

Short communication

## Two new genera of Cantharidae from Burmese amber of the Hukawng Valley (Insecta, Coleoptera)

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### ABSTRACT

In the present paper two new genera and three new species of fossil Cantharidae from Burmese amber are described and figured: *Burmomiles* gen. nov., *Sanaungulus* gen. nov., and *Burmomiles willerslevorum* sp. nov., *Sanaungulus curtippennis* sp. nov., *Sanaungulus ghitaenoerbyae* sp. nov. The new genera present characteristic features as pectinate antennae with only three, four, or seven central antennomeres with long antennal processes (in the antennomeres IV–VI or IV–VII in *Sanaungulus* and in the antennomeres III–IX in *Burmomiles*), unknown until now in the fossil record. *Sanaungulus* gen. nov. differs from *Burmomiles* gen. nov. by possessing shorter elytra, smaller size, longer legs, and different pronotal shape. The new genera described herein, which are assumed to have vesicles for chemical defense, further differs from the similar genus *Ornatomalthinus* Poinar et Fanti, 2016 by possessing different elytral sculpture and pectinate antennae instead of filiform.

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## 1. Introduction

Burmese amber, being rich in inclusions (Ross et al., 2010; Alekseev, 2017; Guo et al., 2017; Ross, 2018), can shed light on many important biogeographic and evolutionary aspects of insects. In this paper, we describe two new genera and three new species of soldier beetles belonging to the extant tribe Cantharini Imhoff, 1856 (subfamily Cantharinae Imhoff, 1856), based on specimens preserved in the Upper Cretaceous Burmese amber of the Hukawng Valley. The new specimens are characterized by pectinate antennae a feature previously illustrated, but never formally described in a publication until now. Currently, only three genera of soldier beetles are known in Burmese amber (Fanti and Ellenberger, 2016; Hsiao et al., 2016; Poinar and Fanti, 2016), and only one Burmese specimen with this habitus (Poinar et al., 2007; Binder, 2008; Oktar [Harun Yahya], 2006–2008; Boucot and Poinar, 2010), and most likely these illustrations regards the same second genus here described.

## 2. Materials and methods

Burmese amber is traditionally assigned to mid Cretaceous, lowermost Cenomanian,  $98.79 \pm 0.62$  MY (Shi et al., 2012). The amber fragments come from square-feed mines, which reach a depth of around 30–80 m and following horizontal layers, where amber is found among the fine-grained classic sedimentary rock matrix and other sediments of the former ancient river bed. These insect inclusions probably originate from Aung-Par-Hmaw mining area in the Hukawng Valley, Myanmar (Cruickshank and Ko, 2003; Kyaw Thu and Khin Zaw, 2017). The pieces have been cleaned and polished to allow proper viewing and photographing of the inclusions. Pictures were taken using a Canon EOS 750D camera mounted on a Leica Macroscope and Olympus BH2 Microscope, or alternately using a Imaging Source DFK 72AUC02 camera attached to the trinocular microscope Nikon SMZ 745T. Images were processed with focus stacking software. Drawings were hand-made with china ink and plates of figures have been processed with PhotoImpact Viewer SE. One holotype is deposited in the SMNS Naturkunde Museum Stuttgart (Germany) amber collection, while the other two will be deposited at the Zoological Museum, University of Copenhagen, Denmark (ZMUC). The terms referring to antennal morphology and syninclusions follow Servadei et al. (1972), Zombori and Steinmann (1999), and Bybee et al. (2015).

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Nomenclatural acts established herein are registered under ZooBank LSID urn:lsid:zoobank.org:pub:53F022AF-81A1-4D5F-8627-88EEF43494BF.

### 3. Systematic paleontology

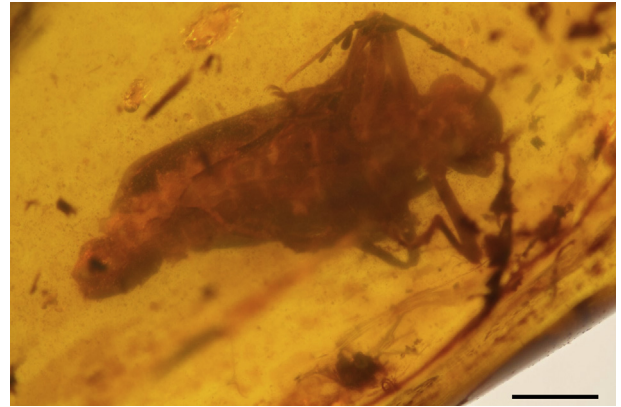
Order Coleoptera Linnaeus, 1758  
 Superfamily Elateroidea Leach, 1815  
 Family Cantharidae Imhoff, 1856 (1815)  
 Subfamily Cantharinae Imhoff, 1856 (1815)  
 Tribe Cantharini Imhoff, 1856 (1815)

Genus *Burmomiles* Fanti, Damgaard et Ellenberger nov.

Type species: *Burmomiles willerslevorum* Fanti, Damgaard et Ellenberger sp. nov., monotypic.

*Etymology.* The name is a combination of the specimen's collection locality Burma (former name of Myanmar), and the Latin noun "mīlēs" = soldier, in reference to the English name of the family Cantharidae = soldier beetles. Gender masculine.

*Diagnosis.* The genus is characterized by short elytra, almost long as the metathoracic wings; elytra bearing shallow but dense and impressed punctation, arranged in striae except on the apex of elytra, and the wings do not cover the last two abdominal segments. Antennae pectinate, bearing long antennal process in the articles III–IX. Pronotum enlarged at sides, appearing very rounded at lateral edges. The head is rounded, the eyes are very large respect other Burmese genera, last abdominal segments resembling a caudal appendage and legs are short. The unequal maxillary palpomeres with the last segment securiform and the pronotum without modified lateral margin permits to assign this new genus belonging to the subfamily Cantharinae Imhoff, 1856.



