



Revision of Bethylinae fossils (Hymenoptera: Bethylidae) from Baltic, Rovno and Oise amber, with comments on the Tertiary fauna of the subfamily

Magno S. Ramos, Evgeny E. Perkovsky, Alexander P. Rasnitsyn, and Celso O. Azevedo

With 53 figures and 1 table

Abstract: The known distribution and taxonomic variation of the previously described species *Lytopsenella kerneggeri* OHL are broadened. Eight new fossil species of Bethylinae are described and illustrated: *Eupsenella aulax* RAMOS & AZEVEDO sp. nov., *E. klesoviana* RAMOS & AZEVEDO sp. nov., *E. rossica* RAMOS & AZEVEDO sp. nov., *E. yantarnica* RAMOS & AZEVEDO sp. nov., *Goniozus definitus* RAMOS & AZEVEDO sp. nov., *Lytopsenella baltica* RAMOS & AZEVEDO sp. nov., *L. maritima* RAMOS & AZEVEDO sp. nov., and *Sierola rovniana* RAMOS & AZEVEDO sp. nov. *Protobethylus* DE PLOËG & NEL, 2004 is considered a junior synonym of *Eupsenella* WESTWOOD, 1874, and *Protobethylus eocenicus* DE PLOËG & NEL, 2004 is transferred from *Protobethylus* to *Eupsenella* as *E. eocenica* comb. nov. A key to the fossil species of Bethylinae is provided. This paper brings the total known fossil species of Bethylinae to 17.

Key words: Insecta, Chrysidoidea, Late Eocene, new combination, Rovno amber, Baltic amber.

1. Introduction

The analysis of fossils is important in understanding the events that shaped the evolutionary history of the planet. Previously, 49 fossil species have been reported for the family Bethylidae (AZEVEDO & AZAR 2012). However, that report omitted *Cretobethylus lucidus* RASNITSYN, 1990 from the Cretaceous of Transbaikalia (RASNITSYN 1990). Most of these species were described by BRUES (1923, 1933, 1939) based on Baltic amber from the Early Oligocene. The geographic distribution of bethylid fossils is limited to a few sites worldwide. Hitherto, nine species have been reported for the subfamily Bethylinae: *Goniozus contractus* (BRUES, 1933) (Oligocene, Baltic amber); *Goniozus respectus* SORG, 1988 (Miocene, Dominican amber); *Lytopsenella crastina* (BRUES, 1923) (Oligocene, Baltic amber); *Lytopsenella kerneggeri* OHL, 1995 (Late Eocene, Baltic amber); *Lytopsenella setigera*

(BRUES, 1923) (Oligocene, Baltic amber); *Lytopsenella simplex* (BRUES, 1923) (Oligocene, Baltic amber); *Prosierola submersa* BRUES, 1933 (Early Oligocene, Baltic amber); *Protobethylus eocenicus* DE PLOËG & NEL, 2004 (earliest Eocene, Oise French amber); and *Sierola hastata* SORG, 1988 (Late Eocene, Baltic amber). Most of these species' types have been lost, except *L. kerneggeri* (deposited at the Geologisch-Paläontologisches Institut und Museum der Universität Hamburg) and *P. eocenicus* (deposited at the Muséum national d'Histoire naturelle, Paris).

Here, eight new species are added to the subfamily, and a new combination is proposed. *Protobethylus eocenicus* DE PLOËG & NEL, 2004, hitherto listed in *Protobethylus*, is transferred to *Eupsenella* as a new combination. Thus, the total known fossil species of Bethylinae are increased to 17.

The main aim of the present paper is to describe and illustrate three new species from the Upper

Eocene Rovno amber and five new species from Baltic amber and to provide a new key to the fossil species of Bethylinae.

2. Material and methods

The specimens from Rovno amber were mined from the Klesov amber deposit (northern Rovno region; see PERKOVSKY et al. 2010) and obtained from the state 'Ukramber' factory (Rovno). The specimens from Baltic amber were extracted in Yantarny, Kaliningrad region, Russia, at a local mine in the Blue Ground of Prussia Formation. Finally, the specimen from Oise French amber was extracted from Le Quesnoy, Chevière, Creil region, in level MP7 of the Dormaal mammal fauna.

Rovno amber is usually considered similar in age to the Baltic amber deposits (Late Eocene, ca. 36–37 million years (My); ALEKSANDROVA & ZAPOROZHETS 2008), whereas Oise amber is much older in age (53 My; see the detailed discussion by NEL et al. 1999).

Institutional abbreviations: MNHN: Muséum national d'Histoire naturelle, Paris; PIN: A.A. Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow; SIZK: I.I. Schmalhausen Institute of Zoology of National Academy of Sciences of Ukraine in Kiev; UFES: Universidade Federal do Espírito Santo, Brazil.

Measurements and indices used in this study are as follows: body length was measured from the anterior most point of the clypeus to the posterior margin of the last metasomal segment, excluding male genitalia or female sting; LH, length of head, was measured in frontal view, from vertex crest to median anterior margin of clypeus; WH, maximum width of head, was measured in frontal view, including

eyes; WF, narrowest width of frons, measured in frontal view, usually around level bottom of eyes; HE, height of eye, was measured in lateral view, across its maximum height (length); OOL, ocello-ocular line, was measured in latero-dorsal view, the shortest distance from eye top to posterior ocellus; WOT, width of ocellar triangle, was measured in frontal view, maximum width, including ocelli; DAO, diameter of anterior ocellus, was measured in frontal view; distance of ocellar triangle to vertex: was measured in dorso-posterior view, distance from posterior ocellus to vertex crest; and VOL, vertex-ocular line, was measured in dorsal view, distance from eye top to vertex crest.

The nomenclature of integument sculpture follows HARRIS (1979), and general terms follow EVANS (1964), AZEVEDO (1999). The nomenclature of wing venation follows RAMOS & AZEVEDO (2012).

Symbols of wing venation: **C:** Costal cell; **R:** Radial cell; **1Cu:** First cubital cell; **1R1:** First radial 1 cell; **2R1:** Second radial 1 cell; **1M:** First medial cell (areolet); **Rsa:** First section of Rs vein; **Rsb:** Second section of Rs vein; **Rsc:** Third section of Rs vein; **M:** M vein; **RS+M:** RS+M vein; **Cua:** First section of Cu vein (more details see RAMOS & AZEVEDO 2012, figs. 1–2).

3. Descriptions

The descriptions were performed with the software DELTA (Descriptive Language for Taxonomy) developed by DALLWITZ (1980), and DALLWITZ et al. (1999). Images were captured using the extended-focus system Leica Application Suite (LAS) – Version 4.1.0 [Build 1264] that feeds image data to a desktop computer. The captured stacks were exported, and combined in a single in-focus image using Helicon Focus v5.2.16, and later edited in Adobe Photoshop.

3.1. Key to fossil species of Bethylinae

1. Forewing with six closed cells (Figs. 3, 7, 11, 16, 25, 35, 38, 44, 48, 49A, 50B) 2
 - Forewing with five or less closed cells (Figs. 31, 53) 12
2. Forewing with 1R1 cell longer than or as long as 2R1 cell (Figs 3, 7, 16, 18, 25); notauli always present (Figs 4, 6, 11, 17, 21, 24) 3
 - Forewing with 1R1 shorter than 2R1 cell (Figs. 35, 38, 44, 48); notauli usually absent (Figs 34, 36, 43, 44) 7
3. Propodeal disc with median longitudinal carina (Figs. 6, 11, 21, 27) 4
 - Propodeal disc without median longitudinal carina (Figs. 1, 4) ... *Eupsenella eocenica* (DE PLOËG & NEL) comb. nov.
4. Notauli uniformly narrow (Fig. 33); 1M cell of forewing subtriangulate (areolet) (Fig. 16) 5
 - Notauli strongly wide posterad (Fig. 27); 1M cell of forewing almost elliptical (areolet) (Fig. 27) *Eupsenella yantarnica* RAMOS & AZEVEDO sp. nov.
5. RS+M vein of forewing shorter than Rsa (Figs. 7, 18) 6
 - RS+M vein of forewing as long as Rsa (Fig. 16) *Eupsenella klesoviana* RAMOS & AZEVEDO sp. nov.
6. Pronotal disc with transversal furrow deep near posterior margin (Figs 5, 6, 9); vertex crest straight (Fig. 8) *Eupsenella aulax* RAMOS & AZEVEDO sp. nov.
 - Pronotal disc without transversal furrow deep near posterior margin (Figs. 17, 21); vertex crest slightly concave medially (Fig. 19) *Eupsenella rossica* RAMOS & AZEVEDO sp. nov.
7. Notauli absent or when present ill-defined (Figs. 34, 36, 43, 47) 8

