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Short communication

A new genus of dasycerine rove beetles from Upper Cretaceous Burmese amber and its phylogenetic implications (Coleoptera, Staphylinidae)

Chenyang Cai [a, *], Margaret K. Thayer [b], Alfred F. Newton [b], Ziwei Yin [c], Diying Huang [d]

[a] CAS Key Laboratory of Economic Stratigraphy and Palaeogeography, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China
[b] Integrative Research Center, Field Museum of Natural History, Chicago, IL 60605, USA
[c] Department of Biology, College of Life and Environmental Sciences, Shanghai Normal University, Shanghai 200234, China
[d] State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China

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ABSTRACT

The rove beetle subfamily Dasycerinae, having specialized latridiid-like body forms, are very distinctive among Staphylinidae. Fossil dasycerines are sparse, with only one species known from the Upper Cretaceous Burmese amber. Here we describe a new and more typical staphylinid-looking Dasycerinae genus and species, *Vetudasycerus burmiticus* gen. et sp. nov., from the Cretaceous Burmese amber (ca. 99 Ma). It exhibits many defining features of the extant Dasycerinae (e.g., acuminate maxillary palpomere 4, verticillate and clubbed antennae, striate and carinate elytra, separated mesocoxae, and 3-segmented tarsi), but retains probably plesiomorphic traits, including short, comparatively compact antennae, greatly shortened elytra, and well-developed hind wings. The discovery reinforces the hypothesis that the Dasycerinae is a subfamily of Staphylinidae, closely related to Neophoninae, Protopselaphinae and Pselaphinae. It also highlights the palaeodiversity of the subfamily Dasycerinae in late Mesozoic.

1. Introduction

The rove beetle subfamily Dasycerinae is a small monophyletic group of Staphylinidae, with only 17 described species placed in the extant genus *Dasycerus* Brongniart, and one extinct species in the fossil genus *Protodasycerus* Yamamoto (Löbl and Calame, 1996; Hansen, 1997; Thayer, 2016; Yamamoto, 2016). *Dasycerus* comprises small mycophagous beetles occurring in the Nearctic, Palaearctic, and Oriental regions (Thayer, 2016). *Dasycerus* was first described by Brongniart (1800) and was compared with pselaphids (now Pselaphinae, a subfamily within Staphylinidae) and tenebrionids. *Dasycerus* was placed in Latridiidae (as Lathridiidae) until Crowson (1955) moved to a separate family placed in Staphylinoidea. Dasyceridae, together with Empelinae, Glypholmatinae, Micropeplidae, Microsilphinae, Neophoninae, Omaliinae, Proteininae, Protopselaphinae, and Pselaphidae, constituted the Omaliine group of Lawrence and Newton (1982, 1995; Newton and Thayer, 1995), based on the presence of a complex gland situated at the basal margin of the eighth abdominal sternite (Thayer, 1987). Newton and Thayer (1992) formalized the staphylinoid classification and placed *Dasycerus* in the Staphylinidae as a group of subfamily rank. A recent molecular study suggests that Dasycerinae (*Dasycerus*) is sister to the monobasic Neophoninae, and they together form a sister group to Pselaphinae (McKenna et al., 2015), although the peculiar subfamily Protopselaphinae (sister of Pselaphinae in Newton and Thayer, 1995) was not sampled in that study. Dasycerinae is very distinctive and easy to identify among the 32 extant subfamilies (Newton et al., 2000), and it has multiple unique autapomorphies: adult with very distinctive body form, including very long elytra nearly covering abdomen (extant taxa), tubercles or spines on the three elytral costae and epipleural fold, antennae inserted on frontal stalks, antennomeres 3–8 very thin and spindle-shaped with sparse long setae, lacinia apically with unique spinose brush, palisade fringe on tergites V–VI only (not VII as usual) of winged species, and larva with uniquely modified rasping mandibles and highly distinctive body form (Newton and Thayer, 1995).

* Corresponding author. Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, 39 East Beijing Road, Nanjing 210008, China.
E-mail address: cycai@nigpas.ac.cn (C. Cai).

