Paleontological Journal, Vol. 30, No. 2, 1996, pp. 217–224. Translated from Paleontologicheskii Zhurnal, No. 2, 1996, pp. 91–99.

Lamellicorn Beetle Species (Coleoptera, Scarabaeidae) with Multistriate Elytra from the Lower Cretaceous Baisa Locality, Transbaikalia

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Received February 23, 1995

Abstract—Two new species of the Mesozoic genus *Proteroscarabaeus*, *P. magnus* and *P. nikritini*, and three new genera with one new species each, *Cretanaides trogopterus* (Hybosorinae), *Cretobolbus rohdendorfi* (Bolboceratinae), and *Hybosorites fissuratus* (subfamily incertae sedis), are described from the Lower Cretaceous of Transbaikalia. A new tribe is created within the Geotrupinae for *Cretogeotrupes*. One new tribe is established within the Hybosorinae, and two more within the extant Bolboceratinae. Cenozoic *Bolboceras tertiarium* is transferred to *Phaeochrous*; doubt is expressed regarding the placement of the monobasic Cenozoic genus *Coprologus* in the Bolboceratinae.

Among lamellicorn specimens collected in the Lower Cretaceous Baisa locality, Transbaikalia, six belong to the species possessing more than 10 elytral striae. So far as numerous striae are characteristic of few lamellicorn taxa, an attempt is made to elucidate the systematic position of these species. One of them was described in the genus *Cretogeotrupes* (Nikolajev, 1992), five more are described below as new. Four specimens are preserved as isolated elytra (Fig. 1), in the fifth one the body and legs are preserved as well.

In addition to *Cretogeotrupes*, more than 10 elytral striae are characteristic of the Mesozoic genus *Proteroscarabaeus* Grabau and several genera of the extant subfamilies Bolboceratinae, Geotrupinae, Hybosorinae, and Ceratocanthinae. Due to the rather large size of the specimens in question, one could exclude the Ceratocanthinae from consideration. Two elytrae are of a peculiar shape, somewhat narrowed towards the apex (Figs. 1a, 1b), similar to those of the type species of *Proteroscarabaeus* (Fig. 2a) and in contrast to *Cretageotrupes* and all recent taxa, having broadly rounded elytrae apically. The systematic position of *Proteroscarabaeus* is still uncertain; it is closest to the monobasic Pleocominae (Nikolajev, 1992) and could be assigned provisionally to the subfamily until a reexamination of the type species. One more elytra (Fig. 1c) bears a very complicated sculpture found only in some genera of the Hybosorinae. Another elytron (Fig. 1d), poorly preserved along the sutural margin and clearly distinct from that of *Proteroscarabaeus*, has insufficient diagnostic characters and could belong to any of the three subfamilies (Bolboceratinae, Geotrupinae, or Hybosorinae).

The last of the specimens discussed, a nearly complete beetle, could be assigned to the recent Bolboceratinae; it differs from the Hybosorinae and Geotrupinae in that the middle coxae are rather broadly separated, and from *Proteroscarabaeus* in that the elytra are broadly rounded lateroapically and the fore tibia is tridentate.

All the specimens described below are from the Baisa locality (Transbaikalia, Buryatia, Eravnenskii Region, left bank of the Vitim River downstream of the mouth of Baisa River; Lower Cretaceous, Valanginian–Hauterivian, Zaza Formation) and deposited in the Paleontological Institute, Russian Academy of Sciences (PIN).

Family Scarabaeidae Laicharting, 1781

?Subfamily Pleocominae Leconte, 1861

Genus *Proteroscarabaeus* Grabau, 1923

***Proteroscarabaeus magnus* Nikolajev, sp. nov.**

Pl. XI, fig. 1

Etymology. From Latin *magnus* (large).

Holotype. PIN 1989/3026, right elytron (part and counterpart); Baisa locality, bed 15 (Martinson, 1961).

Description (Fig. 1a). Large, weakly convex elytra distinctly narrowed apically, with 13–14 striae nearly equidistant from each other. Striae not deep, weakly impressed, with few points. Intervals weakly convex; epipleura rather narrow, distinctly narrower than adjacent interval. Humeral tubercle poorly developed.

