JHR 84: 29–43 (2021)
doi: 10.3897/jhr.84.67749
https://jhr.pensoft.net

RESEARCH ARTICLE

JOURNAL OF Hymenoptera RESEARCH
A peer-reviewed open-access journal
The International Society of Hymenopterists

Braconid parasitoids of ants (Hymenoptera, Braconidae, Euphorinae, Neoneurini) from Baltic amber with a discussion of records of fossil larvae parasitizing ant workers

Sergey A. Belokobylskij[1], Dmitry A. Dubovikoff[2], Andranik R. Manukyan[3], Dmitry M. Zharkov[2]

1 *Zoological Institute of the Russian Academy of Sciences, St Petersburg 199034, Russia* **2** *Saint Petersburg State University, 29 16th line of Vasilievskiy Island, St Petersburg 199178, Russia* **3** *Kaliningrad Amber Museum, 1 Marshal Vasilevskiy Square, Kaliningrad 236016, Russia*

Corresponding author: Sergey A. Belokobylskij (doryctes@gmail.com)

Academic editor: Vladimir Gokhman | Received 22 April 2021 | Accepted 24 May 2021 | Published 24 August 2021

http://zoobank.org/23615AA2-2FA0-4071-8B26-C5336CC42878

Citation: Belokobylskij SA, Dubovikoff DA, Manukyan AR, Zharkov DM (2021) Braconid parasitoids of ants (Hymenoptera, Braconidae, Euphorinae, Neoneurini) from Baltic amber with a discussion of records of fossil larvae parasitizing ant workers. In: Proshchalykin MYu, Gokhman VE (Eds) Hymenoptera studies through space and time: A collection of papers dedicated to the 75th anniversary of Arkady S. Lelej. Journal of Hymenoptera Research 84: 29–43. https://doi.org/10.3897/jhr.84.67749

Abstract

A new record of the fossil genus *Elasmosomites* Brues, 1933 from Baltic amber with an illustrated description of a new species, *E. arkadyleleji* **sp. nov.** and the first description of a male of *E. primordialis* Brues, 1933 are provided. A key to currently known Neoneurini genera is compiled. A new record of fossil braconid larva emerging from an ant worker of *Lasius schiefferdeckeri* Mayr, 1868 is discussed and a correction to previous determination of ant hosts from amber is included.

Keywords

ants, descriptions, fossils, Ichneumonoidea, new male, new species, parasitoid of adult ants

Introduction

The subfamily Euphorinae is a very diverse group of mostly koinobiont braconid wasps featuring a wide spectrum of host orders and their immature stages used for infestation and development of both larval and adult stages within the host (Tobias 1965, 1966; Shaw 1985). The members of this group are relatively common in nature and this subfamily has almost cosmopolitan distribution.

A detailed discussion of recorded fossil Euphorinae genera and species was provided by Belokobylskij (2014). Most fossil euphorine taxa were described from various types of amber (Brues 1933, 1937, 1939; Tobias 1987). They belong to the tribes Centistini, Euphorini, Meteorini, Neoneurini, Oncometeorini, Perilitini, Prosyntretini and Pygostolini. In addition to the rather common euphorine parasitoids of coleopterous and lepidopterous larvae from the genus *Meteorus* Haliday, 1835, imagobionts of beetles and parasitoids of bug nymphs were also recorded. Among them, there are species of the genera *Pygostolus* Haliday, 1833 of the tribe Pygostolini, *Parasyrrhizus* Brues, 1933 of the tribe Centistini; *Microctonus* Wesmael,1835, and perhaps *Onychoura* Brues, 1933 and *Meteorites* Brues, 1939 of the tribe Perilitini as well as *Leiophron* Nees, 1819 (*Euphorus* Nees, 1834) of the tribe Euphorini (Brues 1910).

Two interesting discoveries from Baltic amber include extinct taxa with unknown biologies (Tobias 1987). *Oncometeorus aduncus* Tobias, 1987 belonging to the tribe Oncometeorini Tobias, 1987 has an abnormally hook-like ovipositor. The tribe Prosyntretini Tobias, 1987 for *Prosyntretus calcaratus* Tobias, 1987 is only superficially similar to the tribe Syntretini, parasitoids of hymenopterous aculeates. Both these monotypic tribes are found exclusively in the Eocene.

The specialised and isolated euphorine tribe Neoneurini is represented by a single extinct genus *Elasmosomites* Brues, 1933 (with type species *E. primordialis* Brues, 1933) (Brues 1933). Members of this tribe are known as parasitoids of the adult ants (workers) mainly belonging to the genus *Formica* Linnaeus, 1758. Neoneurini include five extant genera: *Elasmosoma* Ruthe, 1858 (together with *Sinoneoneurus* He, Chen & van Achterberg, 1997); *Euneoneurus* Tobias & Yuldashev, 1979; *Kollasmosoma* van Achterberg & Argaman, 1993; *Neoneurus* Haliday, 1838; and *Parelasmosoma* Tobias & Yuldashev, 1979 (Tobias 1966; Tobias and Yuldashev 1979; van Achterberg and Argaman 1993; Stigenberg et al. 2015; Yu et al. 2016; Belokobylskij 2019; Li et al. 2020).

This article provides an illustrated description of the female of a new species of *Elasmosomites* and the first description of the male of *E. primordialis* Brues from Baltic amber. It also gives details of the second known record of an amber inclusion of a braconid larva emerging from an ant worker, and provides the correct determination of its host.

Material and method

Baltic amber is the most famous and most diverse deposit of fossil insects of the Late Eocene age (33.9±0.1–37.2±0.1 Mya) (Rasnitsyn and Quicke 2002). The source of the resin for these fossils is believed to be mixed pine forests that covered the Scandinavian

territory in the Eocene, with most of the collected material deposited along the eastern part of the south shore of the Baltic Sea.

