

A new genus and three new species of fossil braconid wasps (Hymenoptera, Ichneumonoidea) from Eocene Baltic and Rovno ambers

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Abstract.—New parasitoid wasps of the family Braconidae are documented from Eocene Baltic and Rovno ambers. A new fossil genus belonging to the braconid subfamily Exothecinae, *Palaeocolastes* n. gen., with its type species *P. bruesi* n. sp., is described and illustrated from Baltic amber. This represents the first reliable fossil record for a member of Exothecinae. Two additional new species from Baltic amber are also described: *Ascogaster (Syntaphus) latitibialis* n. sp. (Cheloninae) and *Meteorus arasnitsyni* n. sp. (Euphorinae). Another fossil species, *Microtypus eocenus* n. sp. (Microtypinae), is described from coeval Rovno amber (Ukraine), representing the first braconid species described from this deposit. A new record of a female of *Diospilites brevicornis* Brues, 1933 (Diospilitinae) from Baltic amber, together with variation of some diagnostic features of the species and redescription of its subfamily and genus, are also provided.

UUID: http://zoobank.org/656cb1a3-b9cf-4696-ae24-0d4df9545101.

Introduction

Baltic amber is one of the most well-known and diverse sources of fossil insect deposits for the late Eocene period $(33.9 \pm 0.1 \text{ to} 37.2 \pm 0.1 \text{ Ma})$ (Rasnitsyn and Quicke, 2002). The original source of resin for this amber deposit probably was the pine forests that covered the Scandinavian territory during the Eocene, most of which was deposited along the eastern part of the Baltic Sea, particularly along its southern coast (Rasnitsyn and Quicke, 2002). The number of insects recovered from Baltic amber is considerably large, with >3,000 fossil insect species described so far, many of which belong to the order Hymenoptera. Rovno amber (Priabonian stage, 33.9–37.8 Ma) from Ukraine is the southern coeval of Baltic amber (Perkovsky et al., 2007; Simutnik et al., 2020).

The parasitoid wasps of the family Braconidae found in Baltic amber were primarily studied and described by Brues (1923, 1933, 1939) almost a century ago. Additional descriptions and taxonomic changes of braconid taxa from Baltic amber were subsequently made by Tobias (1987). Currently, there are >100 braconid species and 18 extinct braconid genera described from Baltic amber. In Rovno amber, however, there are far fewer records of fossil hymenopterans, which include taxa mainly belonging to the families Encyrtidae, Proctotrupidae, Formicidae, and Chrysididae (Kolyada and Perkovsky, 2011; Radchenko and Perkovsky, 2018; Martynova et al., 2019; Simutnik and Perkovsky, 2020). To date, there are no descriptions of braconid taxa from this amber deposit, despite their numerous records (E.E. Perkovsky, personal communication, 2020).

Here we describe and illustrate one new braconid genus from Baltic amber belonging to the braconid subfamily Exothecinae, *Palaeocolastes* new genus, with its type species *P. bruesi* new species, as well as two additional species from the subfamilies Cheloninae (*Ascogaster* [*Syntaphus*] *latitibialis* new species) and Euphorinae (*Meteorus arasnitsyni* new species). We also describe a new species from the subfamily Microtypinae (*Microtypus eocenus* new species) from Rovno amber. In addition, we record another female of *Diospilites brevicornis* Brues, 1933 (Diospilitinae) from Baltic amber and provide details of the variation found in some of the species' diagnostic features.

Materials and methods

The four Baltic amber specimens discussed in this paper come from a quarry near Yantarny in Russia's Kaliningrad Province. The remaining amber specimen studied here was found in the Rovno region in Ukraine. Each of the specimens was purchased from a seller (www.amberinclusions.eu) specializing in amber. The seller provided the locality information for the specimens, but had no additional information about the Rovno locality.

Some of the digital photographs were taken at the Instituto de Biología, Universidad Nacional Autónoma de México (IB-UNAM), in Mexico City, with a Leica IC 3D digital camera



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mounted on a Leica MZ16 microscope and using the Leica Application Suite imaging system. Other photographs were taken with a Canon EOS 70D digital camera mounted on an Olympus SZX10 microscope at the Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia. Image stacking was performed using Helicon Focus 5.0. Figures were created with the program Adobe Photoshop CS6.

The terminology employed for morphological features, sculpture, and body measurements follows Belokobylskij and Maetô (2009). Wing venation nomenclature follows Belokobylskij and Maetô (2009), with the terminology of Sharkey and Wharton (1997) shown in parentheses.

Repository and institutional abbreviation.—All specimens examined in this study are deposited in the Palaeontological Institute of the Russian Academy of Sciences, Moscow, Russia (PIN).

Systematic paleontology

Class Insecta Linnaeus, 1758 Order Hymenoptera Linnaeus, 1758 Family Braconidae Nees von Esenbeck, 1811 Subfamily Cheloninae Foerster, 1863

Remarks.—Members of the subfamily Cheloninae are relatively common in fossil deposits, particularly in Eocene Baltic amber (Brues, 1933; Tobias, 1987; Belokobylskij, 2014). Various species of the chelonine genera *Ascogaster* Wesmael, 1835, *Phanerotoma* Wesmael, 1838, *Chelonohelcon* Brues, 1933, and perhaps *Chelonus* Panzer, 1806 were described previously from amber deposits or imprints in sedimentary rocks (Belokobylskij, 2014).

Genus Ascogaster Wesmael, 1835

Type species.—*Ascogaster instabilis* Wesmael, 1835 (= *Chelonus abdominator* Dahlbom, 1833), by subsequent designation (Foerster, 1863).

