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A new family of grylloblattids (Insecta: Grylloblattida) from mid-Cretaceous Burmese amber

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Abstract

The new grylloblattid family Aristoviidae Storozhenko & Gröhn **fam. nov.**, with the type genus and species *Aristovia daniili* Storozhenko & Gröhn **gen. et sp. nov.**, is described from the lowermost Cenomanian amber (Hukawng Valley, Kachin State, northern Myanmar). The new family is similar to the Permian-Triassic family Megakhosaridae and the Permian-Jurassic Blattogryllidae but differs from both by the shape of pronotum and wing venation. Aristoviidae **fam. nov.** is also similar to the extant family Grylloblattidae in body structure, but can easily be distinguished from it by the presence of ocelli, large compound eyes and wings, as well as the lack of the transverse furrow which separates the anterior part of pronotum from its posterior part. The phylogenetic relationships between families Megakhosaridae, Blattogryllidae, Grylloblattidae, and a new family are briefly discussed.

Keywords: fossil insects, grylloblattids, taxonomy, new taxa, lowermost Cenomanian amber, Myanmar

Introduction

Recent grylloblattids, also known as ice crawlers and rock crawlers, are one of the least diverse modern insect orders, in contrast to the rich fossil record of this group, which includes 47 families described from the Late Carboniferous to the Cretaceous. The order Grylloblattida (*sensu* Storozhenko, 1998, 2002) is a polyphyletic taxon (Huang *et al.*, 2008). Attempts to divide it into the orders Eoblattida and Reculida (Aristov, 2015) or to combine the orders Grylloblattodea and Mantophasmatodea as suborders into the order Notoptera (Arillo & Engel, 2006) have been made recently.

Until now, grylloblattids from the mid-Cretaceous

Burmese amber were known by a single nymphal species of the genus *Sylvalitoralis* Aristov, Novokshonov & Pan'kov, 2006, which was placed in an uncertain family of the suborder Grylloblattodea (Zhang *et al.*, 2016). The first adult grylloblattid specimen from Burmese amber, assigned to a new family, genus and species, is described herein.

Material and methods

The second author (CG) obtained several ambers with inclusions from a miner in Myanmar on 12 January 2014. The studied specimen is stored at the Geology and Palaeontology Museum of the University of Hamburg (GPIH), the former Centre of Natural History (CeNak) of the University of Hamburg, now the Leibniz Institute for the Analysis of Biodiversity Change (LIB). In the Museum of GPIH the collection of Carsten Gröhn is separately deposited with abbreviation CCGG.

Photographs of the new species were taken using a Leica M165C stereomicroscope with a Leica DFS425 digital camera. Photographs of extant grylloblattids were taken using an Olympus SZX16 stereomicroscope and an Olympus DP74 digital camera, and then stacked using Helicon Focus software. The final illustrations were post-processed for contrast and brightness using Adobe Photoshop® software.

The morphology nomenclature of body, head, thorax, and legs follows Storozhenko (1998), Kim & Lee (2007), Bai *et al.* (2010), and Wipfler *et al.* (2011).

The wing venation nomenclature generally follows Storozhenko (1998) with minor corrections (Cui, 2012). Wing venation abbreviations: C—costal vein; Sc—subcostal vein; R—radius; RA—anterior branch of radius; RS—radius sector; M—median vein; MA—anterior branches of median

vein; MP—posterior branches of median vein; CuA— anterior cubital vein; CuP—posterior cubital vein; A1–A3— first, second and third branches of anal vein.

Systematic palaeontology

Order Grylloblattida Walker, 1914

Suborder Grylloblattodea Walker, 1914

Family Aristoviidae Storozhenko & Gröhn fam. nov.

Type genus. *Aristovia* gen. nov., here designated.

Diagnosis. The new family is most similar to the Early Permian–Middle Triassic Megakhosaridae and the Middle Permian–Middle Jurassic Blattogryllidae in the large head with relatively large compound eyes and three small ocelli, filiform multi-segmented antennae, orthopteroid mouthparts, 5-segmented tarsi, and wing venation, but differs from both by lacking the paranotalia (lateral expansions of the pronotum) and by Sc ending on RA near the apex in both fore- and hind wings. In Megakhosaridae and Blattogryllidae, the ring of paranotalia is always present and Sc ends in C. The new family is also similar to the wingless Grylloblattidae but easily recognizable from it by the lack of the strong transverse furrow separating the anterior part of pronotum from its posterior part, the character typical for all known extant species of Grylloblattidae.

Description. Medium sized insects (Fig. 1A, B), length of body (from apex of mandibles to apex of wings) 25 mm.