During the present study, braconid specimens were examined using an Olympus SZ51 stereomicroscope. Photographs were obtained using a Canon EOS 70D digital camera mounted on an Olympus SZX10 microscope (Zoological Institute RAS, St Petersburg). A Leica M205C stereo microscope was used for photography and morphological analysis of the worker ant with an emerged larva. Subsequent image processing was performed using Helicon Focus Pro 7 software and Krita 4.4.2. Final plates were prepared in Adobe Photoshop CS6 and Inkscape 1.0.2. The X-ray micro-CT study of the ant with the emerged braconid larva was conducted at St. Petersburg University using a SkyScan1172 system. The specimen was CT scanned at 40 kV and 0.21 mA, generating a resolution of 1.99 μm pixel size and output of 2800 × 2800 pixels per slice. CT scan data were imported to the software Amira 8.0 (FEI-VSG Company) for interactive segmentation and 3D visualization.

The terminology employed for morphological features, sculpture and body measurements follows Belokobylskij and Maetô (2009). Wing venation nomenclature also follows Belokobylskij and Maetô (2009), with the terminology of van Achterberg (1993) shown in parentheses.

The material used for this study is deposited in the collection of the Kaliningrad Museum of Amber (KAM; Russia), except for the specimen with the parasitoid larva (MCZ:ENT:PALE-43618), which will be stored in the Museum of Comparative Zoology, Harvard University (MCZ, USA).

Taxonomy

Class Insecta Linnaeus, 1758
Order Hymenoptera Linnaeus, 1758
Family Braconidae Nees, 1811
Subfamily Euphorinae Foerster, 1863
Tribe Neoneurini Bengtsson, 1918

Genus *Elasmosomites* Brues, 1933
Figs 1–3

Brues 1933: 97; Belokobylskij 2014: 378; Yu et al. 2016.

Type species. *Elasmosomites primordialis* Brues, 1933, by monotypy.

Elasmosomites is a monotypic fossil genus of the euphorine tribe Neoneurini. The genus and type species were described by Brues (1933) on the basis of two female specimens from Baltic amber.

Diagnosis. Head dorsally transversely striate; mesoscutum densely punctate, mesopleuron mainly smooth. Fine occipital carina present at least laterally. Anterior angle of ocellar triangle obtuse. Maxillary palpus relatively long and slender, with 6 segments; la-

bial palpus short, perhaps with 3 segments; labrum rather large. Female antenna with 14 segments (male one with 16 segments), segments of flagellum relatively long; scape distinctly longer than pedicel, pedicel not widened apically; third antennal segment longer than scape and fourth segment. Transverse scuto-scutellar suture on mesoscutum absent; scutellar sulcus (prescutellar depression) relatively narrow, slightly curved and sparsely crenulate. Notauli and precoxal sulcus absent. Prepectal carina present laterally, absent ventrally. Radial (marginal) cell of fore wing strongly shortened, widely open apically, without additional transverse vein. Metacarp (1-R1) shorter than length of pterostigma. Three abscissae of radial vein (r, 3-SR and SR1) present; third abscissa (SR1) sclerotised (tubular) only in basal half and spectral in apical half. Second radiomedial (submarginal) cell small and pentagonal. Recurrent vein (m-cu) postfurcal to first radiomedial vein (2-SR). Discoidal (discal) cell with long petiole (1-SR). Mediocubital vein (M+CU1) almost straight, tubular but unsclerotised and not pigmented. Nervulus (cu-a) slightly inclivous. Brachial vein (CU1b) absent; brachial (subdiscal) cell open distally. Hind wing with 3 hamuli; with distinct plical lobe, anteriorly separated by a deep and narrow gap. Fore coxa enlarged, but distinctly shorter than hind coxa. Outer and inner spurs of female hind tibia slightly longer than hind basitarsus and acute apically. Fore tibia and its spur unmodified. Trochantelli of all legs distinctly differentiated from femora. Hind tarsus shorter than hind tibia. Dorsope of first metasomal tergite present but small. Female hypopygium not far retracted, apically truncate, without medial depression or long setae (hardly visible); male one medio-posteriorly with very deep and narrow split. Ovipositor sheath narrow and distinctly protruding behind tip of metasoma.

Key to genera of the tribe Neoneurini

(Updated after van Achterberg and Argaman 1993, in which morphological illustrations for the all extant genera are present).

1 Antenna of female robust, with 12 segments (that of male with 14–15 segments). Scape shorter than pedicel; third antennal segment shorter than fourth segment. Nervulus (cu-a) and metacarp (1-SRl) of fore wing absent. Outer or inner spurs of female hind tibia usually truncate apically. South Palaearctic ..... ***Kollasmosoma*** **van Achterberg & Argaman**

– Antenna of both sexes more slender, with 13–22 segments. Scape longer than pedicel; third antennal segment about as long as or longer than fourth segment. Nervulus (cu-a) and metacarp (1-SRl) of fore wing present at least basally. Spurs of hind tibia of both sexes apically acute **2**

2 Hind wing without closed cells. Female antenna with 13 segments, male one with 14 segments; female antenna shorter than head and mesosoma combined, but male antenna slightly longer. Nervulus (cu-a) of fore wing strongly reclivous. Holarctic ..... ***Elasmosoma*** **Ruthe**

– Hind wing with two closed cells. Female antenna with 14–16 segments, male one with 16–22 segments; antenna of both sexes longer than head and meso-

soma combined. Nervulus (cu-a) of fore wing subvertical to moderately reclivous **3**

3 Female antenna with 14 segments, male one with 16 segments. Metacarp (1-R1) of fore wing long, completely closing radial (marginal) cell anteriorly. First abscissa of radial vein (r) distinctly longer than second abscissa (3-SR). First medial abscissa (1-SR+M) entirely sclerotised. Occipital and prepectal carinae present laterally, but fine. Eocene, fossil ..... ***Elasmosomites*** **Brues**

– Female antenna with 15–16 segments, male one with 18–22 segments. Metacarp (1-R1) of fore wing short, not closing radial (marginal) cell at long distance anteriorly. First abscissa of radial vein (r) not longer than second abscissa (3-SR). First medial abscissa (1-SR+M) usually desclerotised in distal half. Occipital and prepectal carina completely absent **4**

4 Radial (marginal) cell of fore wing closed subapically by vertical additional vein (SRl). Antenna of both sexes with 16 segments; (very) slender, especially apically. Mesoscutum (rugulose-) coriaceous. Fore femur and tibia of female more or less compressed and sparsely setose; fore coxa enlarged, about as long as hind coxa. Holarctic..... ***Neoneurus*** **Haliday**