Remarks.—The less-derived genus Ascogaster is one of the most common genera of fossil chelonines. The following species of Ascogaster have been described from Baltic amber (Brues, 1933; Tobias, 1987): A. adentata Tobias, 1987; A. dilatata Brues, 1933; A. gracilicornis Brues, 1933; A. longicauda Tobias, 1987; A. pentagona Brues, 1933; A. pinicola Brues, 1933; A. praevolans Brues, 1933; A. robusta Brues, 1933; A. rutilipes Tobias, 1987; A. submersa Brues, 1933; A. sylvestris Brues, 1933; and A. thoracica Tobias, 1987. Three Ascogaster species were described from Bembridge Marls imprints (Belokobylskij, 2014): A. brodiei Belokobylskij, 2014; A. pygmaea Belokobylskij, 2014; and A. yulei Belokobylskij, 2014. Additionally, Syntaphus wheeleri Donisthorpe, 1920, originally described as an ant from the same locality, also belongs to Ascogaster, although with a separate subgenus status (Belokobylskij, 2014). Three additional species of Chelonus Panzer, 1806 described from the Florissant Formation in Colorado, USA (Chelonus depressus Brues, 1910; C. muratus Brues, 1910; and *C. solidus* Brues, 1910) (Brues, 1910) perhaps also belong to *Ascogaster* because they do not show reliable features that help to distinguish the former genus from *Ascogaster*.

Ascogaster (Syntaphus) latitibialis Belokobylskij and Zaldívar-Riverón, new species Figure 1

Holotype.—Female, Baltic amber, # JDC 8315 (PIN collection No. 964/1327). Eastern coast of the Baltic Sea, late Eocene period $(33.9 \pm 0.1 \text{ to } 37.2 \pm 0.1 \text{ Ma})$.

Diagnosis.—This new *Ascogaster* species distinctly differs from the type species of the subgenus *Syntaphus*, *A*. (*S*.) *wheeleri* Donisthorpe, 1920, described from Bembridge Marls (latest Eocene or earliest Oligocene; Belokobylskij, 2014), by having: (1) the recurrent vein (1m-cu) of fore wing subinterstitial (versus distinctly postfurcal); (2) strongly widened hind tibia, which is ~3.5 times longer than its maximum width (versus less strongly widened, only 4.6 times longer than its maximum width); (3) mesosoma longer, 1.6 times longer than its maximum height (versus shorter, only 1.3–1.4 times longer than its maximum height); (4) precoxal sulcus ("sternaulus") distinct (versus absent); (5) propodeum with wide and short lateral corner (versus with rather long lateral processes); and (6) vertex transverse striate in posterior half (versus entirely reticulate-areolate).

Description.—Female. Body length 2.9 mm; fore wing length 2.4 mm.

Head.—Head height without mandible (lateral view) 1.3 times its maximum length. Vertex in posterior half and upper part of temple in transverse striation. Temple (lateral view) ~ 0.8 times as long as transverse diameter of eye. Maximum diameter of eye (lateral view) 1.25 times its transverse diameter. Face weakly convex, 1.5 times higher than maximum diameter of eye, about equal to basal width of mandible. Clypeus weakly convex. Mandible medium length, weakly twisted. Occipital carina dorsally and laterally distinct. Head mainly rugose-reticulate, vertex in its posterior half with coarse transverse dense carinae prolonged laterally until the middle of its temple.

Antenna.—Antenna setiform, weakly thickened before middle, 28-segmented, ~ 0.7 times as long as body. Scape almost 2.0 times longer than maximum width. First flagellar segment 2.5 times longer than apical width, 1.4 times longer than second segment. Penultimate segment 1.3 times longer than its width, almost as long as acuminate apical segment.

Mesosoma.—Mesosoma 1.6 times longer than its maximum height. Precoxal sulcus ("sternaulus") rather deep, wide, coarsely and sparsely crenulate. Pronotum laterally and mesopleuron entirely distinctly and densely areolate-reticulate. Posterior mesosternal furrow deep, crenulate, widened posteriorly. Posterior mesopleural oblique furrow with dense, wide, and coarse crenulate. Propodeum entirely areolate-reticulate, with distinct subpointed break in basal one-third, after which its



Figure 1. Ascogaster latitibialis n. sp., holotype, female. (1) Habitus, left side of amber; (2) habitus, right side of amber. Scale bars = 1 mm.

posterior part subvertical declivous; without any lateral tooth, but with a wide and short corner. Metapleuron with rather wide areolae (larger than on mesopleuron).

Wings.—Fore wing ~ 3.0 times longer than its maximum width. Radial (marginal) cell strongly shortened, rather wide, 2.8 times longer than its maximum width. Metacarpus (R1a) about as long as pterostigma, 1.4 times longer than distance from apex of radial (marginal) cell to apex of wing. Pterostigma wide, almost 3.0 times longer than maximum width. Radial vein (r) arising from 0.7 of pterostigma (distinctly behind middle). First radial abscissa (r) ~ 0.5 times as long as maximum width of pterostigma. Second radial abscissa (3RSa) 1.75 times longer than first radial abscissa (r), 0.2 times as long as the weakly curved third radial abscissa (3RSb), ~0.4 times as long as first radiomedial vein (2RS). Second radiomedial (submarginal) cell 1.8 times longer than maximum width. First medial abscissa ((RS+M)a) almost straight. Recurrent vein (m-cu) perhaps subinterstitial, 0.6 times as long as first radiomedial vein (2RS). Hind wing 4.8 times longer than its maximum width.