**Fig. 2.** *Burmomiles willerslevorum* Fanti, Damgaard et Ellenberger gen. et sp. nov. in Burmese amber. Holotype, ZMUC (No. ALDC0463/ALD.Bu.203), ventral view (Bar = 1.0 mm).

*Burmomiles willerslevorum* Fanti, Damgaard et Ellenberger sp. nov.

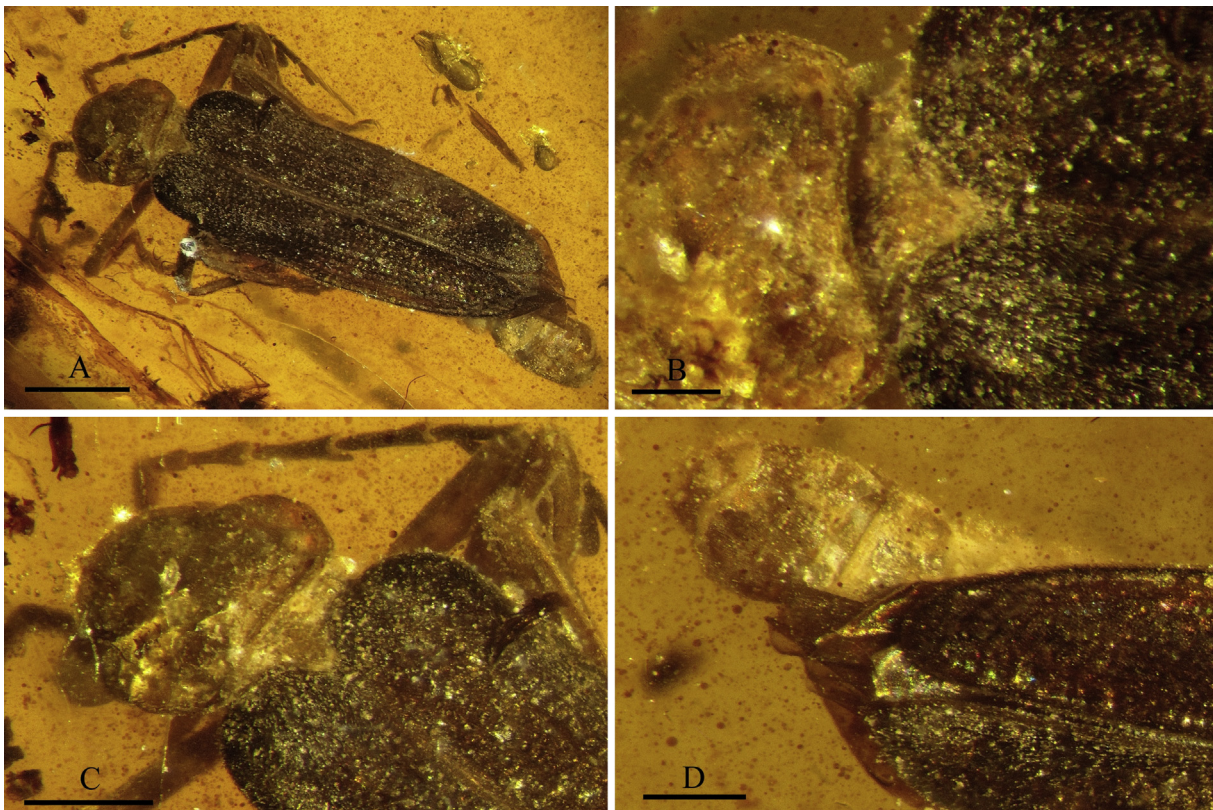
(Figs. 1–3)

*Etymology.* The species is named in honor of the twins Eske and Rane Willerslev, Danish evolutionary geneticist (Eske) and anthropologist (Rane).

*Holotype.* Sex not established, probably male, in Burmese amber, ZMUC (accession No. ALDC0463/ALD.Bu.203).

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

*Type horizon.* The lowermost Cenomanian ( $98.79 \pm 0.62$  Ma), mid-Cretaceous (Shi et al., 2012).



**Fig. 1.** *Burmomiles willerslevorum* Fanti, Damgaard et Ellenberger gen. et sp. nov. in Burmese amber. Holotype, ZMUC (No. ALDC0463/ALD.Bu.203). A. dorsal view (Bar = 1.0 mm); B. detail of scutellum (Bar = 200 µm); C. detail of pronotum (Bar = 0.5 mm); D. detail of last abdominal segments, dorsal view (Bar = 400 µm).



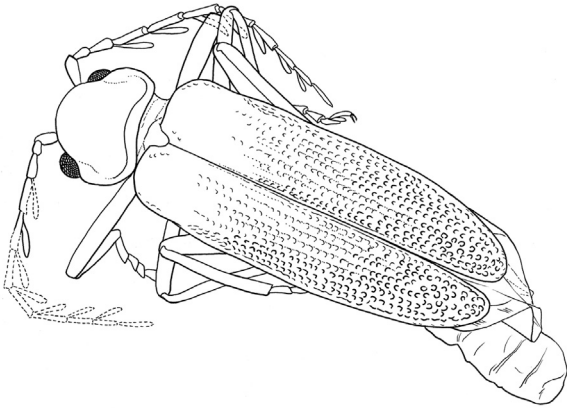


Fig. 3. *Burmomiles willerslevorum* Fanti, Damgaard et Ellenberger gen. et sp. nov. in Burmese amber. Reconstruction habitus, dorsal view (Bar = 1.0 mm).

**Description.** Adult, winged, presumably male due to the narrow last ventrites, big eyes and relatively short antennae. Pronotum and scutellum yellowish with dark brown elytra, and antennae, legs and ventrites brown-testaceous. Body length: 5.6–6.0 mm difficult to determine because the head is folded, pronotum-apex elytra: 4.5 mm.