– Radial (marginal) cell of fore wing open apically and without vertical additional vein (SRl). Female antenna with 15 segments (unknown in *Euneoneurus*), male one with 18–22 segments (unknown in *Parelasmosoma*), antenna less slender. Mesoscutum coarsely punctate. Fore femur and tibia of female unmodified; fore coxa unmodified, shorter than hind coxa. Central Palaearctic **5**

5 Palpi rather slender, at most somewhat flattened. Maxillary palpus with 3 segments. Scutellar sulcus curved and crenulate laterally. First abscissa of medial vein (1-SR+M) (except its base) and recurrent vein (m-cu) of fore wing unsclerotised. Apical costal abscissae (veins SC+Rl and Rl) of hind wing indistinct. Uzbekistan ..... ***Euneoneurus*** **Tobias & Yuldashev**

– Palpi rather strongly flattened, lamelliform. Maxillary palpus with 2 segments. Scutellar sulcus straight and obsolescent laterally. First abscissa of medial vein (1-SR+M) and recurrent vein (m-cu) of fore wing completely sclerotised. Apical costal abscissae (veins SC+Rl and Rl) of hind wing present. Uzbekistan..... ***Parelasmosoma*** **Tobias & Yuldashev**

Elasmosomites arkadyleleji **Belokobylskij, sp. nov.**

http://zoobank.org/A2326A01-D24D-4E23-91CF-7807AF9F6F30

Fig. 1

Type material. ***Holotype***: female, Eocene Baltic amber, # BX 9/21.1 (KAM).

Description. Female. Body length 2.0 mm, fore wing length 1.6 mm.

Head**:** Relatively short and transverse in dorsal view, about 2.5 times wider than medial length. Vertex densely transverse striate. Ocelli slightly enlarged, arranged in

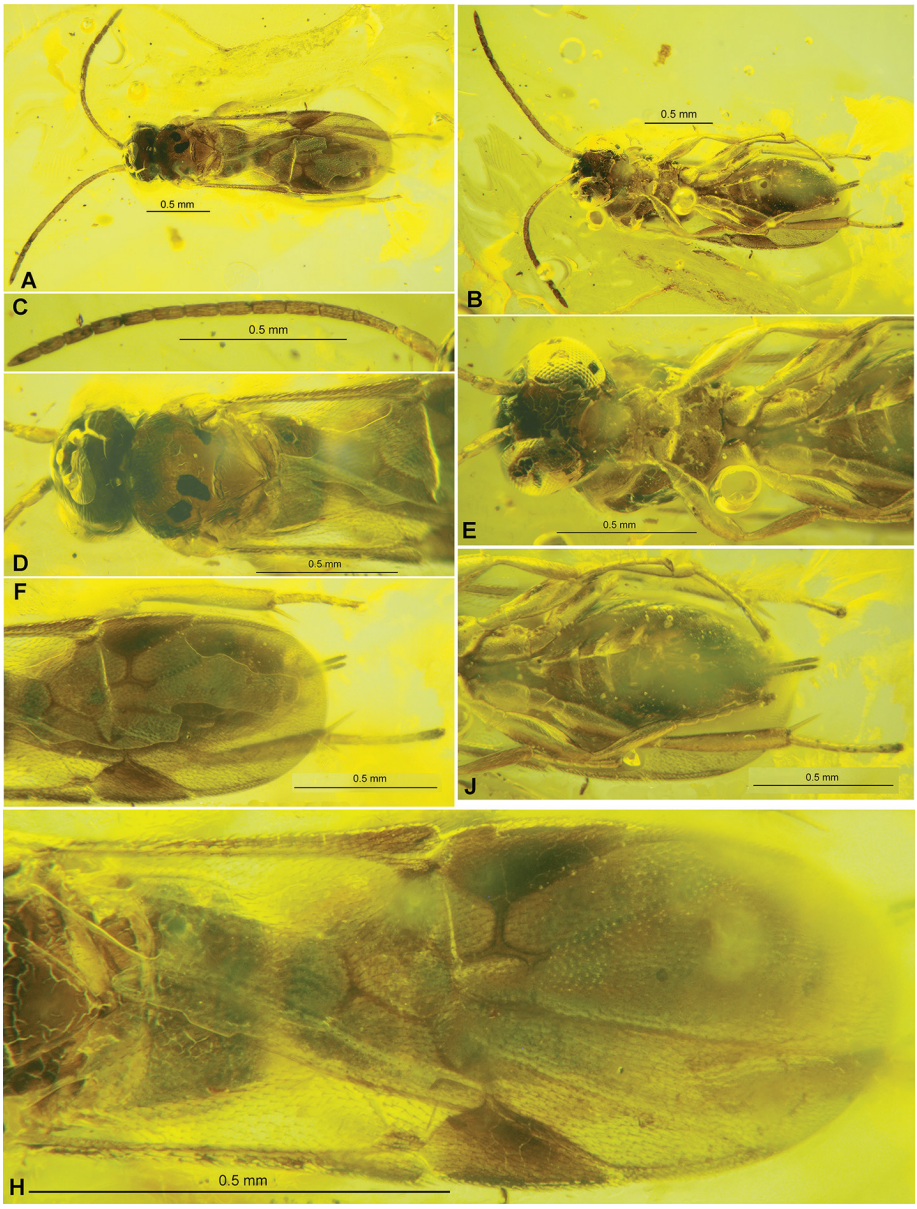

Figure 1. *Elasmosomites arkadyleleji* sp. nov. (female, holotype, Baltic amber, # BX 9/21.1) **A** habitus, dorsal view **B** habitus, ventral view **C** antenna **D** head and mesosoma, dorsal view **E** head, mesosoma and legs, ventral view **F** metasoma and distal part of fore wing, dorsal view **J** metasoma, middle and hind legs, ventral view **H** fore wing.

obtuse triangle with base 1.7 times its sides. POL about 1.6 times OD. Eye oval, approximately 1.4 times as high as broad, below slightly converging to each other. Transverse diameter of eye about 2.5 times length of temple. Malar suture invisible.

