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First larvae of Raphidioptera from Eocene Sakhalinian and Rovno ambers

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Abstract

We describe two larvae of Raphidioptera probably belonging to different genera of Raphidiidae, the first recorded from middle Eocene Sakhalinian amber and late Eocene Rovno amber. The Sakhalinian larva is the first confirmed representative of Raphidioptera from the Cenozoic of Asia, and most probably the oldest larvae of an extant family of the order. The Rovno amber larva is the first European Cenozoic immature raphidiopteran found outside of Russo-Scandia. The terrestrial insect assemblage of the Sakhalinian amber forest is discussed, including snakeflies. An abundance of aphids and rarity of ants distinguishes this assemblage from other Cenozoic amber faunas.

Key words: Fossil larvae, Rovno amber, Sakhalinian amber insect assemblage, snakeflies, ants, micro-CT

Introduction

The Raphidioptera (snakeflies) today include *ca*. 250 species of two families (Inocelliidae and Raphidiidae) that are restricted to the Northern Hemisphere. Snakeflies were most diverse in the Mesozoic, and especially abundant in the Late Jurassic to the Early Cretaceous. Before the Cenozoic, the order was only represented by the extinct families Priscaenigmatidae, Juroraphidiidae, Chrysoraphidiidae, Metaraphidiidae, Mesoraphidiidae, and Baissopteridae, and by three families in the Cenozoic, Baissopteridae, Inocelliidae and Raphidiidae (Liu *et al*. 2014; Makarkin & Archibald 2014).

Fossil larvae of Raphidioptera are only known from amber. They are relatively well-known in mid-Cretaceous Kachin amber (Engel 2002; Perrichot & Engel 2007; Haug *et al*. 2020, 2022) and late Eocene Baltic amber (Pictet-Baraban & Hagen 1856; Weidner 1958; Weitschat & Wichard 1998; Janzen 2002; Scheven 2004; Kobbert 2005; Gröhn 2015, 2020; Haug *et al*. 2022). One or two larvae have been reported from late Barremian Lebanese amber (Jezzine), mid-Cretaceous Charentese amber, Turonian New Jersey amber, and Campanian Canadian amber (Grimaldi 2000; Perrichot & Engel 2007; Engel & Grimaldi 2008).

Here, the first raphidiopteran larvae are described from middle Eocene Sakhalinian amber in Pacific coastal Russia and late Eocene Rovno amber from Ukraine.

Material and methods

This study is based on two larvae, one from Sakhalinian amber and the other from Rovno amber.

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The Sakhalinian larva was collected near the village of Starodubskoye on the east coast of Sakhalin Island. The amber piece after primary treatment was 1.05 grams, coated in artificial resin which was partially removed before photography. The age of Sakhalinian amber, the history of its study, and its biota have been discussed in detail in a number of recent works (Baranov *et al.* 2015; Fedotova & Perkovsky 2016; Marusik *et al*. 2018; Dietrich & Perkovsky 2019; Perkovsky *et al*. 2021; Tikhonenko *et al.* 2021; Tykhonenko *et al.* 2021). Sakhalinian amber is found *in situ* in sediments of the Naibuchi Formation, which Kodrul (1999) convincingly dated as middle Eocene based on geological and paleobotanical data.

The Rovno amber larva was found in the Pugach quarry at Klesov (Sarny District), like nearly all amber housed in the Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine (SIZK), which was collected in 2000–2015 (Mitov *et al.* 2021). The amber piece after primary treatment was 2.3 grams. This is the first raphidiopteran from Klesov. The only known snakefly adult from Rovno amber was described from the Varash District of the Rovno Region (Perkovsky & Makarkin 2019; Kazantsev & Perkovsky 2022 and references therein). Rovno amber is the southern equivalent of the well-known coeval Baltic amber (Sokoloff *et al.* 2018). More than 310 arthropod species have been described from it (Perkovsky & Makarkin 2020; Colombo *et al.* 2021; Tshernyshev & Perkovsky 2021; Simutnik *et al*. 2022a, b; Olmi *et al*. 2022a, b; Telnov *et al*. 2022; Legalov *et al*. 2022 a,b and references therein).

