform, extremely long and thin, without teeth. Last maxillary palpomere elongated, rather robust, with rounded apex. Antennae pectinate, 11-segmented, almost reaching the elytral apex, all antennomeres pubescent including the branches; antennomere I elongated, club-shaped; antennomere II short; antennomeres III–X robust, each with a branch (long, club-shaped) extended from lateral side of the joint near base; antennomere XI clearly elongated, robust, thinner apically. Pronotum strongly transverse, anterior margin nearly straight and bordered, posterior margin rounded expecially near the corners, sides slightly rounded, surface flat and without punctation. Scutellum long, subtriangular-shaped. Elytra very short, which do not cover about five abdominal segments, wider than pronotum, dehiscent apically, rounded apexes, surface finely punctate and strongly pubescent. Posterior wings transparent, well developed, longer than elytra, almost completely covering the last abdominal segment. Metasternum elongated, rounded apically; sternites transverse, wrinkled, and with punctation; last sternite narrow, rounded apically; last tergite narrow, slightly concave in the middle of posterior margin. Aedeagus invisible. Legs very thin, extremely long, slightly pubescent; coxae massive; trochanters elongated, rounded at apex; femora almost straight, subcylindrical, rather thin, slightly sturdier than tibiae; tibiae thin, cylindrical, protibiae shorter than profemora. Tarsal formula 5-5-5; first tarsomere extremely long and thin; second tarsomere about 1.5 times shorter than first; third short, triangular, extended laterally at apex; fourth tarsomere strongly bilobed with lobes very long and rounded apically; fifth tarsomere elongated, thin; claws simple.

Etymology. Derived from the Latin adjectives "*brĕvis*" = short, and "*ālātus*" =

winged. In reference to the abbreviated wings.

Syninclusions. Debris, botanical remains.

Remarks. Piece of clear amber that measures 14 x 10 x 3 mm. The inclusion has some legs only partially preserved.

†*Brevipterus dimidiatus* sp. nov.
(Fig. 4)

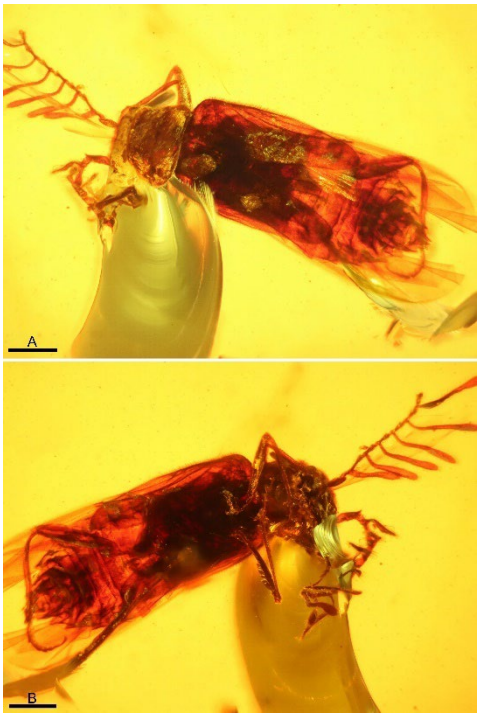

Fig. 4. *Brevipterus dimidiatus* sp. nov. in Burmese amber (code SNHMB.G 8073). A: Holotype, dorsal view, scale bar = 0.5 mm; B: Holotype, ventral view, scale bar = 0.5 mm.

Holotype. Male, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNHMB.G 8073 in the Staatliches Naturhistorisches Museum Braunschweig **(**ex Müller's collection number: BUB3876).

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 very similar to *Brevipterus brachypterus* sp. nov. and differs in the sturdier and shorter antennal processes with apex rounded.

Description. Adult, alate, robust. Male, based on the shape of last abdominal segment. Body length 3.3 mm. Entirely reddish-brown.

Head almost completely exposed, transverse, slightly rounded dorsally, slightly restricted posteriorly, slightly narrower than pronotum, surface with shallow punctation. Eyes rounded and very prominent, inter-ocular dorsal distance about 4.5 times greater than eye diameter. Mandibles falciform. Last maxillary palpomere elongated, securiform. Antennae pectinate, 11-segmented, short, not reaching the elytral apex, all antennomeres pubescent including the branches; antennomere I elongated, club-shaped, robust; antennomere II thinner than first, slightly elongated; antennomeres III–X robust, each with a branch (long, robust, rounded apically) extended from lateral side of the joint near base; antennomere XI clearly elongated, robust apically. Pronotum trapezoidal, wider posteriorly, anterior margin nearly straight and strongly bordered, posterior margin straight and strongly bordered, sides restricted anteriorly and rather bordered, surface almost flat and slightly wrinkled and pubescent. Scutellum long, with rounded apex. Elytra very short, which do not cover some abdominal segments, wider than pronotum, dehiscent apically, rounded apexes, surface smooth and strongly pubescent (very short setae). Posterior wings transparent, well developed, longer than elytra and considerably surpassing the last

abdominal segment. Metasternum elongated, rounded apically; sternites transverse, short, with shallow punctation; last sternite narrow, triangular-shaped; last tergite narrow, lobed with lobes triangular-shaped and robust. Aedeagus invisible. Legs robust, relatively short, pubescent; coxae massive; trochanters elongated, with rounded apex; femora straight, subcylindrical, very robust; tibiae cylindrical, pro- and mesotibiae about as long as pro- and mesofemora, metatibiae longer than metafemora. Tarsal formula 5-5-5; first tarsomere long, robust; second tarsomere slightly shorter and thinner than first; third short, triangular; fourth tarsomere bilobed with lobes short and rounded; fifth tarsomere very elongated, thin, curved; claws simple.

Etymology. Derived from the Latin adjective "*dimidiātus*" = halved. In reference to the abbreviated wings.

Syninclusions. Detritus (very few).

Remarks. Clear and golden amber piece of oval shape that measures 12 x 10 x 6 mm. The inclusion has the right antenna preserved up to eighth antennomere.

Genus †*Hukawngichthyurus* Fanti & Ellenberger, 2018

†*Hukawngichthyurus monstruosus* sp. nov.
(Fig. 5)

Holotype. Male, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNHMB.G 8122 in the Staatliches Naturhistorisches Museum Braunschweig (ex Müller's collection number: BUB4560).

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

Fig. 5. *Hukawngichthyurus monstruosus* sp. nov. in Burmese amber (code SNHMB.G 8122). A: Holotype, dorsal view, scale bar = 0.5 mm; B: Holotype, dorso-lateral view, scale bar = 0.5 mm.

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

Differential diagnosis. The new species is easily recognized from other *Hukawngichthyurus* by the elongated pronotum combined with the filiform antennae with non-enlarged antennomeres (Fanti & Ellenberger 2018; Hsiao et al. 2021; Fanti & Müller 2022).

Description. Adult, alate, slender. Male, based on the shape of the last abdominal segment. Body length: 3.0 mm. Entirely reddish-brown with antennae and legs testaceous-brown.

Head elongated, slightly convex, rounded behind the eyes, surface finely wrinkled and pubescent. Eyes small, prominent, sub-elliptical, inserted laterally to the head. Rostrum elongated. Mandibles falciform, very long. Maxillary palps 4-segmented, last palpomere securiform with rounded apex. Labial palps 3-segmented, last palpomere securiform. Antennae 11-segmented, very short, filiform, not particularly enlarged, slightly surpassing the humeral zone of elytra, insertion of the antennae close to the eyes; antennomere I robust, elongated, not club-shaped; antennomere II short with apex slightly protruded and pointed; antennomeres III-VI elongated, subequal in length, rather robust, slightly enlarged apically; antennomeres VII-X elongated, subequal in length, thinner and shorter than previous ones; antennomere XI elongated with apex rounded; all antennomeres with very short setae. Pronotum very elongated, slightly wider than head, margins undulate and not bordered, posterior margin slightly protruded in the middle in a kind of short and rounded small lobe, sides irregular (almost straight) and slightly bordered, surface irregular with draft and depressions and equipped with very short setae. Scutellum triangular-shaped with rounded apex. Elytra wider than pronotum, parallel-sided, rounded and very slightly dehiscent at apex, rather short and revealing the last two abdominal segments, surface wrinkled in striae without punctation. Posterior wings slightly infuscate, surpassing the elytra and reaching the last abdominal segment. Metasternum large, sub-quadrate; sternites transverse and wide; last urite slightly concave in the middle with two short and asymmetrical apical lobes (at sides) in a kind of fish tail. Legs slender, very long, slightly pubescent; coxae elongated and robust; trochanters elongated with apex rounded; femora elongated, not particularly robust, rather straight and cylindrical; tibiae cylindrical, thin, with spur at apex, slightly longer than femora. Tarsal formula 5-5-5; first tarsomere very elongated, slightly enlarged apically; second tarsomere shorter than first; third tarsomere short, triangular-shaped; fourth tarsomere bilobed with the lobes very long; fifth tarsomere thin, curved; claws simple apparently without denticles or lobes.

Etymology. Derived from the Latin adjective "*monstrŭōsus*" = monstrous. In reference to *habitus*.

Syninclusions. Air bubbles, debris, botanical remains.

Remarks. Piece of clear and yellow amber that measures 15 x 10 x 2.5 mm. The inclusion is complete, except for a median leg preserved up to the tibia and a little part of first tarsomere.

Genus †*Sanaungulus* Fanti, Damgaard & Ellenberger, 2018

†*Sanaungulus ambosae* sp. nov.

(Fig. 6)

Holotype. Sex undefined, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNHMB.G 8276 in the Staatliches Naturhistorisches Museum Braunschweig (ex Müller's collection number: BUB4902)

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 recognizable from other *Sanaungulus* due to the filiform (robust) antennae combined with a pronotum that is elongated, enlarged posteriorly and significantly covers the head (similar to that of the genus *Brevipterus*).

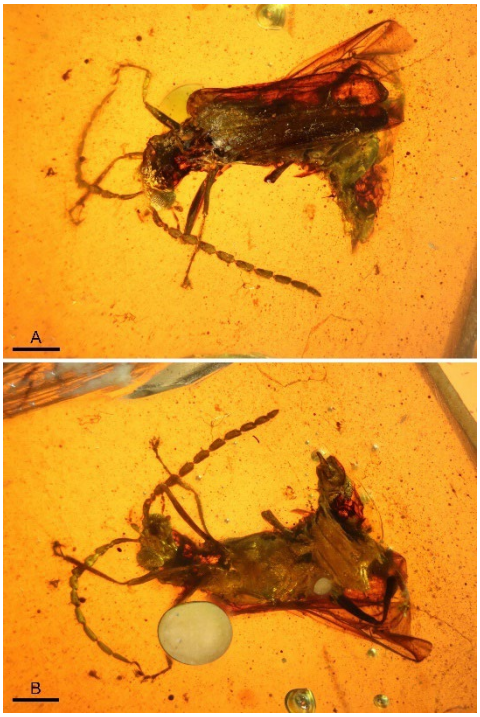

Fig. 6. *Sanaungulus ambosae* sp. nov. in Burmese amber (code SNHMB.G 8276). A: Holotype, dorsal view, scale bar = 0.5 mm; B: Holotype, ventral view, scale bar = 0.5 mm.