Legs.—Hind tibia strongly widened toward posterior third, \sim 3.5 times longer than its maximum width, finely and densely punctate, about as long as hind femur, 1.1 times longer than hind tarsus. Longest hind tibial spur 0.6 times as long as maximum width of hind tibia. Hind basitarsus 0.55 times as long as second to fifth segments combined; second segment 0.5 times as long as basitarsus, about as long as fifth segment (without pretarsus).

Metasoma.—Carapace (lateral view) with rather distinct, but not deep, first and second complete transverse sutures, almost no bend posteriorly on basal side, weakly widened toward posterior margin, the highest in posterior quarter, 3.5 times longer than its maximum height, about as long as mesosoma, 0.7 times as long as the mesosoma and head combined. First part of carapace (along upper part) 1.2 times longer than second part, 1.5 times longer than third part. Ovipositor short, its sheath about as long as the maximum width of metasomal carapace.

Color.—Body black. Palps dark brown. Antenna black. Legs mainly black, hind tibia and tarsus dark brown. Wings distinctly infuscate. Pterostigma entirely black.

Male.—Unknown.

Etymology.—This species is named after its strongly widened hind tibia.

Remarks.—The descriptions of most known fossil species of *Ascogaster* are not comprehensive and often lack distinct diagnostic characters, in many cases because of the condition or quality of the amber and especially imprints. A complete key for determination of all described fossil species of *Ascogaster* has not been created, except for a reduced key suggested by Brues (1933). However, our examined specimen has distinctly developed anterior metasomal sutures on its carapace and a very wide hind tibia, which are the main diagnostic characters of the subgenus *Syntaphus* Donisthorpe. We therefore consider this specimen as the second species of the former monotypic subgenus *Ascogaster* (*Syntaphus*).

Subfamily Diospilitinae Tobias, 1987

Diagnosis.—Hypoclypeal depression perhaps not developed. Occipital carina present, but fine, fused below with hypostomal carina. Ocelli small. Palps short, maxillary palp perhaps 5-segmented, labial palp with two or three segments. Antenna distinctly thickened and 11-segmented. First flagellar segment elongated, slender basally, and distinctly widened towards apex; second to fifth segments inverted subconical and gradually shortened; flagellar segments almost entirely with distinct and dense elongate sensillae. Mesosoma short and high, 1.5-1.6 times longer than high. Notauli, precoxal sulcus, and prepectal carina of mesosoma absent. In fore wing, pterostigma wide and subtriangular. Radial (r) vein originating almost from middle of pterostigma. Radial (marginal) cell not shortened. First abscissa of medial ((RS +M)a) and second radiomedial (r-m) veins present; first and second transverse anal veins (1a and 2a) absent. Recurrent vein (1m-cu) strongly postfurcal to first radiomedial vein (2SR). Brachial (first subdiscal) cell closed distally by brachial (2cu-a) vein, which is shorter than vein 2CUa. In hind wing, recurrent vein (m-cu) absent. First submedial (subbasal) cell large; first abscissa of mediocubital vein (M+CU) much longer than second abscissa (1M). Legs slender; all femora Trochanters and trochantelli present narrow. and distinctly separated. Hind tibia weakly thickened distally; tibial spurs short. Claw simple, but distinctly thickened basally. Metasoma sessile, without delineated laterotergites on second and following tergites. First metasomal tergite relatively short. Suture between second and third tergites present but narrow. Sternites of metasoma strongly sclerotized. Hypopygium strongly developed and distinctly protruding posteriorly. Ovipositor short, apically slender, and simple (unarmed). Visible ovipositor sheath very short, subtriangular shape.

Remarks.—This monotypic, extinct subfamily was erected by Tobias (1987) for the genus *Diospilites* Brues, 1933, which was originally described by Brues (1933) from Baltic amber.

Genus Diospilites Brues, 1933

Type species.—*Diospilites brevicornis* Brues, 1933, by monotypy and original designation (Brues, 1933, p. 98; Tobias, 1987, p. 845 [type genus of subfamily]; Yu et al., 2016 [as members of Aphidiinae: Ephedrini]).

Diagnosis.—Besides the above diagnostic features mentioned for the subfamily Diospilitinae, *Diospilites* can be distinguished by having the following features: body robust, not depressed dorso-ventrally. Head transverse and rather short. Eyes large and bare; temple slightly shorter than eye. Antennae not longer than head and mesosoma combined. First flagellar segments ~1.2 times longer than second segment. Apical segment obtuse distally and without "spine." Neck of prothorax short. Mesoscutum highly and curvedly elevated above pronotum, almost entirely covered by dense and rather short setae. Scutellum and propodeum slightly convex. Fore wing almost 2.0 times longer than its maximal width. Metacarp (R1a) 1.1 times longer than pterostigma. Second radial abscissae (3RSa) about as long as first radiomedial vein (r-m). Recurrent vein (1m-cu) short, distinctly convergent posteriorly with basal vein (1M). Discoidal (discal) cell petiolate, petiole (1RS) short. Nervulus (cu-a) distinctly postfurcal and subperpendicular. Brachial (subdiscal) cell rather short and narrow. Longitudinal anal vein (1-1A) slightly curved. In hind wing, radial vein (RS) perhaps completely absent. First abscissa of mediocubital vein (M+CU) almost 3.0 times longer than second abscissa (1M). Coxa of hind leg relatively large. All tarsi with elongated segments. Metasoma almost entirely smooth (invisibly on first tergite). Second tergite slightly longer than third one.

