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## New species of braconid parasitoid wasps from the subfamilies Doryctinae and Brachistinae from late Eocene Baltic amber

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### Abstract

Three new fossil species of braconid wasps are described and illustrated from late Eocene Baltic amber: *Palaeorhoptrocentrus tenuicornis* **sp. nov.** (Doryctinae), *Taphaeus obscurus* **sp. nov.** (Brachistinae: Diospilini), and *Eubazus electrus* **sp. nov.** (Brachistinae: Brachistini). Keys to the known species of *Palaeorhoptrocentrus* Belokobylskij, 2023 and to species of *Eubazus* Nees, 1812 described from Baltic amber are provided. An illustrated redescription of *Blacus* (*Electroblacus*) *facialis* Brues, 1933 (Brachistinae: Blacini) is also provided, along with digital photographs for the first time of the female of *B. (Electroblacus) facialis*, whose type material was lost during the World War II. We also provide morphological notes and digital photographs of a male belonging to an undescribed species of *Meteorus* (Euphorinae).

**Keywords:** Eocene, parasitoids, wasp, fossil, Diospilini, Blacini, Brachistini, *Meteorus*

### Introduction

Baltic amber is the world's largest amber deposit and the source of an incredible array of fossil insects (Rasnitsyn & Quicke, 2002; Sadowski *et al.*, 2017). The age of Baltic amber is considered to be early Priabonian in age ( $33.9 \pm 0.1$ – $37.2 \pm 0.1$  Mya), within the Late Eocene (Iakovleva *et al.*, 2022; Paleobiology Database, 2023). The original resin was probably produced in coniferous forests that covered the Scandinavian territory during the Eocene (Larsson, 1978). Many of the resulting amber pieces were reworked along the eastern part of the Baltic

Sea, particularly in the Russian Kaliningrad Province (Rasnitsyn & Quicke, 2002). The number of arthropod species recovered from Baltic amber is vast, with more than 3,000 described fossil species, many of which belong to the order Hymenoptera.

Parasitoid wasps of the family Braconidae are found nearly worldwide. They comprise the second largest family of Hymenoptera, with thousands of extant species. The taxonomy of Braconidae from Baltic amber has been studied by Brues (1923, 1933, 1939), Achterberg (1982), Tobias (1987), Belokobylskij *et al.* (2021a, b, 2023), Davidian *et al.* (2022, 2023a, b), and Belokobylskij & Manukyan (2023, 2024). Currently, there are more than 100 fossil braconid species belonging to 21 extinct genera that have been described from Baltic amber.

In this study, we describe and illustrate new braconid species from Baltic amber belonging to the genera *Palaeorhoptrocentrus* Belokobylskij, 2023 (Doryctinae), *Taphaeus* Wesmael, 1835 (Brachistinae), and *Eubazus* Nees, 1812 (Brachistinae). We also redescribe and illustrate a species of *Blacus*, *B. (Electroblacus) facialis* Brues, 1933 (Brachistinae: Blacini), and provide morphological notes and photographs of a male of an unknown species of *Meteorus* Haliday, 1835 (Euphorinae).

### Material and methods

The Baltic amber specimens examined in this study came from a quarry near Yantarny, in Russia's Kaliningrad Province. Digital photographs were taken at the Instituto de Biología, Universidad Nacional Autónoma de

México (IB-UNAM) with a Leica IC 3D digital camera mounted on a Leica MZ16 microscope and using the Leica Application Suite imaging system. Image stacking was performed using Helicon Focus 5.0. Figures were created with Adobe Photoshop CS6. The terminology employed for morphological features, sculpture, and body measurements follows Belokobylskij & Maetô (2009). Wing venation nomenclature follows Belokobylskij & Maetô (2009), with the terminology of Sharkey & Wharton (1997) shown in parentheses.

Generic and suprageneric identification of the examined fossil material was performed using the following references: Achterberg (1993), Wharton *et al.* (1997), and Belokobylskij *et al.* (1998). The material used for this study is deposited in the Colección Nacional de Insectos (CNIN), Instituto de Biología, Universidad Nacional Autónoma de México (IBUNAM), México City, México.

## Systematic palaeontology

### Class Insecta Linnaeus, 1758

### Order Hymenoptera Linnaeus, 1758

### Family Braconidae Nees, 1811

### Subfamily Doryctinae Foerster, 1863

**Remarks.** Fossil members of the braconid subfamily Doryctinae can be distinguished by the combination of the following main characters: head subrounded or weakly transverse, cyclostome depression between the mandibles and clypeus, occipital and prepectal carinae distinct, hind wing with recurrent vein (m-cu), row of spines along the fore tibia (not visible in the examined specimen), basoventral tubercle on the hind coxa often present (but absent in the examined specimen), hind femur thickened, and the presence of two dorsal nodes in the subapical part of ovipositor.

### Genus *Palaeorhoptrocentrus* Belokobylskij, 2023

**Type species.** *Palaeorhoptrocentrus kanti* Belokobylskij, 2023; by original designation.

**Remarks.** Fossil specimens of the subfamily Doryctinae are relatively common in late Eocene Baltic amber (Brues, 1933). Species of the genera *Doryctes* Haliday, 1836 (together with species of *Ontsira* Cameron, 1900, which were previously included in *Doryctes*), *Promonolexis* Brues, 1933, *Semirhytus* Szépligeti, 1902, and *Polystenus* Foerster, 1863, have been recorded from this amber deposit, though the species of the three last genera probably do not belong to Doryctinae (Belokobylskij, 2014; Belokobylskij & Manukyan, 2023).

A new braconid genus, *Palaeorhoptrocentrus* Belokobylskij, 2023, was recently described from Baltic amber (Belokobylskij & Manukyan, 2023). Here we describe a third species of this genus based on another Baltic amber specimen.

*Palaeorhoptrocentrus* can be distinguished from other extinct and extant doryctine genera by the combination of the following features: vertex of head with distinct and wide dorsal crest, first flagellar segment depressed and widened, fore wing recurrent vein (1m-cu) postfurcal and parallel vein (2CUb) not interstitial, propodeum with areas distinctly delineated by carinae, laterotergites behind second metasomal tergite not separated, and pro- and mesopleura mainly smooth.

### *Palaeorhoptrocentrus tenuicornis* sp. nov.

(Fig. 1)

<http://zoobank.org/urn:lsid:zoobank.org:act:862D0F8D-1D31-4592-8D01-F409DEA46090>

**Material.** One female (no syninclusions), JDC 8853 (UNAM collection).

**Etymology.** This species is named after “*tenuis*” (Latin for slender) and “*cornis*” (Latin for horn or projection), referring to its very slender antenna.