- Notauli present and well-defined (see BRUES 1933: 127, Fig. 68) *Lytopsenella simplex* (BRUES)
- 8. Vertex crest convex (Fig. 46); propodeal disc with median longitudinal carina incomplete (Fig. 47) 9
- Vertex crest straight (Figs. 34, 37, 41); propodeal disc without median longitudinal carina (Figs. 34, 42) 10
- 9. Rsa slightly inclined toward tegula (Fig. 49A, B) *Lytopsenella maritima* RAMOS & AZEVEDO sp. nov.
- Rsa subperpendicular to anterior margin of forewing (Fig. 48) *Lytopsenella baltica* RAMOS & AZEVEDO sp. nov.
- 10. Pronotal disc as long as mesoscutum (see BRUES 1933: 126, 128) 11
- Pronotal disc shorter than mesoscutum (Figs. 34, 36, 43) *Lytopsenella kerneggeri* OHL
- 11. Bristly hairs of vertex crest long (see BRUES 1933: 126) *Lytopsenella setigera* (BRUES)
- Bristly hairs of vertex crest short (see BRUES 1933: 128) *Lytopsenella crastina* (BRUES)
- 12. 2R1 cell of forewing open (see BRUES 1933: 128, 129) 13
- 2R1 cell of forewing closed (Fig. 53) 16
- 13. Propodeal disc with pair of anterior pits (see BRUES 1933: 128, 129); triangular area on propodeal disc absent (see BRUES 1933: 128, 129) *Prosierola submersa* BRUES
- Propodeal disc without anterior pits (see SORG 1988, figs. 22B, 136D, E; see BRUES 1933: 130; Fig. 29); triangular area on propodeal disc present (see SORG 1988, figs. 22A, B; 136 D, E; see BRUES 1933: 130; Fig. 29) 14
- 14. Rsc ending abruptly toward anterior margin of forewing (see BRUES 1933: 130; Fig. 28); First medial cell (1M) of forewing almost elliptical (areolet) (see BRUES 1933: 130; Fig. 28) 15
- Rsc ending gently toward anterior margin of forewing (see SORG 1988, Fig. 22 A); 1M cell of forewing subtriangulate (areolet) (see SORG 1988, Fig. 22 A) *Goniozus respectus* SORG
- 15. Pronotal disc longer than mesoscutum (see BRUES 1933: 130); malar space very short (see BRUES 1933, pg. 130); anterior margin of forewing with conspicuous bristly hairs (see BRUES 1933: 130) *Goniozus contractus* (BRUES)
- Pronotal disc shorter than mesoscutum (Fig. 32); malar space evident (Fig. 28); anterior margin of forewing without conspicuous bristly hairs (Fig. 31) *Goniozus definitus* RAMOS & AZEVEDO sp. nov.
- 16. R, 1Cu, and 1M cells nebulous (Fig. 53) *Sierola rovniana* RAMOS & AZEVEDO sp. nov.
- R, 1Cu, and 1M cells tubular (see SORG 1988, fig. 20B) *Sierola hastata* SORG

3.2. Systematic palaeontology

Order Hymenoptera LINNAEUS, 1758
 Family Bethylidae HALIDAY, 1839
 Subfamily Bethylinae DALLA TORRE, 1898
 Genus *Eupsenella* WESTWOOD, 1874

(Syn.: *Protobethylus* DE PLOËG & NEL, 2004:
 75, Type species: *Protobethylus eocenicus*
 PLOËG & NEL, 2004, by monotypy, syn. nov.)

Type species: *Eupsenella agilis* WESTWOOD, 1874, by monotypy.

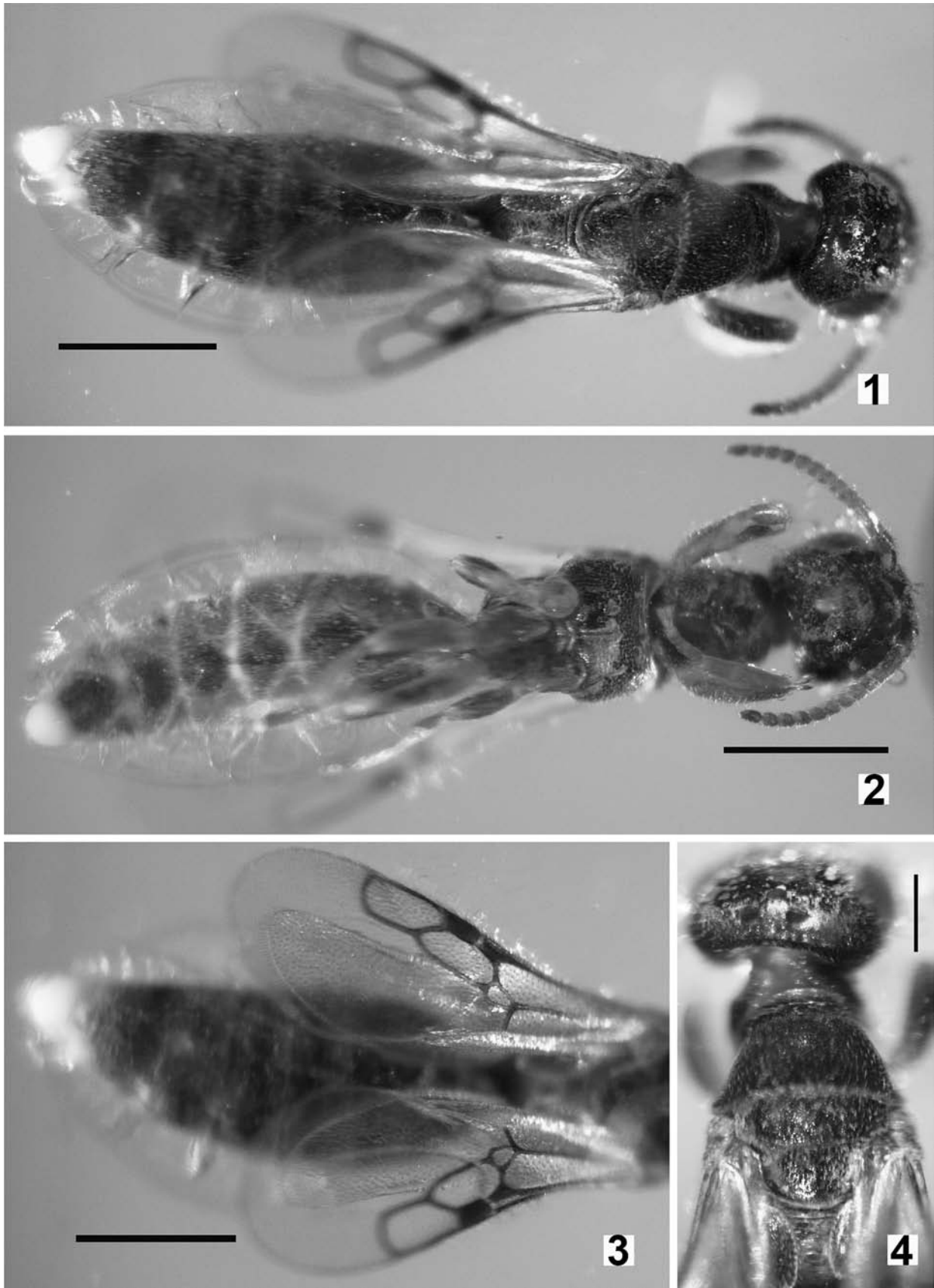
Eupsenella eocenica (DE PLOËG & NEL, 2004)
 comb. nov.
 Figs. 1-4

Material examined: Holotype specimen PA2436, (sex uncertain), in collection DE PLOËG, housed in the Muséum National d'Histoire Naturelle, Paris (MNHN).