Malar space short, about 0.3 times eye height. Face slightly convex, without facial tubercles and spines, its minimum width 0.8 times medial height with clypeus, 0.7 times eye height. Clypeus distinctly curvedly emarginated on lower margin, short, its width about 6.0 times maximum height medially, almost equal to width of face. Mandible and palps not visible. Face seemingly entirely smooth.

***Antenna*:** Slightly thickened, 14-segmented, with short and rather sparse dark setosity, about 0.7 times as long as body. Scape 1.8 times longer than maximum width, about 2.2 times longer than pedicel. Length of first flagellar segment 3.7 times its maximum apical width, 1.3 times length of scape, 1.3 times length of second segment. Length of penultimate segment 1.9 times its width, 0.7 times length of acuminate apical segment.

***Mesosoma*:** Length of mesosoma 1.6 times its maximum width. Mesoscutum 1.4 times wider than its median length, seemingly densely punctate with submedian longitudinal carina in posterior third. Prescutellar depression (scutal sulcus) relatively short, with at least two distinct submedian carinae and slightly sparsely and finely crenulate. Scutellum slightly convex, about as long as wide anteriorly, seemingly slightly punctate. Mesopleuron not visible. Prepectal carina seemingly absent. Mesosoma densely and finely granulate below.

***Wings*:** Fore wing 2.7 times longer than its maximum width, its membrane entirely and densely setose. Costal vein (C+SC+R) distinctly thickened, clearly widened towards apex. Short and vestigial costal cell present distally. Pterostigma wide and relatively short, triangular, 2.3 times longer than its maximum width. Metacarp (1-R1) distinctly and entirely sclerotised, 0.8 times as long as pterostigma. Radial vein (r) arising from basal 0.3 of pterostigma. Radial (marginal) cell distinctly shortened, 3.7 times longer than its maximum width, without additional transverse vein. First radial abscissa (r) long and vertical to pterostigma, 0.6 times as long as maximum width of pterostigma. Second radial abscissa (3-SR) short, 0.8 times as long as first abscissa (r), 0.12 times as long as almost straight third abscissa (SR1), 0.7 times as long as first radiomedial vein (2-SR). Third radial abscissa (SR1) almost complete, but well sclerotised only in basal 0.5 and desclerotised in remaining apical part. Second radiomedial (submarginal) cell rather small, completely delineated by almost entirely sclerotised veins, 1.4 times longer than wide. Second radiomedial vein (r-m) straight, subvertical, desclerotised medially, 0.9 times as long as first radiomedial vein (2-SR). Discoidal (discal) cell with relatively long petiole (1-SR) anteriorly, 1.4 times longer than maximum height; petiole (1-SR) not thickened; parastigma enlarged. First medial abscissa (1-SR+M) almost straight. Recurrent vein (m-cu) short, strongly postfurcal, about 1.5 times longer than second medial abscissa (2-SR+M), 0.9 times as long as first radiomedial vein (2-SR) and second radial abscissa (3-SR). Nervulus (cu-a) strongly postfurcal, distance (1-CU1) between nervulus (cu-a) and basal vein (1-M) equal to nervulus (cu-a) length. Parallel vein (CU1a) distinctly broken basally. Hind wing not visible.

***Legs*:** Fore coxa subglobular. Trochantelli short and distinctly separated from femora on all legs. Fore femur rather wide, almost 3.0 times longer than wide, without tooth. Fore tibia without protuberances or processes, distinctly widened towards apex,

its length 4.7 times maximum width. Fore tarsus slightly longer than fore tibia. Fore tibial spur almost straight, about 0.8 times as long as fore basitarsus. Tarsal segments of middle leg elongate. Hind femur wide, elongate-oval, about 2.8 times longer than its maximum width. Hind tibia distinctly widened towards apex, about 6.0 times longer than maximum width, 1.1 times longer than femur, 0.9 times as long as hind tarsus. Both spurs of hind tibia acute apically, longest spur about as long as hind basitarsus. Hind tarsus relatively slender, all its segments of similar width and not narrowed towards apex.

***Metasoma*:** Almost twice longer than maximum width, 1.3 times longer than mesosoma; its sculpture and pubescence not visible (dorsally covered by wings). First tergite distinctly widened towards apex; its median length about 0.8 times maximum distal width. Segments behind third one distinctly projected; any sutures, if present, not visible. Sternites with distinct median keel. Ovipositor relatively short, its sheath with dense short setae, 0.4 times as long as hind tibia, about 0.2 times as long as metasoma.

***Colour*:** Body reddish brown, with a few dark spots, metasoma in posterior half pale brown. Fore and middle legs yellowish brown, hind leg reddish brown. Wings faintly and evenly infuscate; pterostigma dark brown medially and paler basally and apically.

Male. Unknown.

Comparative diagnosis. The new species differs from the type species *E. primordialis* Brues, 1933, by having the body mainly reddish brown and metasoma in posterior half pale brown (entirely black in *E. primordialis*), antenna basally distinctly pale (entirely black in *E. primordialis*), fore and middle legs yellowish brown (almost black or dark brown in *E. primordialis*), length of first flagellar segment 3.7 times its maximum width (2.8 times in *E. primordialis*), recurrent vein (m-cu) of fore wing longer, about 1.5 times longer than second medial abscissa (2-SR+M) (shorter, not longer than second medial abscissa (2-SR+M) in *E. primordialis*).

Etymology. This species is named in honour of Professor Arkady Stepanovich Lelej, the well-known Russian hymenopterist, dedicated in celebration of his 75th birthday.

Remarks. Most extant species of the tribe Neoneurini are predominantly black in colour, only sometimes legs entirely pale or with a contrasting black and white pattern. *Elasmosomites arkadyleleji* sp. nov. is the first species of the Neoneurini with mainly reddish brown body.

Elasmosomites primordialis Brues, 1933

Figs 2, 3

Brues 1933: 97; Poinar and Miller 2002: 42; Yu et al. 2016.

Material examined. 1 male, Eocene Baltic amber, # BX 9/21.2 (KAM).

Male (first description). Body length 2.5 mm, fore wing length 1.7 mm.