Photographs were taken by A.P. Rasnitsyn using a Leica M165 stereomicroscope and an attached Leica DFC 425 digital camera (Figs 3B, D. E), by L.A. Anisyutkin using a Leica MZ 16 (Fig. 1), by D.A. Dubovikoff using a Carl Zeiss Stemi 305 stereomicroscope with a RisingCam1200KPA digital camera (Fig. 2), and by V.M. Loktionov using a SteREO Discovery V12 stereomicroscope (Fig. 3A, C).

The Sakhalinian amber specimen (PIN 3387/175) was studied by D.A. Dubovikoff using a high resolution X-ray microtomography scanner SkyScan 1172. Arrays of microtomographic sections were obtained at St. Petersburg State University (Resource Center "X-ray diffraction research methods", project No. 103-23769). The sample was scanned with the following parameters: voltage 74 kV, current 80 μA, without filter, with a pixel size of 2.98 microns and a resolution of 4000 × 4000 pixels per slice with continuous rotation by 180° and shutter speed of 990 ms per frame (2589 X-ray projections). Visualization, volumetric rendering and segmentation of tomographic sections of samples were performed in Dragonfly (2021.3.0.1087), 3DSlicer (5.1) and Drishti (3.0) software. The results of volumetric rendering and segmentation turned out to be less informative than photomicrography of the sample, so we do not use the μCT data in this article.

Our experience of using X-ray microtomography of other samples from Sakhalinian amber (mainly ants) has shown that the success of such studies strongly depends on the preservation and/or not sufficienT degree of mineralization of the inclusion, its proximity to the surface, and plastic deformation of the sample due to heating of the amber after deposition. Samples subjected to natural heating to sufficient mineralization are practically ill-suited to study using X-ray microtomography methods. Often, samples clearly visible with the help of optics are practically indistinguishable using X-rays. This is the case with the raphidiopteran larva studied here. This larva is a partly preserved empty exuvium, as confirmed by examination using μCT reconstruction methods.

Systematic paleontology

Insecta Linnaeus, 1758

Raphidioptera Linnaeus, 1758

Raphidioptera fam. gen. sp. indet. A
Figs. 1, 2

Material examined. Specimen PIN 3387/175, deposited in the Paleontological Institute, Moscow, Russia. An empty exoskeleton of a partly destroyed larva; only its head, prothorax, and one foreleg are preserved. Syninclusions include the head of a first instar cockroach larva, other crumpled insect fragments, and numerous fungal hyphae.

Locality and horizon. Russia: Sakhalin Island: Dolinsk District: the village of Starodubskoye; Sakhalinian amber, middle Eocene (Baranov *et al*. 2015).

Description. Head blackish, not narrowed posteriorly, short, *ca*. 2 mm long including mandibles, 1.4 mm wide (*ca*. 1.43 as long as wide). Ecdysial cleavage lines distinct, consisting of frontal and coronal sutures; frontal sutures diverge at obtuse angle. Antennal socket located at swollen, rounded projection (= antennal tubercle of MacLeod 1964). Antenna short; first and third antennomeres elongate, narrow; second antennomere not clearly discernible, probably very short; fourth antennomere poorly discernible, probably much shorter than third antennomere. Stemmata poorly discernible, three detected in dorsal view, one or two in ventral view. Mandibles not protruding, close to head capsule. Palpi not discernible.

Pronotum destroyed, blackish, apparently short, 1.45 mm wide, *ca*. 1.7 mm as preserved.