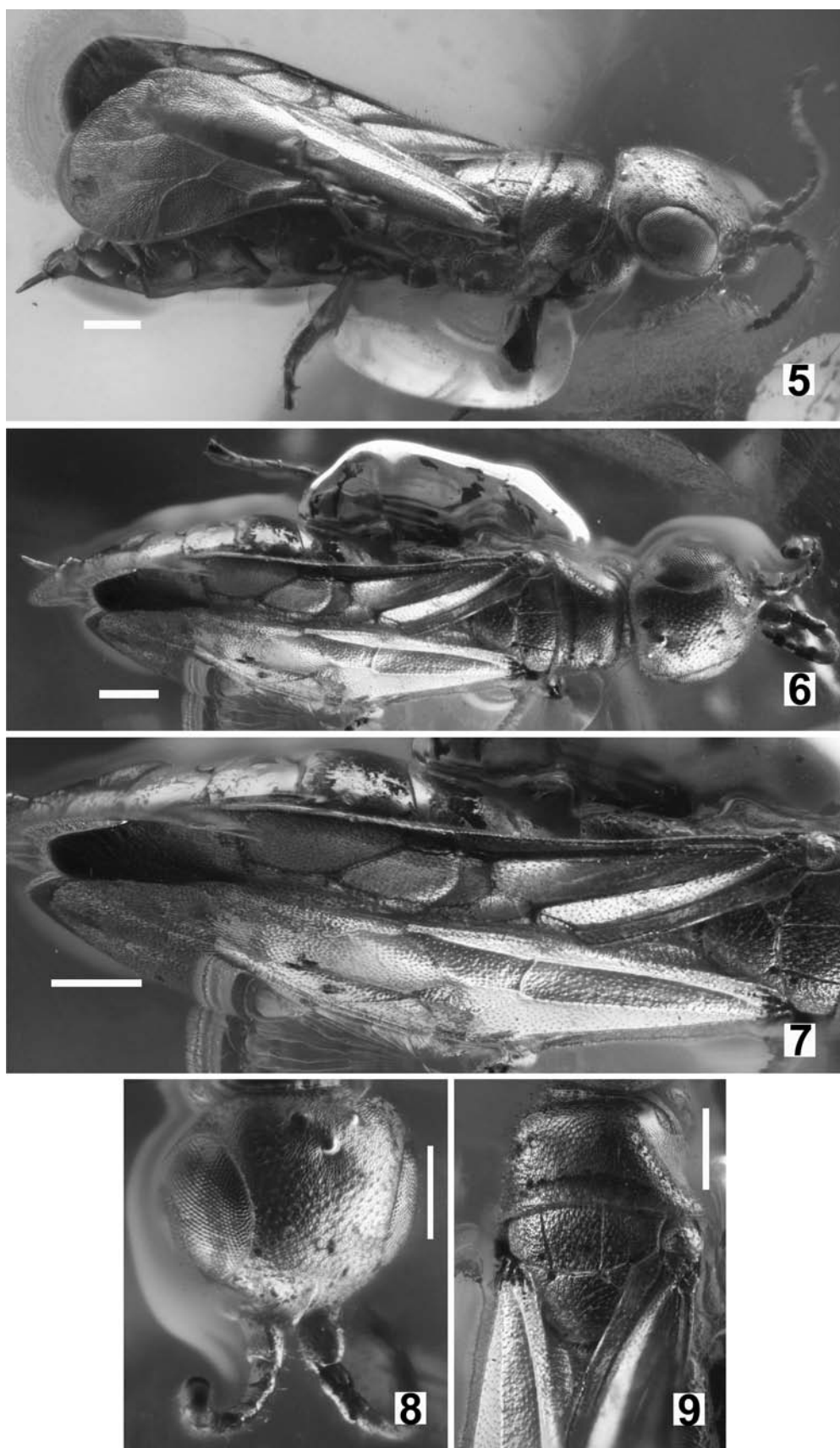
Occurrence: Lowermost Eocene, Le Quesnoy, Chevreire, region of Creil, Oise department, France.

Remarks: This species was originally described as *Protobethylus eocenicus* by DE PLOËG & NEL (2004). *Protobethylus* DE PLOËG & NEL, 2004 was established as a monotypic genus with *P. eocenicus* as its type species. The general habitus of this species closely resembles that of *Eupsenella* WESTWOOD, 1874. According to DE PLOËG & NEL (2004), the generic status of *Protobethylus* is based on its simple hind coxae and propodeal disc with the posterior transverse carina present but weak and the median longitudinal and discal carinae absent. However, the general habitus of *Protobethylus* is superficially similar to that of *Eupsenella*. Based on photographs of the type species, *Protobethylus* exhibits several characters that are also present in all members of *Eupsenella*. The main characters found in both genera are the median clypeal lobe with the median carina continuing well up the frons, the notauli present and well-defined, the prosternum expanded and excavated medially, the forewing with six closed cells, the 2R1 cell ending abruptly toward the anterior margin of the forewing, the 1R1 cell as long as the 2R1 cell, and the complete ventral keel on the petiole.

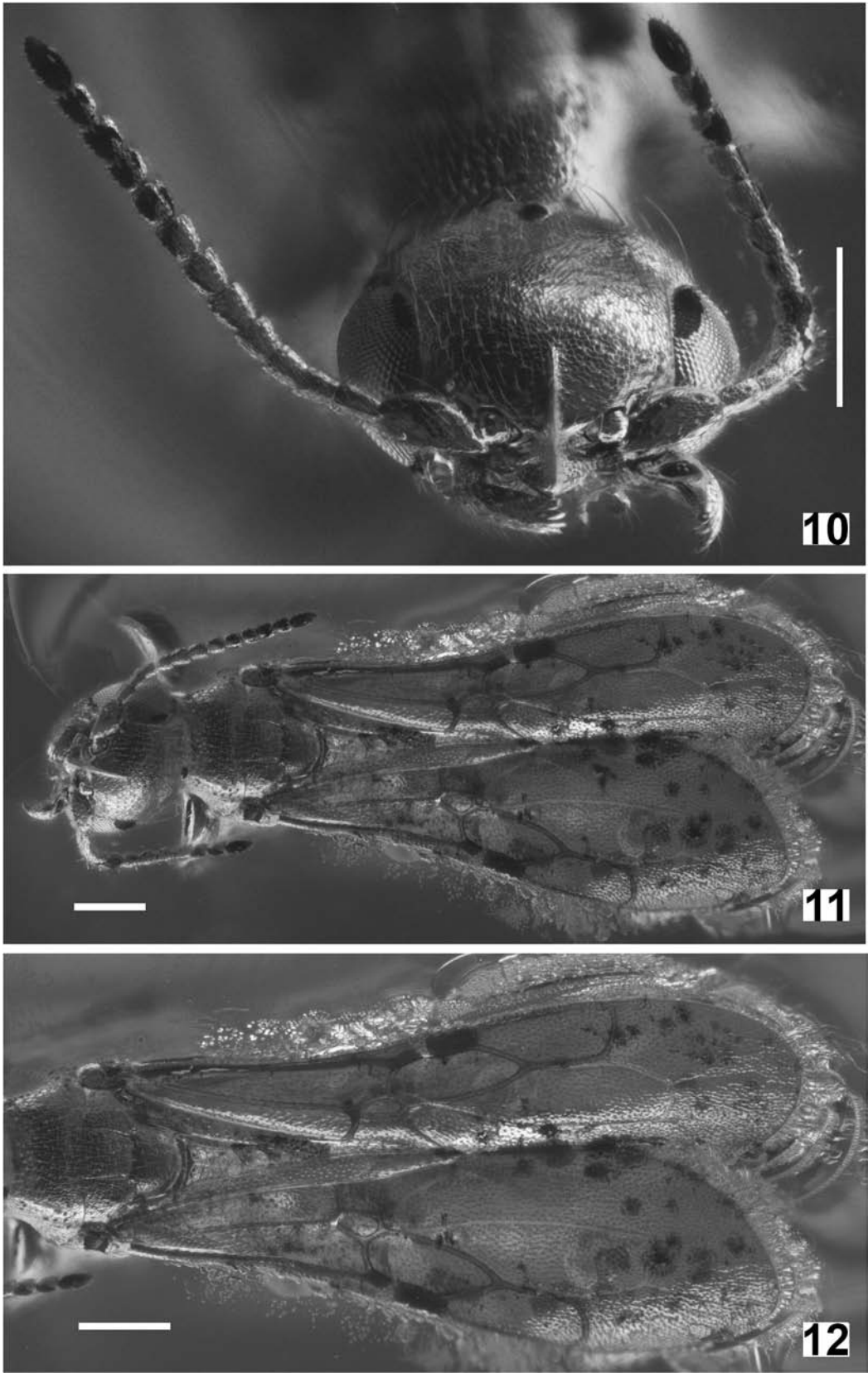
Notably, DE PLOËG & NEL (2004) considered the character of simple, spineless hind coxae to represent a crucial difference between *Protobethylus* and *Eupsenella*. However, this character is also found in some extant *Eupsenella* species, such as *E. inggarda* RAMOS & AZEVEDO, 2012. This character is highly variable among



Figs. 1-4. *Eupsenella eocenica* (DE PLOËG & NEL) comb. nov. **1.** Body in dorsal view. **2.** Body in ventral view. **3.** Left and Right forewings in dorsal view. **4.** Mesosoma in dorsal view. (Scale bar = 300 μ m).



Figs. 5-9. *Eupsenella aulax* RAMOS & AZEVEDO sp. nov. **5.** Habitus. **6.** Body in dorsal view. **7.** Left forewing in dorsal view. **8.** Head in dorsal view. **9.** Mesosoma in dorsal view. (Scale bar = 300 μ m).



Figs. 10–12. *Eupsenella aulax* RAMOS & AZEVEDO sp. nov. **10.** Head in frontal view. **11.** Body in dorsal view. **12.** Left and Right forewings in dorsal view.

Eupsenella species, ranging from almost imperceptible to clearly visible (see RAMOS & AZEVEDO 2012). Therefore, the character of simple, spineless hind coxae does not support the distinction between *Protobethylus* and *Eupsenella*. Considering this evidence, we are convinced that these genera are synonymous. We here propose *Protobethylus* DE PLOËG & NEL, 2004 as a new junior synonym of *Eupsenella* WESTWOOD, 1874 and transfer *Protobethylus eocenicus* DE PLOËG & NEL, 2004 to *Eupsenella*.