Measurements, mm. Elytra length 20; maximal width 11.

Comparison. Distinct from other species in the larger size.

Material. Holotype.

***Proteroscarabaeus nikritini* Nikolajev, sp. nov.**

Etymology. In honor of the entomologist L.M. Nikritin.

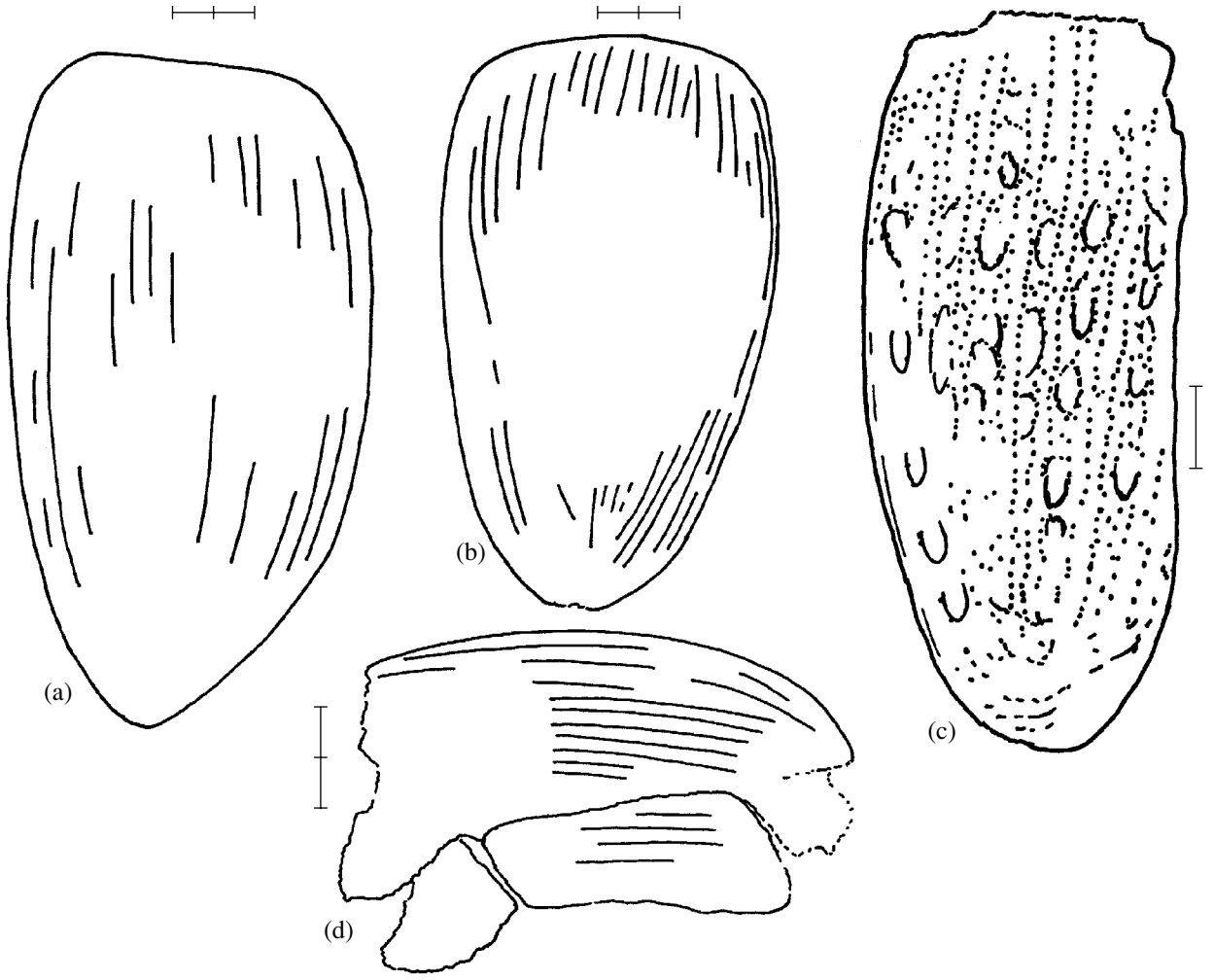

Fig. 1. Scarabaeid elytrae from Baisa locality: (a) *Proteroscarabaeus magnus* sp. nov., holotype PIN 1989/3026; (b) *P. nikritini* sp. nov., holotype PIN 3064/7154; (c) *Cretanaides trogopterus* sp. nov., holotype PIN 4210/706; (d) *Hybosorites fissuratus* sp. nov., holotype PIN 4210/709. Scale unit in all figures 1 mm.

Holotype. PIN 3064/7154, right elytra (part and counterpart); Baisa locality, bed 31 (Martinson, 1961).

Description (Fig. 1b). Large, weakly convex elytra distinctly narrowed apically; its length/width ratio 1.7 : 1. 11 striae between suture and humeral tubercle. Striae deep, with numerous points; first three striae possibly terminate against scutellum. Intervals convex; sutural interval somewhat broader than the next one, remaining of nearly equal width; epipleura somewhat narrower than adjacent interval. Humeral tubercle well developed. Measurements, mm. Elytra length 17.0; maximal width 9.9.

Comparison. Distinct from the type species, *P. yeni* Grabau in the relatively shorter elytrae (length/width ratio of *P. yeni* elytron is 2.3 : 1) (Fig. 2a).

Material. Holotype.

Subfamily Hybosorinae Lacordaire, 1856

?Tribe Anaidini Nikolajev, trib. nov.

Genus *Cretanaides* Nikolajev, gen. nov.

Etymology. From Latin *cretaceus* (Cretaceous) and genus *Anaides*.

Type species. *C. trogopterus* sp. nov.

PLATE XI

Fig. 1. *Proteroscarabaeus magnus* sp. nov.; holotype PIN 1989/3026 (×4.4): (a) cast; (b) counterpart.
Fig. 2. *Cretanaides trogopterus* sp. nov.; holotype PIN 4210/706 (×10).
Fig. 3. *Hybosorites fissuratus* sp. nov., holotype PIN 4210/709 (×7.1).