Description. Adult, alate, rather robust. Sex undefined. Body length: 3.0 mm. Entirely brown.

Head noticeably covered by pronotum, constricted (triangular shaped) behind the eyes (well visible ventrally), surface slightly wrinkled with very small pubescence. Eyes prominent, roundish, large, inserted in the lateral part of the head. Mandibles elongated, falciform. Maxillary palps 4-segmented with last palpomere securiform, almost spatulate-shaped, wide, rounded at apex. Labial palps 3-segmented with last palpomere securiform. Antennae 11-segmented, filiform, robust, relatively long, surpassing half of elytra, approximately reaching half of abdomen, all antennomeres finely pubescent; antennomere I club-shaped, elongated, enlarged approximately from middle to apex; antennomere II very short, rather globular (only slightly extruded-irregular at the base of one side), very small, about 4.9 times shorter than first; antennomere III robust, squared apically; antennomere IV slightly longer and sturdier than antennomere III, squared apically; antennomeres V-VIII robust, sub-equal, slightly longer than previous one, squared apically; antennomeres IX-X slightly shorter and slightly less massive than previous ones; antennomere XI filiform, rounded apically. Pronotum elongated, slightly wider than head, wider at base, anterior margin almost straight, posterior margin almost straight and little bordered, sides irregular, corners rounded-obtuse, pronotum disc wrinkled. Scutellum elongated, triangular-shaped with rounded apex. Elytra short which do not cover some abdominal segments, noticeably wider than pronotum, parallel-sided, not dehiscent, rounded apexes, surface slightly wrinkled with very confused striae. Posterior wings transparent, longer than elytra, almost reaching the last abdominal segments. Metasternum elongated, robust, with apex rounded; sternites strongly transverse, narrow, equipped with shallow punctation and short setae; last abdominal segments enveloping, a long and cylindrical tip protrudes inside. Legs rather thin, slightly pubescent; coxae robust, rather short; trochanters elongated, rounded at apex; femora thin, sturdier than tibiae, slightly curved; tibiae thin, cylindrical, without spurs at apex, protibiae shorter than profemora. Tarsal formula 5-5-5; first tarsomere long; second as long as first; third short, triangular-shaped; fourth tarsomere strongly bilobed with lobes long, robust and rounded apically; fifth tarsomere elongated, thin, curved; claws simple, long, without denticle at the base.

Etymology. Named in honor of Elli Ambos, grandmother of the second author (Patrick).

Syninclusions. Air bubbles (also huge), debris, botanical remains (including stellate hairs), thrips.

Remarks. Piece of clear, gold-yellow, quadratic shape amber that measures 12 x 11 x 3 mm. The inclusion is complete.

†*Sanaungulus beeralissae* sp. nov.
(Fig. 7)

Holotype. Male, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNHMB.G 8266 in the Staatliches Naturhistorisches Museum Braunschweig (ex Müller's collection number: BUB4856).

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

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

Differential diagnosis. The *Sanaungulus* with antennomeres robust and enlarged are only: *Sanaungulus dunlopi* Fanti & P. Müller, 2022, *S. peteriruedeli* Fanti & P. Müller, 2022 and another species described herein. The new species differs from *S. dunlopi* in having the antennomeres V-VIII less robust, and a different pronotum with the anterior margin less rounded (Fanti & Müller 2022). The new species differs from *S. peteriruedeli* in having the antennomeres V-VII less robust, and shorter elytra (Fanti & Müller 2022).

Description. Adult, alate, slender. Male, based on the shape of the last abdominal segment. Body length: 3.3 mm. Entirely brown.

Fig. 7. *Sanaungulus beeralissae* sp. nov. in Burmese amber (code SNHMB.G 8266). A: Holotype, dorso-lateral view, scale bar = 1.0 mm; B: Holotype, ventro-lateral view, scale bar = 1.0 mm; C: Holotype, detail of antenna, head and pronotum, scale bar = 0.5 mm.

Head constricted (triangular shaped) behind the eyes, surface with shallow rugosity and small pubescence. Eyes very prominent, very large, roundish, inserted in the lateral part of the head. Mandibles elongated, falciform. Maxillary palps 4-segmented with last palpomere securiform. Labial palps 3-segmented with last palpomere short and securiform. Antennae 11-segmented, filiform, robust and enlarged, rather short, not completely reaching the elytral apex, all antennomeres slightly pubescent; antennomere I club-shaped, elongated, robust, curved, enlarged apically; antennomere II very short, about 4.0 times shorter than first, globular and extruded-enlarged laterally in the center; antennomere III short, very robust, slightly enlarged externally from middle to apex; antennomere IV robust, thinner and longer than third; antennomeres V-VII rather robust, sub-equal in length, longer and thinner than previous one (progressively less robust each others); antennomere VIII almost filiform, shorter and thinner than previous ones; antennomeres IX-XI filiform, elongated, last antennomere rounded apically. Pronotum elongated, narrower than head, anterior margin feebly rounded, pronotum disc irregular with small drafts and depression. Scutellum short, triangular-shaped. Elytra short which do not cover various abdominal segments, wider than pronotum, parallel-sided, not dehiscent, rounded apexes, surface very feebly wrinkled and pubescent. Posterior wings transparent, longer than elytra and which do not cover some abdominal segments. Metasternum very elongated and robust, with apex almost straight; sternites transverse, very wide, wrinkled and with shallow punctation; last tergite forked with lobes robust and rounded apically; last sternite forked with large lobe at sides and a small concavity centrally. Legs rather robust, rather long, slightly pubescent; coxae robust, elongated; trochanters elongated, rounded at apex; femora robust, cylindrical, not curved, sturdier than tibiae; tibiae, thin, cylindrical, slightly shorter than femora, equipped with very long and pointed spurs at apex. Tarsal formula 5-5-5; first tarsomere very long, thin; second about 2.2-2.3 times shorter than first; third very short, triangular-shaped, enlarged at sides (apically); fourth tarsomere strongly bilobed with lobes long, robust and rounded apically; fifth tarsomere extremely long, thin, slightly curved; claws simple, long, apparently with small and obtuse denticle at the base.

Etymology. Named in honor of Alissa Beer, wife of the second author (Patrick).

Syninclusions. Air bubbles, debris, botanical remains (including stellate hairs), a flower beetle.

Remarks. Piece of gold amber, quadratic shape that measures 15 x 13 x 3 mm. The inclusion is well visible and complete, with posterior leg detached after the femur, of which only the tarsus is preserved in amber.

†*Sanaungulus beerleniae* sp. nov.
(Fig. 8)

Holotype. Sex undefined, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNHMB.G 8261 in the Staatliches Naturhistorisches Museum Braunschweig (ex Müller's collection number: BUB4741).

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 differs from *Sanaungulus curtipennis* Fanti, Damgaard & Ellenberger, 2018, the only other *Sanaungulus* with three antennomeres equipped with an antennal process, by the longer central antennomeres and the last

three antennomeres less robust, and also by the last abdominal segment rounded and pronotum less extruded anteriorly (Fanti et al. 2018).

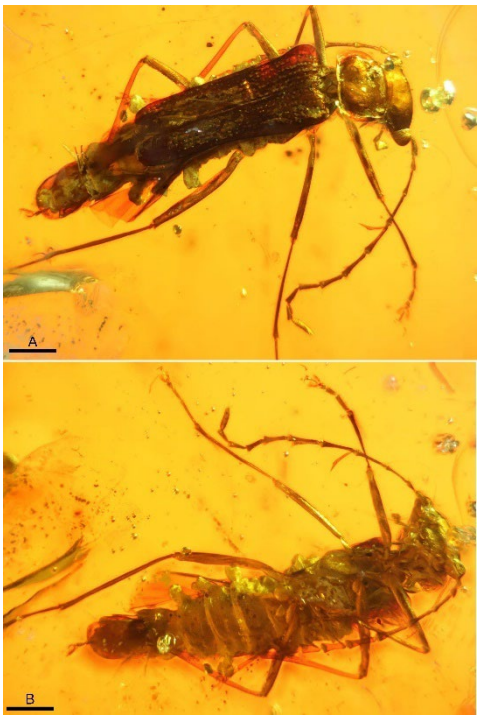

Fig. 8. *Sanaungulus beerleniae* sp. nov. in Burmese amber (code SNHMB.G 8261). A: Holotype, dorsal view, scale bar = 0.5 mm; B: Holotype, ventral view, scale bar = 0.5 mm.

Description. Adult, alate, slender. Sex undefined. Body length: 4.0 mm. Entirely brown-testaceous, with darker elytra.
Head transverse, slightly convex, constricted (triangular shaped) behind the eyes, surface with shallow rugosity and small pubescence. Eyes very prominent, large, roundish, inserted in the lateral part of the head. Mandibles elongated, falciform. Maxillary palps 4-segmented. Labial palps 3-segmented. Antennae 11-segmented, pectinate, thin, relatively long, about reaching the elytral apex, all antennomeres pubescent; antennomere I very slightly club-shaped, elongated, thin, curved; antennomere II short, slightly enlarged apically; antennomere III filiform, long, thin, cylindrical, bulged at apex; antennomere IV filiform, extremely long, longer than third, thin, bulged at apex; antennomere V extremely long, about as long as antennomere IV, thin, very slightly sturdier than previous one, equipped with a long antennal process inserted near the base; antennomere VI shorter than previous one, equipped with an antennal process inserted near the base; antennomere VII shorter than previous one, equipped with an antennal process inserted near the base; antennomere VIII shorter and slightly sturdier than previous one, without antennal process; antennomeres IX-X sub-equal, slightly flat and robust, enlarged apically; antennomere XI quite elongated, robust, rounded apically. Pronotum transverse, anterior margin rounded and very slightly extruded in the middle, posterior margin almost straight and strongly bordered, sides slightly curved and slightly restricted from middle to posterior part, corners rounded, pronotum disc very slightly bulged in the posterior part and slightly pubescent. Scutellum triangular-shaped with rounded apex. Elytra short which do not cover some abdominal segments, wider than pronotum, parallel-sided, slightly enlarged at humeri, not dehiscent, rounded apexes, surface with sparse and rather large impressed punctation (arranged in striae). Posterior wings transparent, longer than elytra. Metasternum elongated; sternites transverse. Legs thin, long, slightly pubescent; coxae robust; trochanters elongated, rounded at apex; femora very elongated, subcylindrical, sturdier than tibiae; tibiae, thin, cylindrical, long, without spur at apex, protibiae shorter than profemora, meso- and metatibiae longer than meso- and metafemora. Tarsal formula 5-5-5; first tarsomere long, second shorter than first; third very short; fourth tarsomere strongly bilobed with lobes long and robust;

fifth tarsomere elongated, thin, curved; claws simple, long, without denticle at the base.