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Probably because of their small body size, Dasycerinae have not been documented as compression fossils to date. Yamamoto (2016) described the first fossil dasycerine, *Protodasycerus aenigmaticus* Yamamoto, from the Upper Cretaceous Burmese amber. *Protodasycerus* is morphologically similar to the extant *Dasycerus*, but differs distinctly from the latter by its much smaller body size (ca. 1.1 mm), slightly transverse metaventrite, only slightly costate elytra, and more importantly, by its truncate elytra, with the apical four abdominal tergites exposed (Yamamoto, 2016). Here, we describe another new genus and species of Dasycerinae based on a well-preserved adult from Cretaceous Burmese amber.

2. Material and methods

The new species is described based on one individual preserved in a transparent yellowish piece of Burmese amber. Diverse organisms have been described from the Burmese amber, including birds (feathers and skeletons), dinosaurs (represented by a tail), fungi, conifers, angiosperms, nematodes, onychophorans, spiders, ticks, and especially insects (e.g., Grimaldi et al., 2002; Ross et al., 2010; Ross, 2017). The typical fossil locality has been mapped in Cruickshank and Ko (2003), Kania et al. (2015), and Yin et al. (2018). Shi et al. (2012) have provided a radiometric date of at least 98.8 million years, or earliest Cenomanian for this deposit. The type specimen was prepared by cutting with a hand-held saw and polishing with sandpapers of different grain sizes and with polishing powder. The specimen was studied with a Zeiss Discovery V20 stereo microscope, measured with an ocular micrometer attached to the same microscope, and also with a Leitz Dialux20 compound microscope using transmitted and incident light. Fig. 1A was taken using a Zeiss Axio Imager 2 compound microscope under normal reflected light. Photomicrographs with green (in the web version) and red backgrounds (Figs. 1B, C and 2) were taken using a fluorescent light source attached to a Zeiss Axio Imager 2 microscope. Multicolored photomicrographs (Fig. 3) were taken with a confocal laser scanning microscope (CLSM) Zeiss LSM 710 with ×10 objectives and using a laser at 488 nm. The nomenclatural acts established herein are registered under ZooBank LSID urn:lsid:zoobank.org:pub:E34DF63C-9ABE-4521-8F91-57FDCA906277.

3. Systematic palaeontology

Order: Coleoptera Linnaeus, 1758
Family: Staphylinidae Latreille, 1802
Subfamily: Dasycerinae Reitter, 1887

Genus: ***Vetudasycerus*** gen. nov.
Type species. *Vetudasycerus burmiticus* sp. nov.

Etymology. The genus-group name is a combination of Latin *vetus*, meaning 'old', and the genus *Dasycerus*; it is masculine in gender. The genus is registered under LSID urn:lsid:zoobank.org:act:2C21D697-C929-40BD-A3AD-F0264189BE67.
Diagnosis. Small (ca. 1.5 mm long), habitus staphylinid-looking. Head with a pair of longitudinal depressions; eye large, protruding laterally; antenna short, comparatively compact, verticillate; antennomere 1 greatly enlarged, more than twice as wide and long as 2, which is wider than 3–8, apical three antennomeres dilated, forming a distinct club; maxillary palpus with palpomere 4 acuminate, much longer and distinctly broader than 3. Pronotum transverse, tuberculate, with elongate setiferous tubercles on lateral margins. Elytron short, exposing abdominal tergites III (in part) –VIII, with apical margins forming obtuse angle; each elytron with three discal costae, without tubercles or spines, with 9 complete longitudinal rows of punctures, epipleural ridge with ctenidium of robust setiferous tubercles. Thorax without foveae. Tarsal formula 3-3-3. Abdomen with 6 segments visible ventrally, abdominal sternite III short.