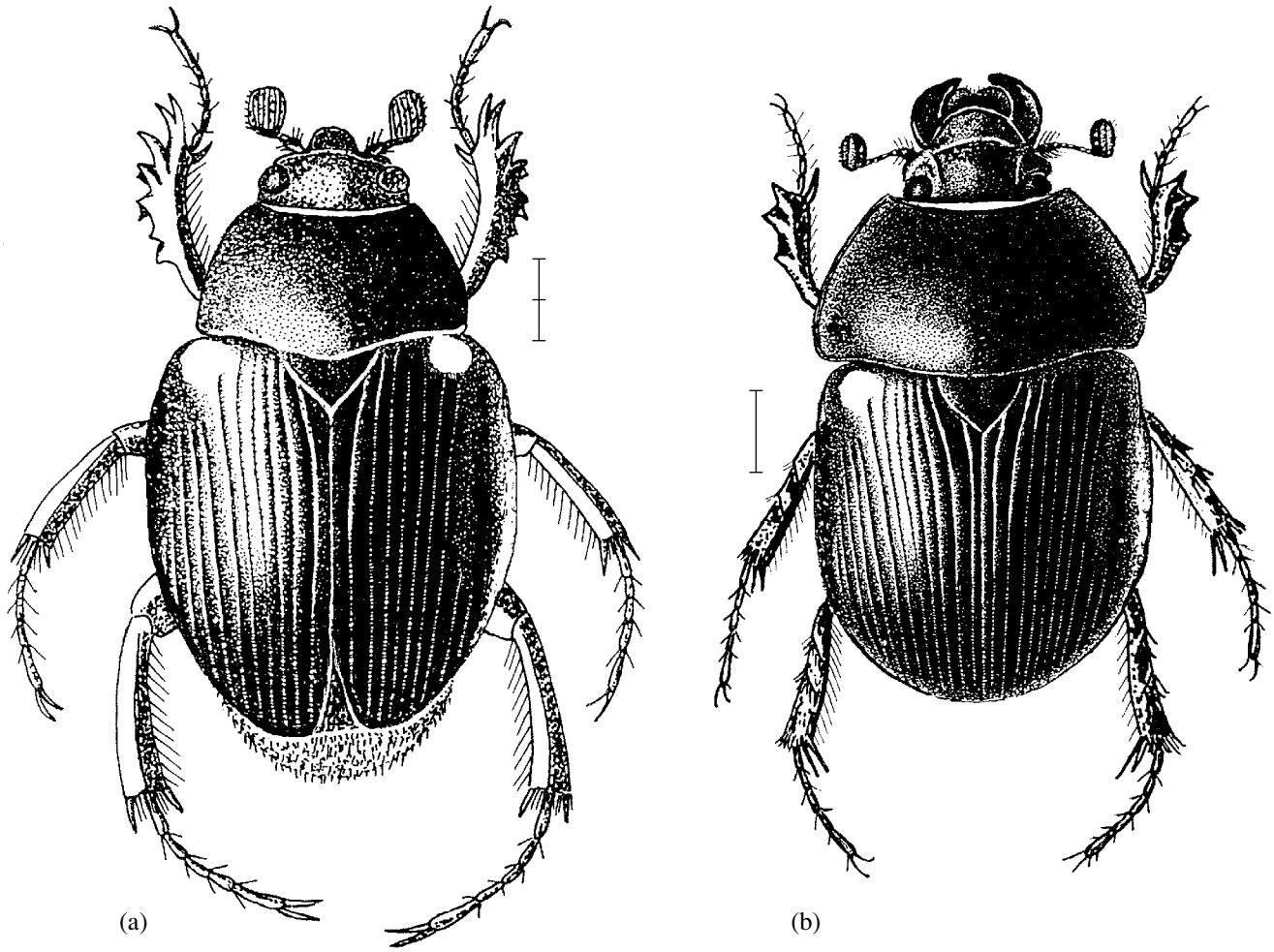

Fig. 2. Reconstructions of Mesozoic Scarabaeidae: (a) *Proteroscarabaeus yeni* Grabau; (b) *Cretogeotrupes convexus* Nikolajev.

Diagnosis. Middle-sized convex beetle. Elytra with numerous (more than 15) punctate striae and weakly convex intervals (some of them bearing elongate tubercles). Fine sutural stria not developed.

Species composition. Monobasic.

Comparison. Distinct from all Mesozoic scarabaeid genera with multistriate elytra, in the complex sculpture of intervals between striae.

Systematic position. Strongly convex, relatively large elytron with complicated sculpture excludes the genus from the Ceratocanthinae. Deeply rounded outer apical margin of elytron prevents association of *Cretanaides* with the Mesozoic *Proteroscarabaeus*, provisionally included in the Pleocominae. The very complex elytral sculpture is unknown in the Geotrupinae. No single character known contradicts the placement of the genus into the Hybosorinae. Within the latter subfamily, the group of American genera (*Anaides* Westwood, *Cryptogenius* Westwood, *Cremastochiloides* Krikken, *Callosides* Howden) (Howden, 1971; Krikken, 1975; Scholtz, D'Hotman, Nel, 1987) demonstrates a similar sculpture of the elytral intervals. In these genera the borders of the elytral striae are vertical (the same is true of at least the first stria in *Cretanaides*), middle and hind tibiae lack transverse carinae, fore tibiae with three large teeth at outer margin, and the wings (studied in *Anaides laticollis* Harold) with a single free vein between the cubital and first anal vein reaching the wing base. The above characters are sufficient for separation of the genera listed into the new tribe Anaidini Nikolajev, trib. nov. The character states could be considered as derived in the Anaidini relative to the Hybosorini s. str.

***Cretanaides trogopterus* Nikolajev, sp. nov.**

Pl. XI, fig. 2

Etymology. From Greek *pteron* (wing) and genus *Trox*.

Holotype. PIN 4210/706, left elytra (part and counterpart); Baisa locality, bed 4 (Martinson, 1961).

