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RESEARCH ARTICLE

Alveoderes gen. nov., the earliest fossil of Bothrideridae from mid-Cretaceous Burmese amber (Coleoptera: Coccinelloidea)

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ABSTRACT. The earliest fossil member of Bothrideridae, *Alveoderes yamamotoi* Li & Cai **gen. et sp. nov.**, is reported from mid-Cretaceous amber of northern Myanmar. *Alveoderes* **gen. nov.** appears to be most similar to extant *Deretaphrus* in the 3-segmented antennal club and pronotal morphology, but is also distinctive among the whole Bothrideridae in having a large cavity (possible glandular opening) at each anterior pronotal angle. Our discovery of a definitive bothriderid beetle from the late Mesozoic highlights the antiquity of the family. A key to the extant and extinct genera of Deretaphrini is added.

KEY WORDS. Bothrideridae, Burmese amber, fossil, Mesozoic, taxonomy.

INTRODUCTION

Bothrideridae, or the cocoon-forming beetles, belongs to Coccinelloidea, with about 27 described genera (Ślipiński et al. 2010, Robertson et al. 2015). The family once also included members now classified in Teredidae (e.g., Pal and Lawrence 1986, Ślipiński and Pakaluk 1991, Philips and Ivie 2002, Ślipiński et al. 2010). However, a molecular phylogenetic study by Robertson et al. (2015) revealed that Teredinae, Anommatinae, and Xylariophilinae (former subfamilies of Bothrideridae s.l.) were not closely related to Bothriderinae, and were therefore classified in a separate family, Teredidae. Robertson et al. (2015) also identified two major lineages in Coccinelloidea, i.e., the bothriderid group and the coccinellid group. Bothrideridae was resolved as the earliest-branching family of the bothriderid group, which has also been supported by further studies (Zhang et al. 2018, McKenna et al. 2019, Cai et al. 2022).

The adults of Bothrideridae are predatory but may also feed on dead insects (Browne 1962, Lei et al. 2003, Wang et al. 2004). The larvae of Bothrideridae are ectoparasites of various wood-boring beetles and other insects (Craighead 1920, Roberts 1980, Wei and Jiang 2011, Mi et al. 2014), which clearly distinguishes them from the free-living larvae of Teredidae (Pal and Lawrence 1986). The biology (e.g., Qin and Gao 1988, Wang and Ogura 1999, Wei et al. 2013, Lyu et al. 2018, Gao et al. 2019, Jiang et al. 2023) and biocontrol application (e.g., Urano 2003, Tang et al. 2012, Li et al. 2013, Gong et al. 2023) of *Dastarcus helophoroides* (Fairmaire, 1881) have been particularly extensively studied, as this species may parasitize the late-instar larvae, pupae, and young adults of numerous longhorn beetles (Yang et al. 2013: figs 3, 4, Zheng et al. 2022: fig. 3).

The fossil record of Bothrideridae is quite sparse, known as only four specimens from Eocene Baltic amber. The two reported by Stein (1881) were assigned to *Bothrideres* Dejean, 1835, although Alekseev (2015) doubted their generic assignment, and the other two reported by Alekseev (2015) were assigned to *Pseudobothrideres* Grouvelle, 1908. While recently several coccinelloid families have been discovered in mid-Cretaceous Burmese amber, including Teredidae (Li et al. 2022a), Anamorphidae (Arriaga-Varela et al. 2024), Corylophidae (Li et al. 2022b), and Endomychidae (Tomaszewska et al. 2018, 2022, Li et al. 2022c, 2023, Arriaga-Varela et al. 2023), Bothrideridae, as one of the earliest diverging lineages of

Coccinelloidea (McKenna et al. 2019, Cai et al. 2022), has not yet been reported from this extraordinary Lagerstätte (e.g., Ross 2019, 2024). In the present study, we describe a new genus and species of Bothrideridae from Burmese amber, representing the earliest record for this family. A key to the extant and extinct genera of Deretaphrini is provided.

MATERIAL AND METHODS

The Burmese (Kachin) amber specimen studied herein originated from amber mines near Noije Bum (26°20'N, 96°36'E), Hukawng Valley, Kachin State, northern Myanmar (e.g., Xuan et al. 2022: fig. 1). The amber specimen is deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China. The amber piece was trimmed with a small table saw, ground with emery paper of different grit sizes, and finally polished with polishing powder.