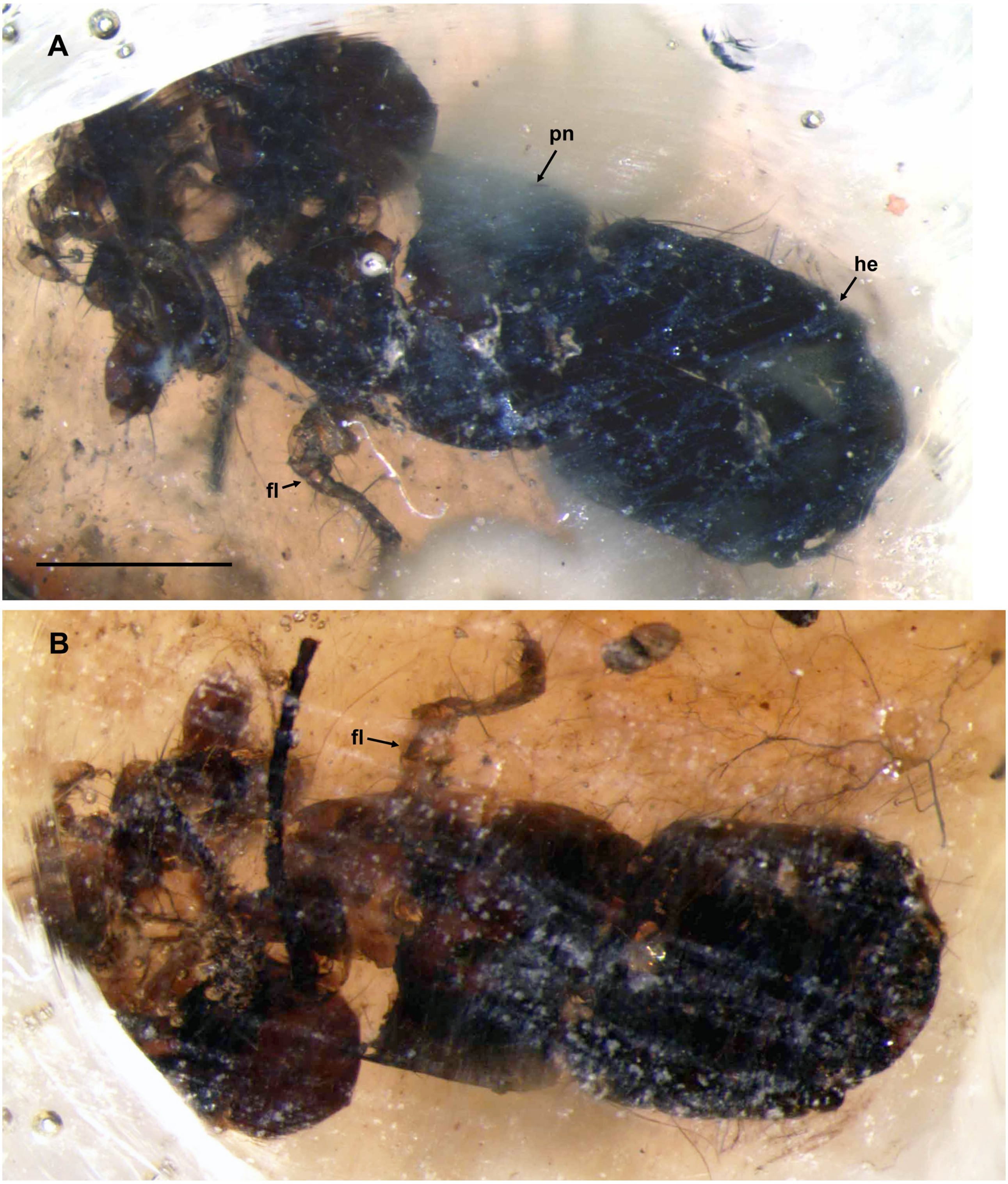

FIGURE 1. Raphidioptera fam. gen. sp. indet. A, specimen PIN 3387/175. A, dorsal view; B, ventral view. fl, foreleg; he, head; pn, pronotum. Scale bar = 1 mm (both to same scale).

Foreleg crumpled. Coxa, trochanter not clearly discernible. Femur short, stout, covered with scarce setae. Tibia appears narrow, covered with relatively dense setae. Tarsus rather stout, clearly not conical, covered with relatively dense setae. Claw slightly curved, with basal dilation (Fig. 2C).

