

A New Subfamily of Lamellicorn Beetles (Coleoptera, Scarabaeoidea) from the Lower Cretaceous of Transbaikalia and Mongolia, and Its Position within the Superfamily

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Abstract—A new subfamily Prototroginae is established for *Prototrox transbaikalicus* gen. et sp. nov. from the Lower Cretaceous of Transbaikalia and Mongolia. The relationship of Prototroginae to other taxa of the Scarabaeoidea are discussed.

INTRODUCTION

The lamellicorn beetles collected in the Semen (Transbaikalia) and Bon-Tsagaan (Mongolia) localities included two specimens belonging to a species that possesses only five visible abdominal sternites. Besides the sternites, the middle coxae are clearly visible indicating that the beetle is a member of the superfamily Scarabaeoidea. The elytra are fully preserved, as well as the right middle tibia showing one clear transverse keel and indistinct traces of another keel. These keels, combined with the reduction of the number of visible abdominal sternites to five suggest that it is possible to determine the species to subfamily.

An abdomen with only five visible sternites is characteristic of a restricted subset of Scarabaeoid taxa; it occurs in most species of Lucanidae and Passalidae, and, within Scarabaeidae, in all Troginae and Glaresinae (Scholtz *et al.*, 1987a, 1994). It also occurs in several members of Hybosorinae (Scholtz *et al.*, 1987b) and Aphodiinae (Nikolajev, 1993a). The broadly oval body of the new species allows most of Lucanidae (except for subfamily Aesalinae where the body is broadly oval), and all Passalidae and Aphodiinae to be excluded from consideration because the body is markedly elongate in these taxa. Besides that, in Aphodiinae the middle coxae are parallel and not contiguous. The sharp edges of all the sternites are clearly visible in the fossil, indicating that the elytra completely covered the pygidium and, moreover, tightly embraced the sternites. The elytra conceal the whole pygidium in all the members of the subfamily Aesalinae (Lucanidae), and in the subfamilies Hybosorinae, Troginae and Glaresinae within Scarabaeidae. However, the beetle in question cannot belong to these taxa, as in Aesalinae the middle coxae are comparatively widely separated, in Troginae they are very small and rounded, and in Hybosorinae and Glaresinae the middle and hind tibiae

bear at most only a single transverse keel. Moreover, in the tribe Anaidini (Hybosorinae) where the abdominal sternite number is reduced to five, the middle and hind tibiae are devoid of transverse keels, and in all Hybosorinae and Glaresinae the lateral margins of the abdominal sternites lack the sharp edges. Taking all the above into consideration, a new taxon of subfamily rank is proposed for the beetle studied.

The material studied is housed in the collection of the Paleontological Institute, Russian Academy of Sciences (PIN).

SYSTEMATIC PALAEONTOLOGY

Family Scarabaeidae Laicharting, 1781

Subfamily Prototroginae Nikolajev, subfam. nov.

Type genus. *Prototrox* gen. nov.

Diagnosis. Middle coxae large, elongate, contiguous; middle tibiae with two transverse keels on outer side; elytra completely covering pygidium; abdomen with five visible sternites; lateral margins of sternites forming sharp edges.

Composition. Type species.

Comparison. Distinct from most recent and extinct families of Scarabaeoidea in the relatively short oval body. Among the taxa with a similar body shape Prototroginae differs: from Geotrupinae, Bolboceratinae and Ochodaeinae in the lower number of abdominal sternites. It differs from Lithoscarabaeinae and the members of the subfamily Aesalinae (Lucanidae) in the contiguous middle coxae, and from Hybosorinae and Troginae in the greater number of transverse keels on the middle tibiae.

Remarks. The apotypic character state of an abdomen with five visible sternites is known in the families Lucanidae and Passalidae, and in the subfamilies Troginae, Glaresinae, Hybosorinae and Aphodiinae in

the family Scarabaeidae. The body shape of all Passalidae is so distinct that this family is unlikely to be closely related to Prototroginae. In Lucanidae, Hybosorinae and Aphodiinae reduction of the abdominal sternite number occurs within certain groups. In Lucanidae and Hybosorinae the number of transverse keels on the middle tibiae is apomorphic relative to the beetle in question; either of these two taxa could be only the sister group to Prototroginae.