Remarks.—This monotypic fossil genus was described from Baltic amber by Brues (1933). A redescription of this genus and its type species for both sexes was provided by Tobias (1987).

Diospilites brevicornis Brues, 1933 Figure 2

Holotype.—Male, Baltic amber, "No. 9020, IV, No, 263" (lost).

Material.—One female, Baltic amber, # 5584 (PIN collection No. 964/1328). Specimen found on the eastern coast of the Baltic Sea, late Eocene period $(33.9 \pm 0.1 \text{ to } 37.2 \pm 0.1 \text{ Ma})$.

Variation of female.-Body length of female 2.8-3.1 mm, of fore wing 2.0 mm; in male, length of body 2.0 mm. Antenna 0.8 times as long as head and mesosoma combined. Only flagellar segments fifth to sixth narrow basally and distinctly straight or weakly widely curved toward middle of apex. Penultimate segment as long as ninth and eleven (apical). Mesosoma 1.4-1.5 times longer than maximum height. Propodeum perhaps with delineated areas. Fore wing equal to or weakly shorter than mesosoma and metasoma combined. Radial (marginal cell) not or weakly shortened. Third abscissa of radial vein (3RSb) 2.0-2.5 times longer than second abscissa (3RSa). Recurrent vein (1m-cu) almost 2.0 times longer than second abscissa of medial vein ((RS+M)b). Hind femur 1.4 times longer than fore femur; its length 4.0-4.8 times the maximum width in posterior half. Hind basitarsus 2.0-2.3 times longer than fifth segment (without pretarsus). Second and following metasomal tergites smooth.

Remarks.—The examined female of *D. brevicornis* undoubtedly belongs to the only described species of this genus. The female of this species was originally described by Brues (1933), and its male was recorded later by Tobias (1987), also from Baltic amber.

Subfamily Euphorinae Foerster, 1863

Remarks.—The subfamily Euphorinae is a diverse group of koinobiont braconid wasps with a wide variety of hosts and stages of infestation (Tobias, 1965, 1966; Shaw, 1985). Members of this group are relatively common and almost



Figure 2. Diospilites brevicornis Brues, 1933, female. Habitus, lateral view. Scale bar = 0.5 mm.

cosmopolitan. Fossil species of the tribe Meteorini have been mainly recorded from the Eocene in Baltic amber and the Bembridge Marls imprints of the Isle of Wight (United Kingdom) (Brues, 1933; Belokobylskij, 2014).

Genus Meteorus Haliday, 1835

Type species.—*Ichneumon pendulator* Latreille, 1799 (= *Ichneumon pendulus* Müller, 1776), by subsequent designation (Haliday, 1840). *Ichneumon* Linnaeus, 1758 is the type genus of the family Ichneumonidae, in which most braconid species were described during the 18th century.

Remarks.—Four species of the genus *Meteorus* Haliday, 1835 —*M. brevis* Brues, 1933; *M. crassicornis* Brues, 1933; *M. elongatus* Brues, 1933; and *M. interstitialis* Brues, 1933 were described from Eocene Baltic amber, whereas "*Meteorus*" *longicornis* Statz, 1938 was described from an imprint in the Rott deposit in Germany (near the Oligocene/ Miocene boundary). The taxonomic position of the species described from Baltic amber is clear, although the status of *M. longicornis* needs confirmation. Two additional species of this genus, *M. applanatus* Belokobylskij, 2014 and *M. crassitergum* Belokobylskij, 2014, were recently described from the Bembridge Marls imprints (Belokobylskij, 2014).

Meteorus arasnitsyni Belokobylskij and Zaldívar-Riverón, new species Figure 3

Holotype.—Female, Baltic amber, # 4641 (PIN collection No. 964/1329). Specimen found on the eastern coast of the Baltic Sea, late Eocene period $(33.9 \pm 0.1 \text{ to } 37.2 \pm 0.1 \text{ Ma})$.

Diagnosis.—This new species is very similar to the fossil species *M. applanatus* Belokobylskij, though it differs from the latter by the face having very dense erect setae (versus such setae indistinct) laterally, the anterior abscissa of basal vein (1RS) long (versus short), and the second radial abscissa (3RSa) longer than the first abscissa (r) (versus almost equal in length to it). Comparison of this taxon with recent *Meteorus* species is considerably complicated by the lack of visibility for most of the important diagnostic features that have been proposed for the genus.



Figure 3. *Meteorus arasnitsyni* n. sp., holotype, female. (1) Habitus, ventral view; scale bar = 1 mm; (2) wings; scale bar = 0.5 mm; (3) head and anterior half of mesosoma, ventral view; scale bar = 0.2 mm.

Description.—Female. Body length 4.2 mm; fore wing length 4.0 mm.

Head.—Width (dorsal view) 1.8 times its median length, 1.2 times wider than mesosoma. Temple behind eye (dorsal view) strongly and weakly roundly narrowed. Transverse diameter of eye (dorsal view) ~2.5 times length of temple. Face narrow, weakly convex, densely and almost entirely transverse striate with rugosity, with very dense, short, and erect white setae, 0.55 times as broad as transverse diameter of eye. Malar space very short. Clypeus distinctly convex, with dense and erect setae, its width 2.8 times larger than maximum height, almost equal to minimum width of face. Tentorial pits distinct and deep, distance between pits 3.5 times distance from pit to eye. Mandible rather small, not twisted. Occipital carina fused with hypostomal carina slightly higher than base of mandible.