Head large (Figs 2A, 4A); cranium (length = 2.7 mm, width = 3.0 mm) about 1.2 times as wide as the pronotum, without setae; compound eyes large, oval; ocelli moderately large. Antennae filiform with at least 25 antennomeres; scapus widest, pedicel narrower than scapus; segments of flagellum narrow, 5.5–6.2 times as long as wide. Mouthparts orthopteroid. Mandibles (length 1.6 mm) highly sclerotized, asymmetrical; inner side of right mandible with a strong preapical tooth; left mandible with two small teeth near the middle. The distal part of maxillae extends past the top of the mandibles; galea sickle-shaped; lacinia as long as mandible, curved, its inner side without preapical teeth and a row of setae near the base (Fig. 4B); maxillary palp 5-segmented, 1st segment short, other segments elongated, 5th segment longest, about 7.5 times as long as wide, with pointed apex.

Pronotum 1.25 times as long as wide with broadly rounded posterior margin; paranotalia, the transverse sulcus at the anterior margin, the median longitudinal suture, and setae absent.

Forewing (Fig. 3C). Membranous, 16.9 mm long, 3.4 times as long as wide; crossveins present between main veins. Sc ending on RA near the apex of wing. Subcostal

area narrow. RA simple, almost straight, parallel to Sc, ending on the anterior wing margin. RA/RS fork slightly after the basal fourth of wing length; RS posteriorly pectinate, with four branches. Area between anterior wing margin and Sc and Sc–RA area slightly narrower than RA–RS area. The base of M absent. MA diverges from CuA in the basal fifth of the wing length, apically with short fork. MP diverges from CuA slightly after the origin of MA, with four branches directed to the posterior wing margin; middle part of MP sclerotised. Cubital vein forks into CuA and CuP near the base of wing; both veins simple, CuA–CuP area with a few straight crossveins. A1 and A3 simple, A2 with fork.

Hind wing (Fig. 3D). Membranous, 16.7 mm long. Anterior margin of wing straight. Sc ending in RA near the apex of wing. Subcostal area narrower than RA–RS area. RA/RS fork slightly before the basal seventh of wing length; R fused with M for a short distance; RS+MA pectinate, with six branches. MP diverges from RS+MA slightly after the origin of RS, with long fork, middle part of MP strongly sclerotised. Cubital vein forks into CuA and CuP slightly before the origin of R. CuA–CuP area without crossveins. Anal veins simple.

Legs (Fig. 4C, D). Femora and tibiae of all legs with dense microsetae (clearly tomentose), spines and long setae absent but apical part of the tibia ventrally contains two relatively short apical spines. Fore leg with enlarged coxa; femur stout, 2.3 mm long; tibia 2.4 mm long. Mid leg similar to fore leg; femur 2.4 mm long; tibia 2.7 mm long, tarsus 5-segmented, apical segment with long tarsal claws, length of claw 0.5 times 5th segment (Fig. 4D). Hind legs well preserved (Fig. 4C); coxa enlarged; trochanter elongated; femur stout, 3.4 mm long, 3.5 times as long as wide; tibia 3.6 mm long, 1.1 times longer than femur; tarsus 5-segmented, length of 1st–4th segments almost equal and each segment ventrally with a pair of euplantulae; 5th segment longest, with large unpaired euplantula and long tarsal claws, arolium absent.

Eggs (Figs 2B, 4E, D). Lengths 1.5–1.6 mm. Capsule elongate; in lateral view, the ventral side S-shaped while dorsal side almost straight; lateral sides with three low longitudinal ridges. Operculum broadly oval.

Composition. Family consists of a type genus only.

Stratigraphic range. The lowermost Cenomanian, mid-Cretaceous, ca. 98.79 ± 0.62 Ma (Cruickshank & Ko, 2003).

Genus *Aristovia* Storozhenko & Gröhn gen. nov.

Type species. *Aristovia daniili* sp. nov., here designated.

Etymology. The new genus is named in honor of the late Russian paleontologist D. S. Aristov (1979–2022). Gender feminine.

Diagnosis. As for family.

Remarks. The new genus differs from *Sylvalitoralis* and especially from *S. cheni* Zhang, Bai & Yang, 2016 described by a single nymph from Burmese amber in absence of setae on the pronotum and stout legs (in *S. cheni*, legs slender and dorsal side of pronotum with numerous long setae).

***Aristovia daniili* Storozhenko & Gröhn sp. nov.**
(Figs 1–4)

Holotype. Adult female, GPIH no. 5084, CCGG no. 11293, stored at the Geology and Palaeontology Museum of the University of Hamburg, Germany.