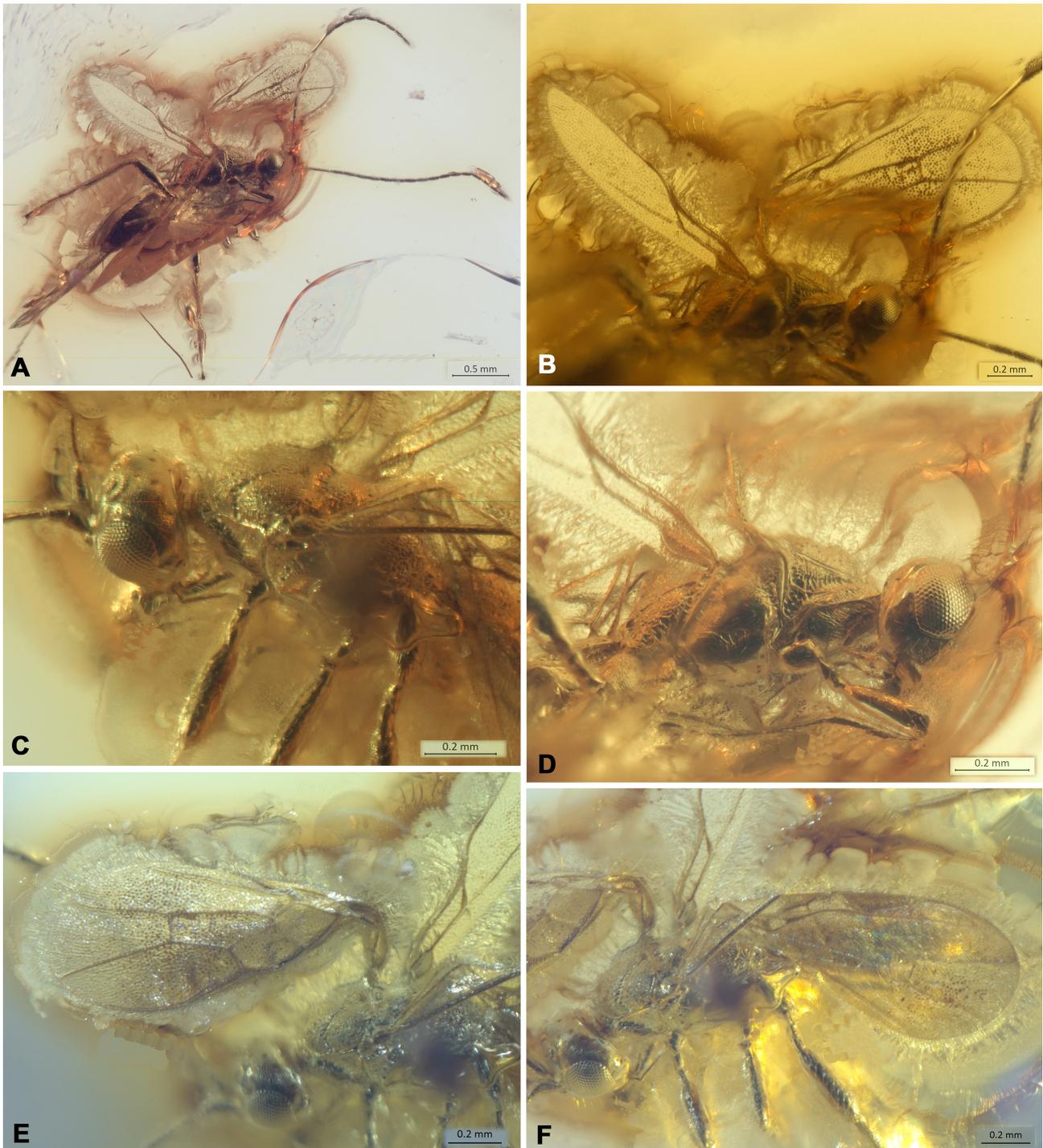
**Diagnosis.** This new species is similar to the type species of the genus, *P. kanti* Belokobylskij, 2023, but differs from it by having the first flagellar segment of antenna slender (wide in *P. kanti*), second radiomedial cell of fore wing (submarginal) narrow (rather wide in *P. kanti*), interstitial nervulus (1cu-a) (postfurcal in *P. kanti*), recurrent vein (m-cu) of hind wing interstitial (antefurcal in *P. kanti*), temple laterally smooth (sculptured in *P. kanti*), side of pronotum and metapleuron distinctly and widely sculptured (widely smooth in *P. kanti*), and precoxal sulcus crenulate-rugose (almost smooth in *P. kanti*).

**Locality and horizon.** Primorskiy quarry, Yantarny, Kaliningrad Province, Russia. Baltic amber from the Late Eocene, Priabonian range.

**Description.** Female. Body length 2.0 mm; fore wing length 1.5 mm.

**Head.** Head distinctly transverse, its height ~1.3 times medial length. Occiput weakly concave. Transverse diameter of eye medially almost 2.0 times longer than temple (lateral view). Ocelli small. Eye 1.3 times as high as broad (lateral view). Malar space about 0.4 times height of eye. Maxillary palpus long.

**Antenna.** Antenna 20-segmented, slender. Scape 1.6 times longer than maximum width, 1.5 times longer than pedicel. First flagellar segment perhaps not wide (poorly visible), ~5.0 times longer than its maximum width; second flagellar segment narrow. Penultimate flagellar segment 4.0 times longer than its maximum width, almost as long as apical flagellar segment; latter acuminate apically.



**FIGURE 1.** *Palaeorhoptrocentrus tenuicornis* sp. nov., holotype, female, Baltic amber, JDC 8853. **A**, Habitus, lateral view. **B**, Head, mesosoma and wings, lateral view. **C**, Head and mesosoma, dorso-lateral view. **D**, Head, basal segments of antenna and mesosoma, lateral view. **E, F**, Wings.

*Mesosoma.* Mesosoma long, 2.1 times longer than its maximum height. Neck of prothorax relatively short. Mesoscutum distinctly curved and elevated above pronotum, its median lobe slightly protruding forward, evenly curved anteriorly, without lateral corners. Notauli distinct and complete. Prescutellar depression (scutellar sulcus) relatively long, ~0.3 times as long as scutellum,

rugulose, with several distinct carinae. Subalar depression relatively shallow, rugose. Precoxal sulcus distinct, short, crenulate-rugose. Lateral carinae between propodeum and metapleuron distinct and complete.

*Wings.* Fore wing wide, 2.7 times longer than its maximum width. Pterostigma wedge-shaped, ~4.0 times longer than its width. Radial vein (r) arising from basal

0.3 of pterostigma. Metacarp (R1a) 1.3 times longer than pterostigma. First (r) and second (3RSa) radial abscissae forming slight obtuse angle; first abscissa (r) 0.8 times as long as maximum width of pterostigma. Second radial abscissa (3RSa) 2.5 times longer than first abscissa (r), 0.5 times as long as almost straight third abscissa (3RSb), 1.2 times longer than the straight first radiomedial vein (2RS). Second radiomedial (submarginal) cell relatively narrow and middle length, 2.8 times longer than its maximum width, 1.9 times longer than brachial (first subdiscal) cell. Recurrent vein (1m-cu) 0.5 times as long as first radiomedial vein (2RS), subparallel posteriorly with basal vein (1M). Discoidal (first discal) cell rather short, 1.6 times longer than its maximum width. Nervulus (1cu-a) interstitial. Parallel vein (2CUb) weakly curved basally, arising almost from middle of the vein (2CUa) closed brachial (subdiscal) cell distally. Brachial (subdiscal) cell relatively short and narrow. Hind wing 5.5 times longer than its maximum width, with dense long setae along its posterior margin. First costal abscissa (C+Sc+R) 0.6 times as long as second abscissa (SC+R). First abscissa of mediocubital vein (M+CU) 0.7–0.8 times as long as second abscissa (1M). Recurrent vein (m-cu) present, distinctly, oblique, interstitial to basal vein (1r-m).

