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## New fossil psocids from Cretaceous Siberian ambers (Psocodea: Trogiomorpha: Atropetae)

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### Abstract

*Empherium rasnitsyni* gen. et sp. nov. (Empheriidae) and *Eolepinotus zherikhini* sp. nov. (Trogiidae), two atropetan trogiomorphan psocids from two Siberian ambers sites, are characterized, described and illustrated. Their taxonomical assignments are discussed. Lists of all fossil empheriids and trogiids are given.

**Keywords:** Russia, Taimyr, Yakutia, fossil insects, Dolgan Formation, Timmerdyakh Formation, Cenomanian, Turonian

### Introduction

Amber-bearing deposits were discovered from various localities in Northern Siberia, Russia. These outcrops are reported from different formations, dating from Lower Cretaceous (Albian) to Upper Cretaceous (Santonian) (Rasnitsyn *et al.*, 2016: fig. 1; Gumovsky *et al.*, 2018: table 1; Perkovsky & Vasilenko, 2019: fig. 1). Fossils are abundant in Siberian ambers, from which many insects were collected and studied (Azar *et al.*, 2007; Kopylov, 2012; Perkovsky & Wegierek, 2017; Gumovsky *et al.*, 2018: tables 1 and 2; Perkovsky & Vasilenko, 2019: table 1). Fossil psocodeans belonging to Psyllipsocidae and Amphientomidae, among others with uncertain assignments, have been recorded and described from Taimyr amber, collected from Nizhnyaya Agapa and Yantardakh in Taimyr Peninsula, Russia (Vishnyakova, 1975; Azar & Engel, 2008; Mockford *et al.*, 2013).

Psocopteran group Atropetae was originally established by Pearman (1936), and later assigned to suborder Trogiomorpha by Roesler (1944). Lienhard

& Smithers (2002) arranged the classification within psocids and elevated Atropetae to the taxonomic status of infraorder. It includes the five families Empheriidae, Archaeatropidae, Psoquillidae, Trogiidae, and Lepidopsocidae (Baz & Ortuño, 2000, 2001; Yoshizawa *et al.*, 2006). Yoshizawa *et al.* (2006) examined the systematics of extant Trogiomorpha based on molecular analyses of partial sequences of the nuclear 18S rDNA and Histone 3 and mitochondrial 16S rDNA genes. They concluded that the monophyly of Atropetae is well-supported at family level. They also identified two morphological synapomorphic characters in the structure of the female terminalia (*i.e.*, external valvulae of gonapophyses elongated and partially joined, and spermathecal sac with one or two glandular accessory bodies) supporting the monophyly of infraorder Atropetae, plus two morphological synapomorphies in the structure of the pretarsal claws (*i.e.*, preapical tooth absent, and enlarged pulvillus throughout its length) supporting the clade (Trogiidae + Psoquillidae).

Phylogenetic relations between Empheriidae and the rest of Atropetae were unclear and controversial for the last century. Enderlein (1911) and Smithers (1972) considered Empheriidae close to Psoquillidae based on the wing shape and venation. Roesler (1944) placed Empheriidae as a subfamily in Trogiidae. Baz & Ortuño (2001) suggested possible relationships with either the clade (Trogiidae + Psoquillidae), or Lepidopsocidae based on the wing's form, venation and setation, but they favored the placement of Empheriidae at the base of (Trogiidae + Psoquillidae). Relying on wing traits, they associated Empheriidae with Psoquillidae (rather than Trogiidae) and proposed that early psoquillids may have been similar to empheriids. They also mentioned that

**TABLE 1.** Fossil Empheriidae known from amber.

Genus	Species	Amber deposit	Age
† <i>Burmempheria</i> Li <i>et al.</i> , 2020	† <i>Burmempheria densuschaetae</i> Li <i>et al.</i> , 2020	Burmese amber	Cretaceous
	† <i>Burmempheria raruschaetae</i> Li <i>et al.</i> , 2020		
† <i>Empheria</i> Pictet-Baraban & Hagen, 1856	† <i>Empheria (Bebiosis) pertinens</i> Enderlein, 1911	Baltic amber	Eocene
	† <i>Empheria (Empheria) reticulata</i> Pictet-Baraban & Hagen, 1856		
† <i>Empherium</i> <b>gen. nov.</b>	† <i>Empherium rasnitsyni</i> <b>sp. nov.</b>	Taimyr amber	Cretaceous
† <i>Empheropsocus</i> Baz & Ortuño, 2001	† <i>Empheropsocus arilloi</i> Baz & Ortuño, 2001	Spanish amber	Cretaceous
	† <i>Empheropsocus margineglabrus</i> Baz & Ortuño, 2001		
† <i>Eoempheria</i> Nel <i>et al.</i> , 2005	† <i>Eoempheria intermedia</i> Nel <i>et al.</i> , 2005	French amber (Oise)	Eocene
† <i>Jerseyempheria</i> Azar <i>et al.</i> , 2010	† <i>Jerseyempheria grimaldii</i> Azar <i>et al.</i> , 2010	New Jersey amber	Cretaceous
† <i>Preempheria</i> Baz & Ortuño, 2001	† <i>Preempheria antiqua</i> Baz & Ortuño, 2001	Spanish amber	Cretaceous
† <i>Trichempheria</i> Enderlein, 1911	† <i>Trichempheria villosa</i> Hagen, 1882	Baltic amber	Eocene