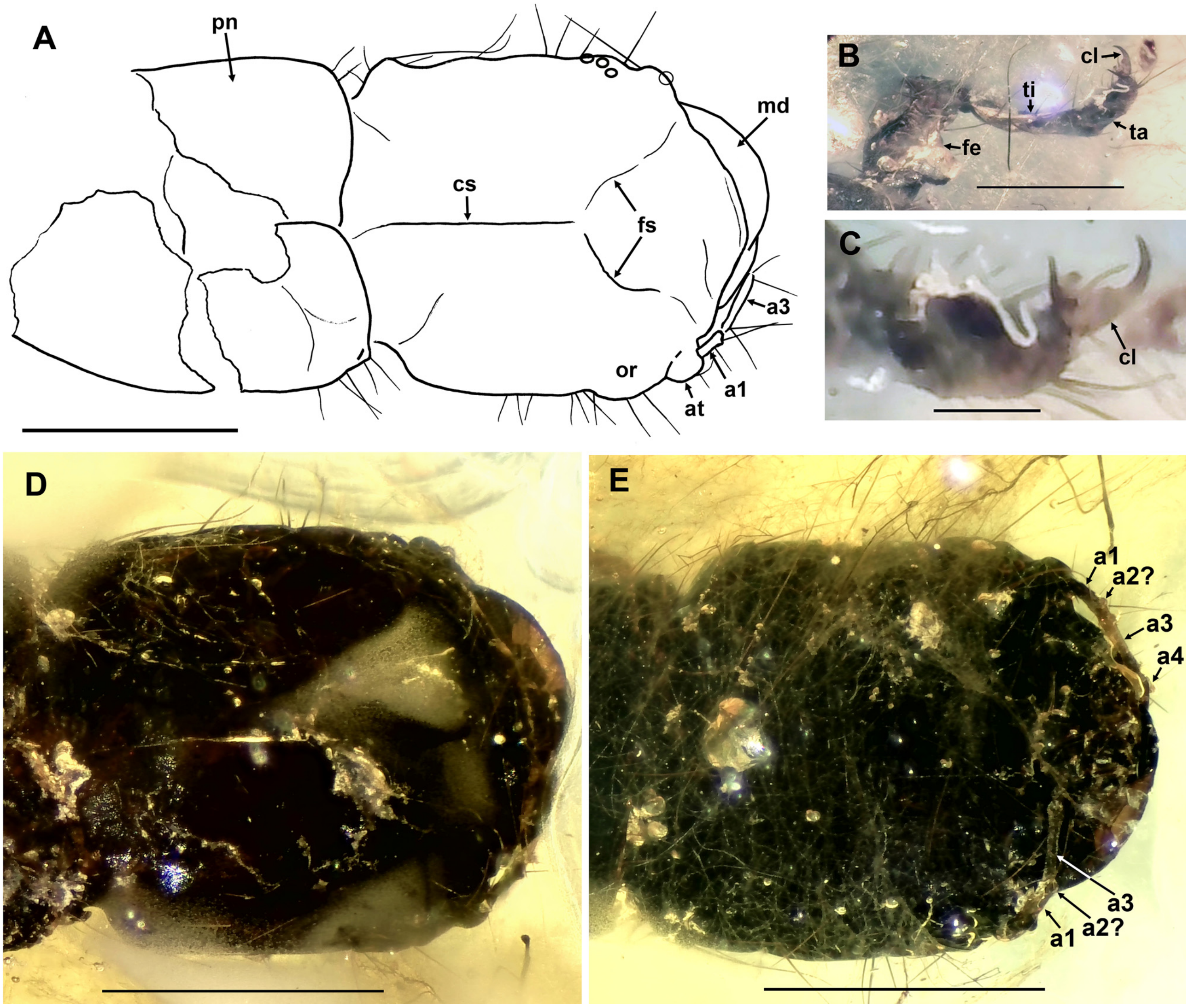

FIGURE 2. Raphidioptera fam. gen. sp. indet. A, details of specimen PIN 3387/175. A, line drawing of the head and pronotum (dorsal view); B, foreleg (ventral view); C, tarsus and claws of foreleg; D, head (dorsal view); E, same (ventral view). a1–a4, 1st to 4th antennomeres; at, antennal tubercle; cl, claw; cs, coronal suture; fe, femur; fs, frontal sutures; md, mandible; or, ocular region; pn, pronotum; ta, tarsus; ti, tibia. Scale bars = 1 mm (A, D, E), 0.5 mm (B), 0.1 mm (C).

Remarks. Its one-segmented tarsus indicates that this insect fragment is a larva, certainly belonging to Raphidioptera. The micro-CT shows that it is probably represented by an empty exoskeleton lacking internal tissues and air bubbles. The larva somewhat resembles those of some Hydrophilidae and Gyrinidae (Coleoptera) (*e.g*., Michat *et al*. 2010; Minoshima & Hayashi 2012), but differs from these by some details, *e.g*., these coleopteran larvae possess the anterior margin of the clypeolabrum furnished with projections; or their antennae are relatively long; or their mandibles are long with the inner teeth. It differs from the larvae of Megaloptera in particular by the relatively long head (it is usually short and rounded in Megaloptera) and the very short coxa (relatively long in Megaloptera).

