First aphidiine wasp from the Sakhalinian amber

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The first ichneumonoid aphidiine wasp species from Sakhalinian amber (middle Eocene) is described. *Ephedrus rasnitsyni* Davidian and Kaliuzhna sp. nov. is the oldest named aphidiine female, the first fossil aphidiine from Asia, and the oldest named species of the *Ephedrus*. *Ephedrus rasnitsyni* Davidian and Kaliuzhna sp. nov. and the two fossil species of *Ephedrus*, i.e., *Ephedrus primordialis* from Baltic amber (late Eocene) and *Ephedrus mirabilis* from Camoins-les-Bains (early Oligocene), presumably belong to the *Ephedrus plagiator* species group of the subgenus *Ephedrus* sensu stricto, and new species differs from them in having a longer petiole and a rather long 3M vein that does not reach the forewing margin. It additionally differs from *E. primordialis* by having longer ovipositor sheaths. The new species is most similar to the extant *Ephedrus validus* and *Ephedrus carinatus*, from which it differs by the less elongated F1, absence of notauli, and by ovipositor sheaths that are 3.0 times as long as wide.

Key words: Hymenoptera, Ichneumonoidea, Braconidae, Aphidiinae, Eocene, Oligocene, Baltic amber, Sakhalinian amber.

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Introduction

Middle Eocene Sakhalinian amber (43–47 Ma) is the typical rumanite from the Dolinsk District (south of Sakhalin Island). It is much older than European sucinites (Kodrul 1999; Perkovsky et al. 2007; Baranov et al. 2015), and its biota is poorly studied (Simutnik 2014, 2015, 2020; Fedotova and Perkovsky 2016; Radchenko and Perkovsky 2016; Marusik et al. 2018; Dietrich and Perkovsky 2019; Azar and Maksoud 2020; Batelka et al. 2020; Perkovsky et al. 2021; Tykhonenko et al. 2021). Aphids are extremely abundant in Sakhalinian amber. Only Late Cretaceous *Baeomorpha* Realm faunas display similar abundance of aphids (Gumovsky et al. 2018). Sakhalinian amber fauna is unique for Cenozoic amber in the rarity of ants (Kazantsev and Perkovsky 2019, and references therein), with only a single species of cantharine beetles as an aphid predator (Kazantsev and Perkovsky 2019). Thus, there is a high abundance of aphid parasitoids in Sakhalinian amber, unknown from any other amber fauna (Rasnitsyn 1980).

Aphidiinae is a small, globally distributed subfamily of specialized aphid parasitoids belonging to Braconidae, Hymenoptera (Yu et al. 2016; Chen and van Achterberg 2019), but it was once considered a separate family within Ichneumonoidea (Starý 1970; Tobias and Chiriac 1986; Davidian 2007, 2018, 2019). According to different estimates, there are 505 (Žikić et al. 2017) to 619 (Yu et al. 2016) extant species of aphidiines recognized worldwide, and the process of generic revision and new species description continues (Rakhshani et al. 2017; Čkrkić et al. 2019; Kocić et al. 2019, 2020; Tomanović et al. 2020). More than half of all species are known from the Palearctic Region (Yu et al. 2016). Aphidiines are an essential part of the aphidophagous guild, and due to their practical importance, this group is well studied (Žikić et al. 2017; Chen and van Achterberg 2019); however, questions remain regarding the evolution and phylogeny of the group (Belshaw and Quicke 1997; Belshaw et al. 2000; Sanchis et al. 2000; Ortega-Blanco et al. 2009; Chen and van Achterberg 2019) and genera therein (Gårdenfors 1986; Kocić et al. 2019, 2020; Čkrkić et al. 2020). The study of fossil material may contribute to resolving these problems.
The fossil fauna of Aphidiinae includes 14 genera and 26 species (Ortega-Blanco et al. 2009). The oldest fossil genus and species, *Archeaphedrus stolamissus* Ortega-Blanco, Bennett, Delelès, and Engel, 2009, was described from a single male specimen from the late Albian (Early Cretaceous) Alava amber of Spain (Ortega-Blanco et al. 2009), and this species was assigned to Ephedrini (Yu et al. 2016). The majority of fossil aphidiines have been described from the early Rupelian (Oligocene) Anna pit in the Alsace potash field (Quilis 1940; Starý 1973, Berger et al. 2005; Ortega-Blanco et al. 2009). Aphidiinae are also found in the late Eocene Baltic (Brues 1933; Starý 1970, 1973) and Rovno amber (MOK and EEP unpublished data). Aphidiines are prevalent in middle Eocene Sakhalinian amber (Rasnitsyn 1980); however, detailed study is in its infancy, with short reports on *Ephedrus* Haliday, 1833, specimens (Kaliuzhna et al. 2019) and the differentiation of possible new species (Kaliuzhna et al. 2020).