**TABLE 2.** Fossil Trogiidae known from amber.

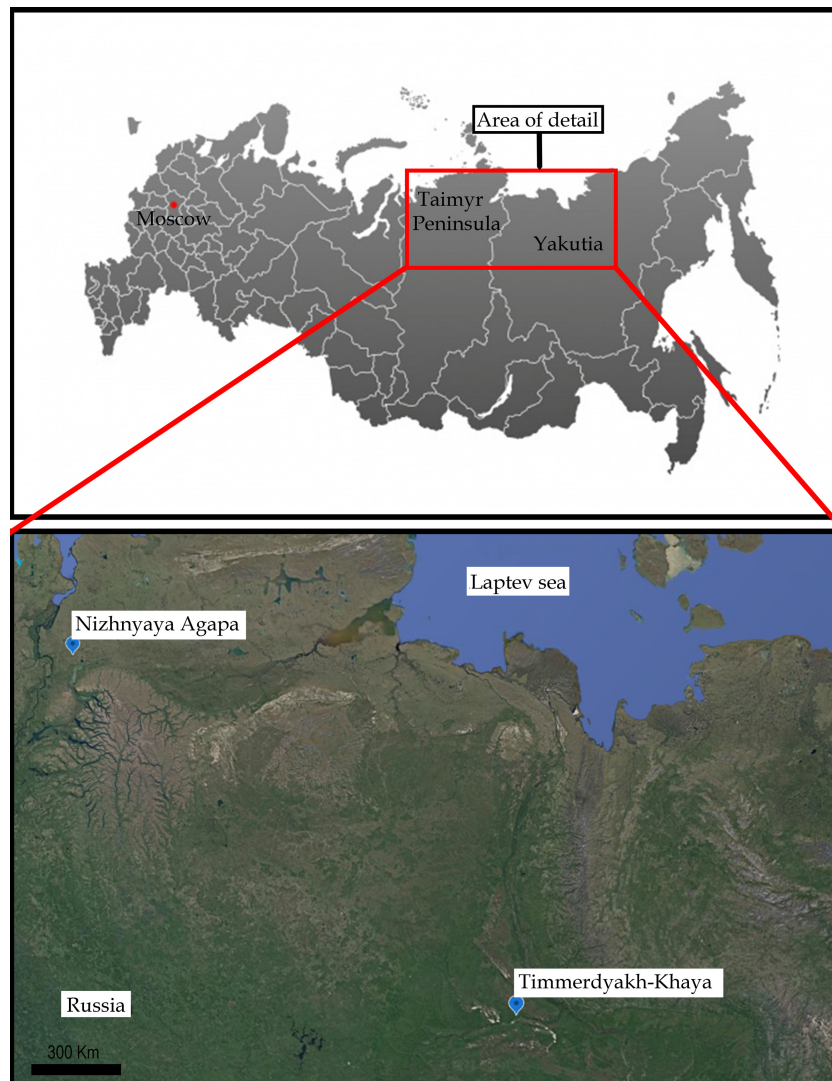
Genus	Species	Amber deposit	Age
† <i>Cretolepinotus</i> Cockx <i>et al.</i> , 2020	† <i>Cretolepinotus tanker</i> Cockx <i>et al.</i> , 2020	Canadian amber (Alberta)	Cretaceous
† <i>Eolepinotus</i> Vishnyakova, 1975	† <i>Eolepinotus pilosus</i> Vishnyakova, 1975	Russian amber (Taimyr)	Cretaceous
	† <i>Eolepinotus zherikhini</i> <b>sp. nov.</b>	Russian amber (Yakutia)	Cretaceous
† <i>Paralepinotus</i> Azar <i>et al.</i> , 2018	† <i>Paralepinotus fushunensis</i> Azar <i>et al.</i> , 2018	Chinese amber (Fushun)	Eocene

some traits typical to the Lepidopsocidae are observed in Empheriidae. Information on the morphology of the spermatheca is necessary for solving this controversy, but this internal structure is not preserved in fossil specimens. Yoshizawa & Lienhard (2020) recently proposed a dated molecular phylogeny of suborder Trogiomorpha in which they placed Psoquillidae as a sister taxon to (Lepidopsocidae + Trogiidae), and assigned Empheriidae and Archaeatropidae to possible basal positions within Atropetae.

Empheriidae are recorded from the Cretaceous in the Spanish, Burmese, and New Jersey (United States) ambers, and from the Eocene in the French (Oise) and Baltic ambers. This extinct family comprises seven genera and ten species (see Tab. 1). Baz & Ortuño (2001) extensively studied the Empheriidae and revised the family diagnosis. They closely compared it to

Archaeatropidae and assigned both families to Atropetae based on the shape and structure of the female ovipositor. They distinguished Archaeatropidae from Empheriidae by the arrangement of setae on the forewing veins, the presence or absence of marginal setae on the hind wings, and some details of the forewing venation. Li *et al.* (2020) questioned the true systematic value of these diagnostic characters, discussing their stability and reliability, and suggested the two families may be synonyms.

Trogiidae is an extant trogiomorphan family, commonly encountered in North America. It is comprised of 11 genera and over 55 species. Though rare in amber, only three monotypic extinct genera have been described (see Tab. 2). Vishnyakova also recorded an undescribed wingless specimen belonging to Trogiidae from Baltic amber (Rasnitsyn & Quicke, 2002). Amongst the limited



**FIGURE 1.** Area of study and sites' locations.

number of described species, the wings' shapes are highly polymorphic in Trogiidae, ranging from apterous to brachypterous (Azar *et al.*, 2018; Vishnyakova, 1975; Cockx *et al.*, 2020). Yoshizawa *et al.* (2006) confirmed the monophyly of the family based on morphological and molecular analyses. The wings are greatly reduced, sometimes absent, and always veinless – a synapomorphic characteristic of the family.

In this study, we describe two new psocopterans *Empherium rasnitsyni* **gen. et sp. nov.** and *Eolepinotus zherikhini* **sp. nov.** from Siberian ambers. Both are assigned to Atropetae and placed respectively within families Empheriidae and Trogiidae.

## Material and methods

The studied material includes two pieces of amber collected in Russia from two separate localities of amber-

bearing deposits (Fig. 1). Each piece contained a single fossilized insect specimen. The type material is housed at the Paleontological Institute of the Russian Academy of Sciences (PIN), Moscow, Russia.

Specimen PIN 3426/34 was collected from the upper Dolgan Formation in the Pyasina River basin, Nizhnyaya Agapa, Taimyr Peninsula, Russia. The amber-bearing deposits are located in a sequence of loose cross-bedded sand with lenses of lignitised wood and tentatively dated to the Upper Cenomanian, upper Cretaceous (Rasnitsyn *et al.*, 2016; Gumovsky *et al.*, 2018: table 1). The collection site is situated on the right bank of the Nizhnyaya Agapa River, 40 km downstream of Lake Ladonnakh (70°9'54.24"N; 86°49'4.19"E).

Specimen PIN 3603/1 was collected from the Timmerdyakh Formation in Timmerdyakh-Khaya, Yakutia, Russia. The amber-bearing deposits are located in a sequence of cross-bedded loose sands and friable sandstones with lenses of siltstone and clay and accumulations of carbonized wood and was dated to the

Cenomanian–Turonian, upper Cretaceous (Rasnitsyn *et al.*, 2016). The collection site is located in the Vilyuy District, on the left bank of the Vilyuy River, 40 km downstream of Kyzyl-Syr village, on Timmerdyakh-Khaya highland (64°3'16"N; 123°34'11"E).

The two amber specimens were manually cut, shaped and polished, then imbedded between two cover slips with Canada balsam medium as indicated in Azar *et al.* (2003). This method allows an optimal observation of the morphological characters. Individuals were observed with a Leitz Laborlux-12 compound microscope and a Nikon SZ10 stereomicroscope and photographed with an AmeScope 9000KPB digital camera and Zeiss Axio Imager 2. Photographs were then stacked and processed using Helicon Focus 6 and Adobe Photoshop CS6. Hand drawings were prepared using a camera lucida, equipped to the compound microscope, then processed using Adobe Photoshop CS6 and Adobe Illustrator CS6.