Antenna.—Antenna perhaps filiform, ~ 0.8 times as long as body. Penultimate segment ~ 2.5 times longer than its width, 1.3 times longer than acuminate apical segment.

Mesosoma.—Mesosoma 1.8 times longer than its maximum breadth. Propleuron and side of pronotum distinctly and rather densely punctate with rugosity. Mesopleuron distinctly and rather sparsely punctate. Mesosternal furrow deep, crenulate, widened posteriorly.

Wings.—Fore wing ~ 3.0 times longer than its maximum width. Radial (marginal) cell not shortened, 3.2 times longer than maximum width. Metacarpus (R1a) 1.2 times longer than pterostigma. Radial vein (r) arising from middle of pterostigma. First radial abscissa (r) ~ 0.7 times as long as maximum width of pterostigma. Second radial abscissa (3RSa) 1.5 times longer than first radial abscissa (r), 0.2 times as long as the straight third radial abscissa (3RSb), 0.65 times as long as first radiomedial vein (2RS). First medial abscissa ((RS+M)a) straight. Recurrent vein (1m-cu) antefurcal, 0.8 times as long as first radiomedial vein (2RS), ~6.0 times longer than second medial abscissa ((RS+M)b), subparallel to basal vein (1M). Discoidal (first discal) cell ~1.5 times longer than its maximum width. Nervulus (1cu-a) distinctly postfurcal. In the hind wing, basal vein (1r-m) 1.4 times longer than second abscissa of mediocubital vein (1M), 1.1 times longer than third abscissa of costal vein (R). Radial (marginal) cell weakly narrowed distally.

Legs.—Fore femur 6.0 times longer than its maximum width. Fore tibia 1.2 times longer than fore femur, about as long as fore tarsus. Hind tibia thickened, 1.7 times longer than hind femur, almost as long as hind tarsus. Hind basitarsus 0.6 times as long as second to fifth segments combined. Second segment of hind tibia 0.5 times as long as hind basitarsus, 1.3 times longer than third segment.

Metasoma.—Metasoma 1.2 times longer than head and mesosoma combined. First tergite invisible, acrosternite relatively short and perhaps basally not fused with tergite lateral borders. Hypopygium straight along posterior margin, without emargination. Ovipositor almost straight; its sheath 0.65 times as long as metasoma, 1.1 times longer than hind tibia, 1.2 times longer than mesosoma, 0.4 times as long as fore wing.

Color.—Body mainly black. Palps brown. Antenna black apically. Legs entirely black. Wings hyaline, very faintly infuscate. Pterostigma entirely brown.

Male.—Unknown.

Etymology.—This new species is named in honor of Professor Alexandr Pavlovich Rasnitsyn, the prominent Russian hymenopterist and paleoentomologist, dedicated in celebration of his upcoming 85th birthday this year.

Remarks.—Baltic and Rott fossil species of *Meteorus* (Brues, 1933; Statz, 1938) have the recurrent (1m-cu) vein distinctly postfurcal (entering the second submarginal cell) or at least interstitial, which contrasts with the Bembridge *Meteorus* species, which have the vein 1m-cu far antefurcal (entering the first submarginal cell well before its apex). We describe here a new species of *Meteorus* from Baltic amber that also has the vein m–cu distinctly antefurcal, thus resembling the Bembridge described taxa.

Subfamily Exothecinae Foerster, 1863

Remarks.—Reliable fossil members of the subfamily Exothecinae s.s. were unknown previous to this study. Brues (1910) described the questionable exothecine *Colastes*

abrogatus (Brues, 1910) from the Florissant (early Oligocene) from an imprint originally belonging to the genus *Exothecus* Wesmael, 1838. The latter species showed features that are unusual for members of *Colastes* Haliday, 1833, namely an almost petiolate metasoma, interstitial position of both nervulus (1cu-a) and recurrent vein (1m-cu), and large second submarginal cell distinctly widened toward its apex.

Genus Palaeocolastes Belokobylskij and Zaldívar-Riverón, new genus

Type species.—Palaeocolastes bruesi Belokobylskij and Zaldívar-Riverón, n. gen n. sp., by present designation and monotypy.

Diagnosis.—As for type species, by monotypy.

Etymology.—Named after "palaeo" (Greek for "ancient") and the generic name of its most similar living genus, *Colastes*, which belongs to the subfamily Exothecinae. Gender: masculine.

Remarks.—The fossil *Colastes abrogatus* (Brues, 1910), from the early Oligocene Florissant, is very similar to this new genus based on its interstitial position of nervulus (1cu-a), and perhaps by having its parallel vein (2Cub) arising from the middle of vein 2CUa. The latter species thus probably belongs to the new genus described here. Examination of the type material of this species is therefore needed to confirm its actual generic status.

Palaeocolastes bruesi Belokobylskij and Zaldívar-Riverón, new species

Figures 4-6

Holotype.—Female, Baltic amber, # 5018 (PIN collection No. 964/1330). Specimen found on eastern coast of the Baltic Sea, late Eocene period $(33.9 \pm 0.1 \text{ to } 37.2 \pm 0.1 \text{ Ma})$.