Head rounded in dorsal view, narrower than pronotum. Eyes large and prominent, roundish, inter-ocular distance about 3.0 times greater than eye diameter. Mandibles elongated and thin (presence or absence of teeth in the inner margin not evaluable). Maxillary palps 4-segmented with last palpomere securiform. Labial palps 3-segmented. Antennae relatively short, 11-segmented, pectinate, slightly surpassing the first half of the elytra, but not reaching half of the abdominal length, inserted on the front and far away from the eyes; scape elongated, stout, club-shaped; antennomere II (pedicel) short and enlarged at apex, about one third length of scape; antennomeres III–IX elongated and each of them provided of one process at apex inserted ventrally and long as the antennal joints and roundish at apex, the V–VII antennal processes are more globular; antennomeres X–XI elongated, filiform and without processes.

Pronotum strongly rounded anteriorly and almost straight posteriorly (only slightly concave in the center), sides very enlarged that appear very rounded; bordered by a ridge to the sides and to the basal margin; surface flat and smooth, presenting very shallow punctation (just perceptible) and bearing very short setae.

Scutellum triangular, small, with rounded apex.

Elytra at base slightly wider than pronotum, elytra short, narrowing posteriorly with rounded apices, and not covering the last two abdominal segments that appear as a large caudal appendage; surface pubescent presenting shallow, dense and strong punctation, gathered in striae. Posterior wings dark, slightly longer and almost completely covered by elytra.

Ventrites short and large covered of pubescence, caudal appendage slightly visible in ventral view and composed of three ventrites: first segment large, second short as sub-quadrangle lobe and the last segment elongated and narrow. Dorsally the caudal appendage is wider.

Legs short; anterior legs longer than the others; coxae massive; trochanters elongated; femora elongated, robust, profemora longer than meso- and metafemora; all tibiae slender and shorter than femora; tarsi 5-segmented, first tarsomere slightly elongated and robust, second and third tarsomere shorter than first, fourth

strongly bilobed with lobes very elongated and roundish at apex, fifth thin; claws simple without denticle.

**Syninclusions.** Wood remains, trichomes (stellate hairs), small air bubbles, and two Acarina ?

**Differential diagnosis.** The genus is monotypic and the species is recognizable for the above and of the genus description. No known fossil have antennae pectinate as the new species, except the following (but with different number of antennal processes) and pronotum so rounded at sides. Furthermore, *Myamalyocerus* Fanti et Ellenberger, 2016 has longer elytra respect *Burmomiles willerslevorum* sp. nov., while *Ornatomalthinus* Poinar et Fanti, 2016 has shorter elytra with different elytral sculpture and pronotum. *Sanaungulus* gen. nov. has triangular head, different pronotum, longer legs and shorter elytra.

**Remarks.** The yellow amber piece measures 11 × 21 × 4 mm and the inclusion is complete; the ventral view of the specimen is slightly opaque and the head is bent and not adequately visible.

Genus *Sanaungulus* Fanti, Damgaard et Ellenberger nov.

**Type species.** *Sanaungulus curtispennis* Fanti, Damgaard et Ellenberger sp. nov., by present designation. The new genus is established on two species.

**Etymology.** In memory of San Aung (22.5.1966–15.4.2017), famous dealer of Burmese amber + the Latin suffix *-ulus* (diminutive) = small. Gender masculine.

**Diagnosis.** The genus is characterized by head triangular behind the large elliptical eyes; short elytra covered with deep and not in relief punctation, organised in striae; antennae pectinate with central antennomeres (from IV to VI or VII) bearing long antennal processes. First seven antennal articles filiform, while the last three antennomeres (and to a lesser extent even the apical fourth) are flat and slightly expanded at sides. Legs, meso- and metathoracics in particular, very long and surpassing the two-thirds of the whole body.

*Sanaungulus curtispennis* Fanti, Damgaard et Ellenberger sp. nov. (Figs. 4–5)

**Etymology.** From Latin “*curtus*” = short, and Latin “*penna*” = wing. Named in reference to the short elytra in comparison to the overall body length.

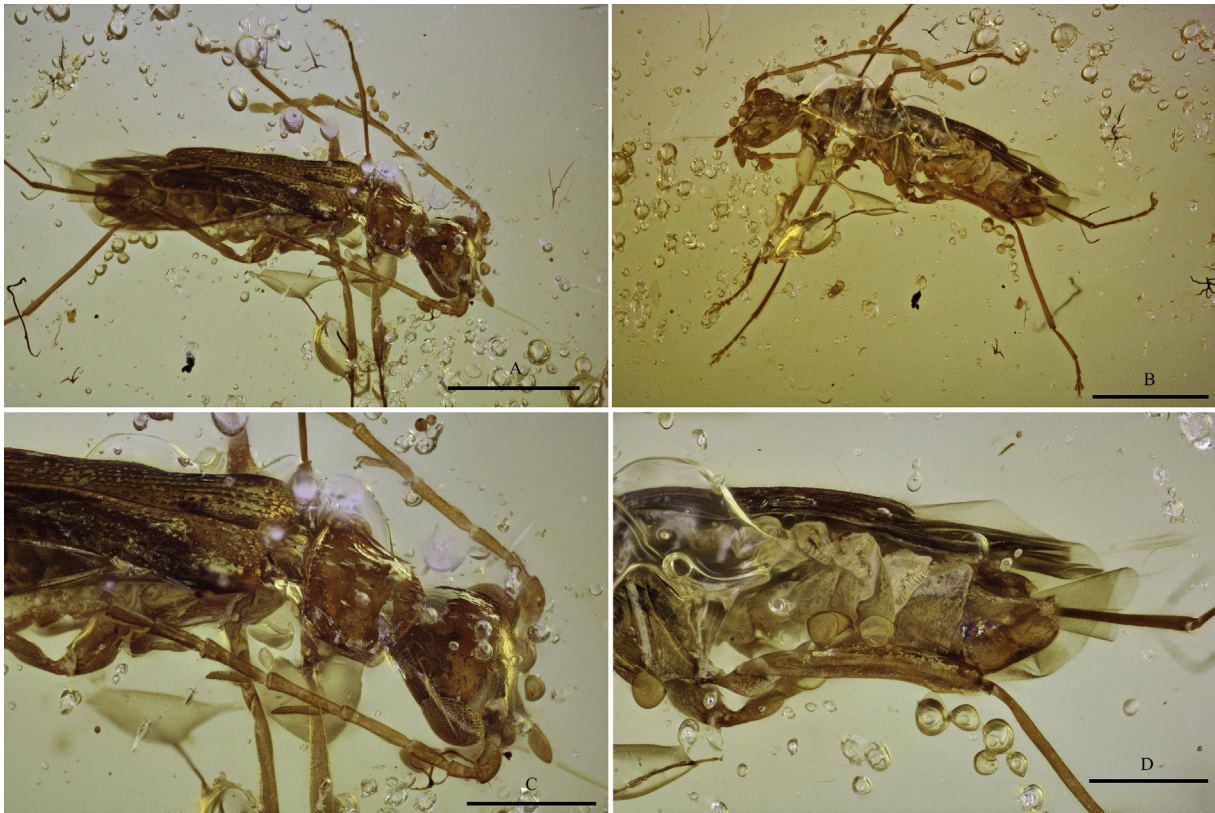
**Holotype.** Possibly female, in Burmese amber, SMNS Naturkunde Museum Stuttgart amber collection, with the accession No. SMNS BU-305.