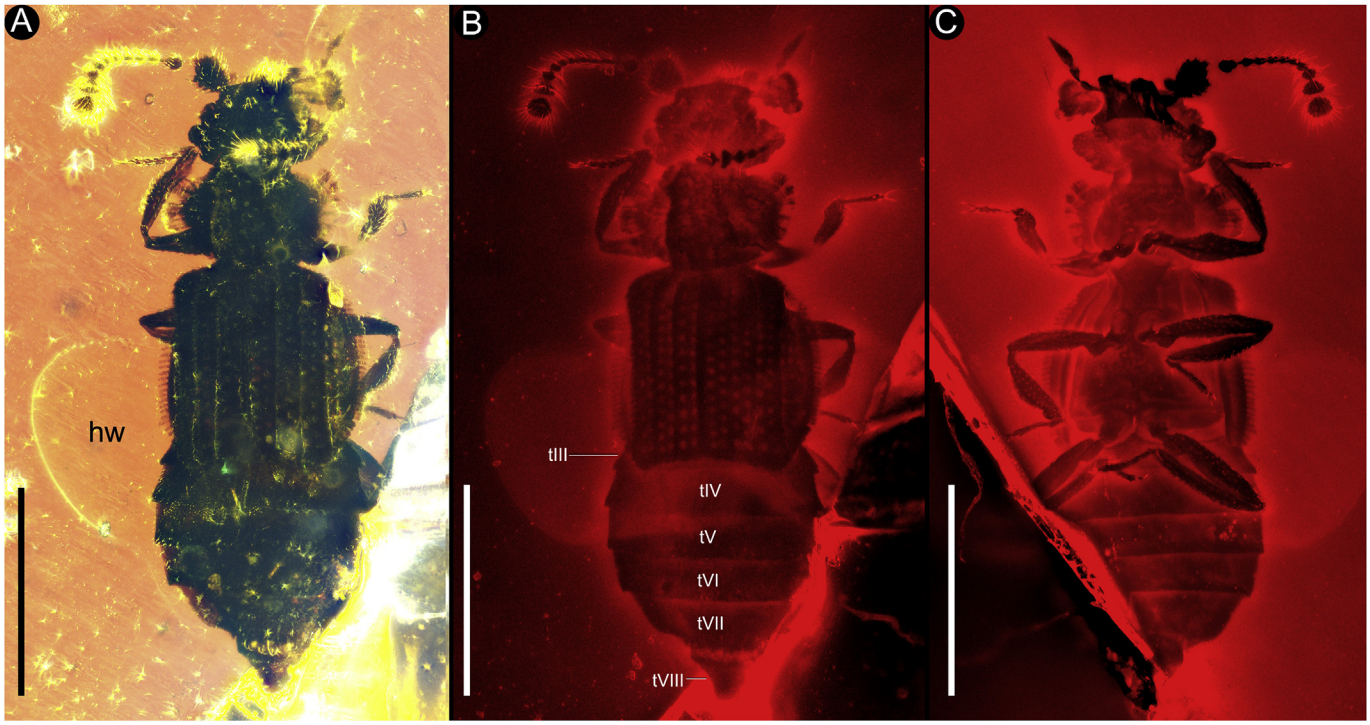

Fig. 1. Microphotographs of holotype (NIGP164823) of *Vetudasycerus burmiticus* gen. et sp. nov. in Upper Cretaceous amber from Myanmar. A under normal reflected light; B and C using fluorescence as light source. A and B, dorsal view; C, ventral view. hw, hind wing; tIII–VIII, tergites III–VIII. Scale bars: 500 μm.