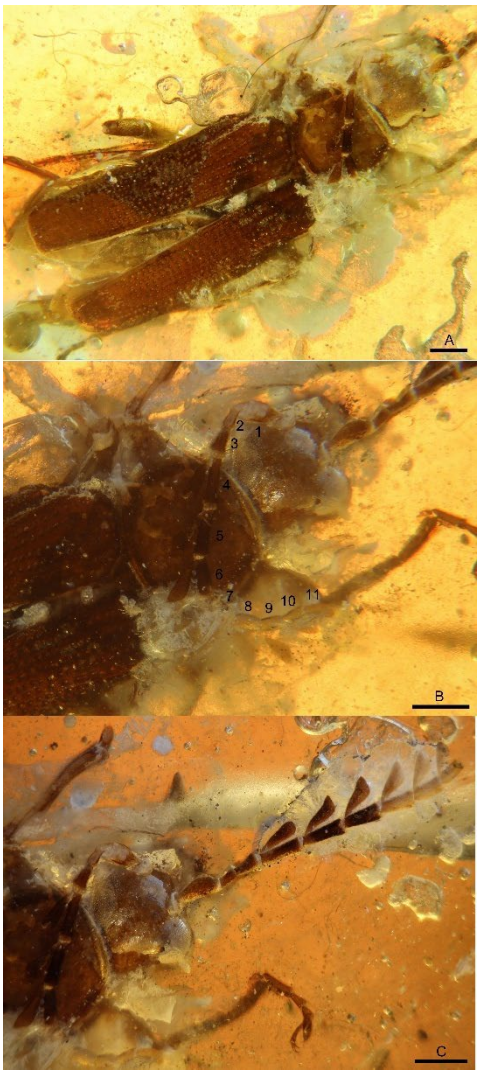

Fig. 9. *Sanaungulus beernalae* sp. nov. in Burmese amber (code SNHMB.G 8093). A: Holotype, dorsal view, scale bar = 0.5 mm; B: Holotype, detail of left antenna, scale bar = 0.5 mm; C: Holotype, detail of antennae, scale bar = 0.5 mm.

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

Syninclusions. Air bubbles, debris, botanical remains.

Remarks. Piece of clear amber that measures 13 x 7 x 3 mm. The inclusion is complete

†*Sanaungulus beernalae* sp. nov.
(Fig. 9)

Holotype. Sex undefined, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNHMB.G 8093 in the Staatliches Naturhistorisches Museum Braunschweig (ex Müller's collection number: BUB1452).

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

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

Differential diagnosis. The most similar species is *Sanaungulus lethi* Fanti & Damgaard, 2020 from which the new species described here differs in the more rounded pronotum and the branches of the antennomeres having a squared apex, where it is rounded in *S. lethi* (Fanti & Damgaard 2020). Furthermore, elytral surface has impressed punctation arranged in nine striae (six striae in *S. lethi*).

Description. Adult, alate, slender. Sex undefined. Body length: 6.0 mm. Entirely dark brown.

Head constricted (triangular shaped) behind the eyes, surface with shallow and plentiful rugosity and small pubescence. Eyes very prominent, large, roundish, inserted in the upper-lateral part of the head. Mandibles elongated, falciform. Maxillary palps 4-

segmented. Labial palps 3-segmented. Antennae 11-segmented, pectinate, thin, rather short, not reaching the elytral apex, all antennomeres slightly pubescent; antennomere I club-shaped, elongated, very robust, curved; antennomere II short, about 2.9 times shorter than first; antennomere III rather robust, bulged at apex, equipped at apex with an antennal process which is rounded apically; antennomeres IV-V rather robust, longer than previous one, equipped at apex with an antennal process which is irregular and squared apically; antennomeres VI-IX rather robust, shorter than previous ones, sub-equal in length, equipped at apex with an antennal process which is irregular and squared apically; antennomere X slightly shorter than previous ones and without antennal process; antennomere XI filiform elongated, rounded apically. Pronotum slightly transverse, wider than head, anterior margin rounded and strongly bordered, posterior margin almost straight and bordered and rounded at corners, sides and corners curved, pronotum disc flat and slightly pubescent. Scutellum short, triangular-shaped with rounded apex. Elytra short which do not cover some abdominal segments, wider than pronotum, parallel-sided, slightly enlarged at humeri, not dehiscent, slightly rounded apexes, surface with impressed and rather large punctation arranged apparently in nine striae. Posterior wings transparent, longer than elytra and slightly surpassing the last abdominal segments. Legs robust, rather short, slightly pubescent; coxae robust; trochanters elongated, rounded at apex; femora very robust, short, sturdier than tibiae; tibiae, thin, cylindrical, long, protibiae longer than profemora and without spurs at apex. Tarsal formula 5-5-5; first tarsomere long, second about 2.2 times shorter than first; third very short, triangular-shaped; fourth tarsomere strongly bilobed with lobes long, robust and very thin apically; fifth tarsomere elongated, thin, curved; claws simple, long, without denticle at the base.

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

Syninclusions. Air bubbles, debris, botanical remains.

Remarks. Piece of clear amber in Cabochon cut that measures 19 x 12 x 3 mm. The inclusion is practically invisible in ventral view, and has the right antenna preserved up to the ninth antennomere.

†*Sanaungulus beernilsi* sp. nov.
(Fig. 10)

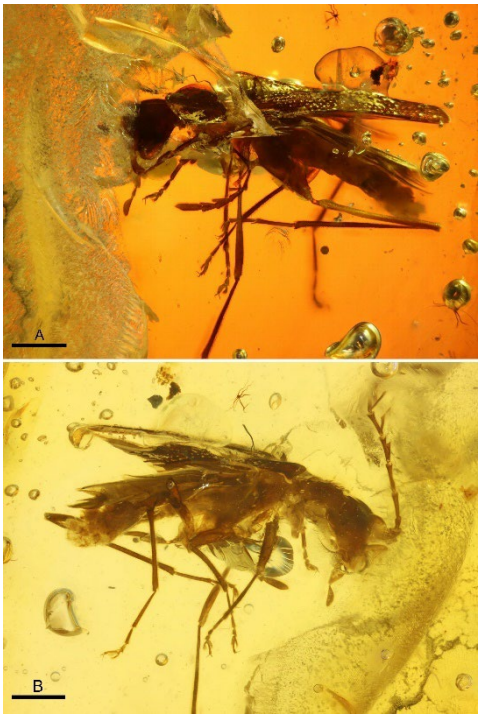

Fig. 10. *Sanaungulus beernilsi* sp. nov. in Burmese amber (code SNHMB.G 8268). A: Holotype, dorso-lateral view, scale bar = 0.5 mm; B: Holotype, ventro-lateral view, scale bar = 0.5 mm.

Holotype. Male, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNHMB.G 8268 in the Staatliches Naturhistorisches Museum Braunschweig (ex Müller's collection number: BUB4870).

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

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

Differential diagnosis. Only four *Sanaungulus* have six antennomeres equipped with an antennal process: *Sanaungulus christensenae* Fanti & Damgaard, 2019, *Sanaungulus myanmaricus* Fanti & P. Müller, 2022, *Sanaungulus imparitibius* Y. Yang, H. Liu & W. Zhao in Yang et al., 2022 and *Sanaungulus longicornis* Y. Yang, W. Zhao & H. Liu, 2024.

S. christensenae is the most similar and differs from the new species in having a different pronotum, more rounded at sides and not particularly enlarged posteriorly, and it also differs in the antennomere IV as long as III, where in the new species the antennomere IV is longer than III (Fanti & Damgaard 2019; Fanti & Müller 2022; Yang et al. 2022, 2024).

Description. Adult, alate, slender. Sex undefined. Body length: 3.0 mm. Entirely brown.

Head constricted (triangular shaped) behind the eyes, surface smooth with pubescence. Eyes very prominent, very large, roundish, inserted in the upper-lateral part of the head. Mandibles very elongated, thin, falciform, without tooth. Maxillary palps 4-segmented with last palpomere securiform. Labial palps 3-segmented with last palpomere securiform. Antennae 11-segmented, pectinate, not particularly long, not reaching the elytral apex, all antennomeres pubescent; antennomere I club-shaped, elongated, robust, curved, enlarged apically; antennomere II short, about 4.0 times shorter than first, filiform; antennomeres III-IV filiform without antennal process, antennomere IV longer than III; antennomeres V-VII pectinate, elongated, slightly enlarged apically, progressively shorter each others, each equipped with an antennal process near the base which is long and squared apically; antennomeres VIII-X pectinate, sturdier and shorter than previous ones, progressively shorter each others, each equipped with an antennal process near the base which is long and rounded apically; antennomere XI filiform, robust, rounded apically. Pronotum as wide as long, approximately as wide as head, wider posteriorly, anterior margin feebly rounded close to the corners, posterior margin straight, sides rather curved, pronotum disc smooth and slightly depressed close to the anterior margin, corners rounded. Scutellum triangular-shaped. Elytra rather long, which do not cover the last two abdominal segments, wider than pronotum at humeri, parallel-sided, rounded apexes, surface with impressed and large punctation arranged in striae. Posterior wings transparent, as long as elytra. Metasternum elongated with apex almost straight; sternites transverse, with shallow punctation; last sternite rounded. Legs thin, rather long, slightly pubescent; coxae robust, rounded; trochanters elongated, rounded at apex; femora robust, cylindrical, sturdier than tibiae, curved; tibiae, thin, cylindrical, longer than femora, equipped with spurs at apex. Tarsal formula 5-5-5; first tarsomere very long, thin; second about 2.1 times shorter than first; third short; fourth tarsomere strongly bilobed with lobes very long and rounded apically; fifth tarsomere extremely long, thin, slightly curved; claws simple, long, with a small denticle at the base.

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

Syninclusions. Air bubbles, debris, botanical remains (including stellate hairs).

Remarks. Piece of clear and yellow amber that measures 12 x 12 x 4 mm. The inclusion is complete.

†*Sanaungulus beerthiloi* sp. nov.
(Fig. 11)

Fig. 11. *Sanaungulus beerthiloi* sp. nov. in Burmese amber (code SNHMB.G 8120). A: Holotype, dorso-lateral view, scale bar = 1.0 mm; B: Holotype, ventro-lateral view, scale bar = 1.0 mm.

Holotype. Male, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNHMB.G 8120 in the Staatliches Naturhistorisches Museum Braunschweig (ex Müller's collection number: BUB4556).

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

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

Differential diagnosis. Other *Sanaungulus* have antennae with seven antennomeres equipped with an antennal process, but the most similar to the new species are: *Sanaungulus havai* Fanti & Müller, 2022 and *Sanaungulus lethi* Fanti & Damgaard, 2020, but both of these species have a pronotum narrower anteriorly with sides curved (Fanti & Damgaard 2020; Fanti & Müller 2022).

Description. Adult, alate, slender. Male, based on the shape of last sternite. Body length: 4.1 mm. Entirely brown.