The head of larval Raphidioptera usually bears projecting mandibles, but this larva is unusual, similar to that of the extant *Phaeostigma notatum* (Fabricius, 1781), in which mandibles do not project (see Beutel & Ge 2008: Fig. 1C).

We follow the antennal segmentation interpretation of Beutel & Ge (2008). This approach seems reasonable. Indeed, as in their understanding, the antennal tubercle of this larva is obviously not a part of the antenna. We think that Haug *et al*. (2022) incorrectly interpreted the antennal segmentation in fossil Raphidioptera larvae. They considered the antennal tubercle as the first antennal antennomere (their 'element'), and the very short second 'element' to be not an antennomere, although it is well discernible as such in some photographs (see *e.g*., Haug *et al*. 2022: Fig. 11a). According to Aspöck *et al*. (1991), the antenna of Raphidioptera larvae is three-segmented; they consider the antennal tubercle as a possible other, basal antennomere, and the second antennomere of Beutel & Ge (2008) as an inconspicuous sclerite between the two long basal antennomeres. According to Tauber (1991), the antenna is four-segmented, but she did not indicate if the fourth antennomere is the antennal tubercle or the second (shortest) antennomere of Beutel & Ge (2008).

Raphidioptera fam. gen. sp. indet. B

Fig. 3

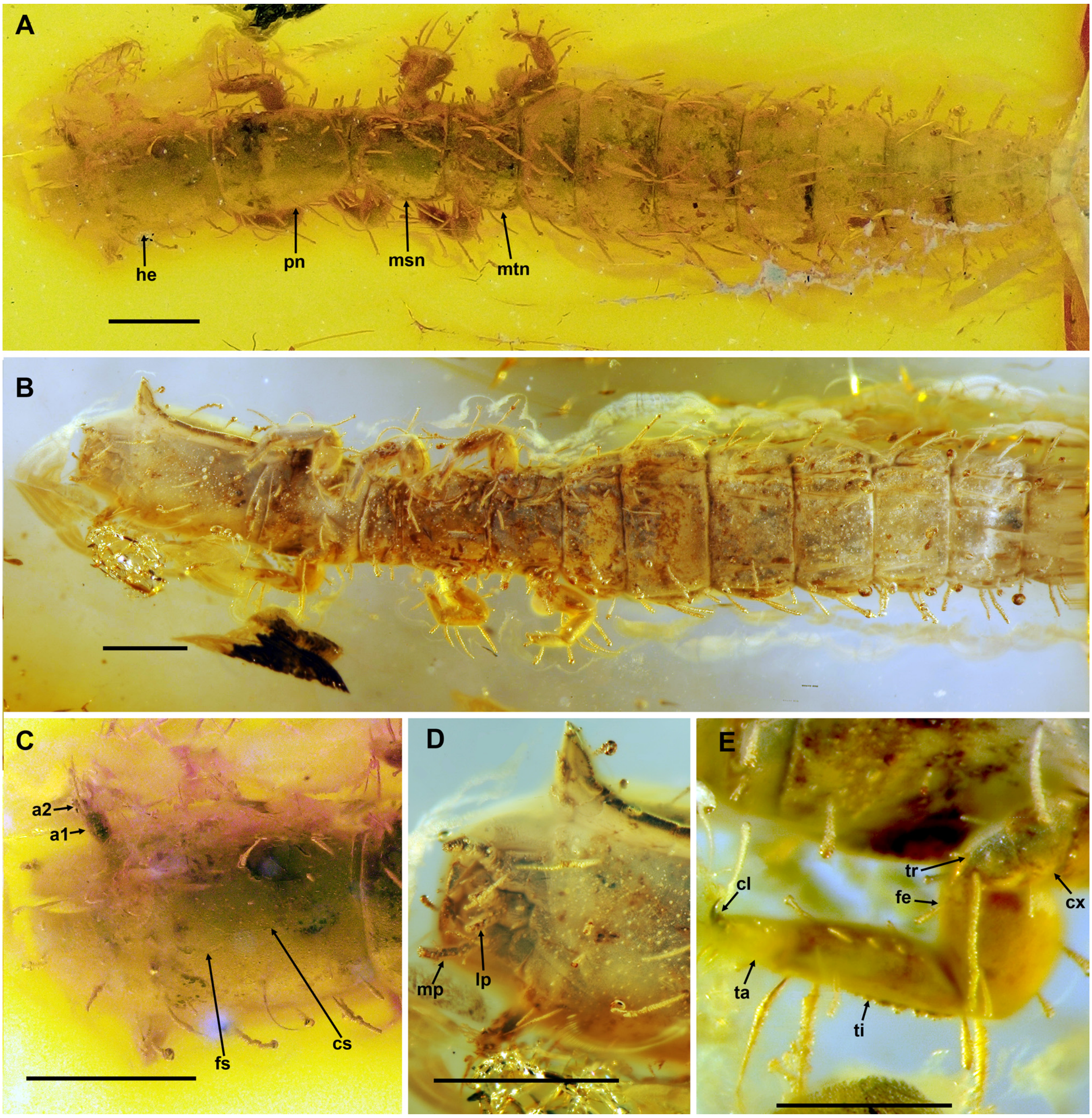

FIGURE 3. Raphidioptera fam. gen. sp. indet. B, specimen SIZK K-8213. A, dorsal view; B, ventral view; C, head, dorsal view; D, anterior part of the head (ventral view); E, right foreleg. a1, 1st antennomere; a2, 2nd antennomere; cl, claw; cs, coronal suture; cx, coxa; fe, femur; fs, frontal suture; he, head; lp, labial palpus; msn, mesonotum; mp, maxillary palpus; mtn, metanotum; pn, pronotum; ta, tarsus; ti, tibia; tr, trochanter. Scale bars = 1 mm (A–D), 0.5 mm (E).

Material examined. Specimen SIZK K-8213, deposited in the Schmalhausen Institute of Zoology, Kiev, Ukraine. An incomplete mature larva lacking the posterior part; details of the head are unclear in part because of a milky covering. Syninclusions: stellate hairs.

Locality and horizon. Ukraine: Rovno Region: Sarny District: Klesov; Rovno amber, late Eocene.

Description. Larva. Preserved length *ca*. 12.5 mm, estimated complete length *ca*. 15 mm.