Eupsenella aulax RAMOS & AZEVEDO sp. nov.

Figs. 5-12

Etymology: The specific epithet *aulax*, from Latin, means 'furrow' in allusion to the transversal furrow deep near the posterior margin of pronotal disc.

Material examined: Holotype. Ukraine, Klesov, Rovno amber, 1 female, n° K-3986 (SIZK); Baltic amber, Baltic seacoast area, 1 female, 1307–1492 (UFES).

Occurrence: Rovno amber, Ukraine, Upper Eocene.

Diagnosis: Mandible with four sharpened apical teeth. Clypeus with median clypeal lobe angulate. Median clypeal lobe with median carina continues on well up the frons. Ocelli small. Vertex crest straight. Pronotal disc with transversal furrow deep near posterior margin, and longer than the mesoscutum. Notaulus present, and uniformly narrow. Forewing with 1M cell present, and closed; 1R1 cell as long as 2R1 cell; C cell widening distally.

Variation: Body lengths 2.5–3.3 mm; LFW 1.8–1.9 mm; clypeus with median carina strongly arched in profile; pronotal disc without transversal furrow; pronotal disc with posterior margin slightly sinuous; notaulus slightly wide posterad; propodeal disc with median longitudinal carina evident.

Description: Holotype, female, body length 3.3 mm, LFW 1.9 mm.

Head. – Head subquadrate in dorsal view, as long as wide. Mandible with four sharpened apical teeth, two lowermost teeth as long as upper ones. Clypeus with median clypeal lobe angulate, with median carina, continues on well up the frons. First five antennal segments in ratio of about 11:6:5:5:5. Eye gibbous, large, $> 0.5 \times$ LH, glabrous. Ocelli small, $\leq 0.30 \times$ WOT, $0.16 \times$ WOT. HE $0.6 \times$ LH. WH $1.0 \times$ LH. WF $0.6 \times$ WH. WF $1.0 \times$ HE. OOL $1.33 \times$ WOT. VOL $0.3 \times$ HE. Vertex crest $6.0 \times$ DAO. DAO $0.05 \times$ WF. Distance between posterior ocelli $6.0 \times$ DAO. Ocellar triangle not compact. Anterior ocellus surpassing imaginary top eye line. Vertex crest straight.

Mesosoma. – Pronotal disc coriaceous, $0.5 \times$ as long as wide, anterior corner rounded, anterior margin straight, posterior margin slightly concave medially; transversal furrow deep near posterior margin, longer than the mesoscutum. Mesoscutum $0.38 \times$ as long as wide, coriaceous. Notaulus present, uniformly narrow, convergent posteriorly. Scutel-

lum with scutellar fovea elliptical, narrowed. Mesopleuron coriaceous, mesopleural pit deep. Prosternum expanded, excavated medially, excavation complete.

Wings. – Macropterous. Tegula without setae. Forewing with 1M cell present, closed, subpentagonal. 1R1 cell of forewing present, 1R1 cell $1.0 \times$ 2R1 cell. C cell widening distally. 2R1 cell closed, $0.19 \times$ LFW. M vein straight. Rsa slightly diagonal to anterior margin of forewing. Rsb straight. Distal margin of Rsc convex, ending abruptly toward anterior margin of forewing. RS+M vein $1.0 \times$ Rsa. M vein $1.5 \times$ Rsa. Cua vein $1.75 \times$ Rsa. Rsa subperpendicular to anterior margin of forewing. Stigma expanded, rectangular, distal stigmal margin truncate. Claws bifid, curved.

Metasoma. – $2.5 \times$ longer than wide.

Male unknown.

Remarks: This species is similar to *Eupsenella rossica* RAMOS & AZEVEDO sp. nov. in having large eyes, an expanded prosternum, and the distal margin of Rsc ending abruptly toward the anterior margin of the forewing. However, *Eupsenella aulax* RAMOS & AZEVEDO sp. nov. has small ocelli and a deep transverse furrow near the posterior margin of the pronotal disc, whereas *Eupsenella rossica* RAMOS & AZEVEDO sp. nov. has large ocelli and lacks a deep transverse furrow near the posterior margin of the pronotal disc.

Eupsenella klesoviana RAMOS & AZEVEDO sp. nov.

Figs. 13-16

Etymology: The specific epithet *klesoviana* in allusion to the Klesov where the specimen was collected.

Material examined: Holotype. Ukraine, Klesov, Rovno amber, 1 female, n° K-5010 (SIZK).

Occurrence: Rovno amber, Ukraine, Upper Eocene.

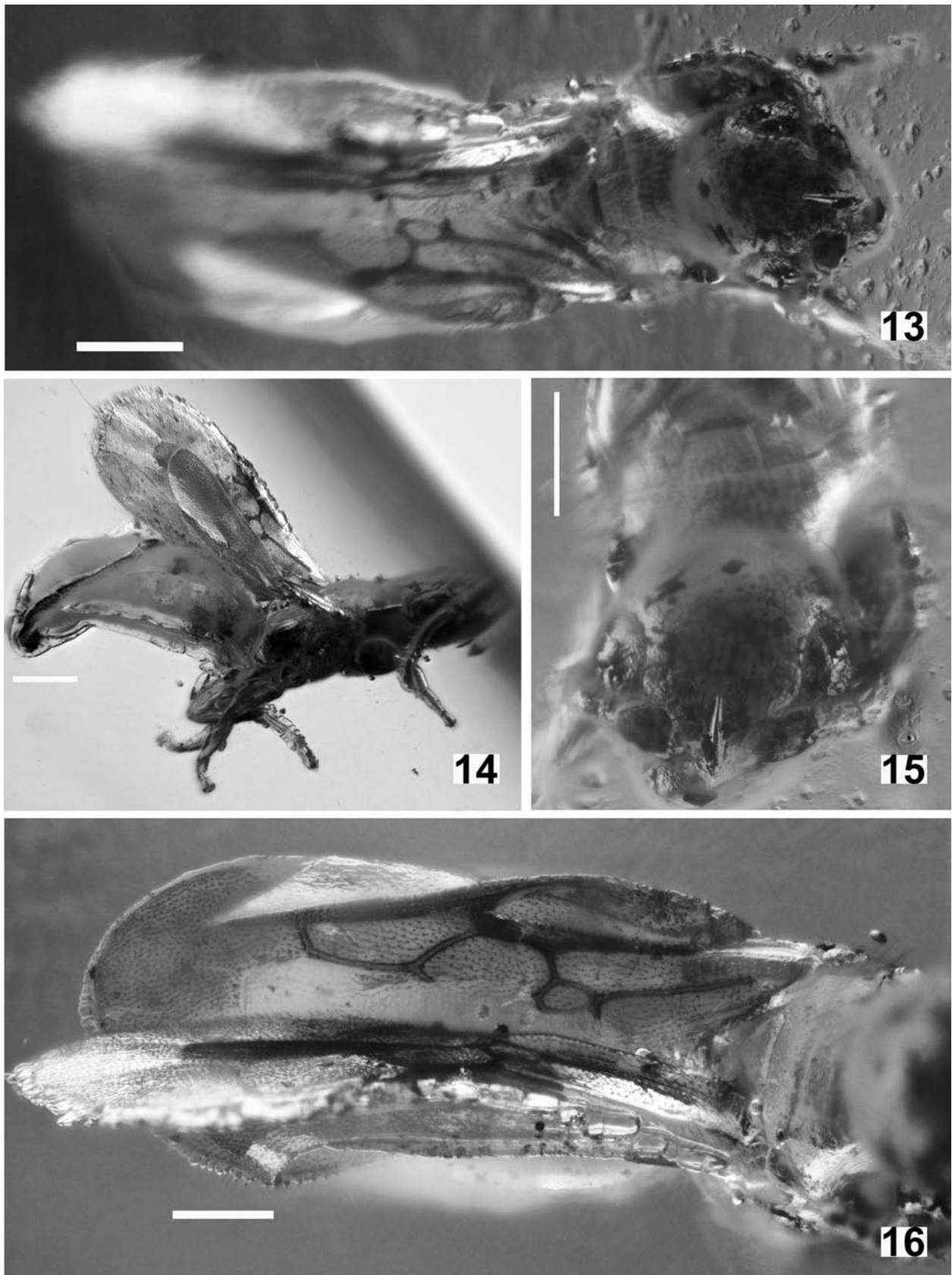
Diagnosis: Clypeus with median clypeal lobe angulate. Median clypeal lobe with median carina continues on well up the frons. Notaulus present, and uniformly narrow. Forewing with the 1R1 cell as long as 2R1 cell; 1M cell subtriangular; the 1R1 cell of forewing shorter than 2R1 cell; C cell evenly narrow; RS+M vein as long as Rsa.

Description: Holotype, female, body length 2.9 mm, LFW 1.8 mm.