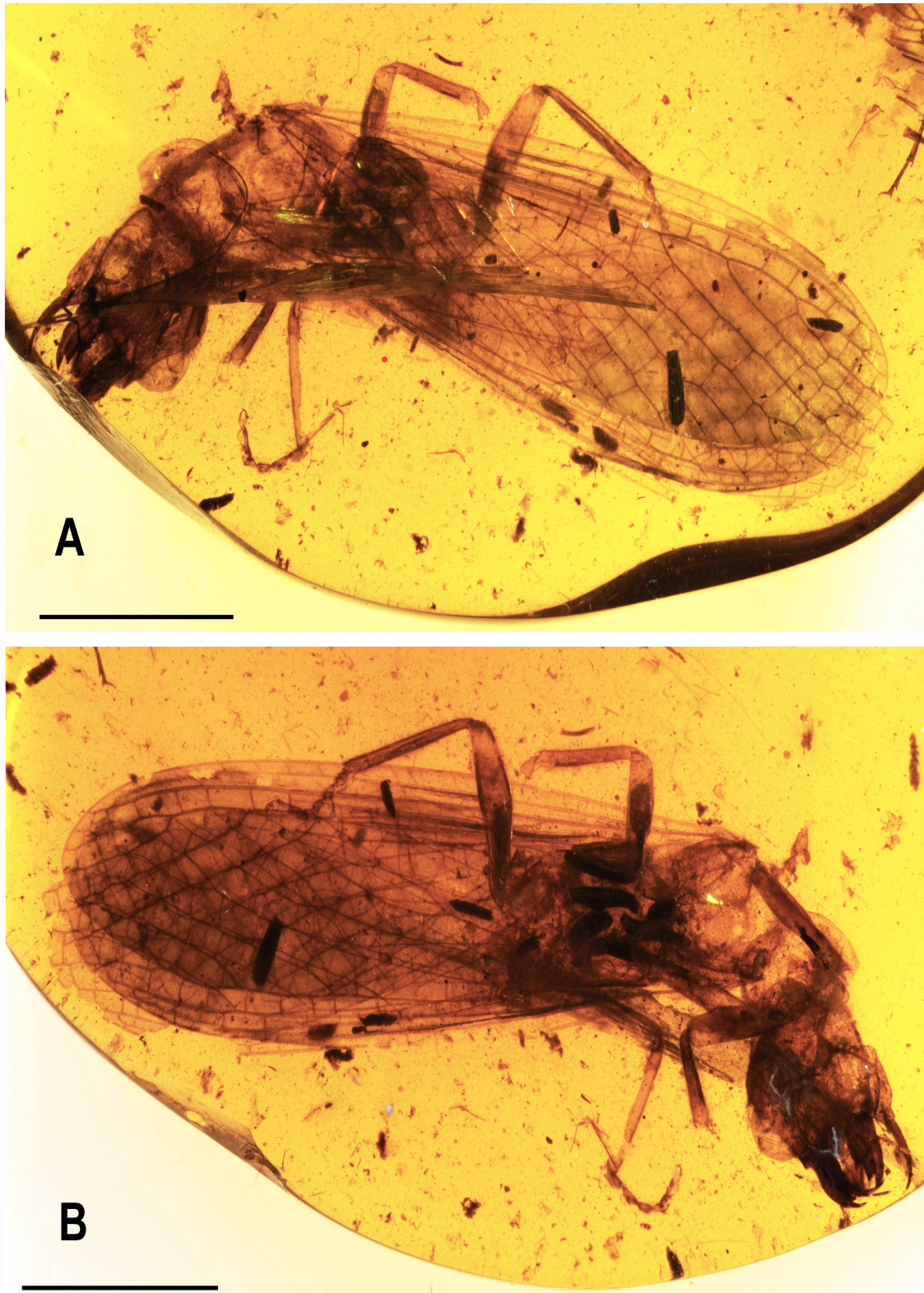


FIGURE 1. *Aristovia daniili* gen et sp. nov., photograph of holotype. **A**, Habitus, dorsal view. **B**, The same, ventral view. Scale bars = 5 mm.