*Legs.* Hind coxa 1.4 times longer than its maximum width. Hind femur 3.2 times longer than its width. Hind tarsus 1.1 times longer than hind tibia. Hind basitarsus 0.55 times as long as second to fifth segments combined. Second segment of hind tarsus 0.6 times as long as basitarsus, 1.4 times longer than fifth segment (without pretarsus).

*Metasoma.* Metasoma slightly shorter than head and mesosoma combined. First metasomal tergite elongate, almost as long as propodeum. Ovipositor straight; ovipositor sheath about as long as metasoma, 1.35 times longer than mesosoma, 0.6 times as long as fore wing.

*Sculpture and pubescence.* Vertex densely granulate, granulae usually situated in dense transversely lines; temple finely granulate upper, smooth at lowest part. Mesoscutum distinctly densely granulate. Mesopleuron smooth medially, reticulate-granulate marginally; scutellum densely granulate. Metapleuron entirely rugose-reticulate. Propodeum rugulose-reticulate, with long and wide antero-lateral areas; areola invisible. Hind coxa dorsally granulate-reticulate with rugosity; hind femur smooth. First metasomal tergite rugose-striate. Second tergite perhaps smooth. Hind tibia with rather sparse and middle length semi-erect setae, their length about 0.7 times maximum width of tibia.

*Colour.* Body almost entirely dark brown to black. Antenna and legs dark brown. Fore wing hyaline. Pterostigma entirely brown.

Male: Unknown.

## Key to species of the genus *Palaeorhoptrocentrus* Belokobylskij, 2023

1. Vertex smooth. Antenna setiform.—First flagellar segment not widened, about 6.0 times longer than its maximum width. Propodeum without areas delineated by carinae. Ovipositor sheath as long as or slightly longer than metasoma. Body length 2.2–2.5 mm.....*P. tertiaria* (Brues, 1933)
- Vertex sculptured, densely transversely striate or granulate with granulae situated in the transverse lines. Antenna filiform..... 2
2. Temple laterally smooth. First flagellar segment about 5.0 times longer than its maximum width. Precoxal sulcus crenulate-rugose. Second radiomedial (submarginal) cell of fore wing relatively narrow and middle length, 2.8 times longer than its maximum width. Nervulus (1cu-a) interstitial. Recurrent vein (m-cu) of hind wing interstitial to basal vein (1r-m). Side of pronotum and metapleuron distinctly and widely sculptured. Body length 2.0 mm.....  
.....*P. tenuicornis* **sp. nov.**
- Temple laterally densely reticulate-granulate. First flagellar segment about 4.0 times longer than its maximum width. Precoxal sulcus smooth. Second radiomedial (submarginal) cell of fore wing wide and relatively long, 2.4 times longer than its maximum width. Nervulus (1cu-a) strongly postfurcal. Recurrent vein (m-cu) of hind wing distinctly antefurcal to basal vein (1r-m). Side of pronotum and metapleuron only partly sculptured, widely almost smooth. Body length 2.0–2.3 mm..... *P. kanti* Belokobylskij, 2023

## Subfamily Brachistinae Foerster, 1863

**Remarks.** Members of the subfamily Brachistinae can be distinguished by a combination of the following morphological features: cyclostome depression between mandibles and clypeus absent, occipital and prepectal carinae distinct and usually complete, notauli distinct and complete, fore wing with second radiomedial vein (r-m) present or not, discoidal (discal) cell sessile anteriorly (on parastigma), recurrent vein (1m-cu) antefurcal to first radiomedial vein (2RS), brachial (subdiscal) cell distally closed but often open, hind wing with recurrent vein (m-cu) absent, claws usually simple but rarely with basal lobe, and ovipositor apically simple, without dorsal nodes and ventral saw.

## Tribe Diospilini

### Genus *Taphaeus* Wesmael, 1835

**Remarks.** The species of the genus *Taphaeus* is characterised by having the occipital carina fused below with the hypostomal carina, second radiomedial vein (r-m) present, second radiomedial (submarginal) cell short and narrowed towards pterostigma, brachial (subdiscal) cell distally closed by the brachial vein (2cu-a), both transverse anal veins (1a, 2a) of fore wing present (not visible in our examined material), second metasomal tergite smooth, claw simple, and ovipositor long.

**Type species.** *Taphaeus irregularis* Wesmael, 1835 (= *Ichneumon hiator* Thunberg, 1822).

**Remarks.** Three fossil species of the genus *Taphaeus* have been previously described. Two of these species were described from incomplete imprints: *Taphaeus cervicalis* (Cockerell, 1921), which was originally included in *Sigalphus* Latreille, 1802 from the Oligocene Bembridge Marls (Cockerell, 1921) and later transferred to *Taphaeus* (Belokobylskij, 2014); and *T. longicornis* (Statz, 1936), originally described within *Aspicolpus* Wesmael, 1838 from near the Oligocene/Miocene boundary of Rott in Germany (Statz, 1936) and subsequently transferred to *Taphaeus* by Belokobylskij (2014). Only one species, *T. praecox* Brues, 1923, was found in late Eocene Baltic amber (Brues, 1923). Additional species that perhaps belong to *Taphaeus* have been described within *Microtypus* Ratzeburg, 1848 by Brues (1933, 1939), who had a broader concept of *Microtypus* and included in this genus several species with a wide and trapezoid (not [sub]triangular) second radiomedial (submarginal) cell. Further examination of the type material of these species is thus necessary to clarify the generic limits between *Taphaeus* and *Microtypus*.

***Taphaeus obscurus* Belokobylskij & Zaldívar-Riverón, sp. nov.**

(Fig. 2)

<http://zoobank.org/urn:lsid:zoobank.org:act:3218A885-0698-41D2-BF6B-E38BECFE738A>

**Material.** One female (with plant remains as syninclusions), JDC 8800 (UNAM collection).

**Etymology.** This species is named based on the Latin word “*obscurus*”, meaning dark, which refers to its dark coloration of body and infuscation of the fore wing.