Description (Fig. 1c). Medium-sized, oblong, convex elytra, slightly narrowed apically. Striae rather deeply punctate; the points separated by a little more than their diameter. First stria (from suture) not deep, with points broader than stria, and borders sharply impressed (vertical); it is uncertain, whether or not remaining striae are of the same structure. No less than 15 striae, but exact number is unknown, since outer striae are faint. Intervals of different width; some of them with tubercles, large and prominent in the 3rd, 7th, 11th and 15th intervals, and superficial but longer in the 5th, 9th and 13th intervals; tubercles well developed on disc but decreasing both basally and apically. Epipleura rather broad (preserved only in basal third of elytron).

Measurements, mm. Length 9.5; width 4.4 (perhaps a little larger, since outer margin and apex are poorly preserved).

Material. Holotype.

Subfamily Bolboceratinae Mulsant, 1842

Genus *Cretobolbus* Nikolajev, gen. nov.

Etymology. From Latin *cretaceus* (Cretaceous) and Latin *bolbus* (bulb), a root of many generic names in the subfamily.

Type species. *C. rohdendorfi* sp. nov.

Diagnosis. Middle-sized convex beetle. Elytra with numerous (no less than 14) punctate striae and weakly convex intervals; fine sutural stria developed. Fore tibiae with three teeth at outer margin. Middle coxae not broadly separated, forming a right angle to each other. Middle tibiae transversely unicarinate.

Species composition. Monobasic.

Comparison. Distinct from other genera of the subfamily in the tridentate fore tibiae, and from all Mesozoic scarabaeids with more than 10 elytral striae, in the fine sutural stria present.

Systematic position. A combination of fine sutural stria and separated middle coxae indicates that the genus could belong only to the Bolboceratinae.

Most authors treat the latter taxon as a tribe within the Geotrupinae (Howden, 1982; Zunino, 1984a, b) rather than a subfamily. However, the character analysis shows the both are sister groups of equal rank. Characters shared by the Bolboceratinae and Geotrupinae (11-segmented antennae, fore tibiae with many teeth along outer margin, wings with two free veins between cubital and first anal vein reaching wing base) are probably symplesiomorphic for the whole superfamily. A combination of the middle coxae separated (plesiomorphy) and the absence of a distinct silky hair spot at the fore femora (apomorphy) in the Bolboceratinae forces us to consider it as a sister group to the Geotrupinae, having the middle coxae contiguous (apomorphy) and fore femora with distinct silky hair spot (plesiomorphy). Apomorphic characters shared by the Bolboceratinae and the Hybosorinae are the 3-segmented antennal club, and middle and hind tibiae with spurs displaced to the same side from tarsal base. The only derived character shared by the Bolboceratinae with Geotrupinae–Scarabaeinae "clade", 3-segmented antennal club, could be regarded as a synapomorphy uniting these taxa in one group (Nikolajev, 1995).

The Bolboceratinae is now separated into the five tribes: monobasic Bolboceratini Mulsant, Athyreini Howden et Martinez (4 genera; Howden, Martinez, 1963), Bolbochromini Nikolajev (3 genera; Nikolajev, 1970), monobasic Gilletinini Nikolajev (Nikolajev, 1990), and Eubolbitini Nikolajev with remaining genera (Nikolajev, 1970). So far as the trend of the outer teeth number to decrease on fore tibia occurs in several tribes of the subfamily, the tridentate condition is not sufficient to separate the genus into one more tribe. The broad scutellum and rather narrowly separated middle coxae preclude the assignment of *Cretobolbus* to the Athyreini or Gilletinini. Contiguous middle coxae distinguish the Bolboceratini from *Cretobolbus*. Almost contiguous middle coxae and also (in most genera) several transverse carinae on middle and hind tibiae in the Bolbochromini separate the tribe from *Cretobolbus* as well. It is only within the Eubolbitini that all the characters of *Cretobolbus* (except for tridentate fore tibia) could be met. However, in my opinion, the tribe Eubolbitini is a conglomeration and deserves separation into at least three tribes.