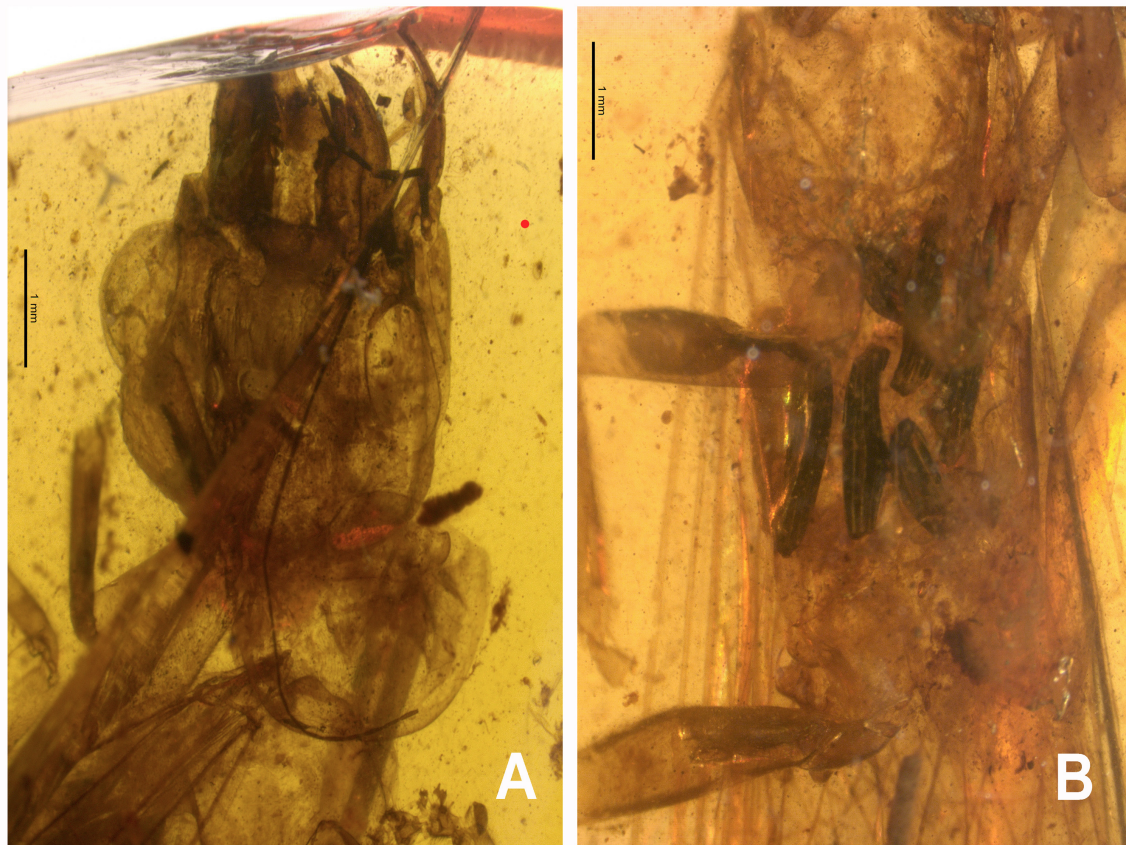


FIGURE 2. *Aristovia daniili* gen et sp. nov., photograph of holotype. **A**, Head and pronotum, dorsal view. **B**, Eggs, ventral view. Photograph by D.E. Shcherbakov. Reproduced with author's permission. Scale bars = 1 mm.

Material. Amber piece of irregular rectangular shape, from left and rear edges widely rounded, approximately $30 \times 25 \times 8$ mm, more or less flat from above and below (directions given according to the position of holotype); transparent. Inclusion includes holotype of new species and fragments of plant debris and insects. The specimen is located in dorsal position, almost intact, but the abdomen is lost, all wings are in resting position, and a few eggs are present (Figs 1, 2).

Etymology. The new species is named in honor of our friend and colleague Daniil Aristov who acquainted us with the study of this species.

Diagnosis. As for the genus.

Type locality and horizon. Hukawng Valley, Kachin State, northern Myanmar; lowermost Cenomanian, mid-Cretaceous.

Description. Body brown. Mandibles, lacinia and maxillary palp blackish brown, galea brown, antennae black. Pronotum light brown. Wings transparent with brown veins. Legs brown, claws light brown. Eggs black with narrow light stripes along longitudinal ridges.

Discussion

There are at least five families of grylloblattids forming

a group of closely related forms, namely Grylloblattidae, Aristoviidae **fam. nov.**, Blattogryllidae, Megakhosaridae, and Tococladidae (Storozhenko, 1998; Storozhenko & Aristov, 2014; Rasnitsyn & Aristov, 2021; present paper). These families are considered as a formal taxon Blattogrylloptera by Cui (2012) or as a central group of the order Eoblattida with 17 extinct families known from the Carboniferous to mid-Cretaceous and one extant family (Aristov, 2015). Moreover, Aristov (2012) and Rasnitsyn & Aristov (2013) demonstrated the relatedness of the succession Eoblattidae—Cacurgidae—Daldubidae—Megakhosaridae—Blattogryllidae—Grylloblattidae.