**Comparative diagnosis.** This species is similar to *T. praecox* Brues, 1923 described from Baltic amber. However, the new species differs from the latter in having the head less transverse, about 2.0 times as wide as long medially (broadly transverse, about 3.0 times as wide as long medially in *T. praecox*), the first flagellar segment 2.2 times longer than its maximum width (4.0 times in *T. praecox*), the penultimate segment of antenna almost as long as its maximum width (2.0 times longer in *T. praecox*), and the second tergite 0.7 times as long as the first tergite (almost equal to the first tergite in *T. praecox*). We could not compare the morphological features of the new species with those observed for the two species of *Taphaeus* that were described from incomplete imprints, *T. cervicalis* (Cockerell) and *T. longicornis* (Statz), since their description was considerably short, and the figures were not detailed.

**Locality and horizon.** Primorskiy quarry, Yantarny, Kaliningrad Province, Russia. Baltic amber from the Late Eocene, Priabonian range.

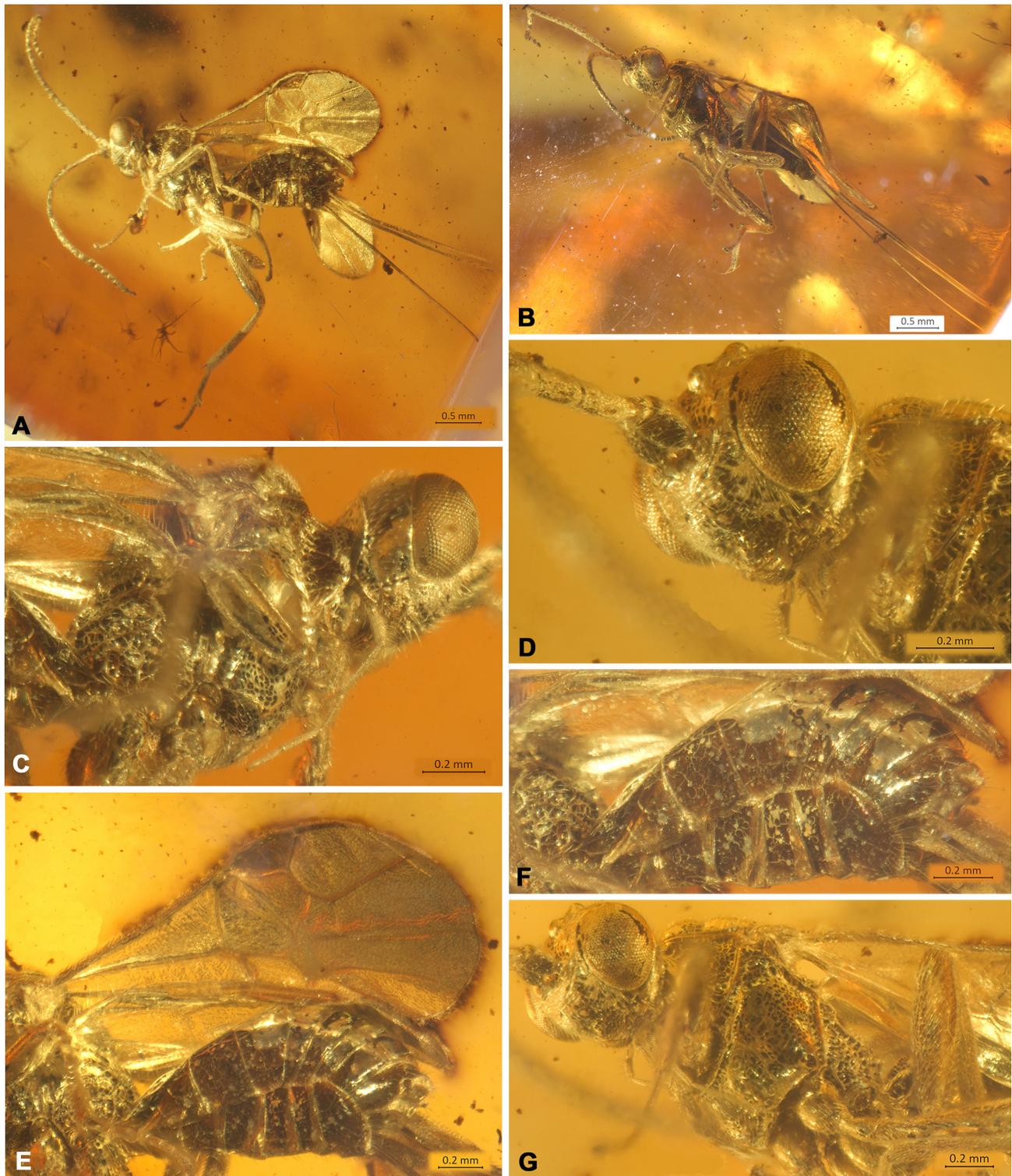
**Description.** Female. Body length 2.9 mm; fore wing length 2.7 mm.

**Head.** Head transverse. Ocelli large and distinctly convex. Frons weakly concave. Eye high and broad, 1.25 times as high as broad (lateral view). Temple relatively short, transverse diameter of eye (lateral view) ~2.5 times longer than temple. Face convex, especially medially. Clypeal suture distinct. Clypeus weakly convex; its ventral margin weakly convex. Malar suture distinct. Malar space rather short, almost equal to base of mandible, about 0.2 times as high as eye. Occipital carina strong, complete, joined below with hypostomal carina distinctly upper than base of mandible. Hypostomal keel wide. Maxillary palp long and slender.

**Antenna.** Antenna 26-segmented, weakly thickened, filiform, about as long as body, its subapical segments short, partly subsquare. Scape relatively short and wide, ~1.6 times longer than maximum width. First flagellar segment 2.2 times longer than its maximum width, 1.2–1.3 times longer than second segments. Penultimate segment as long as its maximum width, 0.7 times as long as distinctly acuminate apical segment.

**Mesosoma.** Mesosoma relatively short, ~1.7 times longer than its maximum height. Mesoscutum highly curved and elevated above prothorax. Median lobe of mesoscutum slightly protruding forward, curved convex anteriorly. Notauli perhaps complete, deep, and sculptured. Subalar depression shallow and relatively narrow, reticulate. Prepectal carina high and complete. Precoxal sulcus present, wide, sinuate, sculptured. Postpectal carina present and coarse. Mesometapleural suture coarsely and densely crenulate. Propodeum with short and thick postero-lateral tubercles.

**Wings.** Fore wing ~2.5 times longer than its maximum width. Pterostigma wide and short, ~2.5 times longer than its width. Metacarp (R1a) 1.3 times longer than pterostigma. Radial (marginal) cell wide, not shortened, ~2.0 times longer than maximum width. Radial vein (r) arising behind middle of pterostigma. First (r) and second (3RSa) radial abscissae forming slightly obtuse angle; first abscissa (r) 0.7 times as long as maximum width of pterostigma, about as long as second radial abscissa (3RSa), 0.6 times as long as the weakly sinuate first radiomedial vein (2RS). Third radial abscissa (3RSb) entirely straight, 4.2 times longer than second radial abscissa (3RSa). Recurrent vein (1m-cu) antefurcal, 0.5 times as long as first radiomedial vein (2RS), distinctly convergent posteriorly with basal vein (1M). Discoidal (first discal) cell narrowly sessile anteriorly, almost as long as its maximum width. Distance between basal vein (1M) and nervulus (1cu-a) about 0.6 times nervulus (1cu-a) length. Brachial (subdiscal) cell wide and short. Transverse anal vein (1a and 2a) not visible. Hind wing. Submedial (subbasal) cell large.