Two plesiotypic character states, separated middle coxae and large number of transverse keels on middle tibiae, are combined in Aphodiinae, implying that this subfamily might be considered ancestral to Prototroginae. However, in Aphodiinae the middle coxae, if contiguous, are set at a much greater angle than in the fossils studied. This makes the above scenario improbable, and suggests that Aphodiinae and Prototroginae could be at best sister taxa.

The remaining subfamilies (Troginae and Glaresinae) could be lineages descended from Prototroginae. Their low number of visible abdominal sternites may be synapotypic with that of the new subfamily, but the number of transverse keels (no more than one) on the middle tibiae is apomorphic in both subfamilies. Another character that the Troginae share with the Prototroginae are the sharp edges of the lateral margins of the abdominal sternites, in contrast with the smoothly rounded steenites of Glaresinae (see Scholtz *et al.*, 1994, text-fig. 28). In my opinion, this character suggests that Prototroginae is more closely related to Troginae than to any other equivalent lineage of Scarabaeoidea.

The short, rounded coxae of Troginae are likely to be an apotypic character state relative to the large, elongate coxae of other scarabaeoid taxa. Besides this character, all Troginae possess eyes that are not divided by genal projection (also an apotypic character state). According to the phylogeny of Scarabaeoidea (Nikolajev, 1995), all the character states diagnostic of the new subfamily can be regarded as primitive relative to those of Troginae.

The eye structure in Prototroginae could either be plesiotypic for the group (i.e., partly divided by genal projection) or apotypic (i.e., not divided); in either case based on this character Prototroginae could be included as a tribe within Troginae.

Questions of the finer relationships of the phyletic lineage Prototroginae–Troginae can not be resolved at present. If, in the phyletic lineage “Geotrupinae–Prototroginae–Troginae–Scarabaeinae”, the subfamilies first diverged in the position of the middle coxae (separated vs. contiguous) or in the position of the apical spurs on the middle and hind tibiae (set on one side of the tarsus vs. on both sides), then Prototroginae–Troginae are more closely related to the Geotrupinae, because their coxae are contiguous. In all known Geotrupinae and Troginae the spurs of the middle and hind tibiae are contiguous; if these taxa constitute one

phyletic lineage, this character state is also synapotypic for the lineage. In this case it is more logical to demote Prototroginae and Troginae to tribes of the Geotrupinae, along with Geotrupini s. str., Lethrini, Taurocerasini and Cretogeotrupini (Nikolajev, 1996).

On the other hand, if the groups of this lineage first diverged in the presence (vs. absence) of the setae on the upper body surface or in the reduction of the number of antennal segment (?synapotypic character state), then Prototroginae–Troginae are more closely related to Scarabaeinae. In either case one can assume the presence of an extinct taxon with 11-segmented antennae, setose upper body surface, 10 elytral striae, narrowly separated middle coxae, and middle and hind tibiae with three transverse keels and with the spurs on both sides of the tarsus. This hypothetical taxon would resemble the common ancestor of the recent subfamilies Scarabaeinae, Geotrupinae and Troginae, as well as the extinct Prototroginae.

From the characters discussed above it is possible to reconstruct some features of Prototroginae not preserved in the fossils. In the phyletic lineages containing the subfamilies Troginae and Glaresinae, all species possess a three-segmented antennal club, a coriaceous border along anterior pronotal margin and distinct silky pubescence along the anterior margin of the front femora. In those taxa in these lineages with elytral striae with steep edges, the antennal segment number is reduced to 9 or 10. In all these subfamilies, the plesiotypic character states are as follows: labrum and mandibles are not concealed by the clypeus, fore tibiae have more than three teeth along the outer margin, and the upper body surface is covered with setae. Probably most of these characters should also be expected in the members of the new subfamily. The development of two free veins between the cubital vein and first anal veins adjoining the wing base is also highly probable.