Photographs under incident light were taken with a Zeiss Discovery V20 stereo microscope. Confocal images were obtained with a Zeiss LSM710 confocal laser scanning microscope, using the 488 nm (Argon) laser excitation line (Fu et al. 2021). Images were semi-manually stacked with Helicon Focus 7.0.2, Zerene Stacker 1.04 and Adobe Photoshop CC, and were further processed in Adobe Photoshop CC to adjust brightness and contrast.

The morphological terminology generally follows Lawrence and Ślipiński (2013).

TAXONOMY

Coleoptera Linnaeus, 1758
Coccinelloidea Latreille, 1807
Bothrideridae Erichson, 1845
Deretaphrini Horn, 1878

Key to extant and extinct genera of Deretaphrini

The identification key herein presented is modified from Heizen (1943).

The tribe as circumscribed here is likely non-monophyletic (Robertson et al. 2015). *Pseudososylus* Grouvelle, 1900 and *Erotylathris* Motschoulsky, 1861 have characters intermediate between Deretaphrini and Bothriderini (Heinze 1943); they were included in Deretaphrini by Heinze (1943), but in Bothriderini by Ślipiński et al. (1989). The validity of *Carbothrus* Aoki, 2012 is doubtful, as it does not seem to differ from *Sosylus* Erichson, 1845 fundamentally.

1. Pronotal disc usually with at most two basal ridges .. 2
1'. Pronotal disc with at least four longitudinal ridges (Heinze 1943: figs 30, 31, Ślipiński et al. 1989: figs 1, 6). Antennal club 2-segmented (Ślipiński et al. 1989: fig. 4) 7
2. Pronotum usually with parallel or rounded sides; disc without median longitudinal groove (Aoki 2008: figs 1, 3; Aoki and Narukawa 2013: fig. 1)..... .....*Sosylus* Erichson & *Carbothrus* Aoki
2'. Pronotum narrowed at base; disc often with a median longitudinal groove (Heinze 1943: figs 18–22, 29, Lord and McHugh 2013: figs 57–81)..... 3
3. Antennal club composed of 2–3 strongly transversely expanded segments (Westwood 1848: fig. 7c of plate XLI, Pascoe 1863: fig. 9 of plate II)..... .....*Petalophora* Westwood
3'. Antennal club normal, not transversely expanded.... 4
4. Antennae club 3-segmented 5
4'. Antennae club 2-segmented (Heinze 1943: figs 23, 25).. 6
5. Pronotum with an oval cavity at each anterior angle (Fig. 5). Antennomere 11 conical (Fig. 8). Elytra each with a single short ridge (Fig. 6)....*Alveoderes* gen. nov.
5'. Pronotum without oval cavity at anterior angles. Antennomere 11 short, apically broadly truncate (Lord and McHugh 2013: figs 44–47). Elytra with multiple longer ridges (Lord and McHugh 2013: figs 80–131).... .....*Deretaphrus* Newman
6. Tarsomere 1 of all legs hardly longer than tarsomere 2..... *Asosylus* Grouvelle
6'. Tarsomere 1 of mid and hind legs at least as long as tarsomeres 2 and 3 combined...*Craspedophilus* Heinze
7. Prosternum not foveate in front of coxae. Scutellum visible. Outer anterior angle of pro- and mesotibiae sharply produced. Tarsomere 1 longer than tarsomere 2..... *Pseudososylus* Grouvelle
7'. Prosternum deeply foveate in front of coxae (Ślipiński et al. 1989: fig. 2). Scutellum not visible. Outer anterior angle of pro- and mesotibiae not produced (Ślipiński et al. 1989: fig. 3). Tarsomere 1 subequal to tarsomere 2.... .....*Erotylathris* Motschulsky

Alveoderes Li & Cai gen. nov.