The extant family Grylloblattidae consists of 34 species in six genera distributed in cool-temperate areas of the United States, Canada, Russia, Japan, Korea and China (Wipfler *et al.*, 2014; Eberhard *et al.*, 2018; Zhou *et al.*, 2023). This family is characterized by the following combination of features: wings absent (apomorphy); the compound eye is composed of less than 50 ommatidia (Gokan *et al.*, 1979) or some cave dwelling species lack eyes (Namkung, 1974; Zhou *et al.*, 2023), and ocelli reduced (apomorphy); lacinia with 1–2 apical teeth (apomorphy); pronotum with strong transverse sulcus at the anterior margin (apomorphy); ring of paranotalia absent (apomorphy) but in the genus *Grylloblattina* Bey-Bienko, 1951 the narrow and poorly sclerotized area posteriad of the hind margin of the pronotum is

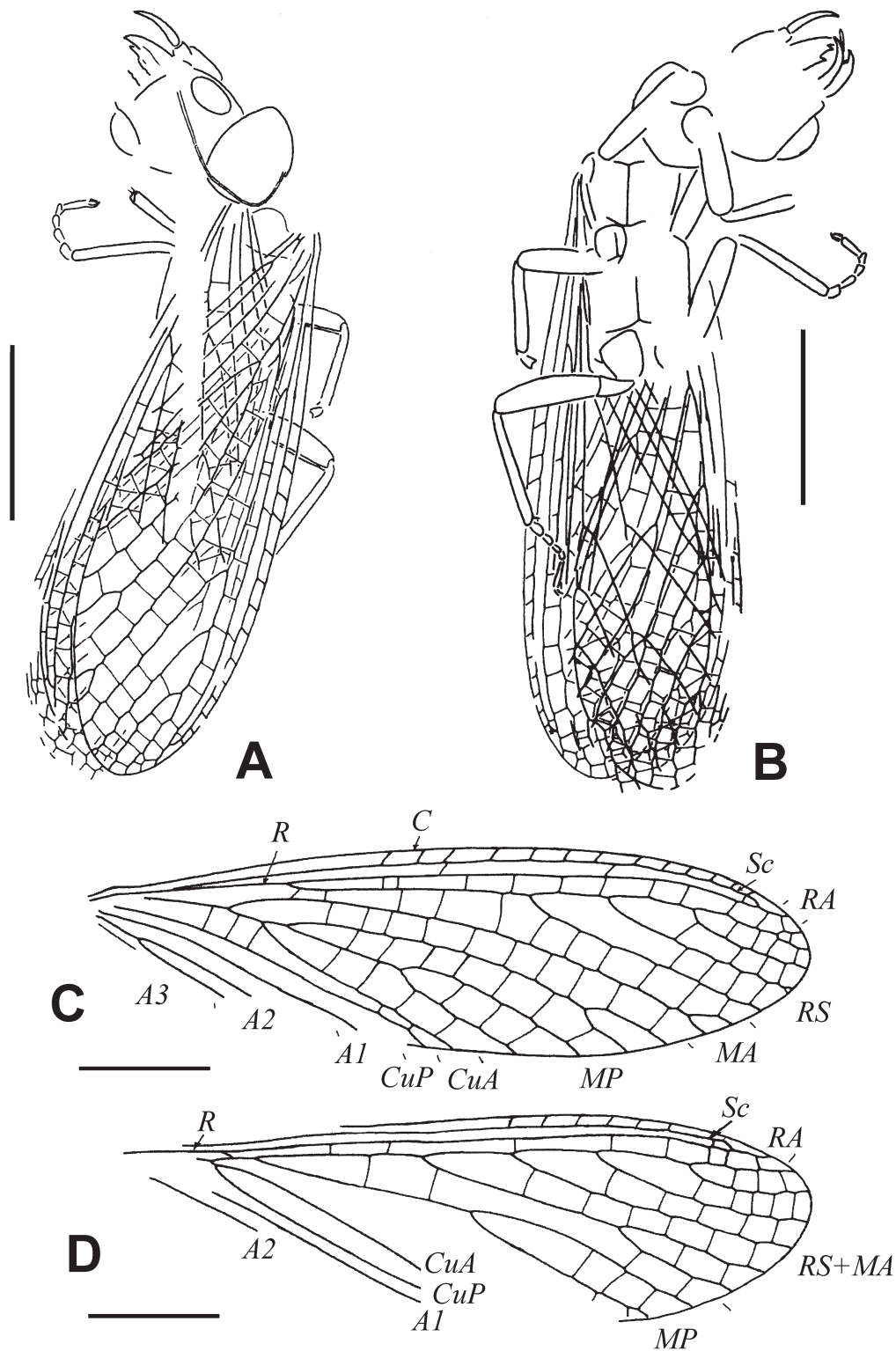


FIGURE 3. *Aristovia danili* gen et sp. nov., sketch drawing of holotype. **A**, Body, dorsal view. **B**, The same, ventral view. **C**, Right forewing. **D**, Combined drawing of right and left hind wings. Scale bars: **A**, **B** = 5 mm; **C**, **D** = 3 mm.

considered as the rest of paranotalia (Fig. 5A); all femora and tibia with long spines (Fig. 5B) (apomorphy); claws long (plesiomorphy); tarsal segments elongate with relatively large euplantulae (plesiomorphy) but in the genus *Grylloprimevala* Zhou, Chen, Ke, Wang, Peng, Wu, Liu, Feng & Ren, 2023 euplantulae reduced (Zhou et

al., 2023). The eggs of Grylloblattidae are oviform with smooth chorion (plesiomorphy) (Ando & Nagashima, 1982).