We follow the wing nomenclature, body terminology, and systematics of Smithers (1972, 1990), Lienhard (1998), and Lienhard & Smithers (2002).

## Systematic palaeontology

### Order Psocodea Hennig, 1966

### Suborder Trogiomorpha Roesler, 1940

### Infraorder Atropetae Pearman, 1936

### Family Empheriidae Enderlein, 1903

## Genus *Empherium* gen. nov.

### Type species. *Empherium rasnitsyni* sp. nov.

**Etymology.** Named after a derivative form of the type genus *Empheria*. Gender: masculine.

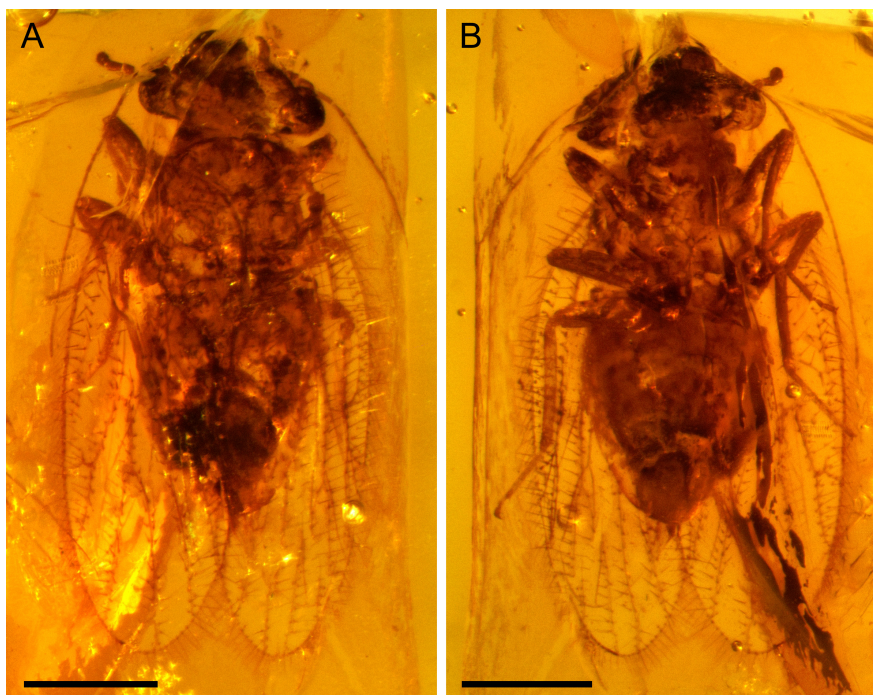
**Diagnosis.** Macropterous. Head with dorsal suture; ocelli present; antennae 25-segmented (23 flagellomeres), last segment being diminutive; sensillum present on middle of second palpomere. Forewing densely setose, setae arranged on either sides of veins and dispersed in some areas of membrane (*e.g.*, pterostigma cell and anal region); branching of  $M_1$  and  $M_2$  basal to branching of  $R_{2+3}$  and  $R_{4+5}$ ; branches of  $M$  long; areola postica relatively short; nodulus absent. Hind wing with  $Sc$  free; basi-radial cell present; stems of  $R$  and  $M$  fused in a short segment before vein  $R_1$ , emerging from common stem  $R+M$ ; veins  $R_s$  and  $M$  bifurcated;  $CuA$  simple. Tarsi three-segmented, basal tarsomere with two rows of four spines, pretarsal claw with pulvillus and without preapical tooth. Female subgenital plate tapering apically.

### *Empherium rasnitsyni* sp. nov.

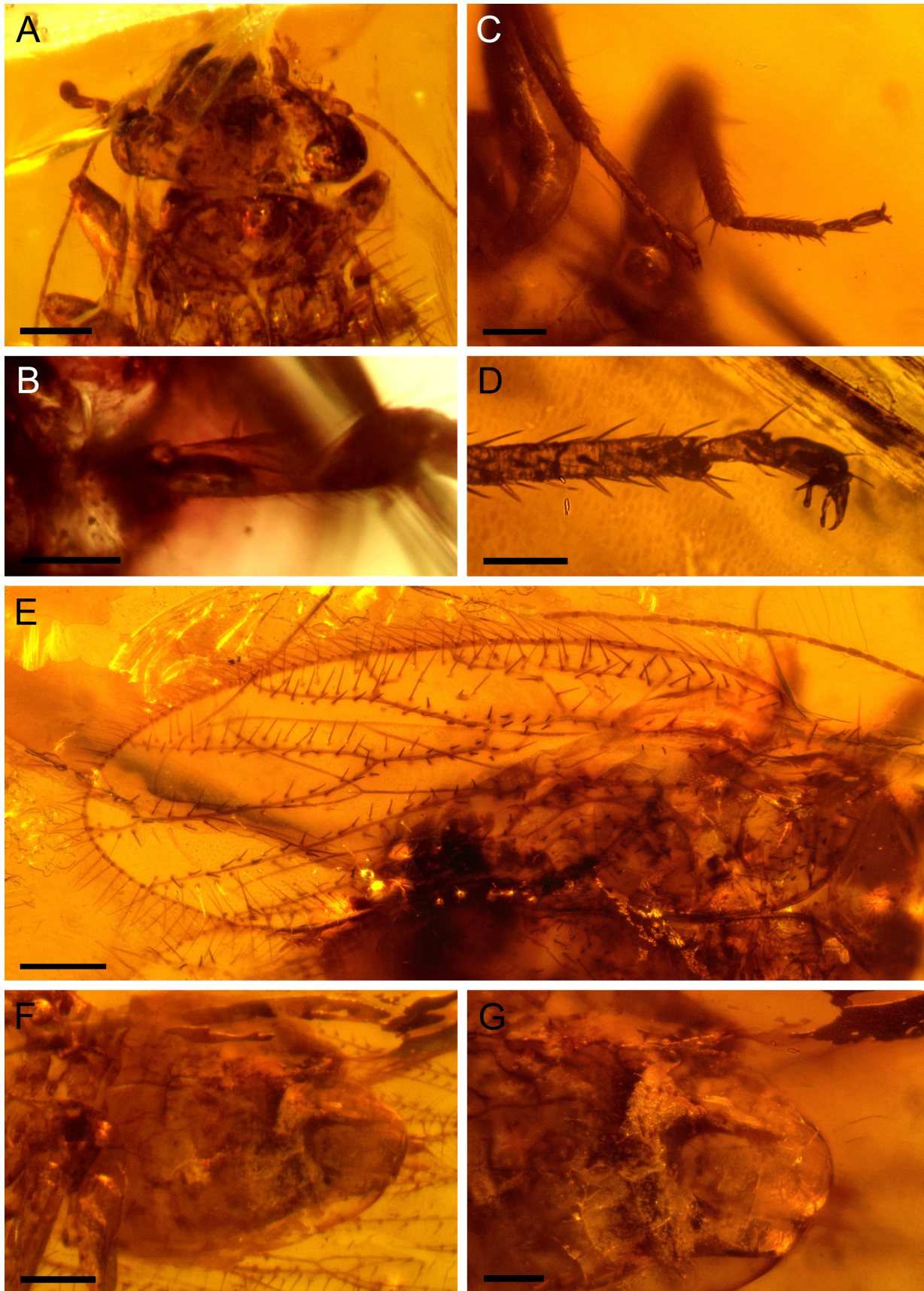
(Figs 2–5)

**Type material.** Holotype specimen PIN 3426/34, female, mostly well-preserved (Fig. 2). Visible breaks in the amber, especially over the head area, creating a mirror effect during observation. No syninclusions observed.