*Ephedrus* contains about 50 living and extinct species altogether, most of which are known from the Palaeartic Region (Yu et al. 2016; Kocić et al. 2019; Tomanović et al. 2020). Among Ephedrini, the *Ephedrus* is the only genus with rich extant fauna and includes two fossil species described from Europe (Oligocene of France and Baltic amber; Yu et al. 2016). Diagnostic morphological characters of the genus are 11-segmented antennae in both sexes (an exception is *E. antennalis* Tomanović, 2020, described from a single female with 12-segmented antennae), complete venation of the forewing, with present 2RS and r-m veins, and also seven complete cells (marginal, 1st and 2nd submarginal, 1st discal, basal, subbasal, and 1st subdiscal). The ovipositor sheaths are more or less elongate, straight or slightly curved upward, usually with sparse setae. According to the review by Kocić et al. (2019), the extant fauna of the *Ephedrus* is represented by three subgenera: *Ephedrus* sensu stricto, *Breviephedrus* Gärdenfors, 1986, and *Fovephedrus* Chen, 1986. The monotypic subgenus *Lysephedrus* Starý, 1958, is assigned by the same authors as a junior synonym of *Ephedrus* sensu stricto, according to the results of molecular analysis (Kocić et al. 2019). The fossil species *Ephedrus primordialis* Brues, 1933, from Baltic amber and *E. mirabilis* Timon-David, 1944, from early Oligocene Camoins-les-Bains Marls near Marseille presumably belong to the subgenus *Ephedrus* sensu stricto as far as we can conclude from the original descriptions (Brues 1933; Timon-David 1944).

**Systematic palaeontology**

Order Hymenoptera Linnaeus, 1758
Superfamily Ichneumonoidea Latreille, 1802
Family Braconidae Nees, 1811
Subfamily Aphidiinae Haliday, 1833
Genus *Ephedrus* Haliday, 1833

*Type species:* *Bracon plagiator* Nees, 1811; Sickershausen, Germany (destroyed); Hermanovce, Prešovské hory, Slovakia (neotype), extant.

*Ephedrus rasnitsyni* Davidian and Kaliuzhna sp. nov.

Figs. 1, 2.

2008 Aphidiinae (Braconidae); Zherikhin et al. 2008: 197, text-fig. 76.


*Etymology:* The species named after famous paleoentomologist Alexander Pavlovich Rasnitsyn.

*Holotype:* PIN 3387/79, single female imago.

*Type locality:* Starodubskoye, Dolinsk District, Sakhalin Province, Sakhalin Island, Russian Federation.

*Type horizon:* Middle Eocene.

**Diagnosis.**—The complete pubescence of the elongate ovipositor sheaths (Fig. 1A4) distinguishes the new species...
from all other species of the *Ephedrus* and places it closer to the extant *E. validus* (Haliday, 1833) and *E. carinatus* Tomanović, 2020. From these two species *E. rasnitsyni* Davidian and Kaliuzhna sp. nov. differs in following characters: first flagellomere (F1) less elongate, 2.5 times as long as wide (Fig. 1A 3), notauli absent, ovipositor sheaths 3.0 times as long as wide (Fig. 1A4) and overall smaller body size. *Ephedrus rasnitsyni* Davidian and Kaliuzhna sp. nov. differs from known fossil species *E. mirabilis* and *E. primordialis* by a longer petiole, and rather long 3M vein that, however, does not reach the forewing margin (Figs. 1A1, A2, 2). The new species additionally differs from the *E. primordialis* by more elongate ovipositor sheaths.