**FIGURE 2.** *Taphaeus obscurus* sp. nov., holotype, female, Baltic amber, JDC 8800. **A**, Habitus, ventro-lateral view. **B**, Habitus, lateral view. **C**, Head and mesosoma, lateral view. **D**, Head, antero-lateral view. **E**, Fore wing, propodeum and metasoma, lateral view. **F**, Propodeum and metasoma, lateral view. **G**, Head and mesosoma, antero-ventro-lateral view.

*Legs.* Hind coxa ~1.5 times longer than wide. Hind femur widened, ~4.5 times longer than its width. Hind tibia weakly thickened; its inner spur 0.4 times as long as hind basitarsus. Hind tarsus 0.9 times as long as hind tibia; second tarsal segment 0.4 times as long as basitarsus. Claw simple, relatively short, and thickened.

*Metasoma.* Metasoma weakly compressed laterally, slightly longer than head and mesosoma combined; tergites behind first one without separated laterotergites; spiracles situated on middle of lateral surfaces tergites. First metasomal tergite slightly elongated, 0.8 times as long as second and third tergites combined, about as long

as propodeum; with dorsople. Suture between second and third tergites present but fine (lateral view). Second tergite ~0.7 times as long as third tergite. Ovipositor long, its sheath 1.3 times longer than mesosoma, 0.9 times longer than fore wing.

**Sculpture and pubescence.** Visible part of head mainly smooth; face medially with coarse, transverse striation at least partially; frons slightly rugulose; malar space at least partly and densely punctate. Mesoscutum perhaps mainly punctate. Mesopleuron mainly smooth. Metapleuron coarsely rugose-reticulate. Propodeum without visible areas delineated by carinae, entirely coarsely rugulose-reticulate. Hind coxa mainly rugulose-reticulate, smooth posteriorly. Hind femur smooth. First metasomal tergite with high sublateral carinae, at least partly rugose. Second and following tergites entirely smooth. Mesoscutum almost entirely covered by dense and relatively short, semi-erect white setae. Hind tibia with dense and short setae.

**Colour.** Body mainly dark brown to black. Antennae and most part of legs dark brown to black, perhaps hind tibia pale in basal 0.4. Fore wing faintly infuscate. Pterostigma entirely brown.

Male: Unknown.

## Tribe Brachistini

### Genus *Eubazus* Nees, 1812

**Remarks.** Members of the genus *Eubazus* are characterised by having the second radiomedial vein (r-m) of fore wing absent and second radiomedial (submarginal) cell not developed, brachial (subdiscal) cell distally closed by brachial vein (2cu-a), transverse anal veins (1a and 2a) of fore wing absent, submedial (subbasal) cell of hind wing long, second metasomal tergite often smooth or only sometimes sculptured, claws simple, and ovipositor long and evenly narrowed apically.

**Type species.** *Eubazus pallipes* Nees, 1812; by subsequent designation by Viereck, 1914: 55.

**Remarks.** In the fossil record, members of the genus *Eubazus* Nees, 1812 are the most common representatives of the tribe Brachistini. Among them are *E. crassicornis* (Brues, 1933) and *E. gracilicornis* (Brues, 1939), both described from Baltic amber within *Blacus* Nees, 1819 (Brues, 1933, 1939; Achterberg, 1982); and *E. normalis* (Brues, 1923) (Baltic amber) and *E. wilmattae* (Brues, 1910) (Florissant) described within *Brachistes* Wesmæl, 1835 and *Calyptus* Haliday, 1835, respectively (Brues, 1910, 1923; Belokobylskij, 2014). Five species attributed to *Eubazus*, *E.?* *brodiei* Belokobylskij, 2014; *E. flavistigma* Belokobylskij, 2014; *E.?* *grandareola* Belokobylskij, 2014; *E.?* *hooleyi* Belokobylskij, 2014; and *E. nanus* Belokobylskij, 2014, were described from

imprint fossils from the Insect Limestone, Bembridge Marls (Belokobylskij, 2014). In addition, *Hecabolus gladiator* Statz, 1936, described from an imprint fossil from Rott am Siebengebirge (Statz, 1936) and originally attributed to Doryctinae, also probably belongs to the brachistine genus *Eubazus* Nees, 1814 (Belokobylskij & Manukyan, 2023). Below we describe the fourth species of *Eubazus* from Eocene Baltic amber.

### *Eubazus electrus* Belokobylskij & Zaldívar-Riverón, sp. nov.

(Fig. 3)

<http://zoobank.org/urn:lsid:zoobank.org:act:4A3074CE-1C78-426C-ACB0-E279906CB910>

**Material.** One female (no syninclusions), JDC 4757 (UNAM collection).

**Etymology.** This new species is named based on the Greek word “*élektron*”, meaning amber, because its holotype specimen was found in Baltic amber.

**Comparative diagnosis.** This new species differs from the three previously described species of *Eubazus* from Baltic amber, *Eubazus crassicornis* (Brues, 1933), *E. gracilicornis* (Brues, 1939), and *E. normalis* (Brues, 1923), mainly by having a multisegmented (with 26 segments) antenna, vs. 17–19 segments in the other described species. Additionally, *E. electrus* sp. nov. differs from *E. crassicornis* by having an infuscate fore wing (hyaline in *E. crassicornis*); from *E. gracilicornis* by its thickened flagellar segments of antenna and weakly transverse penultimate segment (slender flagellar segments of antenna and penultimate segment elongated in *E. gracilicornis*); and from *E. normalis* by its short and wide scape (1.5 times longer than wide), first flagellar segment 3.0 times longer than wide, and ovipositor almost as long as body (scape 2.0 times longer than wide, the first flagellar segment 4.0 times longer than wide, and ovipositor as long as metasoma in *E. normalis*).

**Locality and horizon.** Primorskiy quarry, Yantarny, Kaliningrad Province, Russia. Baltic amber from the Late Eocene, Priabonian range.

**Description.** Female. Body length 2.3 mm; fore wing length 2.1 mm.

**Head.** Head (dorsolateral view) distinctly transverse, about 2.0 times wider than its medial length. Eye high and broad, ~1.2 times as high as broad (lateral view). Temple short, transverse diameter of eye (dorsolateral view) 2.7 times longer than temple. Face convex. Antennal socket weakly protruding.

**Antenna.** Antenna 26-segmented, slightly thickened, filiform, almost as long as body. Scape short and wide, 1.5 times longer than maximum width, ~1.5 times longer than wide pedicel. First segment ~3.0 times longer than its maximum width, almost as long as second segment.