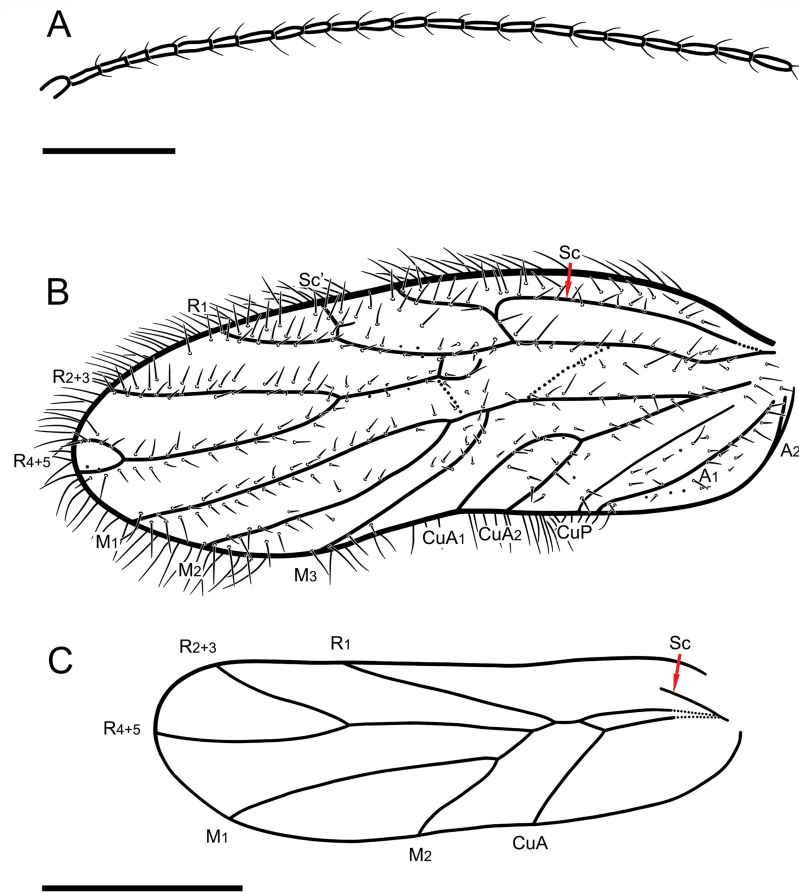
**Etymology.** Named after Professor Alexandr Rasnitsyn.



**FIGURE 2.** *Empherium rasnitsyni* gen. et sp. nov., holotype, female. **A**, Habitus, dorsal view. **B**, Habitus, ventral view. Scale bars = 0.5 mm.



**FIGURE 3.** *Empherium rasnitsyni* gen. et sp. nov., holotype, female. **A**, Details of head, dorsal view. **B**, Details of second maxillary palpus. **C**, Details of tarsomeres. **D**, Details of apical tarsomere and claws. **E**, Details of wings. **F**, Details of abdomen. **G**, Details of female terminalia. Scale bars: 0.2 mm for **A**, **E**, **F**; 0.1 mm for **C**, **G**; 0.05 mm for **B**, **D**.



**FIGURE 4.** *Empherium rasnitsyni* gen. et sp. nov., holotype, female, drawings. **A**, Antenna. **B**, Forewing. **C**, Hind wing. Scale bars: 0.2 mm for **A**; 0.5 mm for **B** and **C**.

**Diagnosis.** As for genus, by monotypy.

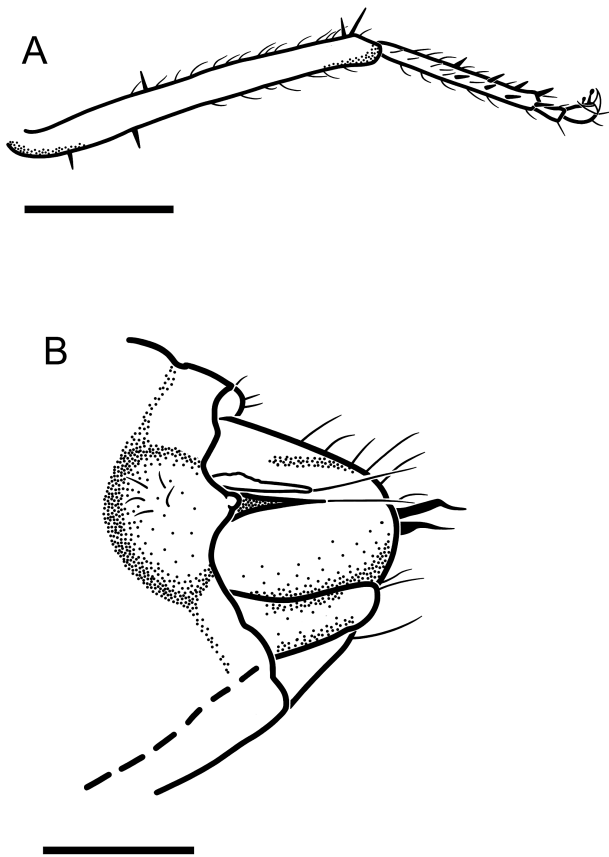
**Locality and horizon.** Nizhnyaya Agapa, Taimyr Peninsula, Russia, Dolgan Formation, Cretaceous (Upper Cenomanian).

**Description.** Head 0.70 mm wide (Fig. 3A); dorsal suture visible, much accentuated. Ocelli present. Compound eyes bare, as long as vertex. Antenna with 25 antennomeres, setae thin and sparse along its length, no secondary annulations; complete antenna with 23 flagellomeres, 0.01 mm wide and 0.05–0.06 mm long, last segment diminutive, with two small and thin apical setae pointing forward. Maxillary palpomeres four-segmented, setose, second palpomere with strong conical sensillum at middle (Fig. 3B). Labial palpomeres two-segmented. Lacinia not visible.