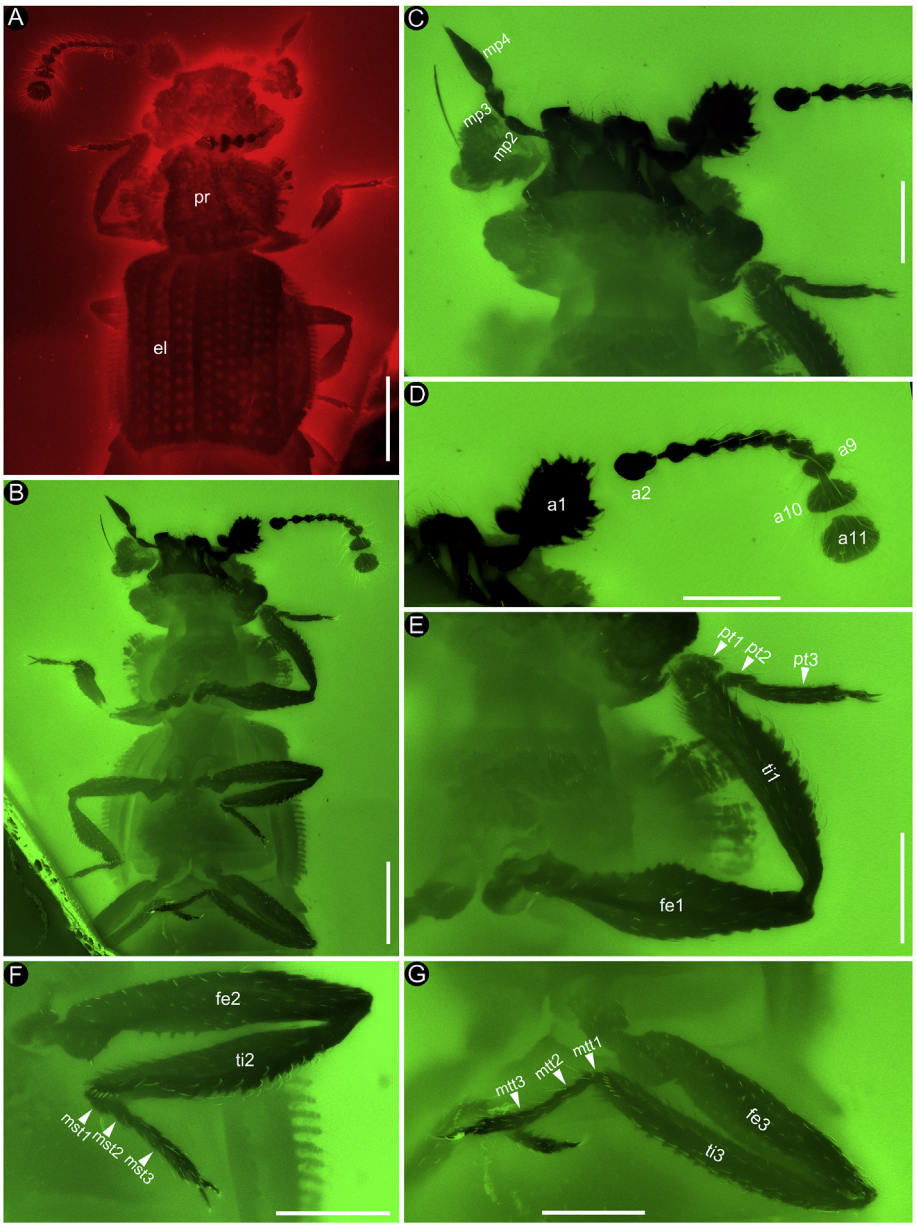

Fig. 2. Enlargements of holotype (NIGP164823) of *Vetudasycerus burmiticus* gen. et sp. nov., under fluorescence. A. forebody, dorsal view; B. forebody, ventral view; C. head, ventral view; D. left antenna, ventral view; E. details of front leg; F. details of middle leg; G. details of hind leg. a1–11, antennomeres 1–11; el, elytron; fe1–3, pro-, meso- and metafemur; mst1–3, mesotarsomeres 1–3; mp2–4, maxillary palpomeres 2–4; mtt1–3; metatarsomeres 1–3; pr, pronotum; pt1–3; protarsomeres 1–3; ti1–3, pro-, meso- and metatibia. Scale bars: 200 μm in A and B, 100 μm in others.

Description. Body robust, more or less parallel-sided (Fig. 1), ca. 1.5 mm long.