The Cretaceous family Aristoviidae **fam. nov.** is characterized by the following combination of features: macropterous (plesiomorphy); the compound eyes large

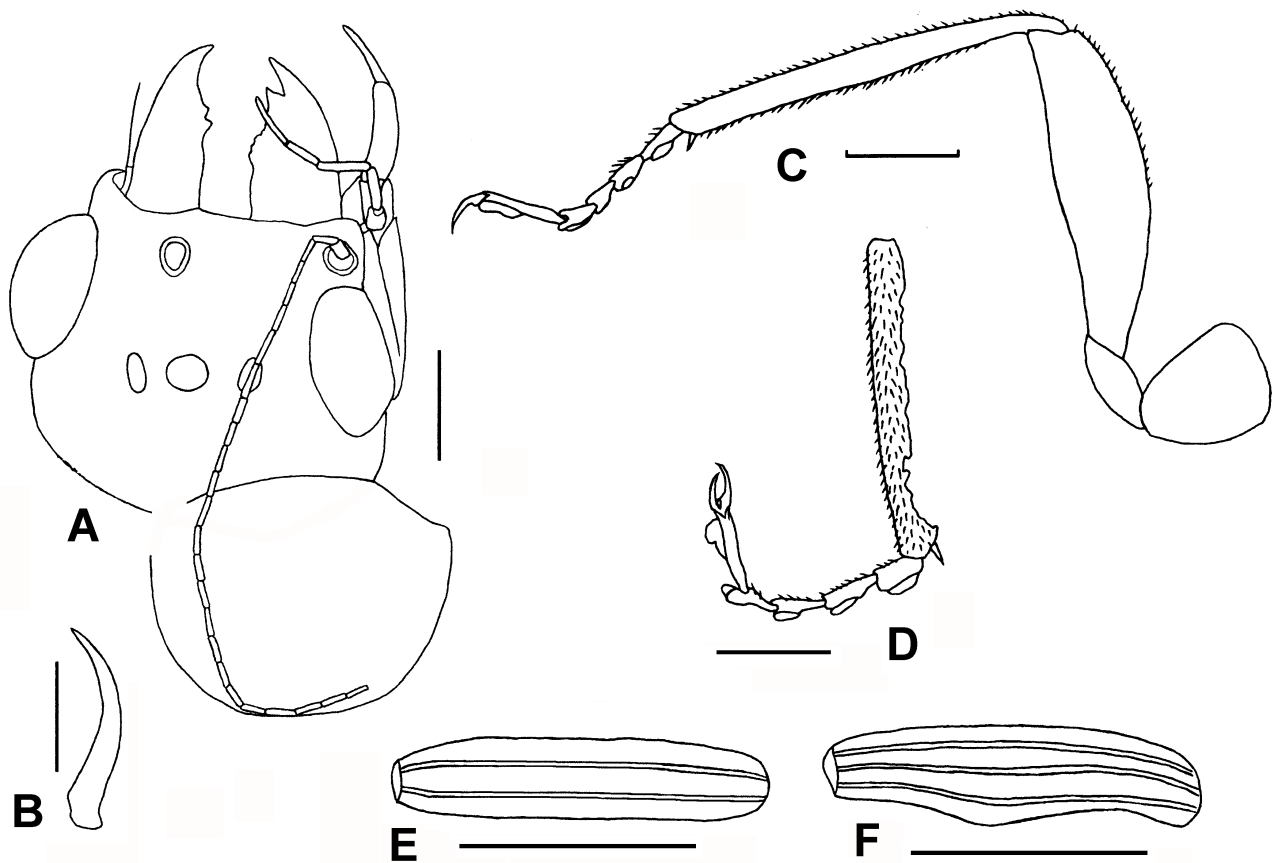


FIGURE 4. *Aristovia daniili* gen et sp. nov., sketch drawing of holotype. **A**, Head and pronotum, dorsal view. **B**, Left lacinia, ventral view. **C**, Mid tibia and tarsus, lateral view. **D**, Hind leg, lateral view. **E**, Egg, dorsal view. **F**, The same, lateral view. Scale bars = 1 mm.

and ocelli present (plesiomorphy); the lacinia without teeth (plesiomorphy); pronotum without transverse sulcus (plesiomorphy); ring of paranotalia absent (apomorphy); all femora and tibia without long spines (plesiomorphy); tarsal segments elongate with large euplantulae (plesiomorphy); claws long (plesiomorphy); the eggs elongate with low longitudinal ridges (apomorphy). In the forewing Sc ending on RA (apomorphy); the base of M absent and MA and MP arise from CuA as separate branches (apomorphy); MP completely sclerotized (plesiomorphy); and the anal area is not transformed into clavus (plesiomorphy).