Thorax 0.60 mm wide; legs with tibia bearing occasional spines along its length and two apical spurs. Tarsi three-segmented (Fig. 3C); ratio of tarsal segments (from base to apex) in fore and mid-legs 3:1:1, in hind-legs 4.5:1:1; basal tarsomere with two rows of four spines but no ctenidiobothria (Fig. 3D); pretarsal claw without

preapical tooth, pulvillus present (long and narrow basally but rounded, sphere-like, apically).

Wings macropterous (Fig. 3E); forewing (1.80 mm long and 0.50 mm wide) with marginal setae; membrane hyaline, setae arranged in two rows around veins and sparsely dispersed in some areas of membrane (e.g., pterostigma cell and anal region); Sc present, curved back and fusing with R, additional veinlet emerging from Sc and reaching costal margin; Sc' reaching margin at 1.09 mm; pterostigma cell closed basally, 0.30 mm long and 0.10 mm wide; R<sub>1</sub> reaching margin at 1.30 mm from base; Rs bifurcated, R<sub>2+3</sub> reaching margin at 1.60 mm and R<sub>4+5</sub> reaching margin at apex; short crossvein r<sub>1</sub>-rs present; M three-branched, veins very long, M<sub>3</sub> separating from common stem M at 0.76 mm, stem M<sub>1</sub> and M<sub>2</sub> very short, fork M<sub>1</sub> and M<sub>2</sub> at 0.86 mm, branches M<sub>1</sub>, M<sub>2</sub> and M<sub>3</sub> reaching margin respectively at 1.50, 1.40 and 1.18 mm; CuA bifurcated at 0.50 mm, CuA<sub>1</sub> and CuA<sub>2</sub> veins short, reaching margin respectively at 0.80 and 0.70 mm; areola postica (AP) cell free, 0.30 mm long and 0.18 mm wide; CuP and A<sub>1</sub> simple; A<sub>1</sub> weakly visible, A<sub>2</sub> short. Hind



**FIGURE 5.** *Empherium rasnitsyni* gen. et sp. nov., holotype, female, drawings. **A**, Hind leg. **B**, Female terminalia. Scale bars = 0.2 mm.

wing (1.38 mm long and 0.40 mm wide) without marginal setae; membrane hyaline, not setose; Sc present, short, not reaching margin; basi-radial cell present, with basal section unclear, potentially absent or weakly visible; stems R and M fused in a short segment, 0.05 mm long;  $R_1$  branching from common stem R+M at 0.40 mm from base, reaching margin at 0.90 mm; common stem Rs as long as branches  $R_{2+3}$  and  $R_{4+5}$ ;  $R_{2+3}$  reaching margin at 1.20 mm and  $R_{4+5}$  at apex; M two-branched, with  $M_1$  reaching margin at 1.20 mm; CuA simple; CuP and A not visible.

Female ovipositor with dorsal and ventral valvulae not visible; external valvulae (V3) elongated, setose (Fig. 3F, G); subgenital plate setose, narrowed apically, with tapered segment rounded; paraprocts with a thick posterior spine each.

**Remarks.** Teratology and aberrations in wing venation seem very common in this family. Within this single specimen, we observe between the pair of forewings several differences that can be attributed to teratological malformations:  $R_{4+5}$  is bifurcated apically in one wing, the shape of Sc differs from one wing to the other, the Sc veinlet is aborted mid-way in one wing, and another

aborted veinlet is observed on the pterostigma of the other (Fig. 4B).

**Family Trogiidae Enderlein, 1911 (sensu Roesler, 1944)**

**Genus *Eolepinotus* Vishnyakova, 1975**

**Type species.** *Eolepinotus pilosus* Vishnyakova, 1975

***Eolepinotus zherikhini* sp. nov.**

(Figs 6–8)

**Type material.** Holotype specimen PIN 3603/1, female, badly preserved but with enough morphological features for clear observation and identification (Fig. 6). No syninclusion.

**Etymology.** Named after the late Professor Vladimir Zherikhin.

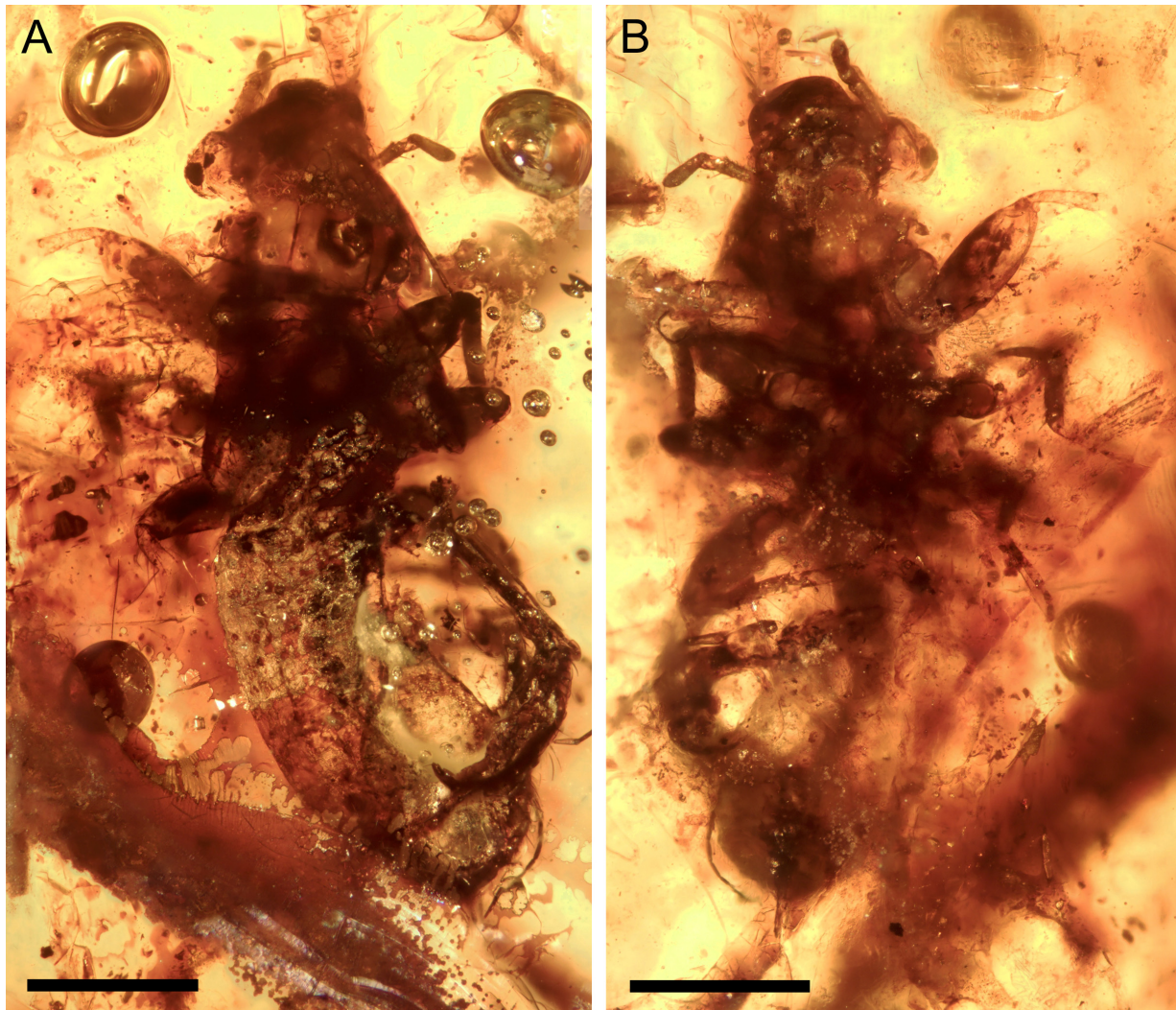
**Locality and horizon.** Timmerdyakh-Khaya, Yakutia, Russia, Timmerdyakh Formation, Cretaceous (Upper Cenomanian–Turonian).