***Head*:** Short and transverse in dorsal view. Occipital carina laterally present but fine, below reaching lower margin of head, perhaps independently from hypostomal

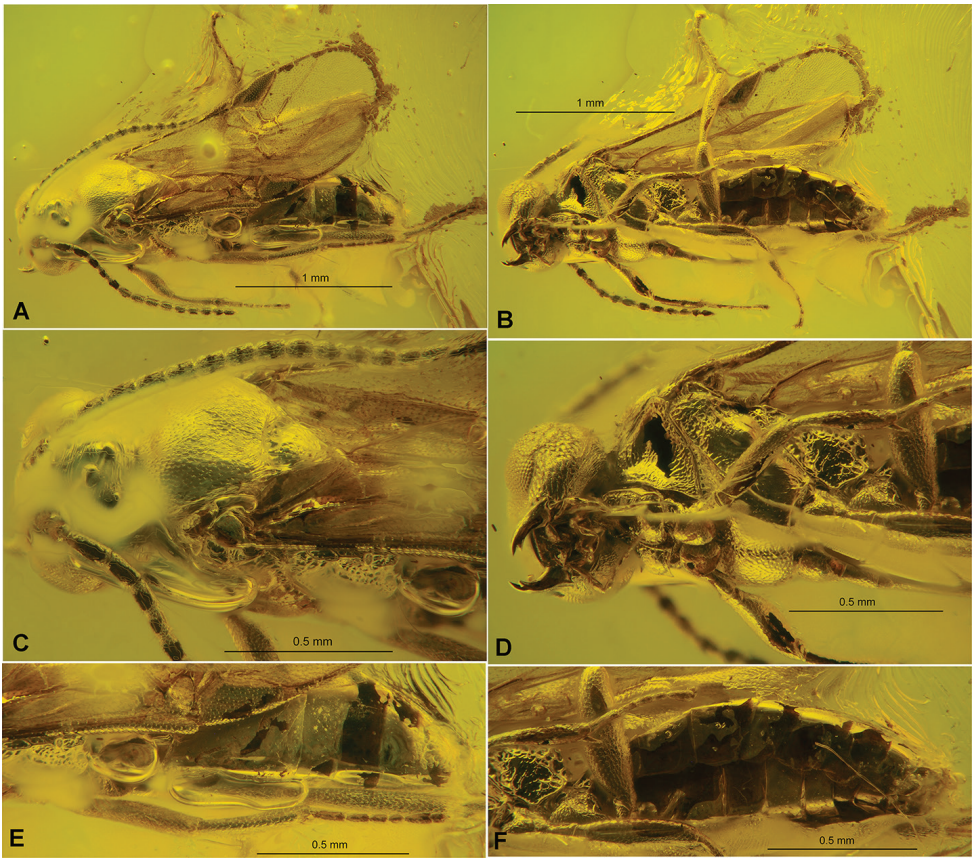

Figure 2. *Elasmosomites primordialis* Brues, 1933 (male, Baltic amber, # BX 9/21.2) **A** habitus, dorso-lateral view **B** habitus, ventro-lateral view **C** head, antenna and metasoma, dorsal view **D** head and mesosoma, ventro-lateral view **E** mesosoma, dorsal view **F** metasoma, ventral view.

carina. Ocelli slightly enlarged, arranged in obtuse triangle with base about 1.5 times its sides. POL about 2.0 times OD. Eyes enlarged, slightly converging ventrally. Malar suture absent. Malar space short, about 0.5 times basal width of mandible. Face convex, without facial tubercles and bristles. Mandible rather long, narrow, slightly twisted, with two pointed teeth, upper tooth distinctly longer than lower tooth. Maxillary palpus rather long and slender, 6-segmented, its second segment slightly thickened. Labial palpus short, perhaps 3-segmented, but third segment very short and subglobular. Vertex and frons with distinct and dense transverse and slightly curved striae. Temple relatively wide and distinctly punctate.

***Antenna*:** Relatively long, slightly thickened, 16-segmented, with short and very dense pale setosity, about 0.6 times as long as body. Scape longer than pedicel. Length of first flagellar segment 2.7 times its maximum apical width, 1.4 times length of second segment. Length of penultimate segment 1.7 times its width, 0.8 times length of acuminate apical segment.

***Mesosoma*:** Mesoscutum about 1.2 times wider than its median length, distinctly and densely punctate with very short and fine submedian longitudinal carina posteriorly. Prescutellar depression (scutal sulcus) relatively short, with several sparse crenulae. Scutellum slightly convex, weakly and sparsely punctate. Mesopleuron slightly convex, mainly smooth in the middle, with fine and sparse marginal punctation. Prepectal carina present and distinct laterally, absent ventrally. Prepectus distinctly rugulose-reticulate. Subalar depression slightly concave, narrow, areolate with oblique transverse striae. Posterior mesopleural suture shallow, narrow and distinctly crenulate. Mesosternal sulcus narrow but distinct and rugose. Metapleuron anteriorly with subvertical crenulate depression, mainly rugose-areolate and with additional reticulation; metapleural lower process short, wide and nearly round distally.

***Wings*:** Fore wing 2.6 times longer than its maximum width, with its membrane entirely and densely setose. Costal vein distinctly thickened, clearly widened towards apex. Short and vestigial costal cell present distally. Pterostigma wide and relatively short, triangular, 2.5 times longer than median width. Metacarp (1-R1) distinctly and entirely sclerotised, 0.8 times as long as pterostigma. Radial vein (r) arising from basal 0.3 of pterostigma. Radial (marginal) cell distinctly shortened, about 3.0 times longer than its maximum width. First radial abscissa (r) long and subvertical to pterostigma, 0.7 times as long as maximum width of pterostigma. Second radial abscissa (3-SR) short, 0.7 times as long as first abscissa (r), 0.5 times as long as sclerotised part of third abscissa (SR1) and 0.15 times as long as almost straight complete third abscissa (SR1), almost equal to first radiomedial vein (2-SR). Second radiomedial (submarginal) cell rather small, completely delineated by sclerotised veins, 1.7 times longer than wide. Second radiomedial vein (r-m) almost straight, slightly oblique, almost as long as first radiomedial vein (2-SR). Discoidal (discal) cell with relatively long petiole (1-SR) anteriorly, 1.6 times longer than its maximum height; parastigma enlarged. First medial abscissa (1-SR+M) very slightly sinuate. Recurrent vein (m-cu) relatively short, distinctly postfurcal, 2.5 times longer than second medial abscissa (2-SR+M), almost as long as first radiomedial vein (2-SR), about as long as second radial abscissa (3-SR). Nervulus (cu-a) distinctly postfurcal, distance (1-CU1) between nervulus (cu-a) and basal vein (1-M) 1.2 times nervulus (cu-a) length. Parallel vein (CU1a) distinctly broken basally. Hind wing poorly preserved, with 3 hamuli; its posterior margin with distinct narrow split in basal third.