Head constricted (triangular shaped) behind the eyes, surface slightly wrinkled with shallow punctation and pubescent. Eyes prominent, roundish, inserted in the upper-lateral part of the head. Mandibles elongated, falciform. Maxillary palps 4-segmented with last palpomere securiform, very elongated. Labial palps 3-segmented with last palpomere securiform. Antennae 11-segmented, pectinate, thin, rather short, slightly surpassing half of elytra, all antennomeres densely pubescent; antennomere I club-shaped, elongated, thin; antennomere II relatively short, about 2.1 times shorter than first; antennomere III filiform, slightly longer and thinner than second; antennomeres IV-VI long, each equipped with an antennal process inserted in the proximity to the base which is rounded apically and not particularly elongated; antennomeres VII-X shorter than previous ones, each equipped in proximity to the base with an antennal process which is rounded apically and not particularly elongated;

antennomere XI filiform, rather robust, very slightly squared apically. Pronotum approximately as long as wide, wider than head, anterior margin straight and strongly bordered, posterior margin almost straight and little bordered, sides almost straight and little bordered, corners rounded, pronotum disc slightly bulged posteriorly, surface slightly pubescent. Scutellum short, triangular-shaped with rounded apex. Elytra short which do not cover some abdominal segments, wider than pronotum, parallel-sided, slightly enlarged at humeri, slightly dehiscent, rounded apexes, surface with some little impressed punctation arranged in confused striae. Posterior wings transparent, longer than elytra, not reaching the last abdominal segments. Metasternum elongated with apex rounded; sternites transverse, with shallow punctation; last tergite elongated in lobe; last sternite in shape of long lobe, strongly narrower than last tergite. Legs robust, rather short, slightly pubescent; coxae very robust, elongated; trochanters elongated, rounded at apex; femora very robust, sturdier than tibiae, short, curved; tibiae thin, cylindrical, short, all very shorter than femora, without spurs at apex. Tarsal formula 5-5-5; first tarsomere long; second about 1.5 times shorter than first; third short, expanded apically (at the sides); fourth tarsomere strongly bilobed with lobes long, robust and pointed apically; fifth tarsomere elongated, thin, curved; claws simple, long, without denticle at the base.

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

Syninclusions. Air bubbles, debris.

Remarks. Piece of clear and yellow amber that measures 15 x 11 x 3 mm. The inclusion is complete but has a leg detached at the femur-tibia height, which is still preserved in the amber piece.

†*Sanaungulus birmanicus* sp. nov.
(Fig. 12)

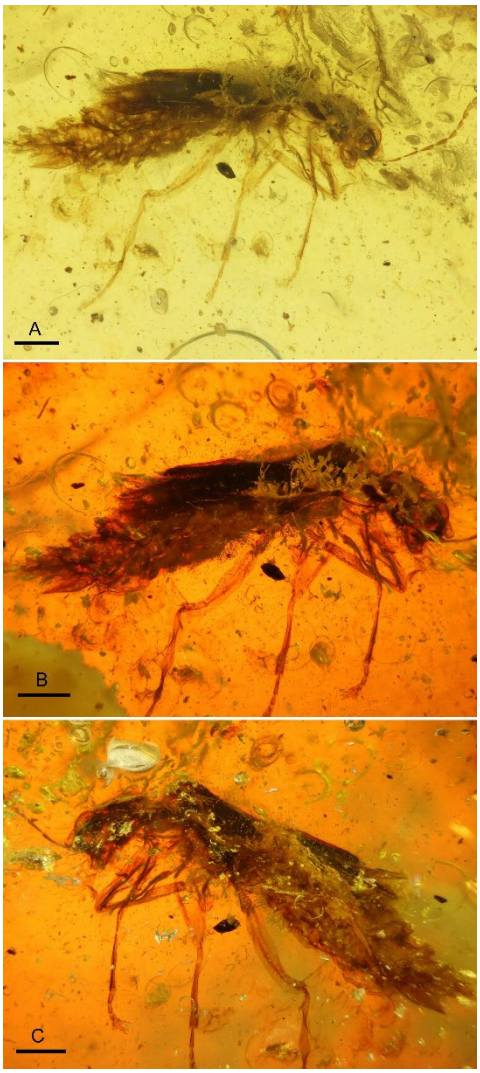

Fig. 12. *Sanaungulus birmanicus* sp. nov. in Burmese amber (code SNHMB.G 8269). A: Holotype, dorso-lateral view, scale bar = 0.5 mm; B-C: Holotype, dorso-lateral view (macro shots), scale bars = 0.5 mm.

Holotype. Male, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNHMB.G 8269 in the Staatliches

Naturhistorisches Museum Braunschweig (ex Müller's collection number: BUB4871).

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

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

Differential diagnosis. Based on the antennae filiform joined to the head and pronotum elongated, the new species is similar to *Sanaungulus nilsi* Fanti & P. Müller, 2022 and *Sanaungulus franziskaeweissbachae* Fanti & P. Müller, 2022, but differs from these taxa for the pronotum gibbous and for the different length and shape of antennomeres (Fanti & Müller 2022).

Description. Adult, alate, slender. Male, based on the shape of last sternite. Body length: 4.1 mm. Entirely brown.

Head slightly constricted (triangular shaped) behind the eyes, elongated, surface smooth with shallow punctation. Eyes very prominent, convex, roundish, inserted in the upper-lateral part of the head. Mandibles elongated, falciform. Maxillary palps 4-segmented with last palpomere securiform. Labial palps 3-segmented with last palpomere securiform. Antennae 11-segmented, filiform, very short, approximately reaching half of elytra, all antennomeres slightly pubescent; antennomere I club-shaped; antennomere II elongated, very thin; antennomeres III-IV very thin and long, with antennomere IV the longest of all antennomeres; antennomere V long, enlarged-bulged from middle to the apex in the external margin; antennomere VI similar to antennomere V but shorter; antennomere VII similar to previous one, but shorter; antennomeres VIII-X short, robust, almost triangular-shaped, antennomere VIII longer than antennomeres IX or X; antennomere XI short, robust, rounded apically. Pronotum extremely elongated, narrower than head, noticeably gibbous, anterior and posterior margins almost straight, corners rounded, surface slightly pubescent. Scutellum triangular-shaped. Elytra short which do not cover some abdominal segments, wider than pronotum, parallel-sided, slightly enlarged and slightly gibbous at humeri, slightly dehiscent, rounded apexes, surface with very small punctation and equipped with some short setae. Posterior wings transparent, longer than elytra, noticeably shorter than last abdominal segments. Metasternum elongated with apex rounded and with shallow punctuation; sternites transverse, robust, pubescent; last tergite elongated with pointed apex, last sternite shorter and noticeably wider than last tergite and lobed at sides whit lobes long and pointed. Legs robust, elongated, pubescent; coxae very robust, elongated; trochanters robust, elongated, rounded at apex; femora very robust, sturdier than tibiae, curved; tibiae thin, cylindrical, short, all approximately as long as femora, apparently without spurs at apex. Tarsal formula 5-5-5; first tarsomere long; second tarsomere about 1.9 times shorter than first; third very short, triangular-shaped; fourth tarsomere enlarged, very robust, bilobed with lobes short and rounded apically; fifth tarsomere elongated, thin; claws simple, short, without denticle at the base.

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

Syninclusions. Air bubbles, several debris and botanical remains.

Remarks. Piece of yellow brownish amber that measures 11 x 10 x 3 mm. The inclusion is not exceptionally visible.

†*Sanaungulus burgardi* sp. nov.
(Fig. 13)

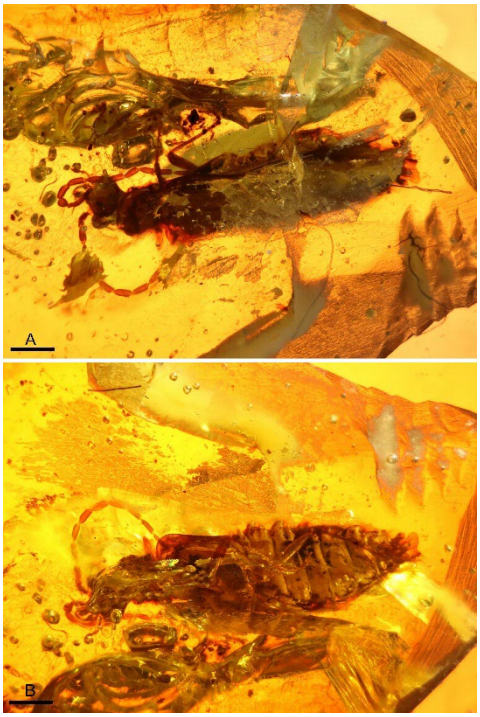

Fig. 13. *Sanaungulus burgardi* sp. nov. in Burmese amber (code SNHMB.G 8272). A: Holotype, dorsal view, scale bar = 0.5 mm; B: Holotype, ventral view, scale bar = 0.5 mm.

Holotype. Male, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNHMB.G 8272 in the Staatliches Naturhistorisches Museum Braunschweig (ex Müller's collection number: BUB4874).

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 has antennae filiform with antennomeres robust, similar to *Sanaungulus beeralissae* Fanti & P. Müller sp. nov. and *S. morellii* Fanti & Damgaard, 2020 (Fanti & Damgaard 2020; present paper). *S. beeralissae* differs from the new species by having more robust and differently shaped antennomeres III-V. *S. morellii* instead, differs from the new species by its antennomeres shorter and more globular (Fanti & Damgaard 2020).

Description. Adult, alate, slender. Male, based on the shape of last sternite. Body length: 3.9 mm. Entirely brown.

Head constricted (triangular shaped) behind the eyes, wide, transverse, surface with shallow punctation and very small pubescence. Eyes prominent, roundish, very large, inserted in the lateral part of the head. Mandibles elongated, falciform. Maxillary palps 4-segmented with last palpomere securiform, rather elongated, with apex thinner and rounded. Labial palps 3-segmented with last palpomere securiform. Antennae 11-segmented, filiform, robust, relatively long, almost reaching the apex of elytra, approximately reaching half of abdomen, all antennomeres very slightly pubescent; antennomere I club-shaped, elongated, robust; antennomere II very short, almost globular, small and not robust, about 4 times shorter than first; antennomere III massive, globular; antennomeres IV-VII sausage-shaped; antennomeres VIII-X slightly shorter and less massive (not particularly sausage-shaped) than previous ones; antennomere XI filiform, robust, rounded apically. Pronotum little transverse, approximately as wide as head, anterior margin almost straight and little bordered, posterior margin almost straight and little bordered, sides slightly irregular and narrower near the apical margin, corners rounded-obtuse, pronotum disc almost flat and little pubescent. Scutellum elongated, triangular-shaped with rounded apex. Elytra short which do not cover some abdominal segments, wider than pronotum, parallel-sided, slightly dehiscent, rounded apexes, surface apparently smooth and equipped with very short setae. Posterior wings transparent, longer than elytra, reaching the

last abdominal segments. Metasternum elongated, robust, with apex almost straight; sternites strongly transverse, narrow, equipped with shallow punctation and short setae; last tergite wider than last sternite, in a squared and wide lobe; last sternite with two rather long and massive lobes. Legs short, rather robust, slightly pubescent; coxae robust, massive, rather short; trochanters elongated, rounded at apex; femora robust, sturdier than tibiae, straight; tibiae thin, cylindrical, metatibiae longer than metafemora, without spurs at apex. Tarsal formula 5-5-5; first tarsomere long; second shorter than first; third short, triangular-shaped; fourth tarsomere strongly bilobed with lobes short, robust and rounded apically; fifth tarsomere elongated, thin, curved; claws simple, long, without denticle at the base.