The genera *Bolbelasmus* Boucomont, *Bolbotrypes* Olsoufieff and *Bolbogonium* Boucomont share the multidentate fore tibiae, numerous transverse carinae on middle and hind tibiae (their number tending to decrease), unmodified clypeus (discal tubercle not tending to fuse with raised anterior border), and basally emarginate wing with radial vein lacking apical extra branches. The tribe Bolbelasmini Nikolajev, trib. nov. is created for these three genera. *Cretobolbus* is distinct from the tribe in the unicarinate middle tibiae.

The Australian genera *Australobolbus* Howden et Cooper, *Bolbobaineus* Howden et Cooper, *Bolborachium* Boucomont, *Blackburnium* Boucomont, *Blackbolbus* Howden et Cooper, *Bolboleaus* Howden et Cooper (Howden and Cooper, 1977), North American *Bolboceras tes* Cartwright and *Bradycinetulus* Cockerell (Cartwright, 1953), African *Prototrupes* Krikken (Krikken, 1977), and Asiatic *Indobolbus* Nikolajev (Nikolajev, 1979) are characterized by the base of elytra emarginated, and discal tubercle of clypeus fused with its anterior border. These genera are separated into the Australobolbini Nikolajev, trib. nov. (a paper with more detailed discussion of taxonomic structure of the Bolboceratinae is in preparation).

The only specimen of *Cretobolbus* is too insufficiently preserved to include the genus into either Eubolbitini or Australobolbini.

Remarks. The descriptions and illustrations of the Cenozoic species from Europe assigned to the Bolboceratinae (Heer, 1848; Deichmüller, 1881) show that