**Type locality.** Myanmar: Kachin state, Myitkyina District, Tanai Township, Hukawng Valley, Aung Bar Maw mine.

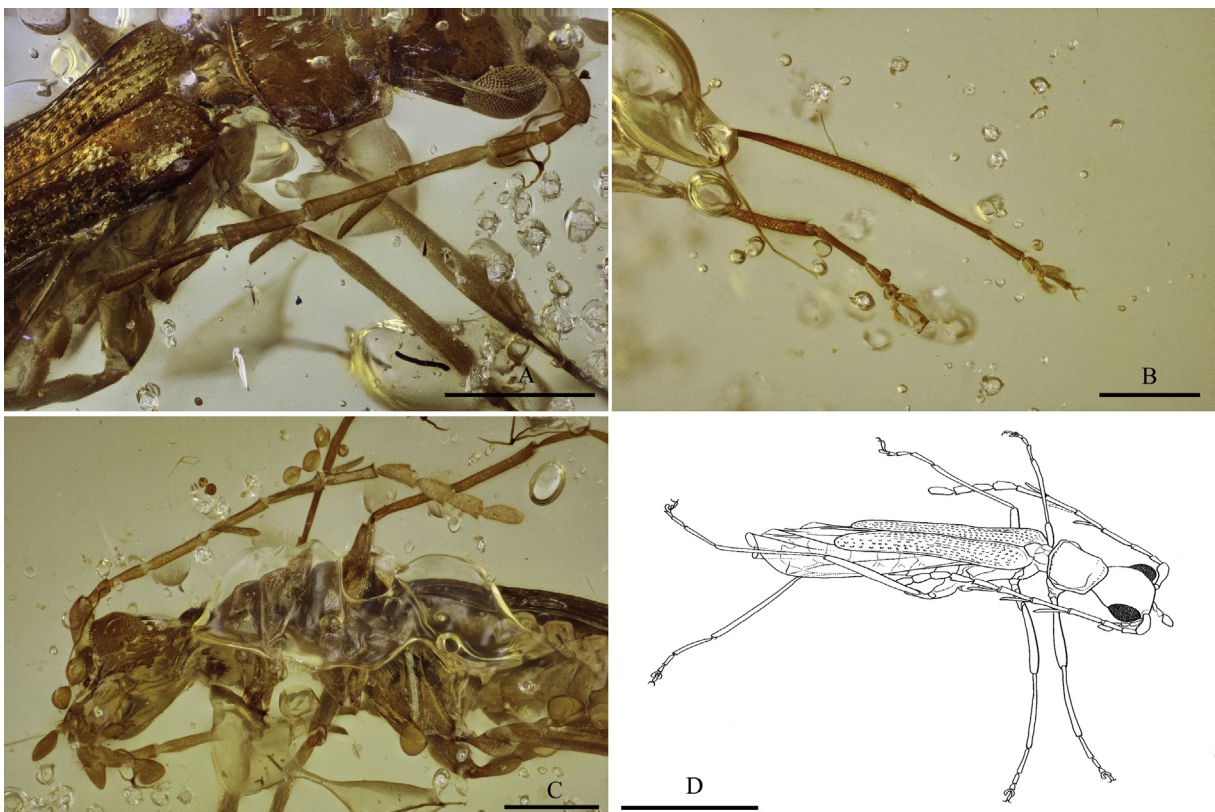
**Type horizon.** The lowermost Cenomanian (98.79 ± 0.62 Ma), mid-Cretaceous (Shi et al., 2012).

**Description.** Adult, winged, slender, possibly female based on the large last ventrite and the general wide appearance of the abdomen. Entirely brown-testaceous with lighter coloured ventrites. Body length: 3.1 mm, longest leg: 2.0 mm but not being fully extended.

Head large, convex, strongly constricted (triangular-shaped) behind the eyes, fitted with very scarce and very shallow punctation (just perceptible), particularly on the front, and bearing few short setae. Eyes elliptical in lateral view and prominent, inter-ocular distance about 3.0 times greater than eye diameter. Mandibles elongated and thin, the presence of a tooth is not visible. Maxillary palps 4-segmented with the first palpomere short and stout, second palpomere long double the length of the first and stout, third of intermediate length between the other two, last palpomere securiform and rather rounded. Labial palps



**Fig. 4.** *Sanaungulus curtippennis* Fanti, Damgaard et Ellenberger gen. et sp. nov. in Burmese amber. Holotype, SMNS No. BU-305, A. dorsal view (Bar = 1.0 mm); B. ventral view (Bar = 1.0 mm); C. detail of pronotum (Bar = 0.5 mm); D. detail of last abdominal segments, ventro-lateral view (Bar = 200  $\mu$ m).