Diagnosis.—This new monotypic genus is similar to *Colastes* Haliday, 1833 by having the hind wing with recurrent vein present and submedial cell considerably large, fore wing with second radiomedial vein present, and recurrent vein running into the first radiomedial cell, mesoscutum elevated high above pronotum, occipital carina probably present only laterally, and ovipositor evenly curved and without nodes or serrations apically. However, *Palaeocolastes* n. gen. differs from *Colastes* by the parallel vein (2CUb) of the fore wing arising almost from the middle of the vein (2CUa) and closing distally the brachial (first subdiscal) cell (versus from its posterior third), and the nervulus (1cu-a) almost interstitial (versus distinctly postfurcal).

Description.—Female. Body length 2.8 mm; fore wing length 2.7 mm.

Head.—Head not depressed, high and transverse, its maximum height 1.6 times its median length (lateral view). Occiput distinctly concave. Occipital carina present laterally and perhaps absent dorsally. Ocelli small. Head behind eyes roundly



Figure 4. Palaeocolastes bruesi n. gen. n. sp., holotype, female. (1) Habitus, lateral view; scale bar = 0.5 mm; (2) head and mesosoma, lateral view; scale bar = 0.2 mm.



Figure 5. *Palaeocolastes bruesi* n. gen. n. sp., holotype, female. (1) Head and anterior half of mesosoma, left side; (2) head and anterior half of mesosoma and fore leg, right side; (3) head and antenna, lateral view. (1, 2) Scale bar = 0.2 mm; (3) Scale bar = 0.5 mm.

narrowed. Frons almost flat. Transverse diameter of eye 3.7 times longer than temple (lateral view). Eye large, without visible emargination opposite antennal sockets, \sim 1.4 times as high as broad (lateral view). Malar suture perhaps present. Malar space 0.15 times as high as eye, \sim 0.5 times as high as basal width of mandible. Face height 0.6 times height of eye and 0.9 times width of eyes (lateral view). Clypeus almost flat, with distinct and rather long lower flange. Hypoclypeal depression rather large. Palps invisible.

Antenna.—Antenna rather slender, almost filiform, 26-segmented. Scape of antenna wide and rather long, \sim 2.0 times longer than its maximum width, without apical lobe or

basal constriction, its ventral margin (lateral view) not longer than dorsal margin. Basal flagellar segment slender. First flagellar segment subcylindrical, 5.5 times longer than its apical width, 0.9 times as long as second segment. Penultimate segments about 4.0 times longer than their width, almost as long as apical segment. Apical segment acuminate distally.

Mesosoma.—Mesosoma rather long, not depressed, its length 2.3 times its height. Neck of prothorax rather long. Pronotum dorsally almost flat, with distinct pronotal carina, mainly rugose dorsally. Mesoscutum rather highly and convex-roundly elevated above pronotum, its median lobe convex, not protruding forward, and without anterolateral corners. Notauli perhaps



Figure 6. Palaeocolastes bruesi n. gen. n. sp., holotype, female. (1) Wings; (2) metasoma and ovipositor, lateral view. Scale bars = 0.2 mm.

complete, crenulate. Prescutellar depression (scutellar sulcus) and scutellum almost invisible. Subalar depression shallow and perhaps partly (anteriorly) crenulate. Precoxal sulcus unclear, perhaps absent. Prepectal carina absent. Propodeum areolate-rugose with invisible areas; lateral tubercles absent, weakly and evenly convex (lateral view).

Wings.—Fore wing 3.3 times longer than its maximum width. Pterostigma wide, 4.3 times longer than width. Metacarpus (R1a) 1.4 times longer than pterostigma. Radial (marginal) cell not shortened, reaching apex of wing, 2.7 times longer than maximum width. Radial vein (r) arising from basal 0.45 of pterostigma. First (r) and second (3RSa) radial abscissae forming very obtuse angle. Second radial abscissa (3RSa) 2.8 times longer than first abscissa (r), 0.45 times as long as the very weakly and evenly curved third abscissa (3RSb), 1.2 times longer than the almost straight first radiomedial vein (2RS). Both radiomedial veins (2RS and r-m) present. Second radiomedial (submarginal) cell wide and rather long, slightly narrowed toward apex, 2.2 times longer than its maximum width, 1.7 times longer than the wide brachial (first subdiscal) cell. Brachial (first subdiscal) cell straight anteriorly. First medial abscissa ((RS+M)a) slightly sinuate. Recurrent vein (1m-cu) convex, antefurcal and distinctly convergent posteriorly with basal (1-M) vein, 0.7 times as long as first radiomedial vein (2RS), 0.7 times as long as basal vein (1M). Discoidal (first discal) cell rather long, 1.5 times longer than its maximum width, petiolate anteriorly, petiole (1RS) not long. Nervulus (1cu-a) weakly postfurcal. Parallel vein (2CUb) arising from middle of apical margin of brachial (second subdiscal) cell. Brachial (second subdiscal) cell short and wide, closed postero-apically by long, sclerotized and distinctly inclivous brachial vein (2cu-a). Transverse anal veins (1a and 2a) absent. Hind wing 5.5 times longer than its maximum width. Radial vein (RS) arising from basal vein (1r-m) rather far from costal vein (SC+R). Radial (marginal) cell weakly widened distally, without additional transverse vein (r). Medial (basal) cell distinctly widened toward apex, 7.0 times longer than wide, 0.4 times as long as hind wing. Nervellus (cu-a) present, slightly curved. Submedial (subbasal) cell long. First abscissa of mediocubital vein (M +CU) about as long as second abscissa (M). Recurrent vein (m-cu) present, pigmented, interstitial, long, weakly curved toward base of wing.