Head relatively broad, not narrowed posteriorly, *ca*. 2.0 mm long (including mandibles), 1.25 mm wide (*ca*. 1.60 times as long as wide). Ecdysial cleavage lines poorly discernible, consisting of frontal and coronal sutures; frontal sutures diverge at a relatively sharp angle. Mandible protruding, poorly discernible. Maxillary palpi relatively long; four distal elongate palpomeres; basal palpomere not discernible. Labial palpi short, three-segmented. Antennal tubercles probably short, but not clearly discernible. Antenna: first antennomere rather short and stout; second antennomere very short, narrow; other antennomeres broken. Stemmata poorly discernible; at least three stemmata visible dorsally.

Thorax covered with long scarce setae. Pronotum relatively short, widest anteriorly; 1.50 mm long, 1.15 mm wide (1.30 times as long as wide); shorter than head (0.79 times as long as head length). Mesonotum nearly quadrate (0.92 times as long as wide), widest caudally. Metanotum transverse (0.70 times as long as wide), widest caudally.

All legs similar in structure, short, covered with long scarce setae. Coxa, trochanter very short, stout. Femur elongate, stout. Tibia nearly as long as femur, rather stout. Tarsus elongate, narrowed toward apex (conical); claws small, slightly curved, basally dilated.

Abdomen wider than thorax; seven preserved segments transverse (their length less than width). Setae long, scarce.

Remarks. The natural color of the larva is altered, with maculation presumed absent. All setae are covered by numerous minute droplets of water. The larva was found in a relatively small piece of amber, so it might be preserved in resin from various parts of the amber tree (*e.g*., any part of the trunk or stout twigs) (Perkovsky *et al.* 2012). The presence of stellate hairs indicates that this resin was exposed to the open air.

Discussion

Raphidioptera have not been reliably recorded from the Cenozoic of Asia. The single specimen reported by Zherikhin (1978) as "a fragmentary remnant" from the Eocene Tadushi Formation (southern Russian Far East) was neither described nor figured, and has not been located in the collections of Paleontological Institute, Moscow (A. Khramov, pers. comm.). Eocene Raphidioptera are only known from North America and Europe (Archibald & Makarkin 2021). Therefore, the Sakhalinian larva is the first confirmed fossil raphidiopteran from the Asian Cenozoic.