Etymology. Named in honor of Rolf Burgard, grandfather of the second author (Patrick).

Syninclusions. Air bubbles, debris, botanical remains.

Remarks. Piece of clear, yellow amber that measures 14 x 9 x 3 mm. The inclusion is complete, partially covered by surface knurling.

†*Sanaungulus carloi* sp. nov.
(Fig. 14)

Holotype. Sex undefined, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNHMB.G 8126 in the Staatliches Naturhistorisches Museum Braunschweig (ex Müller's collection number: BUB4550).

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

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

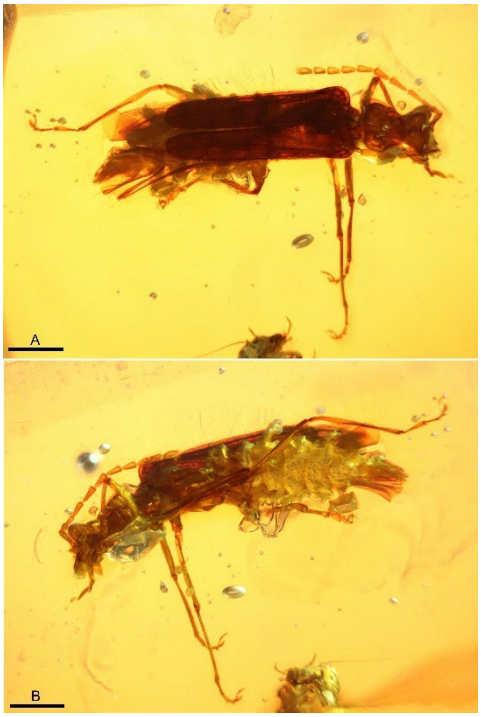

Fig. 14. *Sanaungulus carloi* sp. nov. in Burmese amber (code SNHMB.G 8126). A: Holotype, dorsal view, scale bar = 0.5 mm; B: Holotype, ventral view, scale bar = 0.5 mm.

Differential diagnosis. The new species differs from *Sanaungulus dunlopi* Fanti & P. Müller, 2022, *Sanaungulus ypogaeum* Fanti & P. Müller, 2022 and *Sanaungulus morellii* Fanti & Damgaard, 2020 by its pronotum strongly narrower anteriorly (Fanti & Damgaard 2020; Fanti & Müller 2022). Furthermore, the new species differs from *Sanaungulus rosenzweigi* Fanti & Damgaard, 2020 by its shorter antennae and the different shape and length of antennomeres (Fanti & Damgaard 2020). *S. carloi* sp. nov. has antennomeres less robust than *S. beeralissae* sp. nov.

Description. Adult, alate, slender. Sex undefined. Body length: 3.2 mm. Entirely brown.

Head transverse, constricted (triangular shaped) behind the eyes, surface with shallow punctation and pubescent. 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. Labial palps 3-segmented, with the last palpomere securiform. Antennae 11-segmented, filiform, with robust antennomeres, short, surpassing the humeral zone of elytra but not reaching the half of elytra, all antennomeres pubescent; antennomere I club-shaped, enlarged from middle to apex; antennomere II short, robust; antennomere III about 1.3-1.4 times longer than second; antennomeres IV-V subequal, longer than previous one; antennomeres VI-VII subequal, robust, slightly shorter than previous ones; antennomeres VIII-X shorter than previous ones, subtriangular, robust; antennomere XI quite elongated, robust, rounded apically, margins slightly asymmetrical. Pronotum elongated, hemispherical, with posterior part wider than anterior, anterior margin rounded, posterior margin almost straight and strongly bordered, sides curved and strongly restricted from middle to apex, corners rounded, pronotum disc flat and slightly pubescent. Scutellum triangular-shaped with rounded apex. Elytra short which do not cover some abdominal segments, wider than pronotum, parallel-sided (only slightly enlarged at humeri), not dehiscent, rounded apexes, surface with sparse and rather large impressed punctation (arranged in striae and confused). Posterior wings transparent, longer than elytra. Metasternum elongated and robust; sternites transverse, wide, wrinkled. Legs thin, long, slightly pubescent; coxae massive; trochanters elongated, rounded at apex; femora irregular at margins, very elongated, subcylindrical, very slightly sturdier than tibiae; tibiae, thin, cylindrical, long, without spur at apex, pro- and mesotibiae approximately as long as pro- and mesofemora, metatibiae very longer than metafemora. Tarsal formula 5-5-5; first tarsomere long, second shorter than first; third short, triangular shaped; fourth tarsomere strongly bilobed with lobes long and robust; fifth tarsomere extremely elongated, thin, curved; claws simple, long, without denticle at the base.

Etymology. Named in honor of Carlo Maria Legittimo (Città della Pieve, Umbria, Italy), spiders' expert.

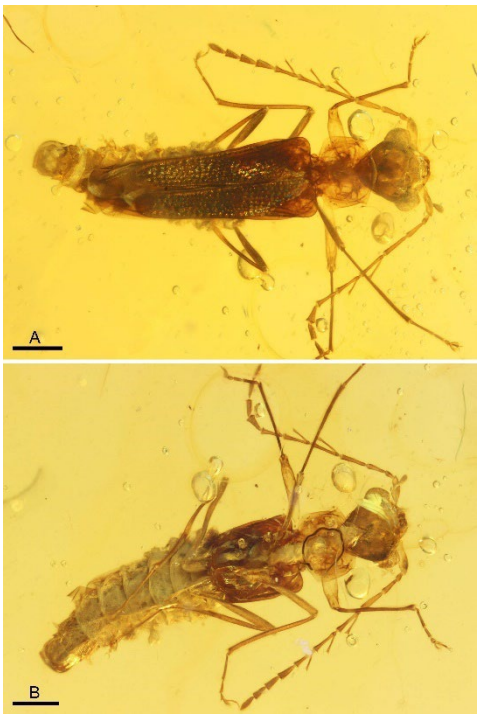

Fig. 15. *Sanaungulus elfriedeae* sp. nov. in Burmese amber (code SNHMB.G 8277). A: Holotype, dorsal view, scale bar = 0.5 mm; B: Holotype, ventral view, scale bar = 0.5 mm.

Syninclusions. Air bubbles, debris, Psocoptera.

Remarks. Piece of clear amber that measures 17 x 7 x 4 mm. The inclusion is complete.

†*Sanaungulus elfriedeae* sp. nov.
(Fig. 15)

Holotype. Female, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNHMB.G 8277 in the Staatliches Naturhistorisches Museum Braunschweig (ex Müller's collection number: BUB4981)

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 very similar to *Sanaungulus curtipennis* Fanti, Damgaard & Ellenberger, 2018 from which it differs for the pronotum with acute anterior corners and by its posterior margin curved, where it is straight in *S. curtipennis* (Fanti et al. 2018). Furthermore, the antennomeres and rami are different in the two taxa.

Description. Adult, alate, slender. Female, based on the shape of last sternite which is rounded. Body length: 4.0 mm. Entirely testaceous-brown.

Head partially covered by pronotum, constricted (triangular shaped) behind the eyes, surface slightly wrinkled with very small pubescence. Eyes very prominent, roundish, large, inserted in the lateral part of the head. Mandibles elongated, falciform, without teeth. Maxillary palps 4-segmented with last palpomere securiform, rather spatulate-shaped, external margin and apex rounded. Labial palps 3-segmented with last palpomere securiform. Antennae 11-segmented, pectinate, thin, relatively long, almost reaching the elytral apex, all antennomeres pubescent equipped with few and long setae; antennomere I club-shaped, elongated, robust; antennomere II short, slightly enlarged apically; antennomere III filiform, long, thin, cylindrical, bulged at apex; antennomere IV filiform, very long, longer than antennomere III, thin, slightly bulged at apex; antennomere V extremely long, slightly longer than antennomere IV, thin, equipped with a long antennal process inserted near the base which is slightly shorter than antennomere and squared apically; antennomere VI very slightly shorter than previous one, equipped with an antennal process inserted near the base (squared apically and shorter than antennomere); antennomere VII shorter than previous one, equipped with an antennal process inserted near the base which is similar to the other rami; antennomere VIII robust, shorter and sturdier than previous one, without antennal process; antennomeres IX-X sub-equal in shape (antennomere IX longer than antennomere X), slightly flat and robust, without antennal proces; antennomere XI robust, rather short, rounded apically. Pronotum transverse, slightly restricted anteriorly, anterior margin curved and protruded in the middle, posterior margin curved, sides straight and very feebly bordered, anterior corners evident and acute, posterior corners rounded, pronotum disc flat and smooth. Scutellum triangular-shaped with rounded apex. Elytra short which do not cover some abdominal segments, slightly wider at humeri than pronotum, parallel-sided, rounded apexes, surface strongly wrinkled with impressed punctuaction. Posterior wings transparent, longer than elytra, not reaching the last abdominal segments. Metasternum robust, with margin curved; sternites strongly transverse; last tergite and last sternite rounded with last tergite wider. Legs thin, pubescent; coxae robust, rather short; trochanters elongated, rounded at apex; femora thin, sturdier than tibiae; tibiae thin, cylindrical, with short spur at apex, protibiae as long as profemora, meso- and metatibiae longer than meso- and metafemora. Tarsal formula 5-5-5; first tarsomere very long; second shorter than first; third triangular-shaped; fourth tarsomere strongly bilobed

with lobes long and rounded apically; fifth tarsomere elongated, thin, curved; claws simple, long, without denticle at the base.

Etymology. Named in honor of Elfriede Müller, grandmother of the second author (Patrick).

Syninclusions. Air bubbles, debris, botanical remains.

Remarks. Piece of clear, oval and golden yellow amber that measures 17 x 12 x 4 mm. The inclusion is complete and exceptionally visible.

†*Sanaungulus feliciaeweissbachae* sp. nov. (Fig. 16)

Fig. 16. *Sanaungulus feliciaeweissbachae* sp. nov. in Burmese amber (code SNHMB.G 8270). A: Holotype, dorsal view, scale bar = 0.5 mm; B: Holotype, ventro-lateral view, scale bar = 0.5 mm.

Holotype. Male, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNHMB.G 8270 in the Staatliches Naturhistorisches Museum Braunschweig (ex Müller's collection number: BUB4872).