Head. – Head subquadrate in dorsal view, as long as wide. Clypeus with median clypeal lobe angulate, with median carina, continues on well up the frons. First five antennal segments in ratio of about 9:6:5:5:5. Eye not gibbous, large, $> 0.5 \times$ LH, glabrous. HE $0.55 \times$ LH. WH $1.0 \times$ LH. WF $0.5 \times$ WH. WF $1.0 \times$ HE. VOL $0.33 \times$ HE.

Mesosoma. – Pronotal disc coriaceous, $0.35 \times$ as long as wide, anterior corner rounded. Mesoscutum $0.22 \times$ as long as wide. Notaulus present, uniformly narrow, convergent posteriorly. Mesopleuron coriaceous, mesopleural pit shallow.

Wings. – Macropterous. Forewing with 1M cell present, closed, subtriangular. 1R1 cell present, 1R1 cell $1.0 \times$ 2R1



Figs. 13-16. *Eupsenella klesoviana* RAMOS & AZEVEDO sp. nov. **13.** Body in dorsal view. **14.** Habitus. **15.** Head in dorso-frontal view. **16.** Left forewing in dorsal view. (Scale bar = 300 μ m).

cell. C cell evenly narrow. 2R1 cell closed, 0.16 x LFW. M vein straight. Rsa slightly diagonal to anterior margin of forewing. Rsb slightly convex. Distal margin Rsc convex, ending abruptly toward anterior margin of forewing. RS+M vein 1.0 x Rsa. M vein 1.33 x Rsa. Cua vein 1.66 x Rsa. Rsa slightly inclined toward tegula. Stigma not expanded, rectangular, distal stigmal margin truncate.

Legs. – Profemur 1.6 x longer than wide. Claws bifid, curved.

Metasoma. – 1.9 x longer than wide.

Male unknown.

Remarks: This species is similar to *Eupsenella yantarnica* RAMOS & AZEVEDO sp. nov. in having the notauli present and convergent posteriorly and the distal margin of Rsc convex, ending abruptly toward the anterior margin of the forewing. However, *Eupsenella klesoviana* RAMOS & AZEVEDO sp. nov. has the notaulus uniformly narrow, the 1M cell subtriangulate, and the 1R1 cell of the forewing shorter than the 2R1 cell, whereas *Eupsenella yantarnica* RAMOS & AZEVEDO sp. nov. has the notaulus strongly widened posterad, the 1M cell elliptical, and the 1R1 cell of the forewing as long as the 2R1 cell.

Eupsenella rossica RAMOS & AZEVEDO sp. nov.

Figs. 17-22

Etymology: The specific epithet *rossica* is in allusion to the standard latinized adjective based on Russia where the specimen was collected.

Material examined: Holotype. Russia, Baltic amber, 1 female, PIN 964/130.

Occurrence: Baltic amber, Russia, Oligocene.

Diagnosis: Mandible with four sharpened apical teeth. Clypeus with median clypeal lobe angulate. Median clypeal lobe with median carina continues on well up the frons. Vertex crest slightly concave medially. Pronotal disc with posterior margin slightly concave medially, and longer than the mesoscutum. Parapsidal furrows ill-defined. Notauli uniformly narrow. Forewing with the 1R1 cell as long as 2R1 cell; M vein straight. C cell evenly narrow.

Description: Holotype, female, body length 2.5 mm, LFW 1.6 mm.

Head. – Head subrectangular in dorsal view, wider than long. Maxillar palpus with six palpomeres. Labial palpus with three palpomeres. Mandible with four sharpened apical teeth, two lowermost teeth as long as upper ones. Clypeus with median clypeal lobe angulate, with median carina, continues on well up the frons. First five antennal segments in ratio of about 10:6:3:3:3. Eye gibbous, large, > 0.5 x LH, glabrous. HE 0.59 x LH. WH 1.14 x LH. WF 0.52 x WH. WF 1.0 x HE. VOL 0.23 x HE. Vertex crest slightly concave medially.

Mesosoma. – Pronotal disc coriaceous, 0.48 x as long as wide, anterior corner rounded, anterior margin straight,

posterior margin slightly concave medially, longer than the mesoscutum. Mesoscutum 0.47 x as long as wide, coriaceous. Notaulus present, uniformly narrow, convergent posteriorly. Parapsidal furrows present, ill-defined. Prosternum expanded, excavated medially, excavation complete.

Wings. – Macropterous. Tegula without setae. Forewing with 1M cell present, closed, subtriangulate. 1R1 cell of forewing present, 1R1 cell 1.0 x 2R1 cell. C cell evenly narrow. 2R1 cell closed, 0.12 x LFW. M vein straight. Rsa slightly diagonal to anterior margin of forewing. Rsb slightly convex. Distal margin of Rsc convex, ending abruptly toward anterior margin of forewing. Rsa slightly inclined toward tegula. Stigma expanded, rectangular, distal stigmal margin truncate.

Legs. – Profemur 0.57 x longer than wide. Claws bifid, curved.

Metasoma. – 2.5 x longer than wide.

Male unknown.

Remarks: This species is similar to *Eupsenella yantarnica* RAMOS & AZEVEDO sp. nov. in having the clypeus with an angulate median clypeal lobe and the median carina continuing well up the frons, the prosternum expanded and completely excavated medially, and the 1R1 cell as long as the 2R1 cell. However, *Eupsenella rossica* RAMOS & AZEVEDO sp. nov. has the vertex crest slightly concave medially, the notaulus uniformly narrow, the pronotal disc longer than the mesoscutum, and the M vein straight, whereas *Eupsenella yantarnica* RAMOS & AZEVEDO sp. nov. has the vertex crest straight, the notaulus strongly widened posterad, the pronotal disc as long as the mesoscutum, and the M vein convex.

Eupsenella yantarnica RAMOS & AZEVEDO sp. nov.

Figs. 23-27

Etymology: The specific epithet *yantarnica* is in allusion to the location Yantarny, where the specimen was collected.

Material examined: Holotype. Russia, Baltic amber, 1 female, PIN 964/120.

Occurrence: Baltic amber, Russia, amber.

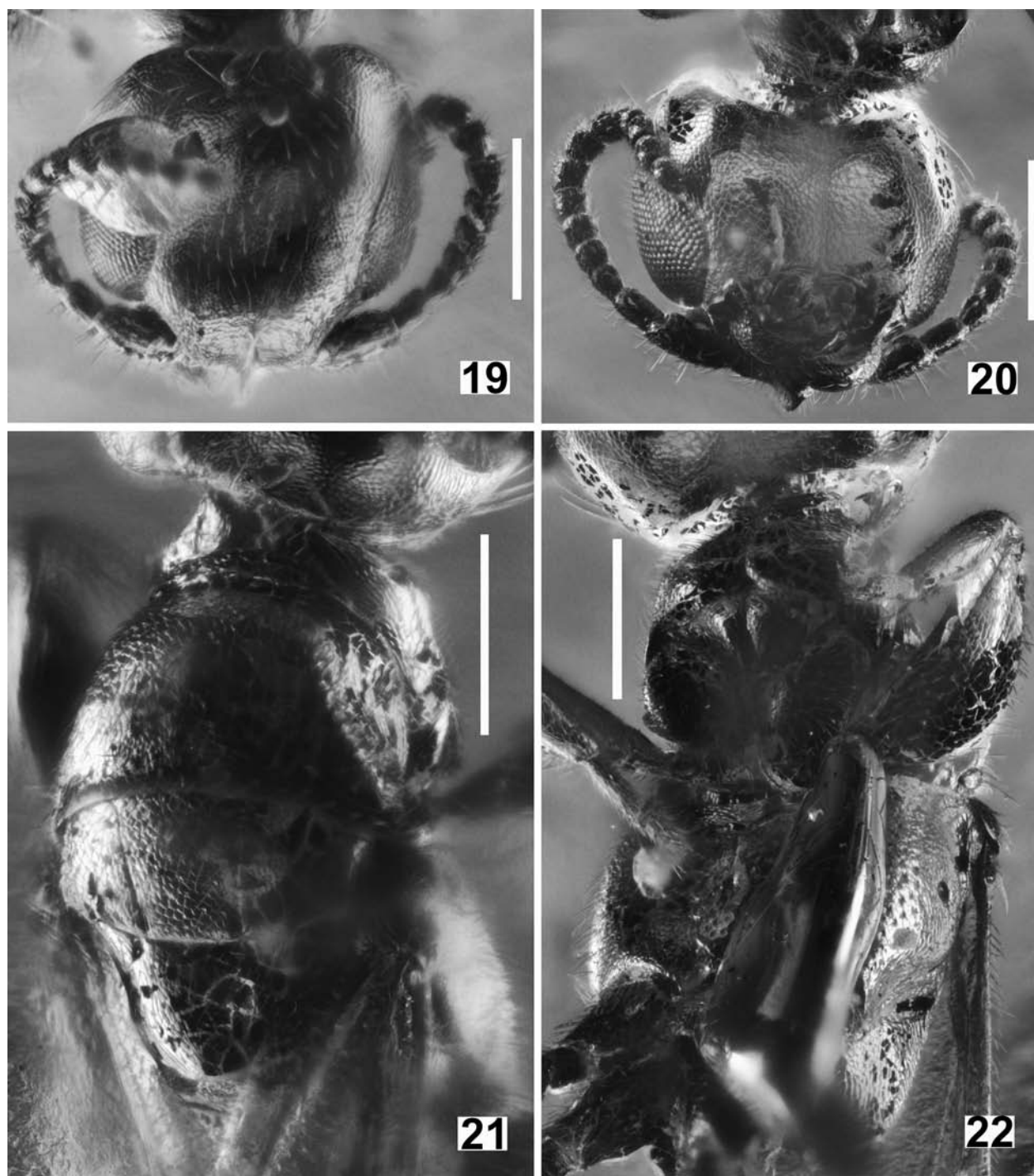
Diagnosis: Clypeus with median clypeal lobe angulate. Median clypeal lobe with median carina continues on well up the frons. Vertex crest straight. Pronotal disc as long as the mesoscutum. parapsidal furrows ill-defined, almost absent. Notaulus strongly wide posterad. Propodeal disc with median longitudinal carina present. Forewing with first medial cell closed, and almost elliptical; 1R1 cell as long as 2R1 cell; 1M cell almost elliptical; the M vein convex; C cell widening distally.