Legs.—Fore femur rather thick and long. Fore tarsus 1.2 times longer than fore tibia. Segments of middle tarsus long and slender. Hind coxa wide and rather long, without basoventral tooth and corner. Fore to hind femora without dorsal protuberances. Hind femur rather thick, ~4.0 times longer than width. Hind tibia widened posteriorly. Hind tibial spurs long and weakly curved. Hind tarsus slender, almost as long as hind tibia, its basitarsus 0.8 times as long as second to fifth segments combined. Second segment of hind tarsus 0.35 times as long as basitarsus, 1.25 times longer than fifth segment (without pretarsus). Claws long, weakly curved, simple.

Metasoma.—Metasoma 0.9 times as long as head and mesosoma combined. First tergite sessile, short, and perhaps wide, weakly convex (lateral view), invisible in dorsal view. Only second and at least partly third tergites with distinctly separate laterotergites (epipleura). Suture between second and third tergites present and distinct. Median length of second 1.6 times length of third tergite. Hypopygium medium sized, densely setose. Ovipositor short and weakly evenly curved, apically without nodes and serration. Ovipositor sheath thick, 0.35 times as long as metasoma, about as long as fore femur, 0.4 times as long as mesosoma, \sim 0.2 times as long as fore wing.

Sculpture and pubescence.—Head mainly smooth. Mesosoma mainly smooth. Propodeum mainly reticulate-areolate, the delineated areas invisible. Hind coxa and femur smooth. Metasoma mainly smooth (first tergite invisible dorsally). First tergite perhaps sculptured. Second and following tergites smooth.

Color.—Body almost entirely black; metasoma ventrally brown to pale brown partly. Antenna mainly black. Legs almost entirely brown. Ovipositor sheaths black. Fore and hind wings entirely and evenly infuscate. Pterostigma entirely dark brown.

Male.—Unknown.

Etymology.—This species is named after Professor Charles T. Brues, pioneer of the study of Hymenoptera from Baltic amber.

Remarks.—This species represents the first reliable fossil of the cyclostome braconid subfamily Exothecinae from Baltic amber. The Exothecinae, together with its closely related extant subfamilies Opiinae and Alysiinae, probably originated during the early Paleogene because this is the period during which there are the first reliable fossil records of these taxa (Brues, 1910; Cockerell, 1913; Théobald, 1937, Statz, 1938; Belokobylskij, 2014).

Subfamily Microtypinae Szépligeti, 1908

Remarks.—The subfamily Microtypinae includes three described genera, with *Microtypus* Ratzeburg, 1848 being the largest one (Yu et al., 2016).

Genus Microtypus Ratzeburg, 1848

Type species.—Microtypus wesmaelii Ratzeburg, 1848, by monotypy.

Remarks.---Nine species of the genus Microtypus Ratzeburg, 1848 were described by Brues (1933) from Baltic amber. However, Brues (1933, p. 73) already mentioned that some of these species "... may go into closely related genera," perhaps in the subfamily Helconinae (Diospilini). According to the original descriptions and the few illustrations provided, at least M. longicornis Brues, 1933; M. terebrator Brues, 1933; M. obliquus Brues, 1933; M. latipennis Brues, 1933; M. leviusculus Brues, 1933; and M. longicaudatus Brues, 1933 have a four-sided second radiomedial (submarginal) cell, and thus do not belong to Microtypus, but perhaps to Aspicolpus Wesmael, 1838 or some other related genera from the subfamily Helconinae. According to our revision, only M. brevicornis Brues, 1933; M. verticalis Brues, 1933; M. triangulifer Brues, 1933; and M. brevicornis Brues, 1933 actually belong to Microtypus.

Cockerell (1921) described *Diospiloides hooleyi* Cockerell, 1921 from the Bembridge Marls and placed it within the

subfamily Helconinae. However, re-examination of the type of this genus and species has shown that it actually belongs to the genus *Microtypus* (Belokobylskij, 2014).

Below, we describe a new species of *Microtypus*, which has the triangular second radiomedial (submarginal) cell of its fore wing distinctly petiolate anteriorly.

Microtypus eocenus Belokobylskij and Zaldívar-Riverón, new species Figure 7

Holotype.—Male, Rovno amber, # JDC 8207 (PIN collection No. 5820/1). Specimen found in western Ukraine (Priabonian stage, 33.9–37.8 Ma).

Diagnosis.—This new species from Rovno amber is similar to *M. triangulifer* from Baltic amber, but differs from it by having the triangular second radiomedial (submarginal) cell petiolate anteriorly (versus sessile), fore wing distinctly infuscate (versus hyaline), and pterostigma almost black (versus light brown). *Microtypus eocenus* n. sp. is similar to the extant *M. algiricus* Szepligeti, 1908 (van Achterberg, 2010), but distinctly differs from the latter species by its dark body color (versus pale brown or yellow color), 25 segments of antenna (versus 49–52 segments), and body length of 3.9 mm (versus 6.5–7.0 mm).

Description.—Male. Body length 3.9 mm; fore wing length 3.1 mm.

Head.—Head maximum height with mandibles 1.5 times its maximum median length (lateral view), smooth dorsally and laterally. Occiput distinctly convex. Head behind eyes perhaps strongly narrowed. Transverse diameter of eye \sim 4.0 times longer than temple (lateral view). Eye large, \sim 1.6 times as high as broad (lateral view). Malar space very short, \sim 0.1 times as high as the eye, \sim 0.25 times as high as basal width of mandible. Face weakly convex, its height 0.75 times height of eye and almost equal to width of eye (lateral view). Clypeus distinctly convex. Mandible wide and short.