**Fig. 5.** *Sanaungulus curtippennis* Fanti, Damgaard et Ellenberger gen. et sp. nov. in Burmese amber. Holotype, SMNS No. BU-305, A. detail of right antenna (Bar = 0.5 mm); B. detail of pro- and mesothoracic leg (Bar = 300  $\mu$ m); C. detail of palps and sternum (Bar = 0.5 mm); D. reconstruction habitus, dorsal view (Bar = 1.0 mm).



3-segmented, with the last elongated and rounded, slightly securiform. Antennae 11-segmented, pectinate, bearing setulation, surpassing the half of the abdomen and surpassing two-thirds of the elytra, antennal insertion in the eyes proximity; scape elongated, stout, club shaped; antennomere II short, about the half of the first; antennomere III filiform, slightly enlarged and feebly longer than second; antennomeres IV–VI filiform, very elongated, each segment with bearing one thin antennal process at apex inserted ventrally and almost as long as the antennal joints and roundish at apex; antennomere VII elongated, slightly shorter than antennomeres IV–VI, without antennal process; antennomeres VIII–X short, flat and enlarged at sides; antennomere XI short, robust and rounded at apex.

Pronotum slightly transverse, narrower than head, with anterior margin protruding onward, partially covering the head, posterior margin almost straight and bordered, lateral margins slightly sinuous, enlarged in the mid; pronotum disc slightly wavy and smooth. Scutellum triangular.

Elytra at base slightly narrower than pronotum, posteriorly parallel-sides with rounded apices, very short which reveals various abdominal segments; surface pubescent bearing scarce, large, very deep and not in relief punctation, gathered in striae. Posterior wings transparent and only slightly blurred, very long, well visible and surpassing the last abdominal segments.

Sternum pubescent, ventrites narrow and sinuous, penultimate ventrite wider, and last elongated, rather large and with apex sinuous with lateral small lobe and central denticle.

Legs extremely long, especially the meso- and metathoracic, covered in dense and short pubescence; coxae massive and enlarged at center; trochanters elongated, wide and globular; femora long, slightly curved, more robust than tibiae, cylindrical

and slightly flattened; tibiae long, cylindrical, thin, bearing one small and short spur near the apex, pro- and mesotibiae almost as long as pro- and mesofemora, metatibiae longer than metafemora; tarsal formula 5-5-5, with the first two articles thin and elongated, first protarsomere long, almost twice than second, first meso- and metatarsomere more than twice as long as second meso- and metatarsomere, third tarsomeres very short and slightly globular, fourth tarsomeres bilobed, fifth slightly elongated and thin; claws simple, small and each of them presenting one evident denticle at base.

*Syninclusions.* Air bubbles, wood remains, trichomes (stellate hairs), and one immature (“nymph”) stage of Hemiptera?

*Differential diagnosis.* *Sanaungulus curtipennis* sp. nov. is less robust than *S. ghitaenoerbyae* sp. nov., has three antennal processes (instead of four) and different pronotal shape.

*Remarks.* The amber piece measures  $19.6 \times 13.7 \times 3.2$  mm and the matrix is extremely transparent and allows a perfect view of all sides of the inclusion.

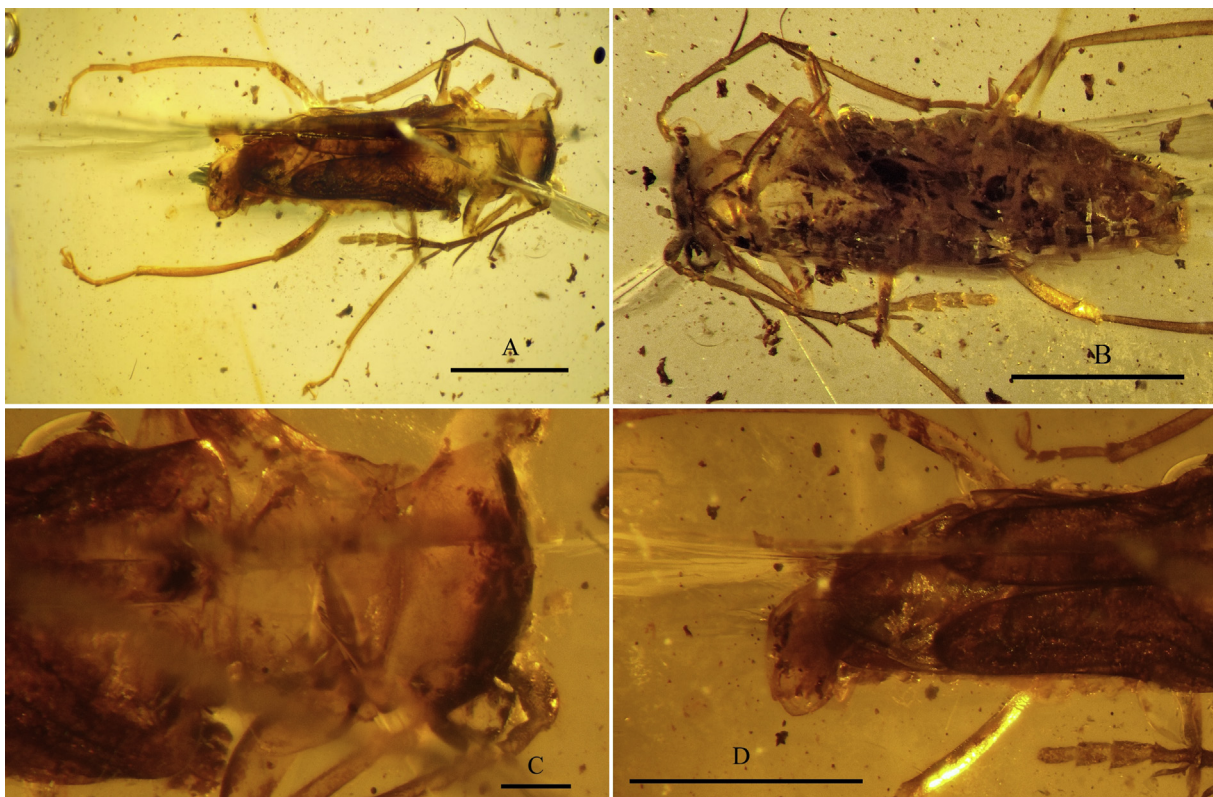
***Sanaungulus ghitaenoerbyae*** Fanti, Damgaard et Ellenberger sp. nov.