Description: Holotype, female, body length 2.7 mm, LFW 2.0 mm.

Head. – Head subquadrate in dorsal view, as long as wide. Clypeus with median clypeal lobe angulate, with median



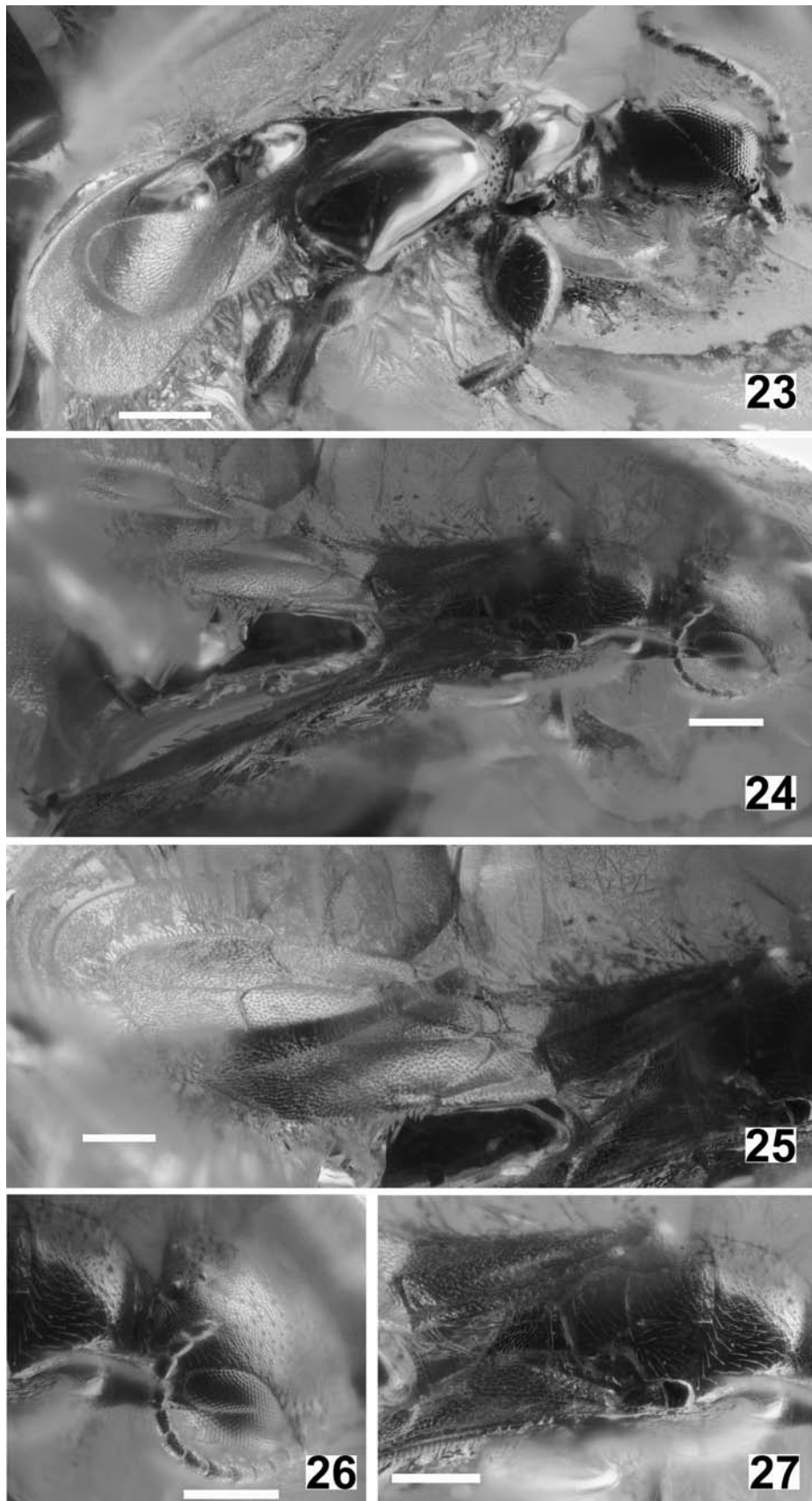
Figs. 17-18. *Eupsenella rossica* RAMOS & AZEVEDO sp. nov. **17.** Body in dorsal view. **18.** Body in ventral view. (Scale bar = 300 μ m).



Figs. 19-22. *Eupsenella rossica* RAMOS & AZEVEDO sp. nov. **19.** Head in dorsal view. **20.** Head in ventral view. **21.** Mesosoma in dorsal view. **22.** Mesosoma in ventral view. (Scale bar = 300 μ m).

carina, continues on well up the frons. First five antennal segments in ratio of about 7:3:3:3:3. Eye not gibbous, large, $> 0.5 \times$ LH, glabrous. Ocelli small, $\leq 0.30 \times$ WOT, $0.30 \times$ WOT. HE $0.54 \times$ LH. WH $1.0 \times$ LH. WF $0.5 \times$ WH. WF $0.94 \times$ HE. OOL $2.0 \times$ WOT. VOL $0.38 \times$ HE. Vertex crest 3.0

$\times$ DAO. DAO $0.13 \times$ WF. Distance between posterior ocelli $1.5 \times$ DAO. Ocellar triangle not compact. Anterior ocellus surpassing imaginary top eye line. Vertex crest straight. Mesosoma. – Pronotal disc coriaceous, $0.5 \times$ as long as wide, anterior corner rounded, anterior margin slightly



Figs. 23-27. *Eupsenella yantarnica* RAMOS & AZEVEDO sp. nov.. **23.** Habitus. **24.** Body in dorsal view. **25.** Left forewing in dorsal view. **26.** Head in latero-dorsal view. **27.** Mesosoma in dorsal view. (Scale bar = 300 μ m).

convex, posterior margin slightly concave medially, as long as the mesoscutum. Mesoscutum 0.44 x as long as wide, coriaceous. Notaulus present, well defined; strongly wide posterad, convergent posteriorly. Parapsidal furrows ill-defined. Scutellum with scutellar fovea elliptical, narrowed. Propodeal disc with median longitudinal carina present. Prosternum expanded, excavated medially, excavation complete.

Wings. – Macropterous. Tegula without setae. Forewing with 1M cell present, closed, almost elliptical. 1R1 cell of forewing present, 1R1 cell 1.0 x 2R1 cell. C cell widening distally. 2R1 closed, 0.11 x LFW. M vein convex. Rsa slightly diagonal to anterior margin of forewing. Rsb straight. Distal margin of Rsc convex, ending abruptly toward anterior margin of forewing. RS+M vein 0.25 x Rsa. M vein 1.0 x Rsa. Cua vein 1.5 x Rsa. Rsa slightly inclined toward tegula. Stigma expanded, rectangular, distal stigmal margin truncate.

Legs. – Profemur 0.45 x as long as wide. Claws bifid, curved. Male unknown.

Remarks: This species differs from the foregoing species in having the parapsidal furrows ill-defined and almost absent, the notaulus strongly widened posterad, the 1M cell almost elliptical, and the M vein convex.

Genus *Goniozus* FÖRSTER, 1856

(Syn.: *Parasierola* CAMERON, 1883: 197; type species:

Parasierola testaceicornis CAMERON, 1883, by monotypy; *Progoniozus* KIEFFER, 1905: 105; type species: *Perisemus floridanus* ASHMEAD, 1887, by original designation; *Parasierola* KIEFFER, 1914: 533; type species: *Parasierola gallicola* KIEFFER, 1905, designated by MUESEBECK & WALKLEY (1951)).