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 has antennae filiform with antennomeres very robust, with only *Sanaungulus peteriruedeli* Fanti & P. Müller, 2022 having even more robust antennomeres (Fanti & Müller 2022). *S. feliciaeweissbachae* sp. nov. has antennomeres similar to: *S. dunlopi* Fanti & P. Müller, 2022 which has a pronotum more elongated with rounded anterior margin and sides straight; to *S. burgardi* sp. nov. which has antennomeres IV-VII sausage-shaped; and to *S. beeralissae* sp. nov. which has antennomere III more robust, and a very different pronotum, more elongated (Fanti & Müller 2022; present paper).

Description. Adult, alate, slender. Male, based on the shape of last abdominal segments. Body length: 3.0 mm. Entirely brown.

Head constricted (triangular shaped) behind the eyes, wide, strongly transverse, surface with shallow punctation and pubescence. Eyes prominent, roundish, rather small, inserted in the lateral part of the head. Mandibles short, robust, falciform, wide at base. Maxillary palps 4-segmented with last palpomere securiform, short, robust. Labial palps 3-segmented with last palpomere securiform. Antennae 11-segmented, filiform, very robust, short, almost reaching the half of elytra, not reaching half of abdomen, all antennomeres very slightly pubescent; antennomere I club-shaped, elongated, very robust; antennomere II short,

almost globular; antennomeres III-V robust, not sausage-shaped; antennomeres VI-IX very slightly longer and less robust than previous ones; antennomere X longer and sturdier than antennomere IX; antennomere XI filiform, robust, rounded apically. Pronotum strongly transverse, approximately as wide as head, anterior margin irregular and protruding in the middle, posterior margin almost straight and finely but evidently bordered, sides slightly irregular and enlarged near the anterior margin, corners rounded-obtuse, pronotum disc irregular and pubescent. Scutellum elongated, triangular-shaped with rounded apex. Elytra short which do not cover some abdominal segments, wider than pronotum, parallel-sided, very slightly dehiscent apically, rounded apexes, surface slightly wrinkled and punctation apparently in relief and arranged in confused striae, equipped with very short setae. Posterior wings transparent, longer than elytra, not reaching the last abdominal segments. Metasternum elongated, robust, with apex rounded; sternites strongly transverse, narrow, equipped with shallow punctation and short setae; last tergite wider than last sternite, in a very long and pointed lobe; last sternite with two rather long lobes. Legs rather long, slightly pubescent; coxae robust, very massive; trochanters elongated, rounded at apex; femora robust, sturdier than tibiae, slightly curved; tibiae thin, cylindrical, pro- and mesotibiae shorter than pro- and mesofemora, metatibiae longer than metafemora. Tarsal formula 5-5-5; first tarsomere not particularly long; second longer than first; third triangular-shaped; fourth tarsomere strongly bilobed with lobes long and rounded apically; fifth tarsomere elongated, thin, curved; claws simple, long, without denticle at the base.

Etymology. Named in honor of Felicia Weissbach, daughter of a big collector in Germany and friend of the second author (Patrick).

Syninclusions. Air bubbles (one huge), debris, botanical remains (including stellate hairs).

Remarks. Piece of clear, yellow amber that measures 11 x 6 x 3 mm. The inclusion is complete.

†*Sanaungulus fossilis* sp. nov.
(Fig. 17)

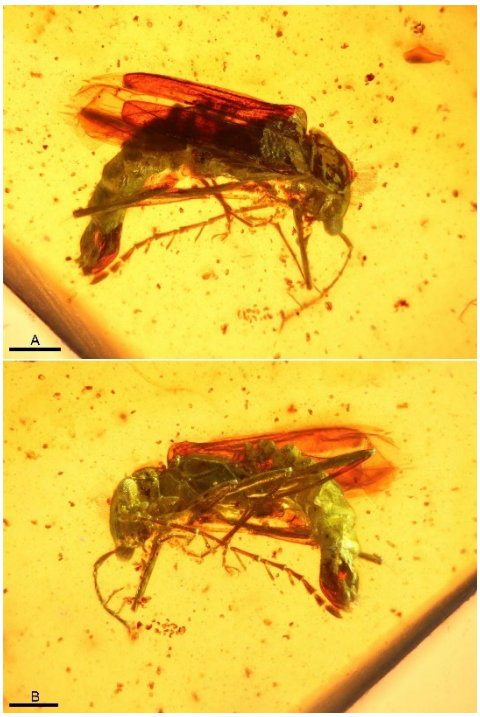

Fig. 17. *Sanaungulus fossilis* sp. nov. in Burmese amber (code SNHMB.G 8125). A: Holotype, dorsal view, scale bar = 0.5 mm; B: Holotype, ventral view, scale bar = 0.5 mm.

Holotype. Male, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNHMB.G 8125 in the Staatliches Naturhistorisches Museum Braunschweig (ex Müller's collection number: BUB4549).

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

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

Differential diagnosis. *Sanaungulus kirstenaeweissbachae* Fanti & P. Müller, 2022, *Sanaungulus ghitaenoerbyae* Fanti, Damgaard & Ellenberger, 2018 and *Sanaungulus troelsikloevedali* Fanti & Damgaard, 2019 have the pronotum more transverse compared to *Sanaungulus fossilis* sp. nov. (Fanti et al. 2018; Fanti & Damgaard 2019; Fanti & Müller 2022). Instead, for the differences with the new species described in this document, see under the following differential diagnoses.

Description. Adult, alate, slender. Male, based on the shape of last sternite. Body length: 3.2 mm. Entirely brown.

Head transverse, constricted (triangular shaped) behind the eyes, surface with shallow punctation and pubescent. Eyes very prominent, large, rounded, inserted in the upper and lateral part of the head. Mandibles elongated, falciform. Maxillary palps 4-segmented with the last palpomere short, securiform. Labial palps 3-segmented, with the last palpomere securiform. Antennae 11-segmented, pectinate, thin, inserted far from the eyes, rather long, about reaching the apex of elytra, all antennomeres pubescent; antennomere I slightly club-shaped, elongated, slightly enlarged from middle to apex; antennomere II short, globular at apex; antennomeres III-IV filiform, thin, long, with antennomere III slightly shorter than antennomere IV; antennomeres V-VI subequal, long, each with a long and thin (squared apically) antennal process inserted near the base; antennomere VII shorter than previous ones, equipped with a long and thin antennal process inserted near the base; antennomere VIII shorter than previous one, equipped with a long antennal process inserted near the base; antennomeres IX-X without antennal process, rather robust and short, antennomere X shorter than IX; antennomere XI filiform, robust, slightly pointed apically. Pronotum elongated, slightly narrower than head, anterior margin rather rounded, posterior margin almost straight and bordered, sides curved and irregular with restriction near the anterior and posterior margins, anterior corners rounded, posterior corners very slightly acute, pronotum disc almost flat and very slightly pubescent. Scutellum triangular-shaped. Elytra short that do not cover some abdominal segments, wider than pronotum, not dehiscent, almost straight apexes, surface with deep punctation mostly present in the humeral zone. Posterior wings transparent, longer than elytra, very shorter than last abdominal segment. Metasternum elongated and rounded apically; sternites transverse and pubescent. Legs thin, long, slightly pubescent; coxae massive, rounded; trochanters elongated; femora straight, subcylindrical, slightly sturdier than tibiae; tibiae, very thin, cylindrical, long, protibiae slightly shorter than profemora, meso- and metatibiae slightly longer than meso- and metafemora. Tarsal formula 5-5-5; first tarsomere extremely long, second shorter than first; third short; fourth tarsomere strongly bilobed with lobes long; fifth tarsomere elongated, thin, curved; claws simple, long, without denticle at the base.

Etymology. Derived from the Latin adjective "*fossĭlis*" (from *fŏdĭo* = to dig, hoe, + *-ĭlis*) = fossil.

Syninclusions. Air bubbles, debris, botanical remains.

Remarks. Piece of clear amber that measures 12 x 9 x 3 mm. The inclusion is folded, and the right antenna is preserved up to the sixth antennomere.

†*Sanaungulus massaronei* sp. nov.
(Fig. 18)

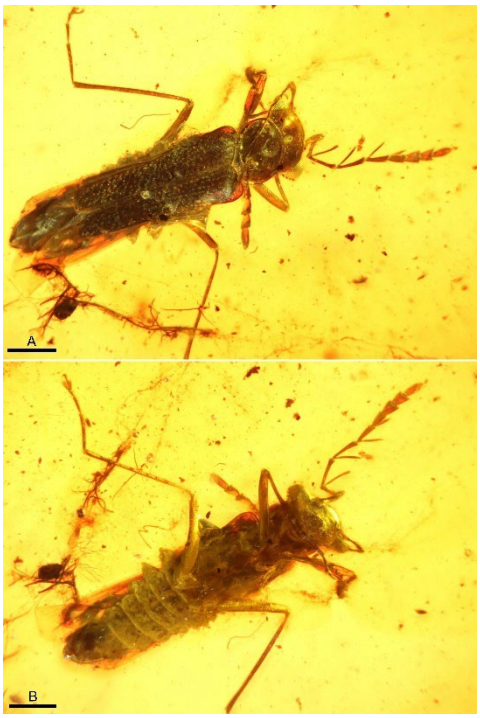

Fig. 18. *Sanaungulus massaronei* sp. nov. in Burmese amber (code SNHMB.G 8124). A: Holotype, dorsal view, scale bar = 0.5 mm; B: Holotype, ventral view, scale bar = 0.5 mm.

Holotype. Sex undefined, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNHMB.G 8124 in the Staatliches Naturhistorisches Museum Braunschweig (ex Müller's collection number: BUB4548).

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 most similar to *Sanaungulus ghitaenoerbyae* Fanti, Damgaard & Ellenberger, 2018 from which it differs for the less transverse pronotum, less dehiscent elytra, and different position of antennal processes (Fanti et al. 2018). Compared to the new species, *Sanaungulus emarginaticollis* Y. Yang, H. Liu & M. Bai in Yang et al., 2022 has the last four antennomeres less robust, and pronotum more enlarged in the middle of the anterior margin (Yang et al. 2022). *Sanaungulus massaronei* sp. nov. differs from *Sanaungulus fossilis* sp. nov. by the pronotum more transverse with sides slightly rounded and non-irregular.

Description. Adult, alate, slender. Sex undefined. Body length: 3.0 mm. Entirely brown.