**Description.**—Description is based on a single female, male forms are unknown.

Head (Fig. 1A1–A2) distinctly densely pubescent. Maxillary palp with three visible palps; labial palp with two palps. Maxillary palp oval, two times as long as wide, completely pubescent, covered with short setae and with two–three long setae apically. Antenna with 11 antennomeres, short, barely reaching the apex of thorax, covered with dense setae that are slightly shorter than the width of F1; each flagellomere also with two semi-erected longer setae apically. F1–F3 parallel-sided (Fig. 1A3) of differing lengths; F1–F3 are longer than the other flagellomeres beginning with F4 are strongly widened towards apex, possibly flattened in amber. The apical flagellomeres

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**Fig. 1.** Aphidiine wasp *Ephedrus rasnitsyni* Davidian and Kaliuzhna sp. nov., holotype PIN 3387/79, Starodubskoye, Sakhalinian amber (Russia), middle Eocene. Specimen in lateral view (A1), explanatory morphology (A2), anterolateral part of the specimen (A3), ovipositor sheaths in lateral view (A4). Abbreviations: body: c, coxa; em+cl, empodium and claws; f, femur; F1–F9, flagellomeres 1–9; mp, maxillary palp; MS5-6, metasomal sternites 5 and 6; MsP, mesopleuron; MsSc, mesoscutum; MsSi, mesoscutellum; MT1 (petiole), first metasomal tergite, petiole; MT2–MT8, metasomal tergites 2–8; MnN, metanotum; MtP, metapleuron; OS, ovipositor sheaths; p, pedicellus; PN, pronotum; PPl, propodeum; PPl, propodeum; s, scape; ti, tibia; tr, trochanter; 1–5, tarsomeres; venation: Pt, pterostigma; R1, metacarp, anterior branch of radius; r, cross vein connecting pterostigma and radial sector; Pt, pterostigma; RS, radial sector; 3RSa, 3RSb, a and b sections of 3rd abscissa of radial sector; 2M, 3M, 2nd, and 3rd abscissa of media; Cu, cubitus.
tightly jointed to each other, forming a club. F1 is broken in basal third, approximately equal in length to F2, 2.5 times as long as wide in the middle; F3 and F4 2.0 times as long as wide, F5 and F6 1.5 times as long as wide; F7 and F8 almost square, i.e., the same length and width; F9 1.3 times as long as wide at base (Fig. 1A1, A2). F1 and F2 with one longitudinal placode; other flagellomeres with two placodes each. 

Mesosoma densely pubescent (Fig. 1A1–A3). Propodeum with central areola. 

The venation (Figs. 1A1, A3, 2) of the forewing complete, including 2RS and r-m veins and seven closed cells, however, only marginal, 1st and 2nd submarginal and basal cells are clearly visible. Pterostigma approximately two times as long as wide. 3RSa slightly longer than 2RS; 3M not reaching wing margin. Hind wing with complete basal cell. The surface of both wings densely covered with long setae. The setae along the wing edge are longer than on the wing surface. 

Legs densely pubescent. First fore tarsomere 2.0 times as long as second tarsomere, first hind tarsomere 2.7 times as long as second tarsomere. 

Metasoma (Fig. 1A1, A2, A4) elongate, lanceolate, densely pubescent. Petiole inverted and its shape is difficult to observe; approximately two times as long as wide at the level of the spiracular tubercles. Eight metasomal tergites clearly visible. Hypopygium and elongate ovipositor sheaths completely covered with short dense setae. Ovipositor sheaths elongate, 3.0 times as long as wide in the middle; dorsal margin of ovipositor sheaths straight, apex rounded, ventral margin slightly curved upwards. Left ovipositor sheath broken at midlength (Fig. 1A4). 

Coloration of the body is brown, antennae and legs are slightly lighter; palpi are light yellow. 

Body length 1.2 mm, the length of antennae 0.5 mm. 

Remarks.—Left side of the specimen is convex towards observer. The head is strongly deformed, it is not possible to observe the eyes and clypeus. The specimen has clearly visible mesosoma, legs, metasomal tergites, ovipositor sheaths; the wings and petiole are partly visible. 