Type species: *Bethylus claripennis* FÖRSTER, 1851, designated by ASHMEAD, 1893.

Goniozus definitus RAMOS & AZEVEDO sp. nov.

Figs. 28–32

Etymology: The specific epithet *definitus*, from Latin, means ‘defined, well-marked’ in allusion to triangular area well-defined of the propodeal disc.

Material examined: Holotype. Russia, Baltic amber, 1 female, PIN 363/138.

Occurrence: Baltic amber, Russia, Oligocene.

Diagnosis: Mandible with four sharpened apical teeth. Median clypeal lobe with median carina continues on well up the frons. Antennal scape not gibbous, and cylindrical. Malar space evident. Ocellar triangle compact. Vertex crest straight. Pronotal disc shorter than the mesoscutum. Notaulus absent. Propodeal disc with triangular area well-defined; median longitudinal carina absent; discal carina absent. Forewing with anterior margin of forewing without

conspicuous bristly hairs; 1R1 cell absent; Rsa subperpendicular to anterior margin of forewing.

Description: Holotype, female, body length 3.1 mm, LFW 2.1 mm.

Head. – Head subquadrate in dorsal view, as long as wide. Mandible with four sharpened apical teeth, two lowermost teeth larger than upper ones. Clypeus with median clypeal lobe angulate, with median carina, continues on well up the frons. Antennal scape not gibbous, cylindrical. Malar space evident. First five antennal segments in ratio of about 9:4:4:4:4. Eye not gibbous, glabrous. Ocelli large, > 0.30 x WOT, 0.4 x WOT. HE 0.5 x LH. WH 1.0 x LH. WF 0.7 x WH. WF 1.4 x HE. OOL 1.4 x WOT. VOL 0.5 x HE. Vertex crest 2.5 x DAO. DAO 0.14 x WF. Distance between posterior ocelli 2.5 x DAO. Ocellar triangle compact. Anterior ocellus not surpassing imaginary top eye line. Vertex crest straight.

Mesosoma. – Pronotal disc coriaceous, 0.6 x as long as wide, anterior corner rounded, posterior margin slightly concave medially, shorter than the mesoscutum. Mesoscutum 0.38 x as long as wide. Notaulus absent. Scutellum with scutellar fovea elliptical, narrowed. Propodeal disc with triangular area well-defined, median longitudinal carina absent, discal carina absent. Mesopleuron coriaceous, mesopleural pit shallow. Prosternum expanded, excavated medially, excavation complete.

Wings. – Macropterous. Tegula without setae. Forewing with 1M cell present, closed, subpentagonal. Anterior margin of forewing without conspicuous bristly hairs. M vein straight. 1R1 cell of forewing absent. C cell evenly narrow. 2R1 cell open. Rsa perpendicular to anterior margin of forewing. Distal margin of Rsa ending abruptly toward anterior margin of forewing. RS+M vein 0.8 x Rsa. M vein 1.2 x Rsa. Cua vein 1.6 x Rsa. Rsa slightly inclined toward tegula. Stigma expanded, rectangular, distal stigmal margin truncate.

Legs. – Profemur 1.9 x longer than wide. Claws bifid, curved.

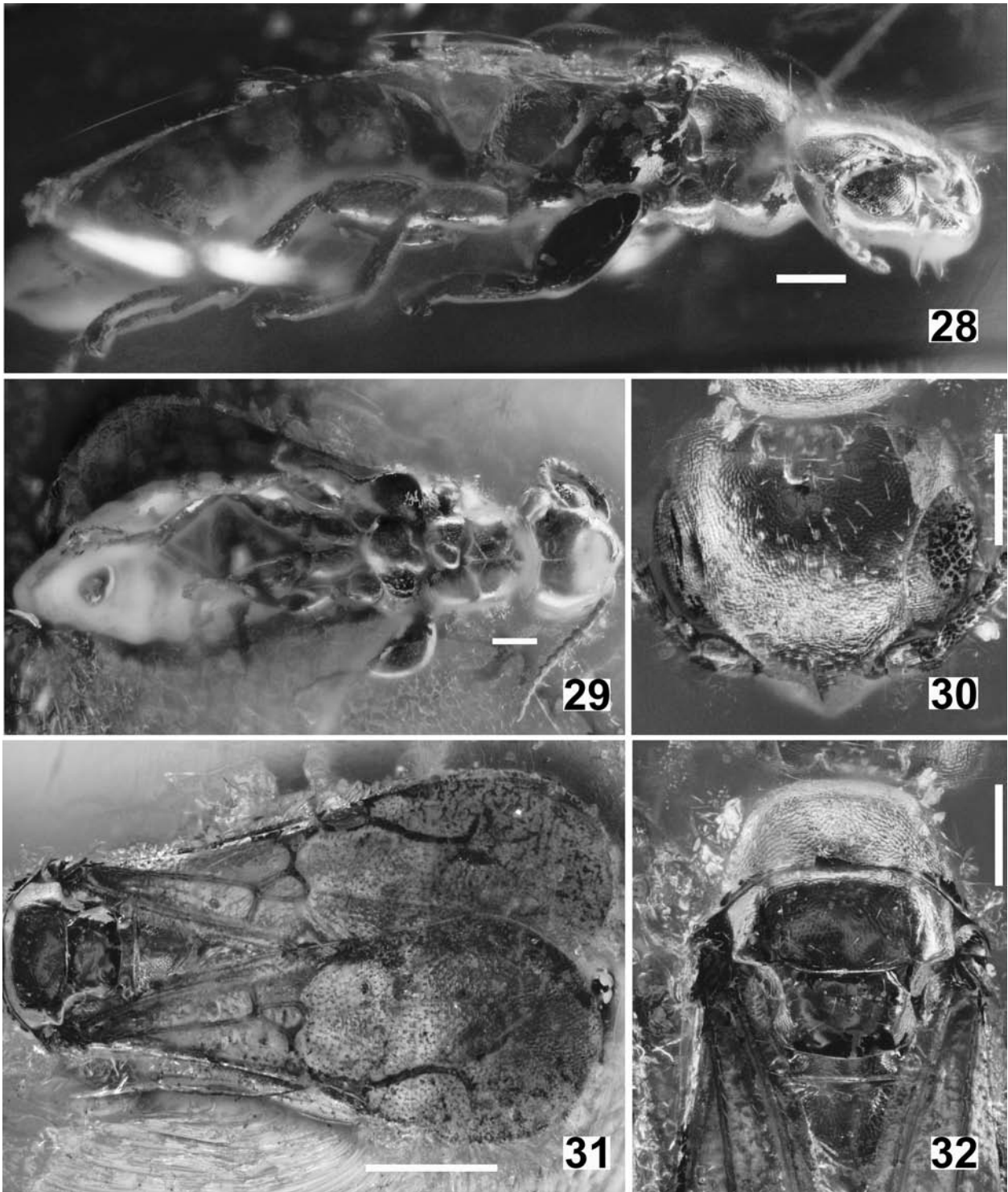
Metasoma. – 2.6 x longer than wide.

Male unknown.

Remarks: This species is similar to *Goniozus contractus* (BRUES, 1933) in having large eyes, the mesoscutum lacking notauli, the propodeal disc lacking a median longitudinal carina, the 2R1 cell open, and the 1M cell closed. However, *G. definitus* RAMOS & AZEVEDO sp. nov. has the antennal scape non-gibbous and cylindrical, the malar space evident, the pronotal disc shorter than the mesoscutum, and the anterior margin of the forewing without conspicuous bristly hairs, whereas *G. contractus* has the antennal scape gibbous and not strongly flattened, the malar space very short, the pronotal disc slightly longer than the mesoscutum, and the anterior margin of the forewing fringed with conspicuous, short, bristly hairs that extend from near the end of the basal cell to the apex of the stigma.

Genus *Lytopsenella* KIEFFER, 1911

Type species: *Eupsenella herbsti* KIEFFER, 1911, by original designation.



Figs. 28-32. *Goniozus definitus* RAMOS & AZEVEDO sp. nov. **28.** Habitus. **29.** Body in ventral view. **30.** Head in dorsal view. **31.** Left and Right forewings in dorsal view. **32.** Mesosoma in dorsal view. (Scale bar = 300 μ m).

Lytopsenella kerneggeri OHL, 1995

Figs. 33–44

Material examined: Holotype. Female: Baltic amber (Upper Eocene), Hamburg (Nr. 24/85), University of Hamburg (Typ.-Kat. Nr. 3621). New material: Ukraine, Klesov, Rovno amber, 1 female, k-7923, 7915–30; 1 female, k-3553 (SIZK); Russia, Baltic amber, 1 female, PIN 964/129.

Occurrence: Rovno amber, Ukraine, and Baltic amber, Russia; Upper Eocene.