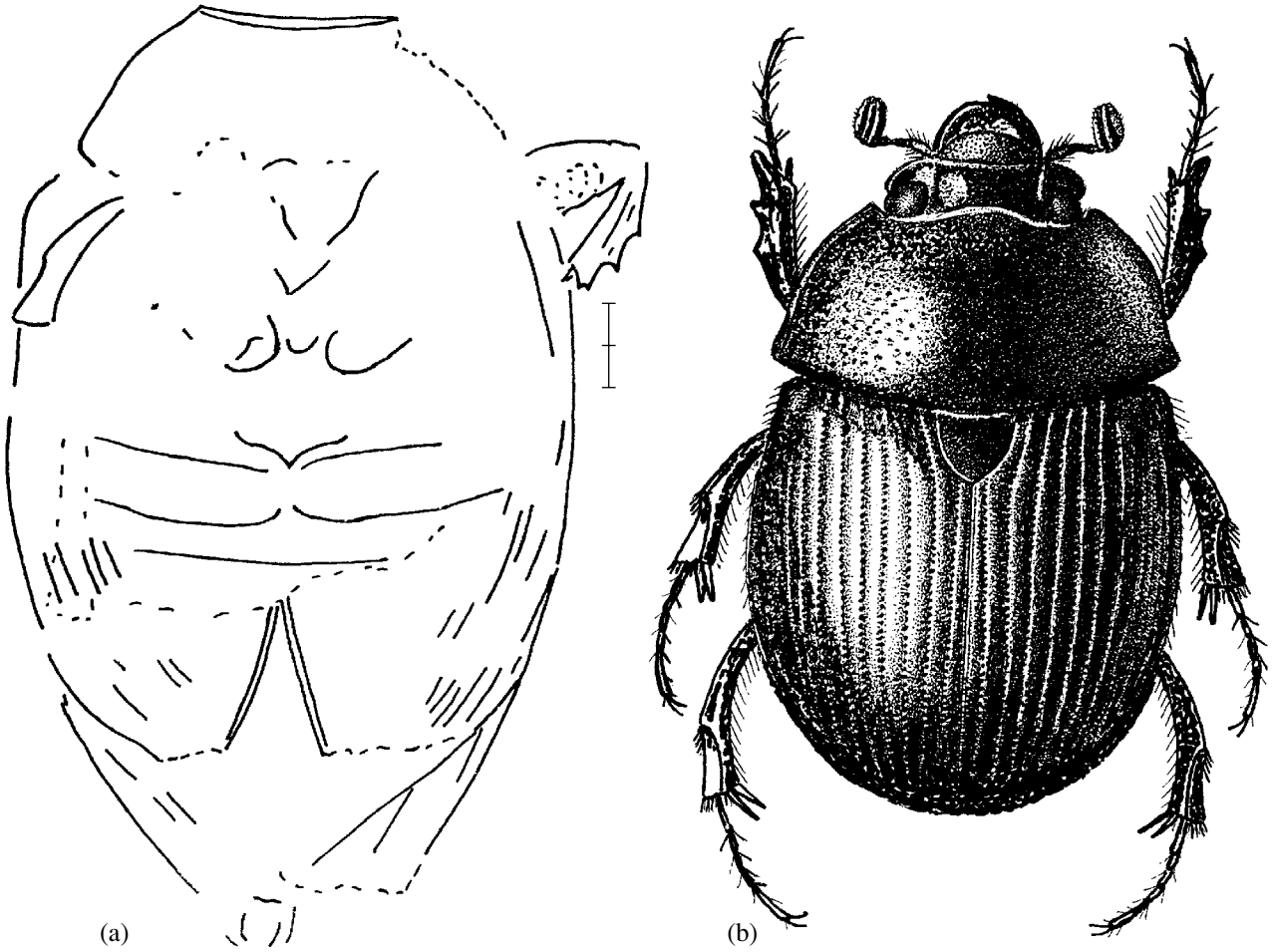

Fig. 3. *Cretobolbus rohdendorfi* sp. nov.: (a) holotype PIN 3064/7137; (b) reconstruction.

they are incorrectly assigned. *Bolboceras tertiarium* Deichmüller should be assigned to the Hybosorinae on account of the middle tibiae lacking transverse carina; the species most probably could be included with *Phaeochrous* Castelnau. *Coprologus gracilis* Heer presumably belongs to the Hybosorinae as well (judging from the description of head shape and labrum), but the holotype should be reexamined to confirm this.

***Cretobolbus rohdendorfi* Nikolajev, sp. nov.**

Etymology. In memory of paleoentomologist B.B. Rohdendorf.

Holotype. PIN 3064/7137, beetle lacking head and most of legs, and the wings projecting from beyond elytra (cast and counterpart); Baisa locality, bed 15 (Martinson, 1961).

Description (Fig. 3). Rather large oval beetle. Pronotum with leathery margin anteriorly, emarginated also laterally and posteriorly. Anterior angles of pronotum obtuse; pronotum slightly emarginate laterally near acute posterior angles. Scutellum large, triangular. Elytra with numerous punctate striae (deeply impressed only laterally) and a deep sutural stria; lateral elytral margin weakly evenly rounded. Fore femur (only right leg preserved) with sparse points at anterior margin (silky hair spot probably "blurred"). Fore tibia with a long longitudinal carina and three large, equidistant teeth on outer margin. Middle coxae clearly separated, forming almost right angle to each other. Middle tibia (left one preserved) with single transverse carina near midlength. Radial vein (traceable in apical part of right wing) possibly branched.

Measurements, mm. Length from anterior pronotal margin to wing apex 22; median length of pronotum 4.5, width 8.1; elytron length 12.5, width 6.6; fore tibia length 3.5; middle tibia length 3.6; space between middle coxae 1.0.

Material. Holotype.

Subfamily Geotrupinae Latreille, 1804

Tribe Cretogeotrupini Nikolajev, trib. nov.

Diagnosis. Relatively small beetles. Elytrae concealing abdomen entirely, each with numerous (more than 11) striae; wings well developed. Fore tibiae

tridentate on outer margin; middle coxae contiguous; middle and hind tibiae transversely bicarinate (see Fig. 2b).

Generic composition. *Cretogeotrupes* Nikolajev, 1992, Lower Cretaceous of Asia.