Head prognathous, large, widest across eyes (Fig. 2A, B). Epistomal suture absent. Vertex with pair of longitudinal depressions (Fig. 2A). Preocular portion of head long. Antennal insertion concealed under frontal shelf (Fig. 2A); antennal fossa small, situated dorsolaterally, above level of eye. Postocular area gradually narrowed toward neck. Antenna short, verticillate, with eleven antennomeres; apical three antennomeres forming a distinct club (Fig. 2D). Eye large, hemispherical, protruding laterally (Figs. 2C and 3A), with tiny setae between some ommatidia. Ocelli absent. Mandible curved, with sharp apex (Figs. 2C and 3A). Lacinia with brush-like apex (Fig. 3A). Maxillary palpus 4-segmented, with scattered pubescence; maxillary palpomeres 2 and 3 strongly thickened apically, palpomere 4 long, aciculate (Figs. 2C and 3A). Labial palpus 3-segmented, very short (Fig. 3A). Neck present (Fig. 2C).

Pronotum transverse, narrowed toward base and apex (Fig. 2A). Disc coarse, with depressions and a pair of nearly longitudinal ridges. Basal area with a pair of short paramedian longitudinal ridges. Laterobasal area depressed. Lateral margins with long setiferous tubercles. Prosternum long, without foveae. Prosternal process relatively long and narrow (Fig. 2B). Procoxal cavity open externally. Protrochantin concealed. Procoxae small, sub-contiguous (Fig. 2B). Visible portion of scutellum very small, triangular.

Elytra distinctly short (Fig. 2A), widest near middle, narrowed from apical fourth toward apex; elytral apex angulate and thickened (Figs. 1B and 3B). Elytral disc with 1 sutural and 3 discal longitudinal costae (Figs. 2A and 3B) consisting of setiferous

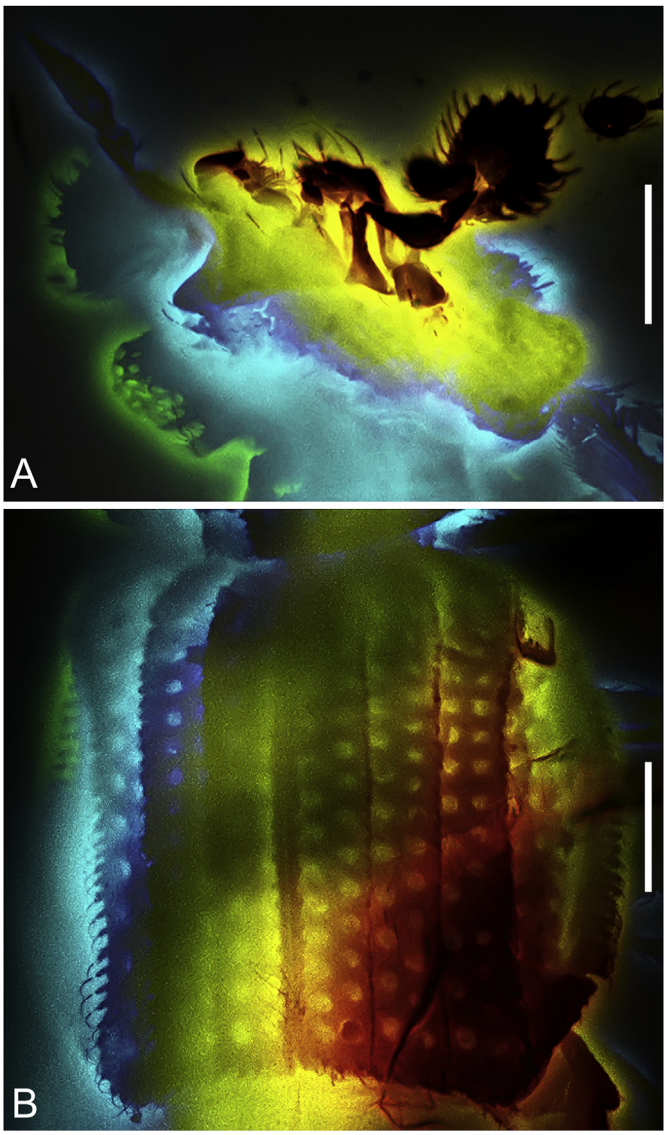

Fig. 3. Head and pronotum of holotype (NIGP164823) of *Vetudasycerus burmiticus* gen. et sp. nov., under confocal laser scanning microscopy. A, ventral view of head, showing eyes and detailed mouthpart structures (e.g., mandibles, maxillary palpi, labial palpi and mentum); B, elytra, dorsal view, showing 9 rows of large and round punctures, 3 discal costae, and sutural and lateral marginal setiferous tubercles on each elytron. Scale bars: 100 μm.