Genus *Prototrox* Nikolajev, gen. nov.

E t y m o l o g y. From Greek *protos* (first) and the genus *Trox*.

T y p e s p e c i e s. *P. transbaikalicus* sp. nov.

D i a g n o s i s. Small convex beetle. Elytra completely concealing pygidium and tightly embracing abdominal sternites; each elytron with no more than 10 striae; striae with steep edges; abdomen with five visible sternites; middle tibiae with two transverse keels on outer side.

C o m p o s i t i o n. Type species.

C o m p a r i s o n. Distinct from all Mesozoic scarabaeid genera in having elytral striae with steep edges in the presence of only five visible abdominal sternites.

R e m a r k s. Differs from the genus *Cretaesalus* Nikolajev (Lucanidae) from the Upper Cretaceous of Kazakhstan (Nikolajev, 1993b) in the contiguous middle coxae.

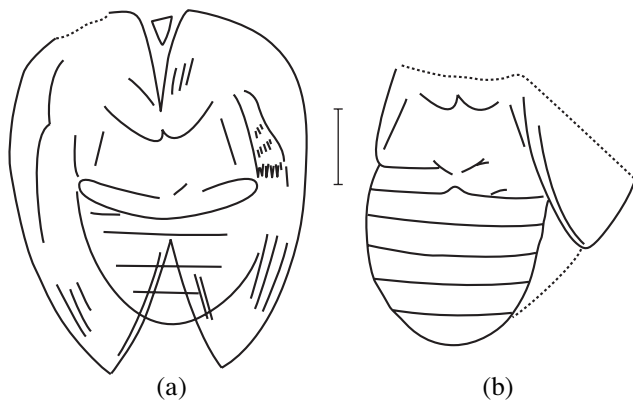


Fig. 1. *Prototrox transbaikalicus* sp. nov.: (a) holotype PIN, no. 2385/1096; (b) paratype PIN, no. 3559/2217.

Prototrox transbaikalicus Nikolajev, sp. nov.

Etymology. From Transbaikalia.

Holotype. PIN, no. 2385/1096, beetle lacking head and pronotum, with right middle tibia poorly preserved (part and counterpart); Semen Creek (Semen locality), Olengui River basin, Chita District, Chita Region, Transbaikalia; Lower Cretaceous, Argun' Formation.

Description (Fig. 1). A small, strongly convex beetle. A coriaceous border is probably developed along the anterior pronotal margin. The scutellum is small, triangular, with the lateral margins weakly rounded. Elytral striae have steep edges; the intervals between the striae are much wider than the striae themselves. The middle coxae are large and contiguous, the hind coxa are narrower but similarly contiguous. The middle tibiae have two transverse rows of setae and contiguous spurs. The apical margins of the second to fourth abdominal sternites have well developed coriaceous borders.

Measurements (mm): scutellum length, 0.5, its basal width, 0.45; elytron length, 5, its width, 2; width of middle coxa, 0.5; width of hind coxa, 0.3; length of middle tibia, 1.1, its apical width, 0.45; basal width of abdomen, 2.4; length of abdominal sternites along midline: second, 0.4, third, 0.4, fourth, 0.3, fifth, 0.35.

Remarks. The elytra have been flattened during fossilization. In life they were possibly strongly convex, therefore the distance from the base to the visible

apex of elytron (equivalent to the elytron length in recent beetles) would have been somewhat shorter.

Occurrence. Lower Cretaceous of Transbaikalia and Mongolia.

Material. Besides the holotype, paratype PIN, no. 3559/2217 is an impression of the lower surface of the beetle lacking the head, pronotum and most of the legs (only middle and hind coxae preserved); foothills of Dund-Uul south of Bon-Tsagaan Lake (Bon-Tsagaan locality), Bayan-Hongor Aymag, Mongolia; Lower Cretaceous, Barremian-Aptian, Bon-Tsagaan Series.

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