_Ephedrus rasnitsyni_ Davidian and Kaliuzhna sp. nov. is the first Aphidiinae species described from Sakhalinian amber, and the oldest named female of subfamily. _Ephedrus rasnitsyni_ sp. nov. presumably belongs to _E. plagiator_ species group of the subgenus _Ephedrus_ sensu stricto (Gärdn fors 1986; Kocić et al. 2019) on the basis of following characters: 11-segmented antennae, complete venation of the forewing, with 3RSa slightly longer than 2RS, and rather long petiole (Figs. 1A1, A2, 2). 

_Ephedrus rasnitsyni_ sp. nov., as well as other studied Sakhalinian Aphidiinae, are much shorter than extant species of the _E. plagiator_ group. This group includes 12 extant species, with only some specimens of two species, i.e., _E. laevicollis_ (Thomson, 1895) (1.3–1.9 mm) and _Ephedrus koponeni_ Halme, 1992 (1.4–1.9 mm), smaller than 1.5 mm, while all known specimens of six species are longer than 1.7 mm, with the largest being _Ephedrus prociphili_ Starý,
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1982 (2.5–3.5 mm; Gärdenfors 1986; Tomanović et al. 2020). Compared to fossil species, *Ephedrus rasnitsyni* Davidian and Kaliuzhna sp. nov. is larger than *E. primordialis* (0.6–0.7 mm) and smaller than *E. mirabilis* (1.56 mm).

**Stratigraphical and geographic range.**—Middle Eocene, Starodubskoye, Dolinsk District, Sakhalin Province, Sakhalin Island, Russian Federation.

**Concluding remarks**

Among studied aphidiine specimens from Sakhalinian amber, the most abundant species are from the genus *Ephedrus*, tribe Ephedrini Haliday, 1833 (29 out of 36 specimens).


Among these genera, *Diospilites* and *Indoephedrus* have been erroneously assigned to Aphidinae in Taxapad (Yu et al. 2016). We agree with Tobias (1987), who reclassified the fossil *Diospilites brevicornis* Brues, 1933, from Baltic amber and erected for him the monotypic subfamily Diosplitinae. The *Indoephedrus* was erected for two parasitoids of Greenideidae from Meghalaya (northeast India): *I. reticulata* Samanta, Pramanik, and Raychaudhuri, 1983, and *I. neoficicola* Samanta, Pramanik, and Raychaudhuri, 1983. According to the description by Samanta et al. (1983), the structure of the head (oval head shape, long temples, narrow face with sparse setae, reticular region between the antennal fossae and simple eyes), venation of the forewings, long antennae (25–segmented in *I. neoficicola* and 33– in *I. reticulata*) as well as the structure of the long narrow ovipositor sheaths completely covered with setae, are similar to those of some genera of the subfamily Braconinae Nees, 1811 (Serjej A. Belokobylskij, personal communication 2020) and does not belong to Aphidinae. This opinion is also shared by other aphidine specialists (Ehsan Rakhshani, personal communication 2020) and does not belong to the list of world aphidiine parasitoids of greenideids (Starý et al. 2010).

The fossil *Archeptedrus stolamissus* Ortega-Blanco, Bennet, Delclòs, and Engel, 2009, was described based on a single male from Early Cretaceous (late Albian) Álava amber (Peñacerrada I) from Spain. It differs from the new species by having 16-segmented antennae that clearly narrow towards the apex and by the 5-segmented maxillary palps.

*Parephedrus* and *Toxares* are represented exclusively by extant species. The Australian *Parephedrus*, despite the absence of notaui, is characterized by sparse pubescence of the ovipositor sheaths, as well as having two thickened setae at the apex of the sheath, similar to species of the *Praon* Haliday, 1833. The *Toxares* occupies an isolated position in the group because it has 16–23-segmented antennae and a plow-shaped ovipositor sheath that is curved downward and widens towards the apex.

*Ephedrus rasnitsyni* Davidian and Kaliuzhna sp. nov. has all of the plesiomorphic features of the *Ephedrus*: 11-segmented antennae, complete wing venation, propodeum with central areola, hind wings with a complete basal cell, a straight, triangular ovipositor sheath. The absence of notaui is characteristic to both previously described fossil *Ephedrus* species and modern *Parephedrus* (Starý 1973; Gärdenfors 1986). Apomorphic features of Ephedrini include posterior position of propodeal spiracles, an elongated petiole, free cuspises of male genitalia, and black colored aphid host mummies (Gärdenfors 1986). The only clearly visible apomorphy of the new species is an elongated petiole; other characters are hardly visible or not present in the available specimen.