***Legs*:** Fore coxa subglobular. Short trochantellus distinctly separated in all legs. Fore femur relatively narrow, 2.8 times longer than wide, apically without tooth. Fore tibia without protuberances or processes, distinctly widened towards apex, its length 5.0 times maximum width in lateral view. Fore tarsus about as long as fore tibia. Fore tibial spur slightly curved, 0.7 times as long as fore basitarsus and 0.2 times as long as fore tibia. Tarsal segments of middle leg elongate. Hind coxa dorsally slightly concave submedially, distinctly and densely punctate, evenly convex anteriorly. Hind femur wide, elongate-oval, 3.3 times longer than its maximum width. Hind tibia distinctly widened towards apex, 4.5 times longer than maximum apical width, 1.1 times longer than femur, about as long as hind tarsus. Both spurs of hind

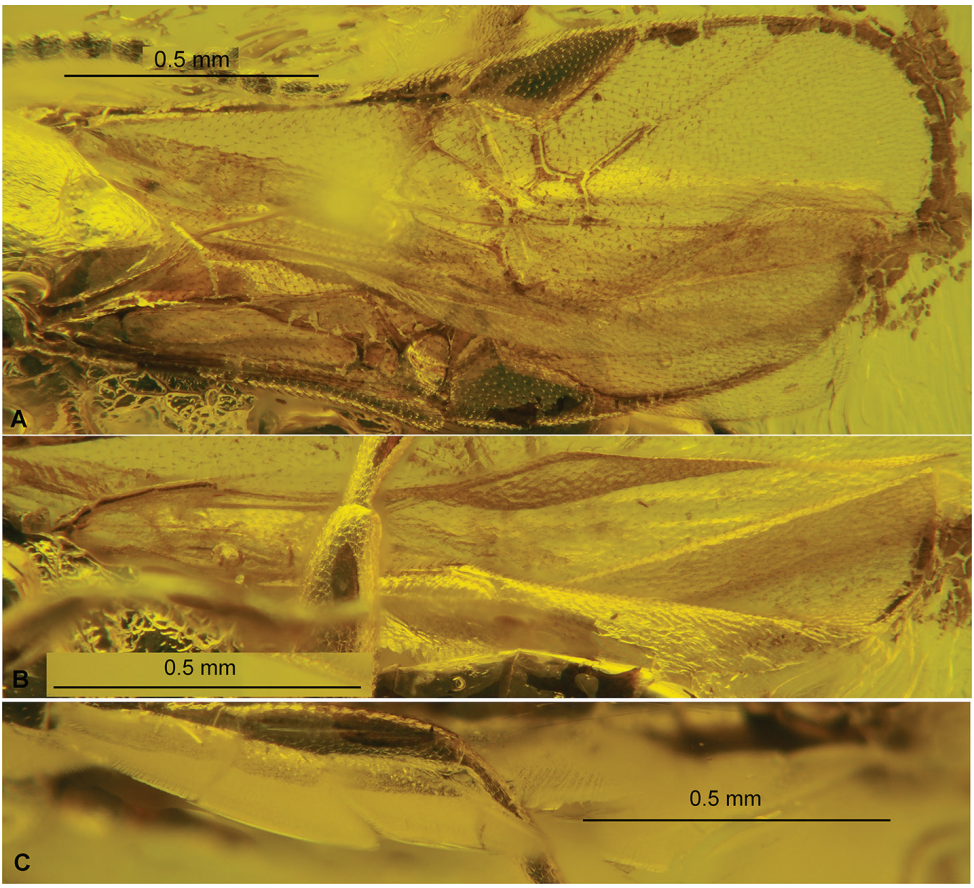

Figure 3. *Elasmosomites primordialis* Brues, 1933 (male, Baltic amber, # BX 9/21.2) **A** fore wing **B** hind wing **C** posterior margin of hind wing.

tibia acute apically, longest spur 0.8 times as long as hind basitarsus. Hind tarsus slender, all its segments of similar width and not narrowed towards apex. All tarsal claws slender and simple.

***Metasoma*:** About 3.0 times longer than maximum width, almost as long as mesosoma and head combined, seemingly entirely smooth and bare, only with sparse short setae in posterior thirds of third and following tergites, with spiracles situated almost at the middle of lateral parts of tergites, without separated laterotergites. First tergite widened towards apex. Suture between second and third tergites absent. Median length of second and third tergites combined about 1.3 times distal width of third tergite. Segments behind third one distinctly projected.

***Colour*:** Body entirely black. Tegula dark brown. Wings faintly and evenly infuscate; pterostigma entirely dark brown.

Remarks. The differences between both known species of the genus *Elasmosomites* are given previously after the description of the new species.

Discussion

The actual evidence of parasitic lifestyle of Hymenoptera is quite rare in the fossil record despite the rather numerous discoveries of the parasitoid adults. The first record of a hymenopterous parasitoid larva emerging from the metasoma of a worker ant (the phenomenon of imagobiosis: Shaw 2004) in Baltic amber was published by Poinar and Miller (2002). However, it is especially noteworthy that the emergence of an ant parasitoid from its host is a rarely observable phenomenon even among extant taxa (Shaw 1993; Gómez Durán and van Achterberg 2011). The previous study of the fossil parasitoid larva in general and its cephalic structure recognized this larva as a member of the genus *Elasmosomites*, perhaps *E. primordialis*, emerging from the host, a worker of probably *Lasius schiefferdeckeri* Mayr, 1868 (Formicinae), because this is one of the most common ants in Baltic amber (Poinar and Miller 2002).