Systematic position. Up to now only three tribes were established within the subfamily: Geotrupini, Lethrini Mulsant et Rey, 1871 and Taurocerastini Germain, 1897. The nominotypical one includes both winged and apterous species, having multistriate elytra and transversely tricarinate (sometimes bi- or even unicarinate) middle and hind tibiae. The monobasic Lethrini is composed only of apterous species (apomorphy) with elytra bearing 10 striae (plesiomorphy) and middle and hind tibiae transversely unicarinate (apomorphy). Therefore, these two tribes could be only in sister group relationship. The Taurocerastini, with only two genera included, demonstrates along with apomorphic characters (10-segmented antennae, middle and hind tibiae transversely unicarinate), one plesiomorphy, the eyes only partly subdivided by the genal projection (completely divided eyes in Geotrupini and Lethrini is an apomorphy). Thus, the Taurocerastini could be only a sister taxon to one of two remaining recent tribes.

The new tribe is certainly a sister group to Lethrini. Lack of data on the head structure prevent the analysis of relationships of two other tribes to the Cretogeotrupini. If *Cretogeotrupes* had the structure of eyes, antennae and mouthparts comparable to those of the Taurocerastini, it could be ancestral to this tribe; if as in the Geotrupini, it presumably would be derivative of the latter tribe.

Remarks. The Geotrupinae constitutes one phyletic lineage with the Troginae, Aphodiinae, and Scarabaeinae. That of all these taxa originate from a common ancestor is beyond doubt. The Aphodiinae (Nikolajev, 1993) and Scarabaeinae are more closely related to each other than to remaining subfamilies of the "branch". It is still possible that contrary to the earlier suggestion (Nikolajev, 1993) the Scarabaeinae is rather a derivative of one of the Aphodiinae subgroups than its sister group. Such a possibility was considered by some authors (e.g., Cambefort, 1987) (for family group taxa, the name Scarabaeinae has priority). Avoiding a discussion on the rank of the three taxa, one could try to elucidate their relationships.

The Geotrupinae and Troginae share the middle coxae contiguous and middle and hind tibial spurs always close-set. These apomorphies often appear in several lamellicorn groups (Nikolajev, 1993) and can not be considered sufficient for uniting the two subfamilies. The Troginae and Scarabaeinae share the other apomorphies, the reduced number of both antennal segments and abdominal sterna. However, these characters appear in many lamellicorn groups as well. Therefore, it is reasonable to treat these three groups as taxa of equal rank, until the relative "weight" of the above characters is determined.

Subfamily incertae sedis

Genus *Hybosorites* Nikolajev, gen. nov.

Etymology. From recent genus *Hybosorus*. Type species. *H. fissuratus* sp. nov.

Diagnosis. Medium-sized beetle. Elytra with numerous striae (more than 11), outer apical margin broadly rounded.

Species composition. Monobasic.

Comparison. Distinct from Mesozoic genera: from *Proteroscarabaeus* in the elytra broadly rounded apically; from *Cretanaides* and *Cretogeotrupes* in the less convex elytra; from *Cretobolbus* in the somewhat smaller size.

Systematic position. The fossil is too large to belong in the Ceratocanthinae, and insufficiently preserved to show diagnostic characters of the Hybosorinae, Bolboceratinae, or Geotrupinae.

***Hybosorites fissuratus* Nikolajev, sp. nov.**

Pl. XI, fig. 3

Etymology. From Latin *fissuratus* (cracked).

Holotype. PIN 4210/709, right elytron; Baisa locality, bed 22 (Martinson, 1961).

Description (Fig. 1d). Epipleura broad, ending at about 3/4 of elytron length. Striae deeply impressed, with large points. Humeral tubercle well developed.

Measurements, mm. Length (as preserved) 11.5, width 6.5 (estimated length of complete elytron below 13).

Material. Holotype.

ACKNOWLEDGMENTS

I am grateful to A.G. Ponomarenko and V.V. Zherikhin (Moscow) for loan their of the fossil specimens and to H.F. Howden (Canada) for the loan of the recent *Anaides* species, and to F.-T. Krell (Germany) who helped with the literature on fossil species. This study was supported by the International Science Foundation and Russian Academy of Natural Sciences.

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