(Figs. 6–8)

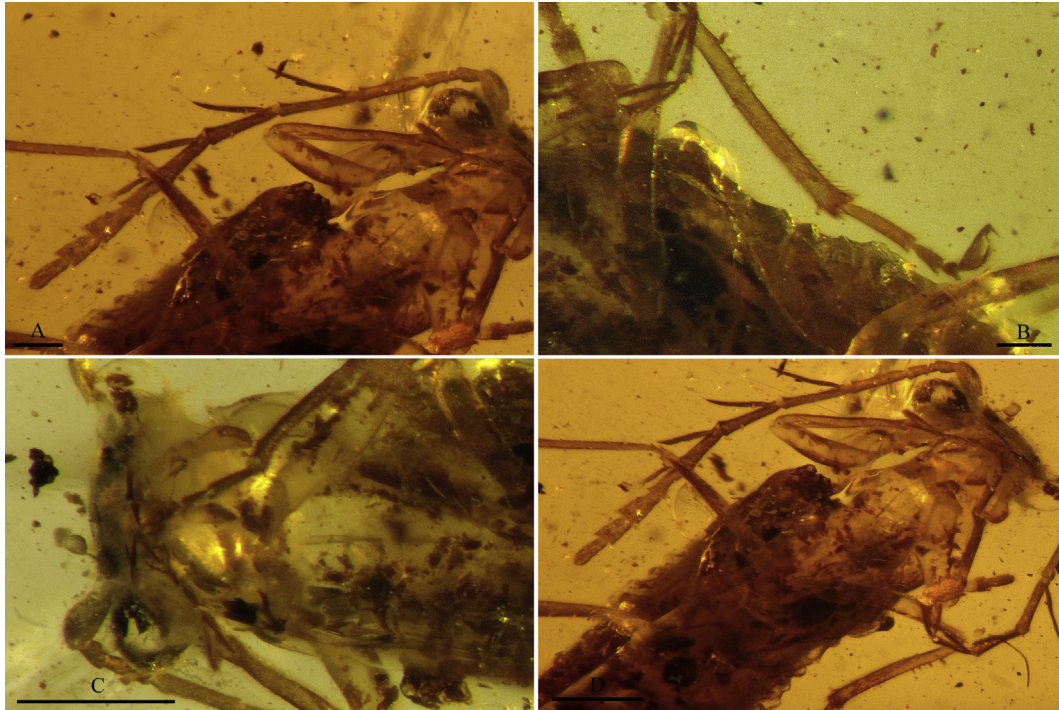
*Etymology.* This new species is named in honor of the Danish actress Ghita Nørby, as thank for decades (over 60 years: 1956–today) of contributions to the Danish theater and film scene.

*Holotype.* Male, in Burmese amber, ZMUC (accession No. ALDC0462/ALD.Bu.202).

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



**Fig. 6.** *Sanaungulus ghitaenoerbyae* Fanti, Damgaard et Ellenberger gen. et sp. nov. in Burmese amber. Holotype, ZMUC (ALDC0462/ALD.Bu.202). A, dorsal view (Bar = 1.0 mm); B, ventral view (Bar = 1.0 mm); C, detail of pronotum (Bar = 200  $\mu$ m); D, detail of apex of elytra (Bar = 1.0 mm).



**Fig. 7.** *Sanaungulus ghitaenoerbyae* Fanti, Damgaard et Ellenberger gen. et sp. nov. in Burmese amber. Holotype, ZMUC (ALDC0462/ALD.Bu.202), A. detail of right antenna (Bar = 200  $\mu$ m); B. detail of leg (Bar = 400  $\mu$ m); C. detail of palps and sternum (Bar = 0.5 mm); D. detail of abdomen (Bar = 400  $\mu$ m).

**Type horizon.** The lowermost Cenomanian ( $98.79 \pm 0.62$  Ma), mid-Cretaceous (Shi et al., 2012).

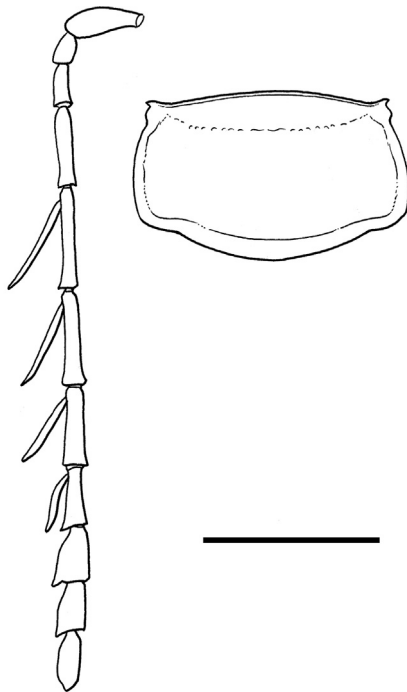
**Description.** Adult, winged, robust, male based on the triangular, small and very narrow last ventrite. Head testaceous behind the eyes and darker anteriorly, elytra reddish-brown with lighter

pronotum, legs and antennae brown-testaceous, abdominal segments brown. Body length: 3.0 mm.