tubercles, with 2 rows of relatively large round punctures between costae and three additional rows between lateral-most costa and epipleural ridge. Epipleural ridge well developed, curved, with a row of regular, laterally-directed finger-like setiferous tubercles forming a ctenidium (Fig. 2A). Epipleuron wide, narrowed toward apex, without puncture row (Fig. 2B).

Mesoventrite long, with convex median area, without foveae (Fig. 2B). Mesoventral posterior process triangular, long, narrowly separating mesocoxae (Fig. 2B). Mesocoxal cavity with slightly raised edge. Mesocoxae separated by narrow mesoventral and wider metaventral processes (Fig. 2B). Metaventrite with anterior margin slightly raised and one narrow antecoxal groove; without foveae. Metanepisternum concealed. Hind wings well developed (Fig. 1A).

Legs short, setose (Fig. 2E–G). Procoxae conical, projecting (Fig. 2E). Mesocoxae oval, not projecting (Fig. 2B). Metacoxae strongly transverse, contiguous (Fig. 2G). Trochanters small, irregular in shape (Fig. 2E–G). Femora robust. Tibiae somewhat fusiform, with apical comb of very small spines. Tarsal formula 3-3-3 (Fig. 2E–G), tarsomeres with coarse setae all around. Claws simple, equal. Empodium without setae.

Abdomen broad, with six visible sternites, gradually widened from sternite III to V, and then narrowed toward apex. Sternite III with obtusely angulate intercoxal process between metacoxae, without foveae (Fig. 2B). Sternites IV–VII each impressed basally. Laterosternites apparently absent. Tergite III largely covered by elytra (Fig. 2A), tergites IV–VIII exposed (Fig. 1B), tergite VIII pygidium-like, with anterior and lateral ridges. Genitalia not visible.

Vetudasycerus burmiticus sp. nov.
(Figs. 1–3)

Etymology. The specific epithet refers to the occurrence of the fossil in Burmite (Burmese amber). The species is registered under LSID urn:lsid:zoobank.org:act:E9E769F6-8E77-45F5-B50D-C14E2E8E10CE.

Holotype. Sex unknown, NIGP164823, lowermost Cenomanian, Hukawng Valley, Kachin State, northern Myanmar; deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China. The holotype is nearly completely preserved, except for the right side of the abdominal sternites.

Diagnosis. As for the genus (*vide supra*).

Description. Body small, 1.52 mm long (measured from apex of mandibles to abdominal apex). Largely dark brown to black, except setae (whitish) and pronotal tubercles (brown).

Head 0.24 mm long and 0.35 mm wide (including eyes), widest across eyes, convex apically, with rim-like neck constriction. Antenna short, as long as head and pronotum combined, densely setose; antennomere 1 (scape) markedly enlarged, widened apically, with setiferous tubercles; antennomere 2 slightly enlarged, much narrower than antennomere 1; antennomere 3 slightly narrower than antennomere 2; antennomeres 4–6 each longer than wide, almost same shape; antennomeres 7 and 8 slightly wider than 6; antennomere 9 transverse, spindle-shaped, distinctly wider than 8; antennomere 10 dilated, subtriangular, much wider than 9; antennomere 11 larger than 10, conical. Maxillary palpus long, with scattered fine setae; maxillary palpomere 1 small; palpomere 2 long, thickened apically; palpomere 3 shorter but wider than 2; palpomere 4 widest and longest, fusiform, acuminate.

Pronotum 0.23 mm long and 0.35 mm wide, widest across middle; pronotal angles not developed; anterior margin nearly straight; posterior margin broadly curved; dorsal surface rough; lateral margin with a row of slender lateral setiferous tubercles.