Antenna.—Antenna distinctly thickened, setiform, with short and dense dark setae, 25-segmented, \sim 0.9 times as long as body. Scape \sim 1.5 times longer than its maximum width. First flagellar segment 1.7 times longer than its apical width, about as long as second segment. Penultimate segment 1.7 times longer than their width, 0.4 times as long as first segment, 0.9 times as long as acuminate apical segment.

Mesosoma.—Mesosoma short and high, its length 1.5 times its height. Median lobe of mesoscutum highly convex, not protruding forwards, entirely and densely setose, with rather dense punctation, without additional granulation between punctures. Notauli distinct and perhaps complete. Scutellum convex. Mesopleuron mainly smooth and partly with sparse punctation. Precoxal suture (sternaulus) distinct, wide, shallow, strongly oblique, entirely and distinctly areolate-rugose. Posterior mesopleural suture entirely coarsely crenulate. Propodeum (lateral view) strongly and almost linearly oblique from anterior onefifth to posterior margin, mainly sculptured.

Wings.—Fore wing 2.3 times longer than its maximum width, 0.7 times as long as body. Pterostigma wide, 3.6 times

longer than width. Metacarpus (R1a) 1.5 times longer than pterostigma; its second abscissa (R1b) rather short. Radial (marginal) cell not shortened, 3.3 times longer than maximum width. Radial vein (r) arising from middle of pterostigma. Second radial abscissa (3RSa+3RSb) weakly sinuate, 5.2 times longer than first abscissa (r), 4.1 times longer than the straight first radiomedial vein (2RS). Second radiomedial vein (r-m) present, but rather weakly sclerotized. Second radiomedial (submarginal) cell triangular, petiolate anteriorly, almost as long as its maximum width, 0.6 times as long as the wide brachial (first subdiscal) cell. First medial abscissa ((RS+M)a) straight. Brachial (first subdiscal) cell straight anteriorly. Recurrent vein (1m-cu) straight, 0.8 times as long as first radiomedial vein (2RS), 1.4 times longer than second medial abscissa ((RS +M)b). Basal vein (1M) distinctly curved, posteriorly convergent with recurrent vein (1m-cu). Nervulus (1cu-a) interstitial. Discoidal (first discal) cell short, sessile anteriorly, 1.25 times longer than its maximum width. Hind wing 3.8 times longer than its maximum width.

Legs.—Hind femur 4.7 times longer than width, densely punctate, and covered entirely with dense and short pale setae. Hind tibia thickened, 6.7 times longer than maximum width; longest tibial spur 0.4 times as long as hind basitarsus. Hind tarsus 0.9 times as long as hind tibia. Second segment of hind tarsus 0.4 times as long as basitarsus, 1.3 times longer than fifth segment (without pretarsus).

Metasoma.—Metasoma 1.1 times as long as head and mesosoma combined. First tergite weakly convex (lateral view), not long, ~0.9 times as long as second and third tergites combined, invisible in dorsal view, perhaps sculptured. Second suture present, complete, and distinct. Median length of second tergite about equal to length of third tergite. Tergites behind first one entirely smooth, tergite behind second tergite is almost entirely covered with dense, short, pale setae. Parameres of male genitalia large, wide, subtriangular.

Color.—Body (including antenna) entirely black. Tarsi of all legs pale, brown. Fore wing entirely and distinctly evenly infuscate, finer distally. Pterostigma entirely dark brown.

Female.—Unknown.

Etymology.—This species is named after the geological period dated for Rovno amber.

Remarks.—Only five fossil species described from Eocene Baltic amber and the Bembridge Marls impression can be confirmed as belonging to *Microtypus* Ratzeburg. The fossil genus *Microtypus* is the morphologically less-derived taxon of the subfamily Microtypinae. The main diagnostic feature of this genus (the developed closed triangular second radiomedial (submarginal) cell of the fore wing) is already present in all Eocene *Microtypus* species.

Conclusions

Of all known amber and fossil imprint deposits from the Eocene period, Baltic amber is by far the richest source of invertebrate fossils. In particular, thousands of hymenopterans have been recovered from Baltic amber, of which >100 fossil braconid



Figure 7. Microtypus eocenus n. sp., holotype, male. Habitus, lateral view. Scale bar = 1 mm.

species have been described. This study documents additional new species and one new genus of Braconidae from Baltic amber belonging to the subfamilies Cheloninae, Euphorinae, and Exothecinae. It also brings to light a new species found in Rovno amber from the subfamily Microtypinae, which represents the first braconid species described from this amber deposit.

The new fossil braconid genus described here from the Eocene period, *Palaeocolastes* n. gen., morphologically resembles the widely distributed, extant exothecine genus *Colastes* Haliday. This new genus represents the first reliable record of

a member of the braconid subfamily Exhotecinae in the fossil fauna. Moreover, the discovery of the second chelonine species of the subgenus *Syntaphus* Donisthorpe (genus *Ascogaster* Wesmael) is also of valuable taxonomic significance. The two currently known species of this subgenus are now only known from the Eocene period in Baltic amber and as an imprint fossil in the Bembridge Marls (Insect Limestone). Moreover, the female of *Diospilites brevicornis* Brues, type species and type genus of the very rare monotypic subfamily Diospilitinae, which is only known from the Eocene period, is illustrated here with digital photographs for the first time, and the variation

of some diagnostic features of the species is documented. Further studies of the Eocene fauna from Baltic, and especially Rovno, amber deposits will continue to increase our knowledge of the braconid taxa present during this geological period, and reveal important information of their morphological features and variation.

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