Taxonomical affinities of the larvae. Larvae of the families Raphidiidae and Inocelliidae dominated Cenozoic Raphidioptera. They are distinguished by only a few details, *i.e*., the number of stemmata (four in Inocelliidae; six to seven in Raphidiidae) and some differences in abdominal maculation (Tauber 1991). Larvae of Baissopteridae are unknown, but this family is recorded in the Cenozoic only in the late Eocene of Florissant (USA: Colorado) (Makarkin & Archibald 2014).

It is very difficult to count the number of stemmata in the larvae described here due to poor preservation. Any abdominal maculation is completely lost in the Rovno larva, and the entire abdomen is missing in the Sakhalinian larva. Therefore, the family affinities of these larvae cannot be determined based on these characters.

All previously known Cenozoic raphidiopteran larvae are from Baltic amber. The first two were described by Pictet-Baraban & Hagen (1856: Pl. 8, Fig. 31), but they mentioned nothing about their eyes (stemmata). Currently, these specimens are thought to be lost and are now treated as "Raphidiidae? gen. sp." (Aspöck *et al.* 1991). Indeed, their prothorax is considerably shorter than their head (*ca*. 0.64 its length based on the figure in Pictet-Baraban & Hagen 1856), consistent with a raphidiid affinity (see below).

One larva was correctly assigned to Inocelliidae, as it possesses four stemmata (Weidner 1958: Fig. 6; Pl. 14. Figs 2, 3). Weidner (1958) treated it as *Inocellia (erigena?)* (Menge in Pictet-Baraban & Hagen 1856), Keilbach (1982) as *Fibla (erigena?)*, and Aspöck *et al*. (1991) as Inocellidae gen. sp. Haug *et al*. (2022: Figs 8a–f) reexamined it and provided detailed photographs, but neither re-described it, nor assigned it to a family or genus. A similar larva was assigned to Inocelliidae by Janzen (2002: Figs 55, 258), but it was again only illustrated, not described. It resembles Weidner's larva by its elongate head and its pronotum, which is 1.70 times as long as wide and 0.90 times the length of its head (Weidner's larva: pronotum 1.78 times as long as wide and 0.95 times the length of its head). Therefore, Janzen's larva is highly likely an inocelliid. A photograph of a similar larva was provided by Scheven (2004: left lower Fig. on p. 66), who assigned it to the inocelliid genus *Fibla* Navás, 1915. Its head and pronotum are very elongate (pronotum 2.0 times as long as wide, 0.88 times the length of its head) and so its inocelliid affinity is very probable.

Eighteen other Baltic amber larvae have been illustrated, but not described or assigned to a family, *i.e*., Weitschat & Wichard (1998: Pl. 52, Fig. c); Kobbert (2005: Figs on p. 104); Gröhn 2015: Fig. on p. 250; Gröhn 2020: Fig. on p. 254; Haug *et al*. 2022: Figs 6–14.

The Rovno larva is similar to those larvae from Baltic amber which have a relatively short pronotum (*e.g*., Weitschat & Wichard 1998: Pl. 52, Fig. c; Haug *et al*. 2022: Figs 6b, 7e, 9). Baltic amber Raphidioptera are dominated by Inocelliidae, with greater taxonomic diversity (four species in three genera of Inocelliidae and two species in one genus of Raphidiidae) and numbers of specimens (nine and four specimens, respectively) than Raphidiidae (Archibald & Makarkin 2021). One raphidiid genus is shared by Baltic and Rovno ambers, although these are different species (Perkovsky & Makarkin 2019). We assume that most larvae from Baltic amber with an elongated pronotum and head belong to Inocelliidae, and those with a relatively shorter pronotum and head belong to Raphidiidae. If this assumption is correct, the Rovno amber larva belongs to Raphidiidae. Unfortunately, this is based on only one larva with stemmata counted (see above) and so it is unreliable. However, three stemmata seen in the dorsal aspect suggest that their total number may be more than four as in extant Raphidiidae larvae (see Beutel & Ge 2008: Fig. 1A), and so that family affinity is highly likely.

The Sakhalinian amber larva appears to belong to a taxon not closely related to those known from Baltic amber. Its head is short and broad so that it appears to be nearly quadrate as the mandibles do not protrude. The pronotum appears to be short, although this is speculative as it is very damaged. The presumed short pronotum and its resemblance to the larva of the extant raphidiid *Phaeostigma notatum* suggest that it may also belong to the Raphidiidae. The possible presence of five discernible stemmata confirms this affinity.