However, our re-examination of the ant fossil presented in the publication by Poinar and Miller (2002) allowed us to re-determine the actual taxonomic status of this ant host. Based on morphological characters in the present photos and drawings (e.g., the general shape of the mesosoma, the shape of the propodeum, the short antennal scape and the shape of the clypeus) we state that this ant specimen belongs to *Ctenobethylus goepperti* (Mayr, 1868) of the subfamily Dolichoderinae. This is the most abundant ant species in the Late Eocene European amber, whereas *L. schiefferdeckeri* is also very common, although less than *C. goepperti* (Dlussky and Rasnitsyn 2009).

Almost 20 years after the publication of the article (Poinar and Miller 2002) with the first finding of an ant adult with a parasitoid larva emerging from it, Artur Michalski from Poland made a new find, which he kindly provided to us for study. In this amber inclusion the ant host undoubtedly belongs to *Lasius schiefferdeckeri.* This piece of Baltic amber includes the ant worker with an emerging hymenopterous larva with more than the half of its body visible from the lower posterior part of the ant's metasoma (Fig. 4). In this specimen, it is possible to study the larval body that is distinctly thickened submedially with six to eight visible segments and the head of the parasitoid larva clearly visible on the top of its most narrow distant part. Unfortunately, it is impossible to study the cephalic structure of this larva because this part of its body is poorly preserved in the amber, but based on the larva from the previous article (Poinar and Miller 2002) we suggest that it is also a member of *Elasmosomites*. However, species identification of the larva is very complicated because there are at least two species (if not more) of this genus.

Extant members of the tribe Neoneurini are mainly known as parasitoids of worker ants of the genus *Formica* Linnaeus, 1758, and more rarely of *Camponotus* Mayr, 1861, *Cataglyphis* Foerster, 1850, *Lasius* Fabricius, 1804 and *Polyergus* Latreille, 1804 (all from the subfamily Formicinae), whereas for fossil members of the genus *Elasmosomites*, hosts belonging to the genera *Ctenobethylus* Brues 1939 and *Lasius* are now known (subfamilies Dolichoderinae and Formicinae, respectively). This is the first record of the ant subfamily Dolichoderinae as the host of a Neoneurini braconid species.

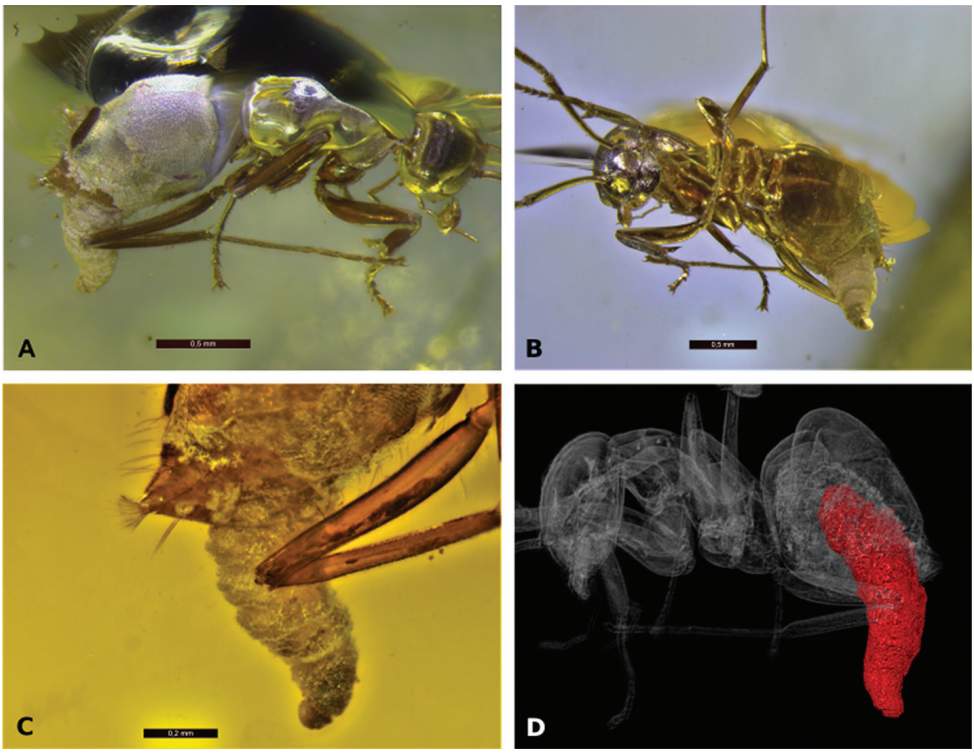

Figure 4. A worker of the ant *Lasius schiefferdeckeri* Mayr, 1868 (Baltic amber) with emerging larva of an *Elasmosomites* species **A** general view, right side **B** general view, left side **C** gastral apex of the ant with *Elasmosomites* larva **D** micro-CT reconstruction showing the position of the parasitoid larva inside the ant.

We don't know much about hosts of this tribe, and the discoveries in fossils that allow us to establish a host-parasitoid relationship of extinct taxa are extremely rare. However, based on the existing two findings, and the available data on the hosts of extant species, it is possible to assume a wider range of hosts for the genus *Elasmosomites* during the Late Eocene. In addition to the two common species mentioned above, it could also be quite numerous in European Late Eocene amber representatives (as potential hosts) of the genera *Formica* (Formicinae) and *Yantaromyrmex* Dlussky & Dubovikoff, 2013 (Dolichoderinae), such as *F. flori* Mayr, 1868 and *Y. geinitzi* (Mayr, 1868).

Acknowledgements

We are sincerely grateful to Artur Michalski (Poland) for the material provided for the study and Madeline Pankowski (Rockville, Maryland, USA) for improving the English. The authors are also very thankful to Prof. Michael J. Sharkey (Redlands, USA), Prof. Cornelis van Achterberg (Leiden, the Netherlands), Dr. Julia Stigenberg

(Stockholm, Sweden) and Dr. Vladimir E. Gokhman (Moscow, Russia) for their very useful suggestions for the first version of the manuscript.