Head very wide and short longitudinally, large as pronotum, slightly triangular behind the eyes, covered by scarce punctation and pubescence. Eyes rounded, slightly elliptical, extremely wide and prominent, inter-ocular distance about 2.0 times greater than eye diameter. Mandibles thin, elongated and with an acute, long and thin tooth, not particularly close to apex. Maxillary palps robust, 4-segmented, first palpomere short, second palpomere robust and third short, last palpomere securiform and with very rounded apex. Labial palps 3-segmented. Antennae 11-segmented, pectinate, surpassing half of the abdomen and surpassing two-thirds of the elytra, antennal insertion in the eyes proximity; scape not very elongated, stout, massive; antennomere II short, about the half of the first; antennomere III filiform, slightly longer than second; antennomeres IV–VII filiform, very elongated and each with very thin antennal process at apex inserted ventrally and as long as (or slightly longer) than the antennal joints, and roundish at apex; antennomere VIII filiform, slightly enlarged at apex, shorter than antennomeres IV–VII, without antennal process; antennomeres IX–X short, flat and enlarged at sides; antennomere XI robust and rounded at apex.

Pronotum strongly transverse, anterior margin almost straight, posterior margin enlarged and rounded in the middle, lateral margin slightly rounded presenting two small denticles at the anterior corners; surface flat, smooth, without pubescence. Scutellum triangular.

Elytra at base slightly wider than pronotum, much narrower after the first third, with rounded apexes, very short which reveals various abdominal segments; surface equipped with scarce and deep punctation, not in relief gathered in striae. Posterior wings dark, long, well visible, surpassing the elytra but not reaching the last abdominal segments.



**Fig. 8.** *Sanaungulus ghitaenoerbyae* Fanti, Damgaard et Ellenberger gen. et sp. nov. in Burmese amber. Holotype, A. reconstructions of pronotum and antenna (Bar = 0.5 mm).



Sternum pubescent, ventrites wide and short, last ventrite triangular-shaped, very small and short, large at base and narrow at apex which is rounded.

Legs extremely long, especially the meso- and metathoracic, pubescent; coxae massive; trochanters elongated and globular; femora long, curved, more robust than tibiae, cylindrical; tibiae long, cylindrical, thin, equipped with small and short spur near the apex, protibiae slightly longer than profemora, meso- and metatibiae much longer than meso- and metafemora; tarsal formula 5-5-5, with the first two articles thin and elongated especially of the meso- and posterior legs, first tarsomere long almost twice as long as second, third tarsomere very short and globular and dilated at sides, fourth tarsomere bilobed, fifth elongated and very thin; claws simple.

*Syninclusions.* Wood remains and air bubbles.

*Differential diagnosis.* The new species has the same size but is easily distinguishable to *Sanaungulus curtippennis* sp. nov. for an additional antennal process (in the article VII) and for the pronotum strongly transverse with anterior margin straight and sides with small denticles in the anterior part. The head is slightly triangular behind the eyes and larger, and the elytra are wider and less tapered to the apex. *Remarks.* The amber measures  $9 \times 13 \times 3$  mm and the inclusion is complete.

#### 4. Discussion

In living species of the subfamily Cantharinae Imhoff, 1856, reduced elytra is a rare condition (Poinar and Fanti, 2016; Fanti and Vitali, 2017) and in only few cases it is associated with complete membranous hind wings (Poinar and Fanti, 2016); furthermore in the fossil record (always regarding the subfamily Cantharinae), until now, was known only in the genus *Ornatomalthinus* Poinar et Fanti, 2016, while the pectinate-flabellate antennae are present in some living specimens such as in some *Lycocerus* Gorham, 1889 (Cantharinae) and *Flabelloontelus* Pic, 1911 (subfamily Dymorphocerinae Brancucci, 1980). Concerning Malthininae Kiesenwetter, 1852, often characterized by the same shortened elytra as the genera here described, *Sanaungulus* gen. nov. (and to a lesser extent *Burmomiles* gen. nov.) appears as intermediate between *Paramalthinus* Brancucci in Brancucci et Wittmer, 1984 (which has pectinate antennae with antennal processes until the last segments, and has longer elytra) and *Falsomalthinus* Pic, 1924 (with head very broad, protruding eyes, short elytra and filiform antennae). Similar antennae are also present in the American genus *Tythonyx* LeConte, 1851 (subfamily Silinae). Chemical defense has been found in the genus *Ornatomalthinus* Poinar et Fanti, 2016 and certainly is also present in *Sanaungulus* gen. nov. since it is the same (or very related) genus, which possesses this defensive mechanism, illustrated in Poinar et al. (2007), and probably is also present in *Burmomiles* gen. nov. (Smejkal et al., 2009; Poinar and Fanti, 2016).

Key to the genera of Cantharidae in Burmese amber:

1. Last maxillary palpomere globular and apically pointed.....*Archaeomalthodes rosetta* Hsiao, Ślipiński et Pang, 2016
- Last maxillary palpomere securiform.....2
2. Elytra and metathoracic wings long, pronotum with central-anterior depression and two thickenings close to the front edge.....*Myamalycoerus vitalii* Fanti et Ellenberger, 2016
- Elytra short and long metathoracic wings.....3
3. Antennae filiform, elytra with striation equipped with relief points.....*Ornatomalthinus elvirae* Poinar et Fanti, 2016

- Antennae pectinate, elytral punctuation not in relief.....4
4. Antennal process in the antennomeres IV–VI or IV–VII, legs extremely long, elytra short, metathoracic wings long and clearly visible.....*Sanaungulus* gen. nov. (*Sanaungulus curtippennis* and *S. ghitaenoerbyae*).
- Antennal process in the antennomeres III–IX, legs short, elytra longer and slightly shorter than metathoracic wings.....*Burmomiles* gen. nov.