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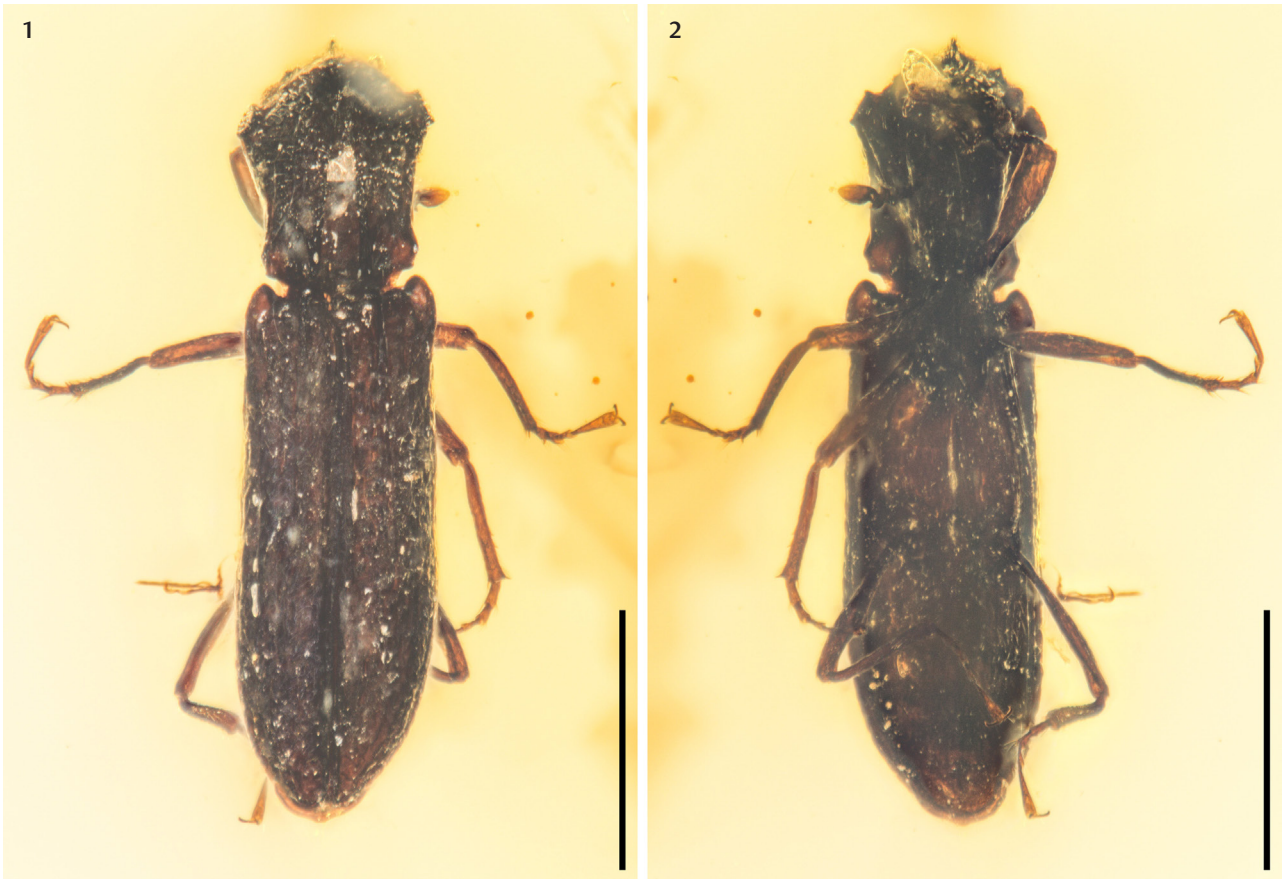
Type species. *Alveoderes yamamotoi* sp. nov., by present designation and monotypy.

Diagnosis. Body elongate. Antennae with 3-segmented club; antennomere 11 conical (Fig. 8). Pronotum (Fig. 5) with



Figures 1–2. General habitus of *Alveoderes yamamotoi* Li & Cai gen. et sp. nov., holotype, NIGP203385, under incident light: (1) dorsal view; (2) ventral view. Scale bars: 500 μm.

oval cavity at each anterior pronotal angle; disc with median longitudinal groove, posteriorly open and posterolaterally bordered by distinct posteriorly directed projections. Procoxae subcontiguous (Fig. 9). Scutellar shield anteriorly emarginate (Fig. 6). Elytra each with one short longitudinal ridge at base (Fig. 6). Mesoventrite with longitudinal carinae (Fig. 9). Protibial spurs unequal; one being enlarged and strongly curved (Fig. 11). Abdominal ventrite 1 with broadly angulate intercoxal process (Fig. 10).

Etymology. The generic name is formed based on the Latin "*alveus*", cavity, and "*deres*", a common suffix for genera in Bothrideridae. The name is masculine in gender.

Alveoderes yamamotoi Li & Cai sp. nov.

Figs 1–13

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Material. Holotype, NIGP203385.

Locality and horizon. Amber mine located near Noije Bum Village, Tanai Township, Myitkyina District, Kachin State, Myanmar; unnamed horizon, mid-Cretaceous, Upper Albian to Lower Cenomanian (Shi et al. 2012, Mao et al. 2018).