**Diagnosis.** Head with dorsal suture well-defined, with anterior arms of frontal sutures; compound eyes bare; antennomeres without secondary annulations; micropterous; wings veinless and setose; pretarsal claws short, no preapical tooth, no pulvilli. Differential characters: forewings narrow and elongated (round and short in *Eolepinotus pilosus*); tibia bearing sparse spines along its length.

**Description.** Head 0.60 mm wide; dorsal suture present, very well defined; anterior arms of frontal sutures visible (Fig. 7A). Ocelli absent. Compound eyes bare, as long as vertex. Both antennae incomplete, with at least 15–16 flagellomeres, no secondary annulations. Maxillary palpomeres four-segmented (Fig. 7B), second palpomere from base with two spurs in apical half, third palpomere with one spur apically, fourth palpomere with one thinner and shorter spur at 2/3 of length and a sensory field of short setae at apex. Labial palpomeres two-segmented. Lacinia not visible.

Thorax badly preserved, pronotum very setose; legs with thick femur in all legs; hind tibia bearing thin spines along its length (Fig. 7C); tarsi three-segmented; basal tarsomere with two rows of small spines; pretarsal claws short without preapical tooth and no pulvillus (Fig. 7D); wings micropterous, veinless (Fig. 7E); forewings setose, elongated and narrowed.

Abdomen partially destroyed and partially covered by debris. Female ovipositor with dorsal and ventral valvulae not visible, either reduced or absent; external valvulae clearly visible, elongated, setose (Fig. 7F). Subgenital plate setose, possibly weakly bilobed apically; paraprocts not visible.



**FIGURE 6.** *Eolepinotus zherikhini* sp. nov., holotype, female. **A**, Habitus, dorsal view. **B**, Habitus, ventral view. Scale bars = 0.5 mm.

## Discussion

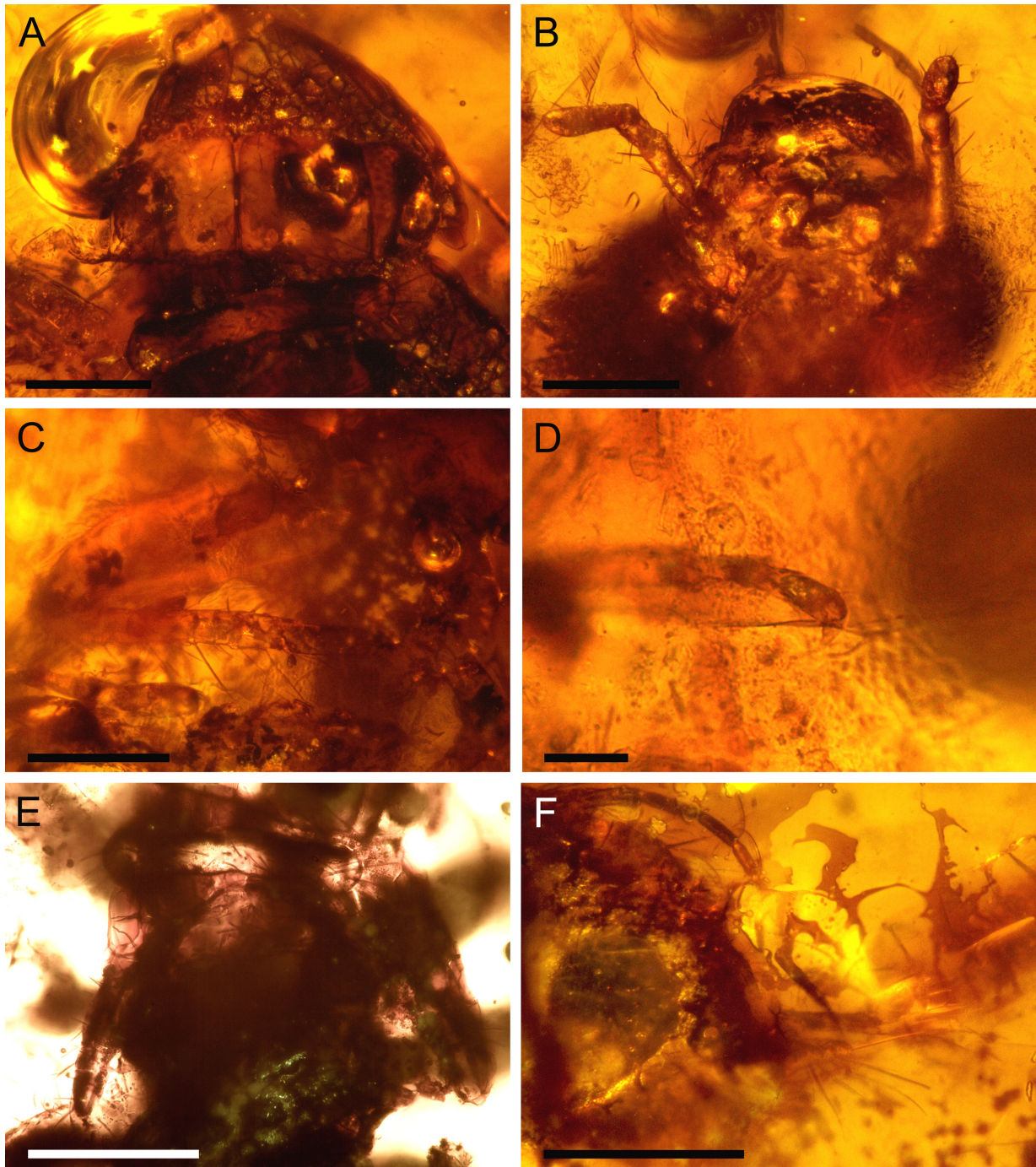
*Empherium rasnitsyni* gen. et sp. nov. and *Eolepinotus zherikhini* sp. nov. fall in Atropetae based on the synapomorphic trait ‘external valvulae of gonapophyses elongated and partially joined together on midline by membrane’ (Yoshizawa *et al.*, 2006). The spermathecal sac is not preserved in fossils and its structure cannot be observed in these extinct taxa. According to the works of Smithers (1972) and Lienhard (1998), *Empherium rasnitsyni* gen. et sp. nov. and *Eolepinotus zherikhini* sp. nov. fall in Trogiomorpha – Atropetae based on the following diagnostic characters: (1) antennae without secondary annulations, (2) tarsi three-segmented, (3) labial palpus two-segmented, (4) female gonapophyses reduced. *Empherium rasnitsyni* gen. et sp. nov. also possesses over 20 antennomeres and paraprocts with a strong posterior spine. According to the work of Baz & Ortuño (2001), *Empherium rasnitsyni* gen. et sp. nov. and