#### 5. Conclusion

Considering that Cantharidae appear to have evolved in the Early Cretaceous or in the Late Jurassic (Fanti, 2017), Burmese specimens and other inclusions of this age could shed some light on many biogeographic aspects. It is interesting how fossil genera reduct considerably different from living genera, suggesting that cantharids went through astonishing evolutionary explosion during the Paleocene–Eocene. We still have to find and understand the relationships, specimens and characteristics that have surpassed the great and important mass extinction of the end of the Cretaceous. The other very useful aspect will be to compare the fauna and the various characters between the Cretaceous remains of various distant geographical areas such as the inclusions of Spanish amber (Peris et al., 2013, 2016) Lebanese amber (Kirejtshuk and Azar, 2013) and maybe even of other localities (New Jersey amber, Canadian amber, Taimyr amber, Ethiopian amber, French amber, Jordan amber).

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#### References

- Alekseev, V.I., 2017. Coleoptera from the middle-upper Eocene European ambers: generic composition, zoogeography and climatic implications. *Zootaxa* 4290 (3), 401–443.
- Binder, H., 2008. Bernstein – Einblicke in vergangene Ökologie II: Käfer beim Einsatz chemischer Waffen erappt. *Studium Integrale Journal* 15 (1), 47.
- Boucot, A.J., Poinar Jr., G.O., 2010. *Fossil Behavior Compendium*. CRC Press, Boca Raton, p. 424.
- Bybee, S.M., Hansen, Q., Büsse, S., Cahill Wightman, H.M., Branham, M.A., 2015. For consistency's sake: the precise use of larva, nymph and naiad within Insecta. *Systematic Entomology* 40, 667–670.
- Cruickshank, R.D., Ko, K., 2003. Geology of an amber locality in the Hukawng Valley, Northern Myanmar. *Journal of Asian Earth Sciences* 21, 441–455.
- Fanti, F., 2017. Catalogo Cantharidae fossili del mondo. *Fossils & Minerals Review* 2, 1–18 [abbreviated Italian version]/World catalog of fossil Cantharidae. *Fossils & Minerals Review*, 2 (Special Issue), 1–52 [extended English version].
- Fanti, F., Ellenberger, S., 2016. *Myamalycoerus vitalii*: A new genus and species of soldier beetle in Burmese amber (Coleoptera Cantharidae). *Cretaceous Research* 71 (2017), 166–169.
- Fanti, F., Vitali, F., 2017. Key to fossil Malthininae, with description of two new species in Baltic amber (Coleoptera Cantharidae). *Baltic Journal of Coleopterology* 17 (1), 19–27.
- Guo, M., Xing, L., Wang, B., Zhang, W., Wang, S., Shi, A., Bai, M., 2017. A catalogue of Burmite inclusions. *Zoological Systematics* 42 (3), 249–379.
- Hsiao, Y., Ślipiński, A., Deng, C., Pang, H., 2016. A new genus and species of soldier beetle from Upper Cretaceous Burmese amber (Coleoptera, Cantharidae, Malthininae). *Cretaceous Research* 69 (2017), 119–123.
- Kirejtshuk, A.G., Azar, D., 2013. Current knowledge of Coleoptera (Insecta) from the Lower Cretaceous Lebanese amber and taxonomical notes for some Mesozoic groups. *Terrestrial Arthropod Reviews* 6, 103–134.
- Oktar, A. [Harun Yahya], 2006–2008. *Atlas of Creation*, vol. 1. Global Publishing, Turkey, Istanbul, p. 904.

- Peris, D., Sánchez-García, A., Soriano, C., Delclús, X., 2013. Beetle fauna in the Early Cretaceous Spanish amber (pp. 74–75). In: The 6th International Congress on Fossil Insects, Arthropods and Amber, Abstract Book, Byblos, Lebanon. April 14–18, 2013 (Poster).
- Peris, D., Ruzzier, E., Perrichot, V., Delclús, X., 2016. Evolutionary and paleobiological implications of Coleoptera (Insecta) from Tethyan-influenced Cretaceous ambers. *Geoscience Frontiers* 7, 695–706.
- Poinar Jr., G.O., Fanti, F., 2016. New fossil soldier beetles (*Coleoptera: Cantharidae*) in Burmese, Baltic and Dominican amber. *Palaeodiversity* 9, 1–7.
- Poinar Jr., G.O., Marshall, C.J., Buckley, R., 2007. One hundred million years of chemical warfare by insects. *Journal of Chemical Ecology* 33 (9), 1663–1669.
- Ross, A.J., 2018. Burmese (Myanmar) amber taxa, on-line checklist v.2017.4, p. 88. <http://www.nms.ac.uk/explore/stories/natural-world/burmese-amber/>.
- Ross, A.J., Mellish, C., York, P., Crighton, B., 2010. Burmese Amber (pp. 209–236). In: Penney, D. (Ed.), *Biodiversity of fossils in Amber from the major world deposits*. Siri Scientific Press, Manchester, p. 304.
- Servadei, A., Zangheri, S., Masutti, L., 1972. *Entomologia generale ed applicata*. Edizioni Cedam, Padova, xvi +, p. 733.
- Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q., Li, X., 2012. Age constraint on Burmese amber based on U–Pb dating of zircons. *Cretaceous Research* 37, 155–163.
- Smejkal, G.B., Poinar Jr., G.O., Righetti, P.G., 2009. Will amber inclusions provide the first glimpse of a Mesozoic proteome? *Expert Review of Proteomics* 6 (1), 1–4.
- Thu, Kyaw, Zaw, Khin, 2017. Chapter 23. Gem deposits of Myanmar (pp. 497–529). In: Barber, A.J., Zaw, Khin, Crow, M.J. (Eds.), *Myanmar: Geology, Resources and Tectonics*. Geological Society, London, Memoirs, p. 776, 48, NP.
- Zombori, L., Steinmann, H., 1999. *Dictionary of Insect Morphology*. In: Fischer, M. (Ed.), *Handbuch der Zoologie (Handbook of Zoology)*, Band/Volume 4, Arthropoda: Insecta, Teilband/Part 34. Walter de Gruyter, Berlin, p. 405.