Diagnosis. As for the genus.

Description. Body elongate, about 1.5 mm long, 0.4 mm wide; surface with scattered setae.

Head declined at base. Compound eyes with short interfacetal setae. Antennae likely 11-segmented; antennomere 1 robust; antennomere 2 wider than 3; antennomeres 3–8 submoniliform to subfiliform; antennomeres 9–11 forming loose club; antennomere 11 conical.

Pronotal disc about 1.1 times as long as wide, widest anteriorly; surface with median longitudinal groove, about 0.8 times as long as pronotal length, anteriorly acute, gradually widened backwards, posteriorly open, posterolaterally bordered by distinct posteriorly directed projections; anterior pronotal angles each with a distinct oval cavity (possibly

Figures 3–4. General habitus of *Alveoderes yamamotoi* Li & Cai gen. et sp. nov., holotype, NIGP203385, under confocal microscopy: (3) dorsal view; (4) ventral view. Scale bars: 500 µm.

a glandular opening). Procoxae subcontiguous (status of coxal cavities unknown).

Scutellar shield elongated oval, anteriorly emarginate. Elytra elongate; surface with indistinct rows of fine punctures; one distinct longitudinal ridge present at base of elytron, anteriorly opposite to respective projection on pronotum, shorter than 1/4 elytral length, gradually weakened posteriorly; elytral humeri distinctly ridged; epipleura narrow. Mesoventrite with median carina and paired parallel carinae continuous with edges of mesoventral process. Mesocoxal cavities narrowly separated. Metaventrite anteromedially slightly tumid, without clear median discrimen; katepisternal suture absent. Metacoxae suboval, moderately separated, laterally separated from elytra by metanepisternum.

Legs well-developed, slender. Trochanters relatively reduced and somewhat concealed. Tibiae with two or three weak spines along outer margin; protibiae with strongly unequal spurs; one being enlarged and strongly curved; meso- and metatibiae with paired equal spurs. Tarsi all 4-segmented; tarsomeres simple, unlobed. Pretarsal claws simple.

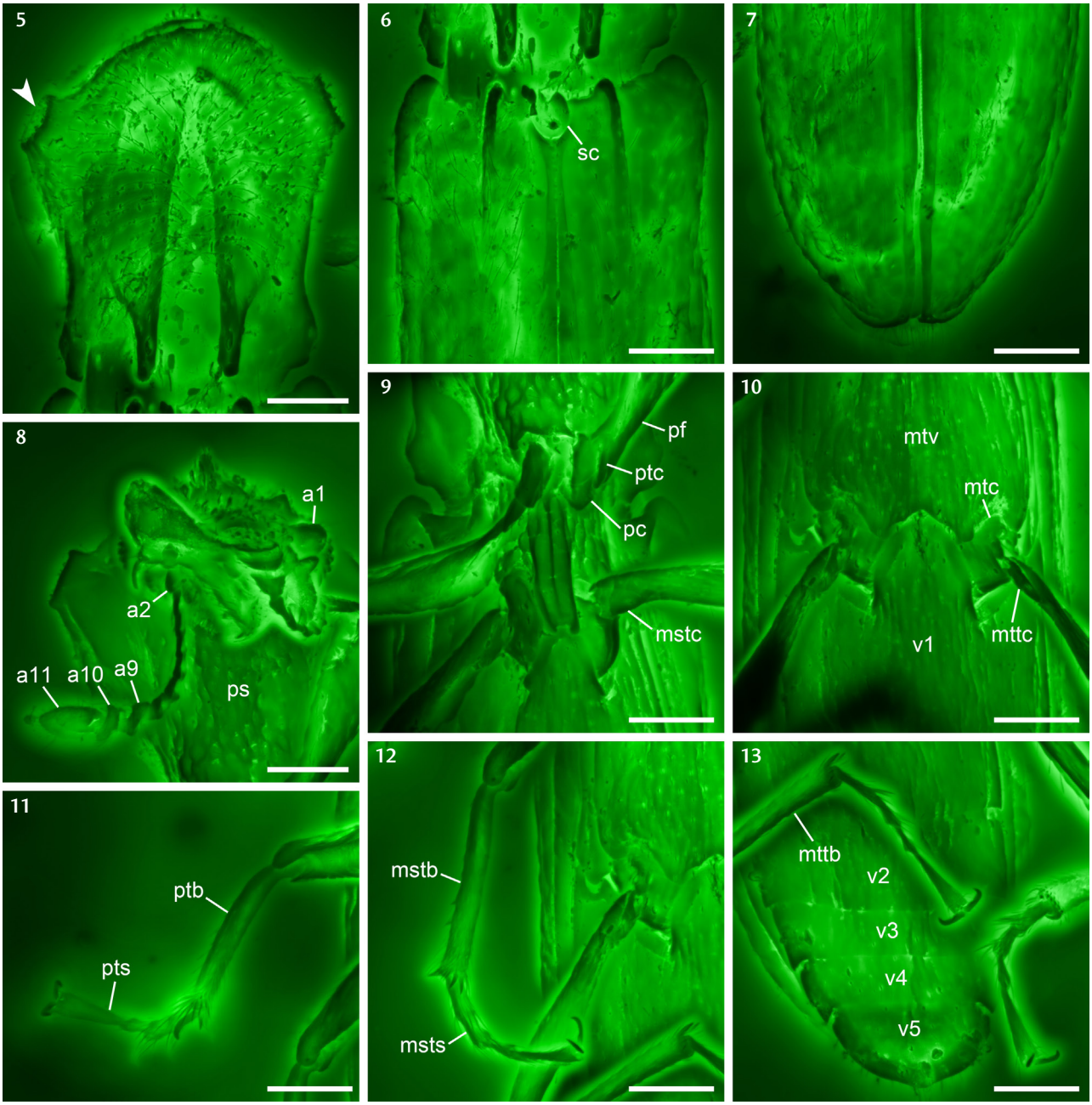
Abdomen with five ventrites. Ratio of ventrite lengths along middle: 5.2:2.0:1.0:1.1:2.0. Ventrite 1 with intercoxal process apically broadly angulate; postcoxal lines absent.