The fossil species *E. mirabilis* and *E. primordialis* can be easily distinguished from the new species. The former has a short petiole and a very short 3M that is approximately equal to $r$ (Timon-David 1944; Starý 1973). *E. primordialis* has a short, wide, and almost square petiole and a long 3M vein that reaches the apical margin of the wing, and rather short, narrow, triangular ovipositor sheaths (the character of pubescence is absent in the description) (Brues 1933; Starý 1973). The new species has a longer petiole, a long 3M vein that does not reach the forewing margin, and more elongated ovipositor sheaths that are completely covered with setae.

*Ephedrus rasnitsyni* Davidian and Kaliuzhna sp. nov. is most similar to the extant *E. validus* and *E. carinatus* in the pubescence of the ovipositor sheaths but differs from these species in the following characters: the F1 is shorter, 2.5 times as long as wide; notaui are absent; and the ovipositor sheaths are 3.0 times as long as wide. In the related extant species, the F1 is much longer (in *E. validus*, it is 4.2–4.7 times as long as wide, and in *E. carinatus*, 5.8 times as long as wide); the notaui are well developed; and the ovipositor sheaths are about two times as long as wide (Starý 1958; Tomanović et al. 2020). Interestingly, *E. validus* was at one time included in the monotypic subgenus *Lysephedrus* established based on morphological and ecological data (Starý 1958). The main diagnostic characters that differentiate *Lysephedrus* from the rest of the subgenera are the reticulated sculpture of the propodeum and petiole and the continuous pubescence of the ovipositor sheath. *Lysephedrus* was also considered a subgenus in the *Ephedrus* monograph by Gärdenfors (1986). In several other studies, *Lysephedrus* was considered as a genus (Mackauer 1968; Starý 2006; Davidian 2018, 2019). On the other hand, *Ephedrus carinatus* (*Ephedrus sensu stricto*) from Austria was described from a single female already in the nominate subgenus (Tomanović et al. 2020). This species, like *E. validus*, is characterized by pubescent ovipositor sheaths. This morphological character could be an adaptation to the
parasitization of root aphids (e.g., subfamily Eriosomatinae), such as in *E. validus* (Starý and Schlinger 1967; Tobias and Chiriac 1986; Davidian 2007; Yu et al. 2016) and a similar host was assumed by Tomanović et al. (2020) for *E. carina tatus*. Eriosomatidae are known from Sakhalinian amber as well (Piotr Węgierek, personal communication 2020), and because *E. rasnitsyni* Davidian and Kaliuzhna sp. nov. has the same character, it could also be a parasite of root aphids.

Sakhalinian amber is potentially the best source to reveal the crucial information in understanding the early stages of aphid-aphidiine coevolution. The Sakhalinian amber biota existed after the rise of ants and after the establishment of close ant-aphid relationships (Perkovsky and Węgierek 2018, and references therein), but ants are rare in this amber—four times less abundant than in Baltic and Rovno ambers (Perkovsky et al. 2007; Radchenko and Perkovsky 2018, and references therein). The authors are grateful to Alexandr P. Rasnitsyn and Irina D. Sukatsheva (both PIN), who provided the amber material; to Andranik R. Manukian (Senior Researcher of the Kaliningrad Regional Amber Museum, Kaliningrad, Russian Federation) who kindly helped in separating inclusions and polishing amber; to Elshan Rakhsani (University of Zabol, Zabol, Iran), Dmitri V. Logunov (Curator of Arthropods at the Manchester Museum, the University of Manchester, UK), and Hirotsugu Ono (National Museum of Nature and Science, Tokyo, Japan), who provided a copy of the *Indoidea* description. Piotr Węgierek (Silesian University, Katowice, Poland) is thanked for discussion and Sarah C. Crews (California Academy of Sciences, San Francisco, USA) for editing the English text. Authors are grateful to reviewers of this article Sergey A. Belokobylskij (Zoological Institute of Russian Academy of Sciences, St. Petersburg, Russian Federation) and Michael Sharkey (University of Kentucky, Lexington, USA) for useful recommendations and corrections.

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