**FIGURE 3.** *Eubazus electrus* sp. nov., holotype, female, Baltic amber, JDC 4757. **A**, Habitus, lateral view. **B**, Head, antenna and mesosoma, dorso-lateral view. **C**, Wings and metasoma, lateral view.

Flagellar segments in apical half subsquare or weakly transverse. Penultimate segment weakly transverse,  $\sim 0.8$  times as long as its maximum width, 0.5 times as long as weakly acuminate apical segment.

*Mesosoma.* Mesosoma short and high,  $\sim 1.5$  times longer than its maximum height. Mesoscutum distinctly curved and elevated above prothorax. Median lobe of mesoscutum slightly protruding forward. Notauli distinct anteriorly (lateral view), perhaps complete. Precoxal sulcus not visible.

*Wings.* Fore wing 2.8 times longer than its maximum width. Pterostigma relatively narrow,  $\sim 4.0$  times longer than its width. Radial vein (r) arising behind middle of

pterostigma. First (r) and second (3RSa) radial abscissae forming slightly obtuse angle; first abscissa (r) almost equal to maximum width of pterostigma, 0.15 times as long as second radial abscissa (3RSa), 0.5 times as long as first radiomedial (2RS) vein. Second radial abscissa (3RSa) distinctly curved in basal 0.3, straight on remaining part. Radial (marginal) cell wide, slightly shortened, about 2.8 times longer than maximum width. Recurrent vein (1m-cu) distinctly antefurcal, 0.5 times as long as second abscissa of medial vein ((RS+M)b), subparallel posteriorly with basal vein (1M). Discoidal (first discal) cell narrowly sessile anteriorly, 1.3 times longer than its maximum width. Distance between basal

vein (1M) and nervulus (1cu-a) 0.6 times nervulus (1cu-a) length. Brachial (subdiscal) cell wide. Hind wing ~4.3 times longer than its maximum width.

*Legs.* Hind femur relatively slender, ~4.5 times longer than its width. Hind tibia only slightly widened towards apex. Hind tarsus almost as long as hind tibia. Hind basitarsus 0.6 times as long as remaining segments combined. Second segment of hind tarsus 0.4 times as long as basitarsus, almost as long as fifth segment (without pretarsus). Hind claw relatively long and curved.

*Metasoma.* Metasoma slightly compressed laterally, slightly longer than mesosoma; tergite behind first one without separated laterotergites. First metasomal tergite slightly elongated, ~1.3 times longer than its posterior width. Suture between second and third tergites present but weak. Second tergite perhaps as long as third tergite (poorly visible). Ovipositor slender, evenly narrowed distally, without apical armament. Ovipositor sheath long, about as long as body, 1.1 times longer than fore wing.

*Sculpture and pubescence.* Visible part of head smooth. Side of prothorax densely rugose-reticulate. Mesoscutum densely punctate-reticulate anteriorly (especially near notauli), punctate on remaining part. Mesopleuron almost entirely smooth. Propodeum at least partly rugulose-reticulate. Hind coxa dorsally densely rugulose; hind femur smooth. First metasomal tergite without visibly dorsal carinae, almost entirely rugose-reticulate. Second and following tergites entirely smooth. Hind tibia in with dense and short setae.

*Colour.* Body dark brown to black. Antenna mainly black, but brown basally. Legs dark brown. Fore wing faintly infusate. Pterostigma entirely brown.

Male: Unknown.

### Key to species of the genus *Eubazus* Nees, 1812 from Baltic amber

1. Antenna 26-segmented. Fore wing infusate. Body length 2.3 mm..... *E. electrus* sp. nov.
- . Antenna 17–18-segmented. Fore wing hyaline..... 2
2. Penultimate segment elongate, 1.3 times longer than its width. Malar space high, almost equal to basal width of mandible.—First flagellar segment about 4.0 times longer than maximum width. Body length 2.3 mm.....  
.....*E. gracilicornis* (Brues, 1939)
- . Penultimate segment square, as long as its width. Malar space short, much less than basal width of mandible..... 3
3. First flagellar segment about 4.0 times longer than maximum width. Ovipositor sheaths as long as metasoma. Body length 2.5 mm.....*E. normalis* (Brues, 1923)
- . First flagellar segment about 3.0 times longer than maximum width. Ovipositor sheaths as long as mesosoma and metasoma combined. Body length 1.6–2.3 mm.....  
.....*E. crassicornis* (Brues, 1933)

## Tribe Blacini

### Genus *Blacus* Nees, 1818

**Remarks.** Members of the genus *Blacus* are characterised by having antennae often 16–17-segmented, thickened, and moniliform; fore wing with second radiomedial vein (r-m) absent and the second radiomedial (submarginal) cell not developed; brachial (subdiscal) cell distally open; transverse anal veins (1a, 2a) absent; propodeum without areolation and entirely rugose-reticulate; second metasomal tergite always smooth or rarely partly sculptured; claws simple; and ovipositor short. A previous revision of the fossil species of *Blacus* Nees, 1818 enabled us to propose new combinations and helped us to provide a key to the valid fossil species of the genus (Achterberg, 1982). The author had kept the following species in this genus: *B. facialis* (Brues, 1933), *B. andreei* Brues, 1933, *B. fritschii* Brues, 1933, and *B. multiarticulatiformis* Shenefelt, 1969 (originally named as *B. multiarticulatus* Brues, 1923). However, the multisegmented antenna and long ovipositor of the species redescribed here raises serious doubts about their generic placement. Additionally, the late Eocene genus and species *Promonolexis klebsi* Brues, 1933 from Baltic amber was originally assigned to Doryctinae but without mentioning in the text nor in the figure the hypostomal cavity on the head. Based on its remaining external morphological features, this species also probably belongs to the brachistine genus *Blacus* Nees, 1818 (Belokobylskij & Manukyan, 2023).

**Type species.** *Bracon humilis* Nees, 1811; by subsequent designation (Haliday, 1840: 62).

### *Blacus* (*Electroblacus*) *facialis* Brues, 1933

(Fig. 4)

*Electroblacus facialis* Brues, 1933: 86.

*Blacus* (*Electroblacus*) *facialis*: Achterberg, 1982: 94; Yu *et al.*, 2016.

**Material.** One female (no syninclusions), JDC 8921a (UNAM collection).

**Redescription.** Female. Body length 1.9 mm; fore wing length 1.5 mm.

*Head.* Head (lateral view) 1.5 times higher than its medial length. Eye high and rather narrow, almost 2.0 times as high as broad (lateral view). Temple long, transverse diameter of eye (lateral view) 0.7 times as long as temple. Face weakly convex. Antennal socket distinctly protruding. Malar space rather high, perhaps about 0.4 times height of eye.

*Antenna.* Antenna 16-segmented, slightly thickened, moniliform, with sparse and long setae, about 0.55 times as long as body. Scape short, ~1.6 times longer than maximum width, and ~1.7 times longer than wide pedicel.



**FIGURE 4.** *Blacus (Electroblacus) facialis* Brues, 1933. Female, Baltic amber, JDC 8921a. **A**, Habitus, lateral view. **B**, Antenna, head and mesosoma, lateral view. **C**, Wings. **D**, Mesosoma and metasoma, lateral view.