Etymology. The species is named after the coleopterist Dr. Shûhei Yamamoto.

Remarks. The antennomere 11 of the left antenna is not preserved in the specimen. The prosternal process cannot be observed, and the state of procoxal cavities cannot be confidently determined.

DISCUSSION

Based on the elongate body shape and 4-4-4 tarsi, *Alveoderes* mostly resembles Bothrideridae and Teredidae of Coccinelloidea. Some members of Colydiinae (Tenebrionoidea: Zopheridae) also have a similar elongate appearance



Figures 5–13. Details of *Alveoderes yamamotoi* Li & Cai gen. et sp. nov., holotype, NIGP203385, under confocal microscopy: (5) prothorax, dorsal view, with the cavity at anterior pronotal angle indicated (arrowhead); (6) elytral base, dorsal view; (7) elytral apex, dorsal view; (8) head and prothorax, ventral view; (9) mesothorax, ventral view; (10) abdominal base, ventral view; (11) fore leg, showing strongly unequal protibial spurs; (12) mid leg; (13) abdominal apex and hind legs, ventral view. (a1–11) antennomeres 1–11, (mstb) mesotibia, (mstc) mesotrochanter, (msts) mesotarsus, (mtc) metacoxa, (mttb) metatibia, (mttc) metatrochanter, (mtv) metaventrite, (pc) procoxa, (pf) profemur, (ps) prosternum, (ptb) protibia, (ptc) protrochanter, (pts) protarsus, (sc) scutellum, (v1–5) ventrites 1–5. Scale bars: 100 µm.

and 4-4-4 tarsi. However, *Alveoderes* can be readily separated from colydiines by the long ventrite 1 (Fig. 10) typically present in many coccinelloids, even though other important characters, such as the state of antennal insertions (Lawrence 1980), cannot be determined.