Elytra very short, 0.5 mm long and each 0.26 mm wide, covering most of tergite III, 1.75 times as long as pronotum. Elytral humerus well developed. Each with 9 distinct rows of large, round punctures, two rows per interval between sutural and discal costae, three between lateral costa and epipleuron; rows 1–6 each with 12–14 punctures; rows 7–9 with fewer.

Legs finely setose. Profemur distinctly dilated in middle, inner margin with small teeth; protibia with external margin curved, with row of small setiferous tubercles; protarsomere 1 slightly longer than protarsomere 2, protarsomere 3 much longer than 1 and 2 together. Mesofemur thinner than profemur, inner margin with about 5 teeth near base; mesotibia with external margin curved, with setiferous tubercles; mesotarsomeres 1 and 2 combined shorter than mesotarsomere 3. Metafemur longer than mesofemur, inner margin with a small tooth at base; metatibia slender, with small setiferous tubercles on external margin; metatarsomere 1 very short, metatarsomere 2 slightly longer; metatarsomere 3 much longer than metatarsomeres 1 and 2 combined.

Abdomen broad, nearly glabrous, dilated in middle; lateral margin curved. Sternite III short; sternites IV–VI successively shortened; sternite VII longer than sternite VI.

4. Discussion

Vetudasycerus has a generalized body form of Staphylinidae, including elongate shape, short elytra (exposing 6 abdominal segments) and contiguous procoxae. *Vetudasycerus* is very distinctive among all known staphylinids because of its unique combination of: 1) densely setose and distinctly clubbed antennae; 2) maxillary palpi long, with apical palpomere acuminate; 3) tarsal formula 3-3-3; and 4) elytra with regular rows of punctures and longitudinal costae. Among all 32 subfamilies of staphylinids, striate and costate elytra are confined to two atypical rove beetle subfamilies: Dasycerinae and Micropeplinae (Campbell, 1968; Löbl and Calame, 1996; Cai and Huang, 2014). The 3-segmented tarsi are relatively rare in Staphylinidae, and they occur in Dasycerinae, Neophoninae, Protopselaphinae, nearly all Pselaphinae, and some Aleocharinae, Osoriinae, Oxytelinae, Proteininae, Leptotyphlinae, and one Pseudopsinae (Newton et al., 2000). *Vetudasycerus* differs obviously from members of Micropeplinae by having 11-segmented antennae (9-segmented in Micropeplinae) and 3-segmented tarsi (4-segmented in Micropeplinae, although superficially appearing as 3-segmented); from Neophoninae by costate elytra and unmodified tarsi (first tarsomere with expanded adhesive setae in Neophoninae); from Protopselaphinae and Pselaphinae by presence of elytral puncture rows; from Aleocharinae by concealed antennal insertions; and from Oxytelinae with 3-3-3 tarsi by lack of exposed abdominal sternite II. *Vetudasycerus* can be placed in Dasycerinae mainly based on its specialized elytral and tarsal morphological characters. In addition, the conspicuously setose and clubbed antenna with enlarged scape and pedicel, the elongate maxillary palpus with elongate and acuminate apical palpomere, and the widespread setiferous tubercles including those on the pronotum are suggestive of this placement as well. Extant Dasycerinae (the sole genus *Dasycerus*) is very distinctive among Staphylinidae, characterized by very long non-truncate elytra, antennal flagellum verticillate, extremely slender and hair-like, and lacinia with a unique enlarged brush of short spines; all these characters are regarded as autapomorphies for this group (Newton and Thayer, 1995). The recent discovery of an extinct transitional genus and species (*Protodasycerus aenigmaticus* Yamamoto) of Dasycerinae from mid-Cretaceous Burmese amber expanded the definition of the subfamily. *Protodasycerus* displays many morphological similarities to extant *Dasycerus*, but primitively retains comparatively shorter, truncate and non-costate elytra (Yamamoto, 2016; elytra 2.8 times as long as pronotum). Our examination of additional material of *P. aenigmaticus* reveals very low-profile elytral costae in at least some specimens and elytra up to 3.8 times as long as pronotum. It is striking that the new genus *Vetudasycerus*, also from Burmese amber, shows more plesiomorphic characters than the extinct *Protodasycerus* and the extant *Dasycerus*, but also shares some presumably derived features with *Dasycerus*. Putatively ancestral characters include: short antennae; short legs; absence of foveae on thorax; short (1.75 times as long as pronotum) and truncate elytra entirely exposing apical five abdominal segments, and fully developed hind wings. *Vetudasycerus* shares with *Dasycerus* the presence of prominent setiferous tubercles on the elytral costae and lateral margins, whereas *Protodasycerus* has only small tubercles on the costae and none on the lateral margins. *Vetudasycerus* differs strikingly from both *Protodasycerus* and *Dasycerus* in having a greatly enlarged antennomere 1 bearing setiferous tubercles; in the other two genera, antennomeres 1 and 2 are similar in size and lack setiferous tubercles.