The family Blattogryllidae consists of 13 fossil genera: one genus is known from the Middle Permian only, one genus—from the Late Permian to the Middle Triassic, four genera—from the Triassic only, three genera—from the Triassic to Jurassic, and four genera—from the Jurassic only (Aristov, 2015). The body structure is known for species of the genera *Blattogryllus* Rasnitsyn, 1976, *Protoblattogryllus* Storozhenko, 1990, *Costatoviblatia* Storozhenko, 1992, and *Plesioblattogryllus* Huang, Nel & Petrulevičius, 2008 (Rasnitsyn, 1976; Storozhenko, 1990, 1992; Huang *et al.*, 2008; Aristov, 2011; Ren

& Aristov, 2011; Cui, 2012), while other taxa were described from isolated wings. Blattogryllidae is characterized by the following combination of features: macropterous (plesiomorphy); the compound eyes large and ocelli present (plesiomorphy); pronotum without transverse sulcus (plesiomorphy); ring of paranotalia wide (plesiomorphy); all femora and tibia with a few long spines (apomorphy); tarsal segments short, 5th segment with extremely large euplantula almost reaching apex of claws (apomorphy); claws short (apomorphy). In forewing Sc ending in C (plesiomorphy); the base of M absent and MA and MP arise from CuA as separate branches (apomorphy); MP unsclerotized near the mid of wing (apomorphy); and clavus absent (plesiomorphy). The Triassic *Costatoviblatia aenigmatica* Storozhenko, 1992, the Jurassic *Plesioblattogryllus magnificus* Huang, Nel & Petrulevičius, 2008 and *P. minor* Ren et Aristov, 2011 have the fusiform eggs with strongly sclerotized longitudinal ribs (apomorphy).

The family Megakhosaridae consists of 20 genera, of them 14 genera are known from the Early, Middle and Late Permian, two genera—from the Middle Permian to the Middle Triassic, and four genera—from the Middle