*Eolepinotus zherikhini* sp. nov. fall in Trogiomorpha—Atropetae based on the following additional diagnostic characters: (1) labial palpus with minute basal segment and rounded distal segment, (2) forewing lacking a sclerotized pterostigma, (3) ovipositor strongly reduced, with V3 elongated and bearing long apical setae. *Empherium rasnitsyni* gen. et sp. nov. also possesses paraprocts with a stout spine on free margin near the middle.

*Empherium rasnitsyni* gen. et sp. nov. falls in Empheriidae based on the following diagnostic characters: (1) forewing with Sc well-developed, curving back to meet with R, (2) presence of crossvein  $r_1$ -rs, (3) veins setose, with setae arranged on both sides along veins, (4) hind wing without fringe (Baz & Ortuño, 2001).

*Empherium* gen. nov. is mainly distinguished from all empheriids in the forewing venation: (1) the crossvein  $r_1$ -rs is basal to the pterostigma cell, (2) the areola postica is shorter, (3) the common stem  $M_1+M_2$  is very short (less than half the length of veins  $M_1$  and  $M_2$ ), and



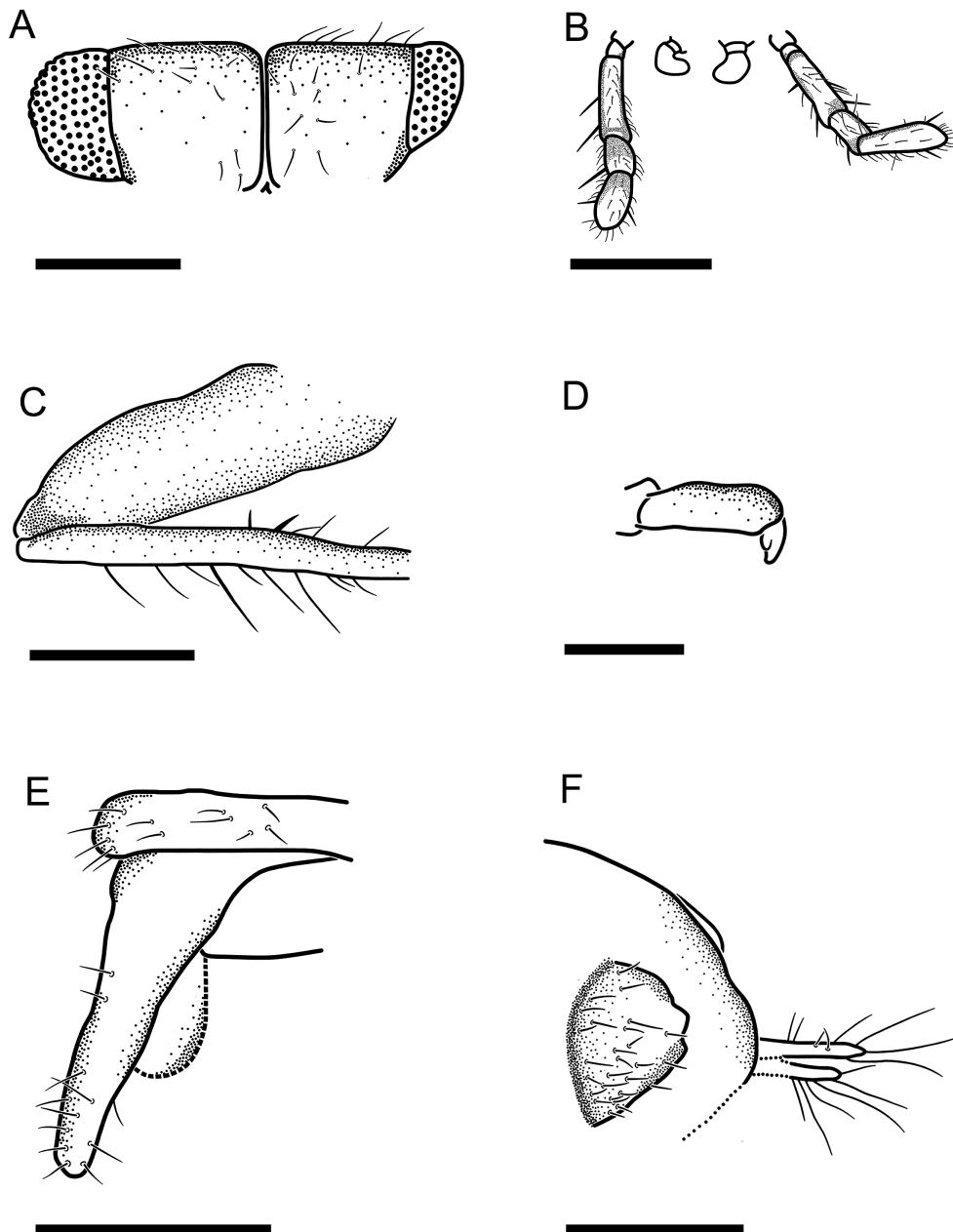


**FIGURE 7.** *Eolepinotus zherikhini* sp. nov., holotype, female. **A**, Details of head, dorsal view. **B**, Details of head, ventral view. **C**, Details of hind tibia. **D**, Details of pretarsal claw. **E**, Details of wings. **F**, Details of female terminalia. Scale bars: 0.2 mm for A–C, F; 0.3 mm for E; 0.05 mm for D.

the fork  $M_1$  and  $M_2$  is basal to the fork  $R_{2+3}$  and  $R_{4+5}$ , which results in longer branches of  $M$ . *Jerseyempheria*, *Empheropsocus*, *Burmempheria* and *Preempheria* have the fork  $R_{2+3}$  and  $R_{4+5}$  basal to the fork  $M_1$  and  $M_2$ , while *Empheria*, *Trichempheria* and *Eoempheria* have the fork  $R_{2+3}$  and  $R_{4+5}$  almost at the same level as the fork  $M_1$  and  $M_2$ . *Empherium* gen. nov. is also distinguished from other empheriids, except for *Burmempheria* and *Empheropsocus*, in the presence of an additional veinlet

between  $Sc$  and the anterior margin (vs. veinlet absent) in the forewing. In *Empheropsocus margineglabus*, the veinlet emerging from  $Sc$  curves forward and reaches  $Sc'$  instead of the wing margin.