Head transverse, slightly constricted (triangular shaped) behind the eyes, surface with shallow punctation and pubescent. Eyes very prominent, large, subelliptical, inserted in the upper and lateral part of the head, inter-ocular dorsal distance about 4.0 times greater than eye diameter. Mandibles elongated, falciform. Maxillary palps 4-segmented with the last palpomere elongated, securiform. Labial palps 3-segmented, with the last palpomere securiform. Antennae 11-segmented, pectinate, thin, short, about reaching the half of elytra, all antennomeres pubescent; antennomere I club-shaped, elongated, enlarged at base and apex and strongly thinner in the middle; antennomere II short, robust; antennomere III thinner and longer than second; antennomere IV longer than third; antennomeres V-VI subequal, extremely long (the longest), each with a very long and thin antennal process inserted near the base; antennomere VII shorter than previous ones, enlarged apically, equipped with a very long and thin antennal process inserted near the base (similar to the previous ones in length and shape); antennomeres VIII-X robust, quite flat, enlarged apically (antennomere VIII equipped with a long antennal process near

the base, antennomeres IX-X without antennal process), progressively reduced in length from each other; antennomere XI filiform, short, rather robust, rounded apically. Pronotum transverse, about as wide as head, anterior margin rather rounded and strongly bordered, posterior margin almost straight, sides very slightly curved, corners rounded, pronotum disc flat and very slightly pubescent. Scutellum triangular-shaped. Elytra short which do not cover some abdominal segments, wider than pronotum, dehiscent, rounded apexes, surface with several punctation arranged in striae and in relief. Posterior wings transparent, longer than elytra, about as long as last abdominal segment. Metasternum elongated, rounded apically; sternites transverse. Legs thin, long, slightly pubescent; coxae massive; trochanters elongated, rounded at apex; femora almost straight, subcylindrical, sturdier than tibiae; tibiae, thin, cylindrical, long, with a robust spur at apex, tibiae very longer than femora. Tarsal formula 5-5-5; first tarsomere extremely long, second shorter than first; third short, slightly elongated; fourth tarsomere strongly bilobed with lobes long; fifth tarsomere elongated, thin, slightly curved; claws simple, long, without denticle at the base.

Etymology. Named in honor of Carlo Massarone, expert of the family Cerambycidae.

Syninclusions. Air and enhydro bubbles, debris, botanical remains.

Remarks. Piece of clear amber in Cabochon cut that measures 14 x 10 x 2 mm. The inclusion is well visible but two legs are missing.

†***Sanaungulus rosaemariae*** **sp. nov.**
(Fig. 19)

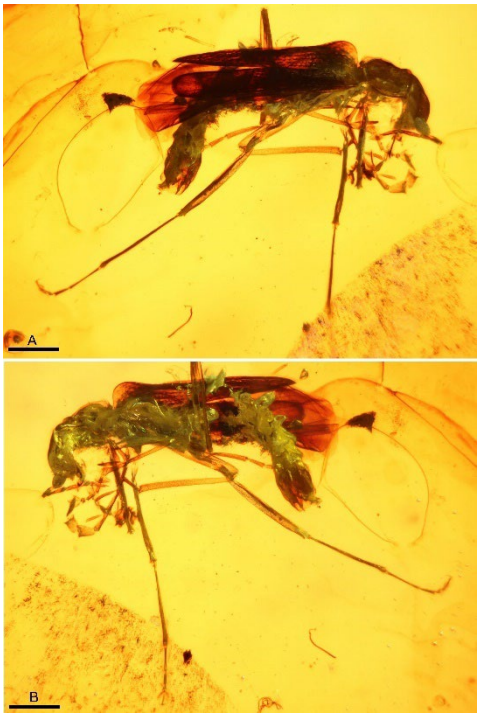

Fig. 19. *Sanaungulus rosaemariae* sp. nov. in Burmese amber (code SNHMB.G 8127). A: Holotype, dorsal view, scale bar = 0.5 mm; B: Holotype, ventral view, scale bar = 0.5 mm.

Holotype. Male, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNHMB.G 8127 in the Staatliches Naturhistorisches Museum Braunschweig (ex Müller's collection number: BUB4551).

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 differs from *Sanaungulus emarginaticollis* Y. Yang, H. Liu & M. Bai in Yang et al., 2022 by its pronotum more elongated without protrusion at the center of the anterior margin, anterior corners not

emarginated, and antennomeres IX-X more robust (Yang et al. 2022). Furthermore, the new species has different last abdominal segments (Yang et al. 2022). The new species differs from *Sanaungulus massaronei* sp. nov. by its more elongated pronotum with concavity near the anterior margin (disc flat in *S. massaronei* sp. nov.), and by the different shape of antennomeres (in particular, antennomeres VIII and XI). *Sanaungulus rosaemariae* sp. nov. is very similar to *Sanaungulus fossilis* sp. nov. from which it differs in the pronotum non-flat and with sides rounded (non-irregular), and in shorter antennae. *S. elongaticollis* Y. Yang, W. Zhao & H. Liu, 2024 instead has a more elongated pronotum (Yang et al. 2024) than *S. rosaemariae* sp. nov.

Description. Adult, alate, slender. Male, based on the shape of last sternite. Body length: 3.0 mm (curled). Entirely brown.

Head elongate, constricted (triangular shaped) behind the eyes, surface with shallow punctation and slightly pubescent. Eyes very prominent, elliptical, inserted in the upper and lateral part of the head. Mandibles elongated, falciform. Maxillary palps 4-segmented with the last palpomere very elongated, securiform. Labial palps 3-segmented. Antennae 11-segmented, pectinate, thin, relatively long, surpassing the half of elytra and not reaching the apex, all antennomeres pubescent; antennomere I slightly club-shaped, elongated, thin; antennomere II short, robust, elongated; antennomere III filiform, long, thin, cylindrical; antennomere IV filiform, longer than third, extremely thin; antennomere V extremely long (the longest), thin, sturdier than previous one, equipped with a very long antennal process inserted near the base; antennomeres VI-VII subequal, long, shorter than previous one, each with a very long (and squared apically) antennal process inserted near the base; antennomere VIII shorter than previous ones, enlarged apically, equipped with a long antennal process inserted near the base (similar to the previous ones); antennomeres IX-X very robust, quite flat, enlarged apically, without antennal processes; antennomere XI filiform, elongated, thin, rounded apically. Pronotum elongated, narrower than head, anterior margin straight and strongly bordered, posterior margin slightly rounded and bordered, sides curved at the posterior part, posterior corners rounded, anterior corners obtuse, pronotum disc smooth and irregular with small concavity near the anterior margin. Scutellum triangular-shaped. Elytra short, which do not cover some abdominal segments, wider than pronotum, parallel sides, rounded apexes, surface with several punctation arranged in striae and rather in relief. Posterior wings transparent, longer than elytra, which do not cover the last abdominal segment. Metasternum elongated; sternites transverse; last sternite elongated with lobes. Legs very thin, extremely long, slightly pubescent; coxae massive; trochanters elongated, rounded at apex; femora almost straight, subcylindrical, slightly sturdier than tibiae; tibiae, thin, cylindrical, pro- and mesotibiae longer than pro- and mesofemora, metatibiae shorter than metafemora. Tarsal formula 5-5-5; first tarsomere extremely long, second tarsomere shorter than first; third short, triangular; fourth tarsomere strongly bilobed with lobes very long; fifth tarsomere elongated, thin; claws simple, long, without denticle at the base.

Etymology. Named in honor of Rosa Maria Di Lauro (Poggiomarino, Campania, Italy).

Syninclusions. Air bubbles, debris, botanical remains.

Remarks. Piece of clear amber that measures 15 x 9 x 3 mm. The front legs and antennae are quite tangled.

†*Sanaungulus sucinus* sp. nov.
(Fig. 20)

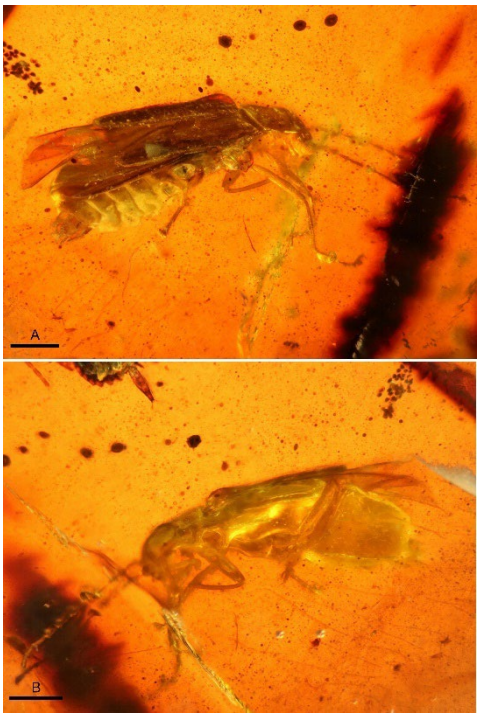

Fig. 20. *Sanaungulus sucinus* sp. nov. in Burmese amber (code SNHMB.G 8267). A: Holotype, dorsal view, scale bar = 0.5 mm; B: Holotype, ventro-lateral view, scale bar = 0.5 mm.

Holotype. Male, adult specimen in a Burmese (Kachin) amber piece: Catalog number SNHMB.G 8267 in the Staatliches Naturhistorisches Museum Braunschweig (ex Müller's collection number: BUB4869).

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 has antennae filiform with antennomeres very thin, and it differs from *Sanaungulus ruicheni* (Hsiao & Huang, 2018) in having the antennomere II more robust, the antennomere III longer than II, and a different pronotum (Hsiao & Huang 2018). Furthermore, *Sanaungulus nalae* Fanti & P. Müller, 2022 has a different pronotum with a more rounded anterior margin, and *Sanaungulus rosenzweigi* Fanti & Damgaard, 2020 has the antennomere II less robust, and antennomeres IV-IX sub-equal (not sub-equal in *Sanaungulus sucinus* sp. nov.), and also a different pronotum (Fanti & Damgaard 2020; Fanti & Müller 2022).

Description. Adult, alate, robust. Male, based on the shape of last sternite. Body length: 2.9 mm. Entirely brown.
Head constricted (triangular shaped) behind the eyes, wide, surface with shallow punctation and small pubescence. Eyes prominent, roundish, inserted in the upper-lateral part of the head. Mandibles elongated, falciform. Maxillary palps 4-segmented with last palpomere securiform, robust and short. Labial palps 3-segmented with last palpomere securiform. Antennae 11-segmented, filiform, thin, relatively long, not reaching the apex of elytra, approximately reaching half of abdomen, all antennomeres pubescent; antennomere I club-shaped, elongated, robust; antennomere II short, rather robust especially in the middle, about 1.4-1.5 times shorter than first; antennomeres III-VI elongated, thin, sub-equal; antennomere VII slightly shorter than previous ones; antennomeres VIII-X shorter than previous one, rather robust and short; antennomere XI filiform, robust, rounded apically. Pronotum sub-squared, approximately as wide as head, anterior margin almost straight and little bordered, posterior margin almost straight and little bordered, sides slightly curved and very little bordered, corners rounded-obtuse, pronotum disc almost flat and only very little depressed in the center with surface pubescent. Scutellum elongated, triangular-shaped with rounded apex. Elytra short which do not

cover some abdominal segments, wider than pronotum, parallel-sided, dehiscent, rounded apexes, surface slightly wrinkled equipped with short setae. Posterior wings transparent, longer than elytra, reaching the last abdominal segments. Metasternum elongated with apex rather roundish; sternites transverse, robust, with shallow punctation; last sternite with long and narrow lobe at sides. Legs robust, not particularly long, slightly pubescent; coxae robust, elongated; trochanters elongated, rounded at apex; femora robust, sturdier than tibiae, very slightly curved; tibiae thin, cylindrical, all very shorter than femora, without spurs at apex. Tarsal formula 5-5-5; first tarsomere long; second shorter than first, robust, slightly enlarged apically at sides; third short, triangular-shaped; fourth tarsomere strongly bilobed with lobes short, robust and rounded apically; fifth tarsomere elongated, thin, curved; claws simple, long, without denticle at the base.