First flagellar segment short, 1.8 times longer than its maximum width, as long as second flagellar segment. Penultimate flagellar segment slightly transverse, approximately 0.8 times as long as its maximum width, 0.5 times as long as weakly acuminate apical flagellar segment.

*Mesosoma.* Mesosoma long, ~2.2 times longer than its maximum height. Mesoscutum slightly curved and

elevated above prothorax. Median lobe of mesoscutum slightly protruding forward. Notauli distinct at least anteriorly (lateral view). Subalar depression rather shallow and narrow, mainly smooth. Precoxal sulcus invisible. Mesometapleural suture distinct and densely crenulate. Propodeum evenly and distinctly convex.

*Wings.* Fore wing almost 3.0 times longer than its maximum width. Pterostigma narrow ~6.0 times longer

than its width. Radial vein (r) arising almost from middle of pterostigma. First (r) and second (3RSa) radial abscissae forming slight obtuse angle; first abscissa (r) 1.1 times longer than maximum width of pterostigma, 0.4 times as long as first radiomedial (2RS) vein. Second radial abscissa (3RSa) almost entirely straight. Radial (marginal) cell narrow, slightly shortened, about 4.0 times longer than maximum width. Recurrent vein (1m-cu) distinctly antefurcal, 0.55 times as long as first radiomedial vein (2RS), slightly convergent posteriorly with basal vein (1M). Discoidal (first discal) cell 1.5 times longer than its maximum width. Distance between basal vein (1M) and nervulus (1cu-a) about 0.5 times nervulus (1cu-a) length. Brachial (subdiscal) cell narrow. Hind wing ~4.5 times longer than its maximum width.

**Legs.** Hind coxa ~1.5 times longer than wide. Hind femur widened, ~2.8 times longer than its width. Hind tibia slightly widened towards apex. Hind tarsus almost as long as hind tibia. Hind claw relatively long.

**Metasoma.** Metasoma weakly compressed laterally, as long as head and mesosoma combined; tergite behind first one without separated laterotergites; spiracles situated on middle of lateral surfaces tergites. First metasomal tergite rather short, 0.8 times as long as second and third tergites combined, 0.9 times as long as propodeum; with dorsople. Suture between second and third tergites present but fine (lateral view). Second tergite 1.3 times longer than third tergite. Ovipositor evenly narrowed distally. Ovipositor sheath short, 0.4 times as long as metasoma, 0.25 times as long as fore wing.

**Sculpture and pubescence.** Visible part of head smooth. Mesoscutum and mesopleuron mainly smooth. Propodeum at least partly rugulose-reticulate, with at least basal medial carina and basolateral areas delineated by carinae. Hind coxa and femur smooth. First metasomal tergite with high dorsal carinae, at least partly rugose-striate. Second and following tergites entirely smooth. Mesoscutum perhaps entirely covered by rather dense and short white setae. Hind tibia in dense and short pale setae. Ovipositor sheaths covered by relatively dense, short, and pale setae.

**Colour.** Body including antennae and legs dark brown to black. Fore wing faintly infusate. Pterostigma entirely brown.

Male: Unknown.

**Remarks.** The specimen examined here was identified as *B. facialis* based on the original description of this species (Brues, 1933) and following Achterberg's (1982) revision of fossil *Blacus* species. It clearly belongs to this species since it has the following diagnostic features: antenna 16-segmented, ovipositor about as long as half of metasoma, and length of body 1.5–1.9 mm.

## Subfamily Euphorinae Foerster, 1863

### Genus *Meteorus* Haliday, 1935

**Type species.** *Ichneumon pendulator* Latreille, 1799; by subsequent designation by Haliday, 1840: 61.

**Remarks.** *Meteorus* Haliday is one most speciose euphorine genus, with numerous described living and fossil species. Four *Meteorus* species have been described from Baltic amber: *M. brevis* Brues, 1933; *M. crassicornis* Brues, 1933; *M. elongatus* Brues, 1933; and *M. interstitialis* Brues, 1933 (Brues, 1933). Three species of this genus have been described from imprints (Statz, 1938; Belokobylskij, 2014): "*Meteorus*" *longicornis* Statz, 1938, from Rott depositary in Germany (Oligocene/Miocene boundary), though it probably does not belong to this genus; *M. applanatus* Belokobylskij, 2014 and *M. crassitergum* Belokobylskij, 2014, from the Insect Limestone, Bembridge Marls (Belokobylskij, 2014). We found an additional male specimen of *Meteorus* from Baltic amber.

Member of the genus *Meteorus* are characterised by having a multisegmented antenna; fore wing with the second radiomedial vein (r-m) present; second radiomedial (submarginal) cell isolated, short, and with four or five sides; brachial (subdiscal) cell open distally; propodeum without areas; first metasomal tergite distinctly elongated, widened posteriorly and subpetiolate; second tergite usually smooth; and claws usually simple.

#### *Meteorus* sp.

(Fig. 5)

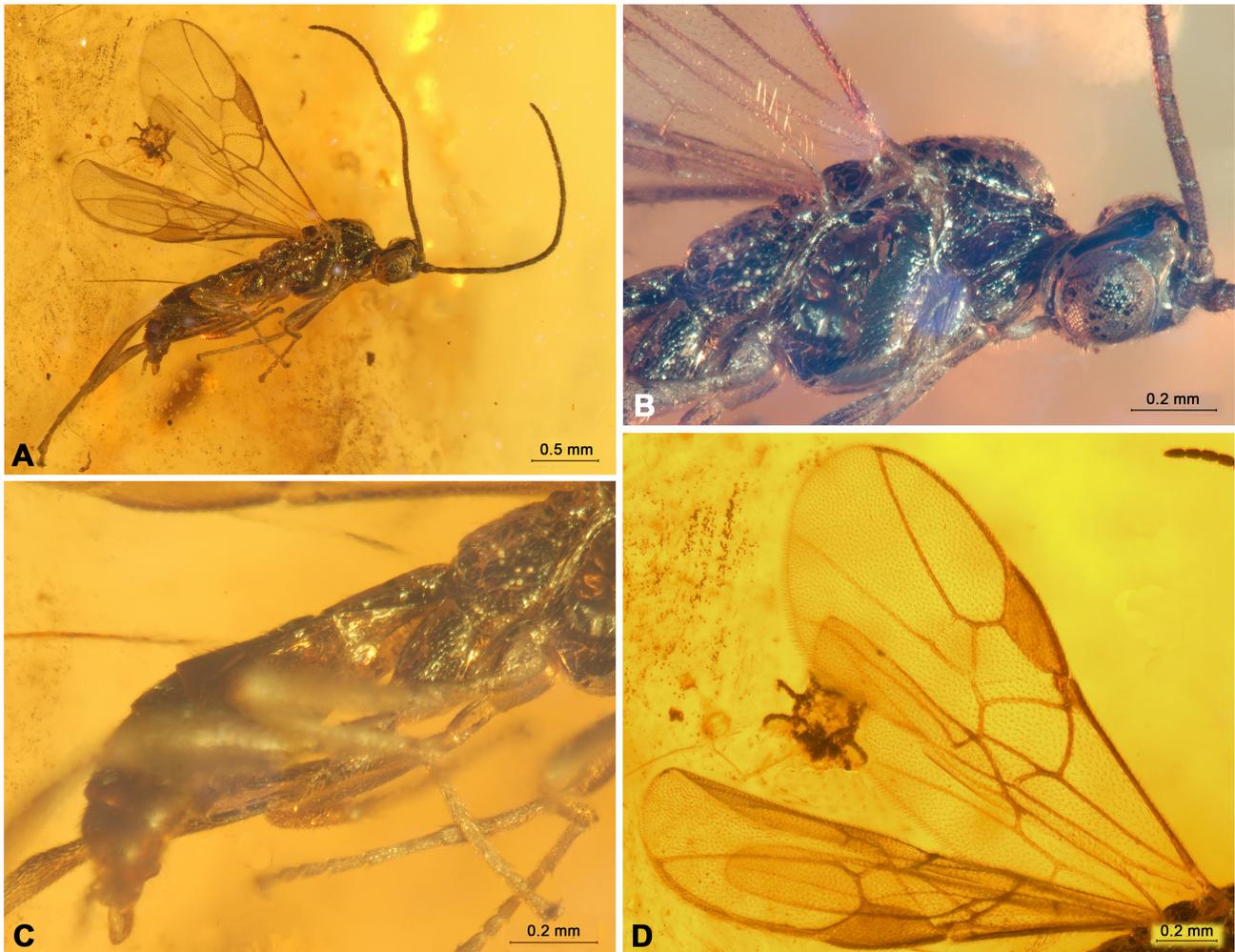
**Material.** One male (with mite as syninclusion), JDC 8811 (UNAM collection).