The photographs and micro-CT data of the fossil ant with a braconid larva were taken using the equipment of the Science Park of St. Petersburg State University (Resource Centers "Microscopy and Microanalysis" (project No. 112–11405) and "Centre for X-ray Diffraction Studies" (projects No. 103–21316 and 103–11527). The article was made with support from the Ministry of Science and Higher Education of the Russian Federation in accordance with agreement No. 075–15–2020–922 date 16.11.2020 on providing a grant in the form of subsidies from the Federal Budget of the Russian Federation. The grant was provided for state support for the creation and development of a World-class Scientific Center "Agrotechnologies for the Future" for DAD.

References

Belokobylskij SA (2014) Family Braconidae. In: Antropov AV, Belokobylskij SA, Compton SG, Dlussky GM, Khalaim AI, Kolyada VA, Kozlov MA, Perfilieva KS, Rasnitsyn AP (Eds) The wasps, bees and ants (Insecta: Vespida = Hymenoptera) from the insect limestone (Late Eocene) of the Isle of Wight, UK. Earth and Environmental Sciences Transactions of the Royal Society of Edinburgh 104(3–4): 335–446. https://doi.org/10.1017/S1755691014000103

Belokobylskij SA (2019) New data on the tribe Neoneurini (Hymenoptera: Braconidae: Euphorinae) of Russia. Far Eastern Entomologist 396: 1–9. https://doi.org/10.25221/fee.396.1

Belokobylskij SA, Maetô K (2009) Doryctinae (Hymenoptera, Braconidae) of Japan. Fauna mundi, Vol. 1, Warszawa, Warshawska Drukarnia Naukowa, 806 pp. https://doi.org/10.3161/067.058.0107

Brues CT (1910) The parasitic Hymenoptera of the Tertiary of Florissant, Colorado. Bulletin of the Museum of Comparative Zoology at Harvard College 54(1): 4–125.

Brues CT (1933) The parasitic Hymenoptera of the Baltic amber. Bernstein Forschungen (Amber Studies) 3: 4–178.

Brues CT (1937) Superfamilies Ichneumonoidea, Serphoidea, and Chalcidoidea. In: Carpenter FM, Folsom JW, Essig EO, Kinsey AC, Brues CT, Boesel MW, Ewig HE (Eds) Insects and arachnids from Canadian amber. University of Toronto Studies. Geological Series 40: 27–44.

Brues CT (1939) New Oligocene Braconidae and Bethylidae from Baltic amber. Annals of the Entomological Society of America 32: 251–263. https://doi.org/10.1093/aesa/32.2.251

Gómez Durán J-M, van Achterberg C (2011) Oviposition behaviour of four ant parasitoids (Hymenoptera, Braconidae, Euphorinae, Neoneurini and Ichneumonidae, Hybrizontinae), with the description of three new European species. ZooKeys 125: 59–106. https://doi.org/10.3897/zookeys.125.1754

Dlussky GM, Rasnitsyn AP (2009) Ants (Insecta: Vespida: Formicidae) in the Upper Eocene amber of Central and Eastern Europe. Paleontological Journal 43: 1024–1042. https://doi.org/10.1134/S0031030109090056

Li J, van Achterberg C, Zheng M, Chen J (2020) Review of Neoneurini Bengtsson (Hymenoptera: Braconidae: Euphorinae) from China. Zoological Systematics 45(4): 281–289. https://doi.org/10.11865/zs.202034

Poinar Jr G, Miller JC (2002) First fossil record of endoparasitism of adult ants (Formicidae: Hymenoptera) by Braconidae (Hymenoptera). Annales of the Entomological Society of America 95(1): 41–43. https://doi.org/10.1603/0013-8746(2002)095[0041:FFROEO]2.0.CO;2

Rasnitsyn AP, Quicke DLJ [Eds] (2002) History of insects. Kluwer Academic Publishers, New York, Boston, Dordrecht, London, Moscow, 517 pp.

Shaw SR (1985) A phylogenetic study of the subfamilies Meteorinae and Euphorinae (Hymenoptera: Braconidae). Entomography 3: 277–370.

Shaw SR (1993) Observations on the ovipositional behavior of *Neoneurus mantis*, an ant-associated parasitoid from Wyoming (Hymenoptera: Braconidae). Journal of Insect Behavior 6: 649–658. https://doi.org/10.1007/BF01048130

Shaw SR (2004) Essay on the evolution of adult-parasitism in the subfamily Euphorinae (Hymenoptera: Braconidae). Proceedings of the Russian Entomological Society 75(1): 82–95.

Stigenberg J, Boring CA, Ronquist F (2015) Phylogeny of the parasitic wasp subfamily Euphorinae (Braconidae) and evolution of its host preferences. Systematic Entomology 40(3): 570–591. https://doi.org/10.1111/syen.12122

Tobias VI (1965) Generic grouping and evolution of parasitic Hymenoptera of the subfamily Euphorinae (Hymenoptera, Braconidae). I. Entomologicheskoe Obozrenie 44: 841–865. [In Russian]

Tobias VI (1966) Generic grouping and evolution of parasitic Hymenoptera of the subfamily Euphorinae (Hymenoptera, Braconidae). II. Entomologicheskoe Obozrenie 45: 612–33. [In Russian]

Tobias VI (1987) New taxa of Braconidae from Baltic amber (Hymenoptera). Entomologicheskoe Obozrenie 66(4): 845–859. [English translation: Entomological Review 67(4): 18–32] [In Russian]

Tobias VI, Yuldashev EYu (1979) Three new remarkable species and two new genera of braconids (Hymenoptera, Braconidae, Euphorinae, Neoneurini). Proceedings of the Zoological Institute of the USSR Academy of Science 88: 95–102. [In Russian]

van Achterberg C (1993) Illustrated key to the subfamilies of the Braconidae (Hymenoptera: Ichneumonoidea). Zoologische Verhandelingen 283: 1–189.

van Achterberg C, Argaman Q (1993) *Kollasmosoma* gen. nov. and a key to the genera of the subfamily Neoneurinae (Hymenoptera: Braconidae). Zoologische Mededelingen 67(5): 63–74.

Yu DS, van Achterberg C, Horstmann K (2016) Taxapad 2016, Ichneumonoidea 2015. Database on flash-drive: Nepean, Ontario.