Etymology. Derived from the Latin adjective "*sūcĭnus*" = of amber.

Syninclusions. Air bubbles, debris, botanical remains, a cockroach larva (Blattodea).

Remarks. Piece of clear and gold amber that measures 11 x 11 x 2.5 mm. The inclusion is complete but not very visible ventrally.

Subfamily Silinae Mulsant, 1862
Genus *Silis* Charpentier, 1825
Subgenus *Silis* Charpentier, 1825

†*Silis* (*Silis*) *aztecimaya* sp. nov.
(Fig. 21)

Holotype. Male, adult specimen in a Mexican amber piece: SNHMB.G 8087 in the Staatliches Naturhistorisches Museum Braunschweig (ex Müller's collection number: MEX002).

Fig. 21. *Silis* (*Silis*) *aztecimaya* sp. nov. in Mexican amber (code SNHMB.G 8087). A: Holotype, dorsal view, scale bar = 0.5 mm; B: Holotype, ventral view, scale bar = 0.5 mm; C-D: Holotype, lateral views, scale bars = 0.5 mm.

Type locality. Simojovel de Allende, Chiapas, Mexico, mine unknown.

Type horizon. Early-Middle Miocene: Balumtun Sandstone or Mazantic Shale (13-19 mya, or 15-20 mya) or 13-22.8/23 mya including La Quinta Formation.

Differential diagnosis. The lateral margins of pronotum lobed, also if only slightly, and the shape of last abdominal segment indicate that the specimen is male.
The specimen considered here was assigned to the genus *Silis* based on a combination of the following morphological characters (Champion 1915; Leng & Mutchler 1922; Ramsdale 2002; Constantin 2009, 2010, 2017, 2024): (1) the pronotum strongly transverse (less transverse in *Discodon*, *Grandesilis*); (2) the anterior margin of pronotum not explanate and not reflexed (explanate and reflexed in *Grandesilis*); (3) claws simple (anterior meso- and metatarsal claws of male apically cleft in *Discodon, Pygodiscodon*; tarsi each with one claw cleft at tip in *Ditemnomorphus*; all anterior tarsal claws of male tendentially with a broad basal tooth in *Polemius*; anterior claw of male protarsi bifid at tip in *Parasilis*); (4)

scutellum without projected long lamella (with long projection in *Peltariosilis*); (5) caudal abdominal tergite produced (not produced in *Ditemnus*); (6) head short and last abdominal segment not forcipiform (strongly projecting head and last abdominal segment of the male bilobed and forcipiform in *Silidiscodon*); (7) head not covered by pronotum and this latter not semicircular (head covered by pronotum that is semicircular in *Photinomorpha*); (8) first antennomere club-shaped not enlarged (scape-shaped and enlarged in *Tylocerus*).

The shape of eighth sternite (= ventrite) and posterior margin of seventh sternite are not clearly visible in the new species, but the caudal abdominal tergite strongly produced is very similar to *Plectonotum excisum* sensu Ramsdale. This latter is considered by Ramsdale (2002) as potential new genus (subfamily Silinae) with several additional undescribed species in Arizona and Mexico. Only further findings will be able to highlight the possible affinity between the new fossil species and *Plectonotum excisum*.

Furthermore, it is worth noting that it is difficult to differentiate the Neotropic species of *Silis* and *Polemius* (Constantin 2009) since many Neotropical *Silis* have the pronotum without spines and lobes, and similar basal lobe in the claws, however based on Constantin (2009, 2024) the genus *Polemius* also presents: the pronotum widest near the anterior margin, lateral margin of the pronotum notched in the apical half, and elytral pubescence velvety. All these features are not present in the new species.

Silis aztecimaya sp. nov. differs from *Silis chiapasensis* Wittmer, 1963, the only other fossil soldier beetle known from Mexican (Chiapas) amber, for the longer elytra comparated to abdominal length, and for the pronotum without a long process on the sides (Wittmer 1963).

Description. Adult, alate. Male defined on the basis of pronotum with lateral lobes. Body length: 4.2 mm. Entirely brown.

Head small, slightly elongated, narrower than pronotum, restricted behind the eyes, finely punctate and pubescent, only partially covered by pronotum. Eyes rounded and strongly protruded, convex, inserted in upper and lateral part of head. Mandibles falciform. Maxillary palpi 4-segmented, palpomeres unequal in length with last palpomere strongly elongate and slightly securiform. Labial palps 3-segmented with last palpomere securiform. Antennae inserted in frons and away from eyes, reaching back approximately to half of elytra, 11-segmented, filiform, all antennomeres covered with sparce setae; antennomere I elongate and slightly enlarged in the basal-middle part; antennomere II short, triangular shaped, enlarged apically and slightly elongated basally; antennomere III long and robust, about 2.2-2.3 times longer than second; antennomere IV long, thinner than third; antennomeres V-X long, progressively slightly shorter from each other; antennomere XI filiform, oblong, with rounded apex. Pronotum strongly transverse, surface almost flat, with semi-erect setae and with small rugosity; anterior margin rounded at the center and not explanated, posterior margin straight, sides with a kind of two very small lobes, anterior lobe obtuse and close to the corners and more evident than posterior one, posterior lobe very small (in a kind of obtuse tooth) located between the posterior and central margins of pronotum, anterior corners rounded, posterior corners obtuse. Scutellum wide, triangular-shaped with apex rounded. Elytra wider than pronotum, elongate, not reaching the last abdominal segment, parallel-sided, smooth with some semi-erect setae, apex rounded. Posterior wings longer than elytra, rather transparent. Metasternum sub-quadrate with rounded posterior margin; abdominal segments robust, transverse and

pubescent; last tergite broad with two lobes at posterior corners and undulating and rounded at the middle; last ventrite wide with two central lobes triangular-shaped having apex rounded. Legs relatively short, slender and pubescent; coxae elongated and robust; trochanters long with rounded apex; femora enlarged and almost straight; tibiae cylindrical, thinner than femora, with apical spurs, pro- and mesotibiae shorter than pro- and mesofemora, metatibiae very slightly longer than metafemora. Tarsal formula 5-5-5; first tarsomere elongated; second tarsomere approximately 1.2 times shorter than first; third tarsomere shorter than tarsomere II; fourth tarsomere deeply bilobed at sides; fifth tarsomere elongate, slender and curved; claws simple with an extremely small and obtuse basal tooth. Female unknown.

Etymology. Derived from the ancient peoples: Aztecs (= in Latin "*Azteci*") and Maya. In reference to the fact that these indigenous peoples were the first to use this amber for various medical and religious purposes or for incense. Epithet is to be treated as noun in apposition.

Syninclusions. Air bubbles, debris.

Remarks. Piece of clear and yellow amber that measures 13 x 10 x 4 mm. The inclusion is complete except for the left anterior leg preserved up to the tibia and part of the tarsus. The inclusion is barely visible even ventrally.

DISCUSSION

The origin and evolution of the Cantharidae is not yet well known, however it can be traced back between the Middle-Late Jurassic (Fanti 2017): maximum 162 mya (Bocák et al. 2016), 165 mya (Cai et al. 2022) or 152 mya (Kusy et al. 2018), and the Early Cretaceous (McKenna et al. 2015): Berriasian age 141.4 mya with an interval of 118.5-166.2 mya (Motyka et al. 2023).

Therefore, the Cantharidae preserved in Burmese amber are very important because they are almost at the beginning of evolution. The remains of this resin have provided a good number of species which, however, concern genera that are currently completely extinct. Interestingly, Spanish amber (Peris & Fanti 2018), Agdzhakend amber (Kazantsev & Perkovsky 2019; Motyka et al. 2023: page 563) and Burmese amber have yielded remnants of the subfamily Cantharinae, with few representatives of the subfamily Malthininae only for Burmese amber. The attribution to Cantharinae *incertae sedis* of Burmese soldier beetles, made by various authors (Hsiao et al. 2021; Yang et al. 2021, 2022, 2024; Motyka et al. 2023) is purely hypothetical and without morphological evidence (see: Fanti & Müller 2022; Zhao et al. 2022), and the attribution to Silinae (Hsiao & Huang 2018) is totally incorrect (Fanti & Müller 2022; Motyka et al. 2023). All the characters present in these fossils are found in the current Cantharinae, while the few fossil remains of the Malthininae subfamily (Hsiao et al. 2016; Li et al. 2022) in Burmese amber, have some characters not currently present in the Malthininae (Fanti 2022: Li et al. 2022) and therefore, if anything, it is the latter that should be included in *incertae sedis* and not the representatives of Cantharinae. These fossil remains in three Cretaceous ambers, therefore, suggest that Cantharinae evolved earlier than recently suggested by Motyka et al. (2023). In addition, in Motyka et al. (2023) we find as "*incertae sedis* Burmite Cantharinae", the genus *Cnathrion* Kazantsev & Perkovsky, 2019 which is an Eocene genus of Sakhalinian amber (47.0-43.0 Mya) and therefore evidently cannot be a Burmite cantharid, much less *incertae sedis*, being among other things considered even in the original description, and without

doubt, as belonging to the subfamily Cantharinae (Kazantsev & Perkovsky 2019).

The genus *Brevipterus* Y. Yang, H. Liu & W. Zhao in Zhao et al., 2022 was established recently due to slight differences compared to the genera *Sanaungulus* Fanti, Damgaard & Ellenberger, 2018 and *Burmomiles* Fanti, Damgaard & Ellenberger, 2018 as short elytra that reveal one more abdominal segment, and small differences in pronotum (variable even for the authors) and position and shape of the antennal branches (Zhao et al. 2022). These characters, however, are certainly not sufficient and valid at generic level, for example the insertion of the branches is subject to considerable plasticity (Motyka et al. 2023: supporting information). Furthermore, the authors themselves change their opinion from one work to another, in fact in Yang et al. (2024) it is clearly said that the elytral length of species in Burmese amber is not a reliable character. However, *Brevipterus* differs from *Sanaungulus* for its rounded head and only slightly triangular posteriorly, in a sort of short neck. For us, this character is a valid character at generic level and would confirm the validity of the genus *Brevipterus*. However, the authors of *Brevipterus* did not even consider the shape of the head and mistakenly believe (Zhao et al. 2022) that it is not a stable character, so if the systematics of these authors were followed, the genus *Brevipterus* would be considered synonymous with *Sanaungulus*. Agree with Fanti (2025), *Sanaungulus strungei* Fanti & Damgaard, 2019 has a head rather rounded in dorsal view but triangular in ventral view (Fanti & Damgaard 2019) as *S. ambosae* sp. nov., but does not have an elongated neck, therefore the move to *Brevipterus* made by Zhao et al. (2022) is hereby confirmed to be erroneous.

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