The characters of the Sakhalinian and Rovno amber larvae clearly show that these belong to different taxa, most probably to different genera within Raphidiidae.

Raphidioptera in the terrestrial insect assemblage of Sakhalinian amber. The larvae of all extant snakeflies and adults of Raphidiidae are entomophagous. Adults of Raphidiidae distinctly prefer aphids and other Sternorrhyncha. Larvae of snakeflies live on or under bark and in soil, feeding on various soft-bodied arthropods (Aspöck 2002). It is likely that adults of the Eocene Sakhalin snakeflies also largely fed on aphids and other Hemiptera like leafhoppers (see Dietrich & Perkovsky 2019), which would have been plentiful, as the insect assemblage of Sakhalinian amber is strongly dominated by aphids (Davidian *et al.* 2021a). Hitherto, only one predator (except ants) which might be associated with aphids was known from this amber, *i.e*., *Cnathrion sakhalinense* Kazantsev & Perkovsky, 2019 (Coleoptera: Cantharidae). The described larva of snakeflies is the largest insect found in Sakhalinian amber. In addition to these, known arboreal predators could include very rare spiders, the first representative of which was recently described from Sakhalinian amber (Marusik *et al*. 2018), and predatory midges of the genus *Eohelea* Petrunkewitch, 1957 (Diptera: Ceratopogonidae), which might have preyed on chironomids (Szadziewski 1990; Perkovsky 2013).

Ants are so rare in Sakhalinian amber that this was the basis for its incorrect dating (La Polla *et al.* 2013; Radchenko & Perkovsky 2016). Sakhalinian amber contains only 20 specimens of ants belonging to nine species (DD, pers. data), and only one snakefly, while in the collection of Rovno amber from Klesov (Perkovsky 2018; Radchenko *et al.* 2021) there are more than 1000 ant specimens of 71 species and one snakefly (EP, pers. data). Hemiptera, and most importantly aphids, did not have the effective defense provided by symbiotic ants in the Sakhalinian amber community. This is indicated in aphids by a unique abundance of their parasitoids, *i.e*., aphidiine wasps (Davidian *et al*. 2021a, b), which are many times more numerous than ants. Many of the numerous encyrtids (Hymenoptera) in Sakhalinian amber (Simutnik 2021; Simutnik *et al.* 2021) could be connected with scale insects (Sternorrhycha: Coccomorpha) (S. Simutnik, pers. comm.). An abundance of aphids and rarity of ants distinguishes the Sakhalinian amber insect assemblage from all other Cenozoic amber faunas. However, the rarity of ants may be explained by swampy environments in the Sakhalinian amber forest, which is confirmed by its mosses (Ignatov & Perkovsky 2013; Radchenko & Perkovsky 2016). High humidity in the Sakhalinian amber forest would have promoted an abundance of cockroaches and the low viscosity of the resin would have provided a strong selection bias resulting in only very young and small cockroach larvae being trapped in it. A single fossil triungulin of the cockroach parasitoid *Rhipidius* Thunberg, 1806 (Ripiphoridae) (Batelka *et al*. 2020) was described from Sakhalinian amber. The free life of a triungulin is limited to four-five hours in which it must find a host (Besuchet 1956), and so the presence of this triungulin is the indication of the great abundance of cockroaches. The snakefly larva is very damaged; micro-CT examination showed the absence of internal tissues. The numerous fungal hyphae (likely related to zygomycetes) also indicate high humidity. This peculiarity in the Sakhalinian insect assemblage might, therefore, represent a local environmental condition.

The rise of crown ants, most of which are symbionts of aphids in Northern Hemisphere mid-latitudes, presumably led to the extinction of all families of Late Cretaceous long-proboscis aphids at the Cretaceous–Paleogene boundary (these aphids were not associated with ants: Perkovsky & Wegierek 2018), and could be at least one of the reasons for the extinction of Cretaceous Raphidioptera species. Therefore, the study of the Sakhalinian amber insect assemblage in which predation pressure of ants is minimal for the Northern Hemisphere Cenozoic, and the abundance of aphids is comparable only with the Late Cretaceous faunas of the *Baeomorpha* Realm (Gumovsky *et al.* 2018; Perkovsky 2022) may be important for understanding the ecological evolution of Cenozoic Raphidioptera.

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