*Empherium* gen. nov. further differs from *Jerseyempheria* in the number of flagellomeres (23 vs. 19), the setae arrangement on the forewing membrane (completely setose in *Jerseyempheria*), and  $R_1$  emerging from stem  $R+M$  instead of  $R$  in the hind



**FIGURE 8.** *Eolepinotus zherikhini* sp. nov., holotype, female, drawings. **A**, Head. **B**, Maxillary and labial palpomeres. **C**, Hind leg. **D**, Pretarsal claw. **E**, Wings. **F**, Female terminalia. Scale bars: 0.2 mm for **A–C**, **F**; 0.3 mm for **E**; 0.05 mm for **D**.

wing. *Empherium* gen. nov. is further distinguished from *Empheria*, *Trichempheria*, and *Eoempheria* in the absence of a long common basal stem R+M+Cu in the forewing, and in the presence of a basi-radial cell in the hind wing (vs. absent). *Empherium* gen. nov. also differs from *Trichempheria* in the arrangement of setae on the forewing membrane (setose, except for costal and subcostal cells in *Trichempheria*), and from *Eoempheria* in the number of flagellomeres (23 vs. at least 29) and vein Sc free in the hind wing (vs. reaching costal margin). The new genus differs from *Empheropsocus marginelabrus* and *Preempheria* in the number of flagellomeres (23 vs.

27 in both), and from *Burmempheria* in the number of flagellomeres (23 vs. over 30), the absence of a nodulus in forewings, and the presence of a pulvillus (vs. absence). Baz & Ortuño (2001) observed several similarities in body structures of Empheriidae and Archaeatropidae, including the antennae, the pretarsal claws and the maxillary palpomeres, and presumed that these families could be related. They relied on wing venation and setation to differentiate the two families (Baz & Ortuño, 2001: fig. 1), but several new species described after the establishment of Archaeatropidae do not properly conform to some of the diagnostic traits of Empheriidae

and Archaeatropidae. For instance, the presence of a nodulus in the forewings is a major character used by Baz & Ortuño (2001) to distinguish Archaeatropidae from Empheriidae; *Burmempheeria*, while possessing a typical setae arrangement of Empheriidae, has veins CuP and A meeting in a nodulus. Similarly, archaeatropid species *Propriionoglaris axioperi erga* Azar *et al.*, 2014 possesses diagnostic features of Empheriidae, *i.e.*, forewings with vein Sc' directed forward and setae disposed in two rows on each side of the veins. Li *et al.* (2020) suggested possible synonymy between Archaeatropidae and Empheriidae, which highly agree in morphology, arguing that wing characters are too unstable and polymorphic in Trogiomorpha for reliable insight on the taxonomy of the group at family level. The systematic value of these diagnostic characters clearly needs re-evaluation, along with a comprehensive revision of the generic content of Archaeatropidae and Empheriidae.

According to the work of Yoshizawa *et al.* (2006), *Eolepinotus zherikhini* **sp. nov.** belongs to Trogiidae based on the synapomorphic character 'wings greatly reduced and veinless, sometimes absent'. According to the works of Smithers (1972) and Lienhard (1998), *Eolepinotus zherikhini* **sp. nov.** belongs to the Trogiidae based on the following diagnostic characters: (1) antennae of many flagellomeres, without secondary annulation, (2) ocelli absent, (3) maxillary palpomeres with sensillum on second segment, (4) labial palpomeres two-segmented, (5) wings rudimentary, (6) body and wings not scaly, (7) tarsi three-segmented, (8) claws without preapical tooth, with pulvillus, (9) female gonapophyses reduced to an elongate external valve, with or without a small dorsal valve remnant. Following the keys of Smithers (1990) to psocopteran families, *Eolepinotus zherikhini* **sp. nov.** falls in Trogiidae based on: (1) micropterous, (2) tarsi three-segmented, (3) body and wing rudiments without scales, (4) forewings elytriform, (5) venation absent, and (6) antennae with 15 or more flagellomeres.

*Eolepinotus zherikhini* **sp. nov.** is assigned to *Eolepinotus* based on the following diagnostic characters: (1) posterior margin of the head homogenous, (2) compound eyes without setae, (3) presence of a long sensillum on second maxillary palpomere, (4) fourth maxillary palpomere elongated, not widened at apex, (5) wings reduced, (6) basal hind tarsomere with rows of spines on the lower surface, (7) pretarsal claws without a basal setae, and (8) external valvulae of the ovipositor elongated with short hairs and one long apical setae. The presence of a fully developed female terminalia negates the possibility of the specimen being a psocid nymph.

*Eolepinotus zherikhini* **sp. nov.** differs from *Eolepinotus pilosus* in the shape of the forewings: while rudimentary in both, the wings are longer and narrower in *Eolepinotus zherikhini* **sp. nov.** Further distinctions

between the two species are found in the tibiae which bear long spurs aside from the apical spines in *Eolepinotus zherikhini* **sp. nov.** (*vs.* tibiae with only apical spurs), and the claws lacking a pulvillus (*vs.* with). Due to the bad state of preservation of specimen PIN 3603/1 and the large number of similarities observed with *Eolepinotus pilosus*, we refrain from establishing a new genus until further discoveries. *Eolepinotus zherikhini* **sp. nov.** differs from *Paralepinotus* by having the compound eyes bare (*vs.* setose), the forewing micropterous (*vs.* brachypterous), and the claws without pulvilli (*vs.* with). *Eolepinotus zherikhini* **sp. nov.** differs from *Cretolepinotus* by having the wings micropterous (*vs.* apterous).

The fossil records appear to support the results of the molecular analysis by Yoshizawa *et al.* (2006) concerning Trogiidae. They concluded that the reduction of the wings, which are always veinless, is a synapomorphy of this family. This condition is present in all fossil trogiid taxa, as no extinct trogiid with macropterous wings, or one with developed veins, has been described. The discovery of more fossil trogiids accompanied by a comprehensive morphological analysis including both extant and extinct taxa can shed more light on this matter and give a clearer insight on the evolution of the family and its relationships with other Atropetae.

## Conclusion

The systematics of extant Atropetae have mostly been treated through molecular analysis, but controversies regarding extinct taxa are yet to be resolved. The newly discovered material offers additional data on families Empheriidae and Trogiidae during the Cretaceous and contributes to future morphological and phylogenetic analyses on Atropetae.

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