**Description.** Male. Body length 2.4 mm; fore wing length 1.9 mm.

**Head.** Head (dorsolateral view) transverse. Eye broad, ~1.1 times as high as broad (lateral view). Temple short, transverse diameter of eye (lateral view) ~5.5 times longer than temple.

**Antenna.** Antenna 28-segmented, slightly thickened, almost filiform. Scape short and wide, ~1.4 times longer than wide pedicel. First segment 3.3 times longer than its maximum width, 1.3 times longer than second segment. All flagellar segments elongated. Penultimate segment ~1.5 times longer than its maximum width, 0.75 times as long as obtuse apical segment.

**Mesosoma.** Mesosoma 1.7 times longer than its maximum height. Mesoscutum highly and subperpendicularly elevated above prothorax. Precoxal sulcus absent. Propodeum (lateral view) weakly narrowed in anterior 0.8 and distinctly abruptly in posterior 0.2.



**FIGURE 5.** *Meteorus* sp., male, Baltic amber, JDC 8811. **A**, Habitus, lateral view. **B**, Antenna basal, head and mesosoma, sublateral view. **C**, Propodeum and metasoma, lateral view. **D**, Wings.

**Wings.** Fore wing 2.6 times longer than its maximum width. Pterostigma wide, 2.8 times longer than its width. Radial (marginal) cell not shortened. Radial vein (r) arising weakly before middle of pterostigma. First radial abscissa (r) almost equal to second abscissa (3RSa), 0.5 times as long as maximum width of pterostigma, 0.4 times as long as first radiomedial vein (2RS). Third radial abscissa (3RSb) almost straight, 8.5 times longer than second abscissa (3RSa). Recurrent vein (1m-cu) strongly antefurcal, 0.6 times as long as first radiomedial vein (2RS), weakly convergent posteriorly with basal vein (1M). Discoidal (first discal) cell shortly petiolate anteriorly, 1.6 times longer than its maximum width. Distance between basal vein (1M) and nervulus (1cu-a) 0.5 times nervulus (1cu-a) length. Brachial (subdiscal) cell wide and relatively short. In hind wing submedial (subbasal) cell large.

**Legs.** Hind femur relatively slender, ~3.7 times longer than its width. Hind tibia distinctly thickened. Hind tarsus almost as long as hind tibia. Hind claw without basal tooth and not thickened.

**Metasoma.** First metasomal tergite elongated, ~1.2 times longer than propodeum, equal to second and third tergites combined. Suture between second and third tergites indistinct.

**Sculpture and pubescence.** Visible part of head smooth. Mesoscutum and mesopleuron almost entirely smooth. Propodeum at least partly rugulose-reticulate. Hind coxa dorsally partly rugulose. First metasomal tergite almost entirely striate. Second and following tergites perhaps smooth.

**Colour.** Body entirely black. Antenna entirely black, but brown basally. Legs reddish brown. Fore wing faintly infusate. Pterostigma entirely brown.

**Remarks.** The examined specimen of *Meteorus* from Baltic amber deposited at IBUNAM is similar to *M. interstitialis* Brues, 1933 by its relative slender antenna and the “four sided” second radiomedial (submarginal) cell of fore wing (Brues, 1933: 100). However, our examined species mainly differs from the latter species by its strongly antefurcal position of

recurrent vein (1m-cu) of the fore wing (interstitial to the first radiomedial vein (2RS) in *M. interstitialis*). We therefore believe that it actually represents an undescribed species, though a female specimen is necessary before we can describe it.

## Discussion

More than 100 fossil braconid species have been described from late Eocene Baltic amber, and this amber represents the richest source of invertebrates found in fossilised resin. Helping to fuel this biodiversity was a humid warm-temperate climate in the areas where Baltic amber formed, as well as a variety of habitats that included coastal swamps and mesophytic conifer-angiosperm forests with meadows (Erwin, 2009; Sadowski, 2017; Sadowski *et al.*, 2017; Parisi & Fanti, 2020; Pankowski & Fanti, 2022). Our study documents additional braconid species from this amber deposit belonging to the subfamilies Doryctinae and Brachistinae (tribes Diospilini and Brachistini, respectively). The hosts of the extant members of these two subfamilies mainly are larvae of bark-boring and xylophages beetles. The extant members of *Meteorus* are predominantly endoparasitoids of lepidopteran larvae, though some species (*e.g.*, *M. corax* Marshall, 1898) are parasites of beetle larvae.

Unfortunately, some braconid taxa originally described from this Eocene deposit (*e.g.*, by Brues, 1923, 1933, 1939) were incorrectly assigned to the genera examined in this study. The loss of most of the Königsberg amber collection during World War II (Achterberg, 1982), together with the scarce morphological information included in their original descriptions and illustrations, impeded us in many cases to make a taxonomic decision for most of these taxa. However, here we redescribe and illustrate with digital photographs for the first time the female of *B. (Electroblacus) facialis* Brues, 1933, whose type material was lost during World War II. Further studies of additional material from Baltic amber will undoubtedly increase our knowledge of the braconid taxa present during the Eocene period.

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