Another defining character of Dasycerinae is the highly specialized mouthparts. All extant dasycerines bear an enlarged dense brush of short spines on the apex of the lacinia, a character possibly indicative of mycophagous habits, as suggested by the fact that they are associated with the fruiting bodies of various fungi (reviewed by Newton and Thayer, 1995; Löbl and Calame, 1996). Detail visible in the holotype under the compound microscope suggests the presence of a similar structure, although it is not visible with the lower resolution shown in the figures. This lacinial structure is more clearly visible in a specimen that we believe represents an undescribed second species of *Protodasycerus*.

It is thus probable that *Vetudasycerus* represents a very basal lineage of the subfamily Dasycerinae. Its typical staphylinid-looking appearance reinforces the hypothesis that Dasycerinae is a part of the hyperdiverse Staphylinidae. Furthermore, the fact that the two extinct genera (*Protodasycerus* and *Vetudasycerus*) have elytra that are significantly shorter than extant *Dasycerus* reinforces earlier hypotheses (e.g., by Lawrence and Newton, 1982; Newton and Thayer, 1995; Grebennikov and Newton, 2009, 2012) that all those Staphylinidae with very long elytra that nearly or completely cover the abdomen are derived from short-elytra ancestors. In their review and discussion of ancestral elytral length in staphylinids, Grebennikov and Newton (2012) noted the example of the staphylinid subfamily Scydmaeninae, in which all of the more than 5000 extant species have long elytra, even though phylogenetic studies (e.g., Grebennikov and Newton, 2009) nested this group well within a large clade of short-elytra staphylinids; this surprising phylogenetic conclusion was strongly supported by the subsequent discovery of Cretaceous scydmaenines with much shorter elytra than any modern taxa (e.g., Chatzimanolis et al., 2010). The discovery of short-elytra dasycerines in the Cretaceous adds a new, parallel example supporting this general conclusion that extant staphylinids with long elytra are derived from ancestors with shorter elytra. However, a more precise phylogenetic connection among *Dasycerus* and the two extinct genera (*Protodasycerus* and *Vetudasycerus*) remains to be explored. Our discovery of *Vetudasycerus* from Burmese amber also highlights the palaeodiversity of Dasycerinae in the mid-Cretaceous, showing that the subfamily was more morphologically disparate in the late Mesozoic than it is at present.

5. Concluding remarks

Our discovery of *Vetudasycerus burmiticus* gen. et sp. nov. from the Upper Cretaceous Burmese amber represents the second fossil record for the extant small subfamily Dasycerinae. The staphylinid-looking body form (rather than latridiid-looking) and many defining features (e.g., setose and clubbed antennae, 3-segmented tarsi, and punctate and costate elytra) of Dasycerinae suggest *Vetudasycerus* is a very basal lineage of the subfamily. This find also highlights the palaeodiversity of Dasycerinae, and is of potential significance for understanding the phylogenetic relationships between Dasycerinae and other related Omaliine groups of subfamilies, including Neophoninae, Protopselaphinae, and Pselaphinae. Finally, it contributes to our understanding of the evolution of elytral length within Staphylinidae.

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