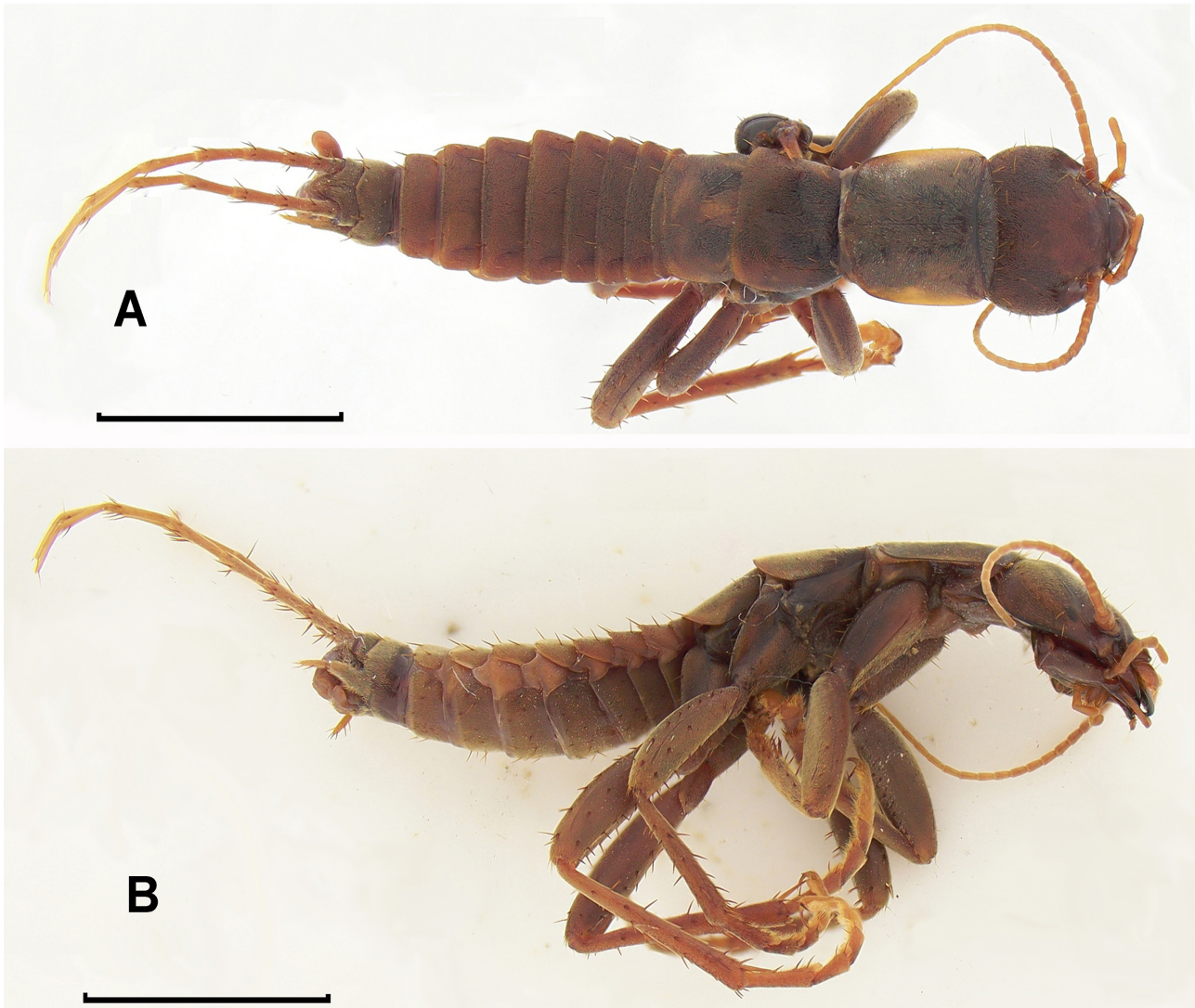


FIGURE 5. *Grylloblattina djakonovi* Bey-Bienko, 1951, male (Russia: Primorsk Territory). **A**, Habitus, dorsal view. **B**, The same, lateral view. Scale bars = 5 mm.

Triassic only (Aristov, 2015). Almost all species of this family were described from isolated wings; the parts of body are known for Permian *Sylvakhosara martynovi* Storozhenko, 1993, *Megakhosarina miniscula* Aristov, 2008 and Triassic *Metakhosara sharovi* Storozhenko, 1993 and *Parakhosara nasuta* Storozhenko, 1993 (Storozhenko, 1993; Aristov, 2008). The most important feature for separation of Megakhosaridae from Blattogryllidae and Aristoviidae **fam. nov.** is the position of bases of M, MA and MP in the forewing. The genera with the base of M in the forewing distinctly separated from CuA (plesiomorphy) or with MA and MP arising from CuA as a single vein (in this case the base of M always present) are assigned to Megakhosaridae (Aristov, 2015), while in Blattogryllidae and Aristoviidae **fam. nov.** MA and MP in the forewing arise from CuA separately (synapomorphy). Megakhosaridae is characterized by the following combination of features: macropterous (plesiomorphy); the compound eyes large and ocelli present (plesiomorphy);

pronotum without transverse sulcus (plesiomorphy); ring of paranotalia wide (plesiomorphy); all femora and tibia with a few spines (apomorphy); tarsal segments elongated (plesiomorphy); claws relatively long (plesiomorphy). In forewing, Sc ending on C (plesiomorphy); the base of M present (plesiomorphy); MP completely sclerotized (in Permian *Megakhosara* Martynov, 1937, *Megakhosarodes* Storozhenko, 1933, *Ideliopsis* Carpenter, 1948 and other genera) or partially unsclerotized near the middle of wing (in Permian *Sylvakhosara* Storozhenko, 1993 and *Megakhosarella* Sharov, 1961, Permian-Triassic *Protoblattogryllus* Storozhenko, 1990, and Triassic *Mesoblattogryllus* Storozhenko, 1990); clavus absent (plesiomorphy).

The Early Permian family Tococladidae consists of three genera and is most similar in body structure and forewing venation to Megakhosaridae (Rasnitsyn & Aristov, 2021). This family is characterized by the following features: wings present (plesiomorphy);

compound eyes large and ocelli present (plesiomorphy); pronotum without transverse sulcus (plesiomorphy); ring of paranotalia present (plesiomorphy); in the forewing Sc ending on RA (apomorphy); M not fused with R or CuA (plesiomorphy); MP completely sclerotized (plesiomorphy); and clavus present (apomorphy). Within discussed grylloblattids, this family is characterized by the most plesiomorphic position of bases of M, MA and MP in the forewing, but Tococlididae cannot be considered as ancestral to Megakhosaridae because of having such important apomorphic features as Sc ending on RA near the middle of the forewing and the anal area modified into a clavus.

Each of the above-discussed families is characterized by unique combination of plesiomorphic and apomorphic features but the majority of plesiomorphic conditions are found in Megakhosaridae. Therefore, this family seems to be the ancestral group for Blattogryllidae, Aristoviidae **fam. nov.**, and Grylloblattidae, which are considered here as sister groups.

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