Members of Bothrideridae and Teredidae resemble each other in general adult morphology and had long been treated as a single family until the comprehensive molecular study by Robertson et al. (2015). As proposed by Pal and Lawrence (1986), bothriderids are characterized by the unequal protibial spurs and reduced and more or less concealed trochanters, while teredids have subequal and unhooked protibial spurs and unreduced trochanters. Bothriderids also often have variable sculpture on the pronotum and elytra (e.g., Heinze 1943, Ślipiński et al. 1989), whereas in most teredids there are no distinct ridges or depressions on the dorsal surface (exceptions include paired pronotal depressions in *Kocherius* Coiffait, 1984, *Rustleria* Stephan, 1989 and *Oxylaemus* Erichson, 1845, and elytral ridges in *Sysolus* Grouvelle, 1908 – Coiffait 1984, Lawrence 1985, Ślipiński and Pal 1985, Stephan 1989, Recalde Irurzun and San Martín Moreno 2007). *Alveoderes* has relatively reduced trochanters (Figs 9, 10), strongly unequal protibial spurs (Fig. 11), and peculiar sculpture on the pronotum and elytra (Figs 5, 6). Thus, it could be confidently placed in the family Bothrideridae. The procoxae are subcontiguous in *Alveoderes* (Fig. 9). Although Ślipiński and Pal (1985) proposed the broad prosternal process as one of the diagnostic characters for bothriderids, the width of the prosternal process actually varies within the family (e.g., Lee et al. 2017: figs 1D, 2D), and in *Sosylus* and *Carbothrus* the prosternal process can be very narrow with procoxae appearing almost contiguous (Hinton 1946, Pope 1980, Aoki 2012, Aoki and Narukawa 2013).

Two tribes are currently recognized in Bothrideridae, i.e., Bothriderini and Deretaphrini (Pope 1961, Ślipiński and Pal 1985, Pal and Lawrence 1986). Bothriderini has metacoxae widely separated by the apically truncate intercoxal process of abdominal ventrite 1 (e.g., Dajoz 1980, Lim et al. 2012: fig. 6, McElrath et al. 2016: fig. 1b, Aoki and Ito 2017: fig. 5, Lim et al. 2023: fig. 2B). Deretaphrini has metacoxae less widely separated by the apically broadly rounded (or angulate) intercoxal process (e.g., Heinze 1943, Lord and McHugh 2013: figs 2, 28). *Alveoderes* possesses a broadly angulate intercoxal process of abdominal ventrite 1 and moderately separated metacoxae (Fig. 10), and therefore should belong to the tribe Deretaphrini. Nevertheless, it should be noted that the presently defined Deretaphrini may not be monophyletic (Robertson et al. 2015).

Within Deretaphrini, *Sosylus* and *Carbothrus* have overall simple pronotal disc (although there might be some short or indistinct ridges) (Hinton 1946, Pope 1980, Aoki 2008, 2012, Aoki and Narukawa 2013), and *Pseudososylus* and *Erotylathris* have at least four distinct longitudinal ridges on pronotal disc (Heinze 1943), both of which are different from *Alveoderes*. The pronotal sculpture of *Alveoderes* (Fig. 5) is similar to some members of *Petalophora* Westwood, 1848, *Asosylus* Grouvelle, 1908, *Craspedophilus* Heinze, 1943, and *Deretaphrus* Newman, 1842; in these genera, the pronotal disc has a median longitudinal groove, posteriorly open and posterolaterally bordered by distinct ridges (Pascoe 1863, Heinze 1943, Lord and McHugh 2013: fig. 67). *Alveoderes* differs from *Petalophora* by the unmodified antennal club (Fig. 8) and less broad pronotum (antennomeres of the club strongly transverse and expanded in *Petalophora* – Westwood 1848, Pascoe 1863), and from *Asosylus* and *Craspedophilus* by the 3-segmented antennal club (antennal club 2-segmented in *Asosylus* and *Craspedophilus* – Heinze 1943). *Alveoderes* appears to be most similar to *Deretaphrus*. However, *Alveoderes* can be separated from *Deretaphrus* by the conical antennomere 11 (Fig. 8) and elytra each with a single short ridge (Fig. 6), whereas in *Deretaphrus* the antennomere 11 is broadly truncate and multiple long ridges are present on elytra (Lord and McHugh 2013).

Alveoderes is distinctive in Bothrideridae in having a large cavity at each anterior pronotal angle (Fig. 5). While external exoskeletal cavities have been widely reported in Coleoptera (Grebennikov and Leschen 2010), such prominent cavities at anterior pronotal angles are nevertheless uncommon. Similar cavities at anterior pronotal angles have been reported in *Cretoboganium* Cai & Huang, 2018 of Boganiidae and *Trematosphindus* Li & Cai, 2021 of Sphindidae, both from Burmese amber (Cai and Huang 2019, Li et al. 2021). Some extant Anamorphidae, Boganiidae and Cryptophagidae also have callosity at anterior pronotal angles, albeit only with a much smaller glandular pore (or pores) on it (Crowson 1990, Otero and Johnson 2013, Escalona et al. 2015, Otero and Pereira 2019, Arriaga-Varela et al. 2024).

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