Variation: Body length 3.0–3.54 mm; LFW 1.9–2.5 mm; median longitudinal carina present, very short; mesoscutum clearly longer than the mesoscutum; posterior margin of propodeal disc strongly concave; RS+M vein 0.75 x Rsa; M vein 1.5 x Rsa; Cua vein 1.75 x Rsa; Rsa slightly inclined toward tegula; C cell clearly widening distally; vertex crest with several long, and wide setae; the 2R1 cell 1.35 x 1R1 cell.

Remarks: This species was previously known only from a single specimen from Baltic amber and is here recorded for the first time from Rovno amber.

Lytopsenella baltica RAMOS & AZEVEDO sp. nov.

Figs. 45–48

Etymology: The specific epithet *baltica* is in allusion to the coast of the Baltic Sea, where the specimen was collected.

Material examined: Holotype. Baltic amber, coast of Baltic Sea, 1 female, 0906–0991 (UFES).

Occurrence: Baltic amber, coast of Baltic Sea, Upper Eocene.

Diagnosis: Clypeus with median clypeal lobe angulate. Median clypeal lobe with median carina continues on well up the frons, straight in profile. Vertex crest convex. Notaulus absent. Forewing with the distal margin of Rsc convex. 1M cell subquadrate.

Description: Holotype, Female, Body length 2.6 mm, LFW 2.2 mm.

Head. – Head subtriangular in dorsal view, longer than wide. Clypeus with median clypeal lobe angulate, with median carina, continues on well up the frons, almost straight in profile. First five antennal segments in ratio of about 7:2:3:3:3. Eye gibbous, large, > 0.5 x LH, glabrous. Ocelli large, > 0.30 x WOT, 0.33 x WOT. HE 0.54 x LH. WH 0.88 x LH. WF 0.56 x WH. WF 0.9 x HE. OOL 1.66 x WOT. VOL 0.3 x HE. Vertex crest 3.0 x DAO. DAO 0.1 x WF. Distance between posterior ocelli 3.0 x DAO. Ocellar triangle not compact. Anterior ocellus not surpassing imaginary top eye line. Vertex crest convex.

Mesosoma. – Pronotal disc coriaceous, 0.4 x as long as wide, anterior corner rounded, anterior margin slightly convex, posterior margin slightly concave medially; as long as wide the mesoscutum. Mesoscutum 0.50 x as long as wide,

coriaceous. Notaulus absent. Scutellum with scutellar fovea elliptical, narrowed.

Wings. – Macropterous. Tegula with setae. Forewing with 1M cell present, closed, subquadrate. 1R1 cell of forewing present, 1R1 cell 0.86 x 2R1 cell. C cell widening distally. 2R1 cell closed, 0.22 x LFW. M vein straight. Rsa slightly diagonal to anterior margin of forewing. Rsb arched. Distal margin of Rsc convex, ending gently toward anterior margin of forewing. RS+M vein 0.8 x Rsa. M vein 1.0 x Rsa. Cua vein 1.4 x Rsa. Stigma expanded, rectangular, distal stigmal margin truncate. Claws bifid, curved. Rsa subperpendicular to anterior margin of forewing.

Metasoma. – 2.6 x longer than wide.

Male unknown.

Remarks: This species is similar to *Lytopsenella kerneggeri* OHL in having large eyes, the vertex crest with a series of long bristly hairs, the notauli absent, and the costal cell (C) widening distally. However, *Lytopsenella baltica* RAMOS & AZEVEDO sp. nov. has a median clypeal lobe with the median carina nearly straight in profile, the vertex crest convex, the distal margin of the third section of the Rs vein (Rsc) convex, and the 1M cell subquadrate, whereas *L. kerneggeri* OHL has a median clypeal lobe with the median carina strongly arched in profile, the vertex crest straight, the distal margin of Rsc nearly straight, and the 1M cell subpentagonal.

Lytopsenella maritima RAMOS & AZEVEDO sp. nov.

Figs. 49A, B, 50C, D

Etymology: The specific epithet *maritima*, from Latin, means ‘seacoast’ in allusion to the coast of the Baltic Sea, where the specimens were collected.

Material examined: Holotype. Baltic amber, coast of Baltic Sea, 1 female and 1 male allotype, 0911–1050 (UFES).

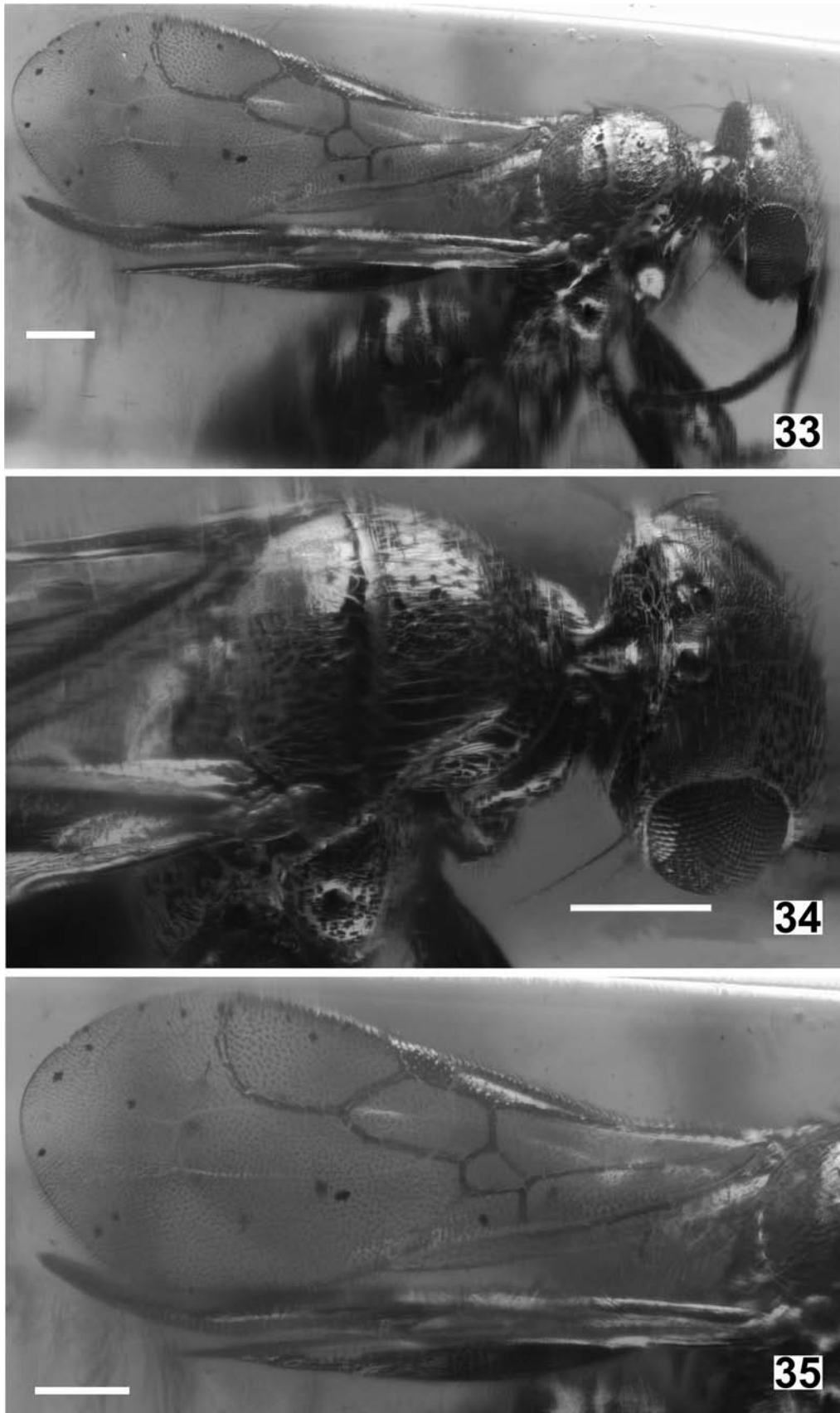
Occurrence: Baltic amber, coast of Baltic Sea, Oligocene.

Diagnosis: Clypeus with median clypeal lobe angulate. Vertex crest convex, without a series of long bristly hairs. Pronotal disc very short. Notauli absent. Propodeal disc with median longitudinal carina incomplete.

Description of the female: Holotype, female, body length 2.0 mm, LFW 1.3 mm.

Head. – Head subquadrate in dorsal view, longer than wide. Maxillar palpus with six palpomeres. Clypeus with median clypeal lobe angulate, straight in profile. First five antennal segments in ratio of about 7:3:2:2:2. Eye not gibbous, glabrous. HE 0.45 x LH. VOL 0.7 x HE.

Mesosoma. – Pronotal disc coriaceous, 0.3 x as long as wide, very short, anterior corner rounded, anterior margin slightly convex, posterior margin slightly concave medially; shorter than the mesoscutum. Mesoscutum 0.5 x as long as wide, coriaceous. Notaulus absent. Scutellum with scutellar fovea elliptical, narrowed. Propodeal disc with median longitudinal carina incomplete.



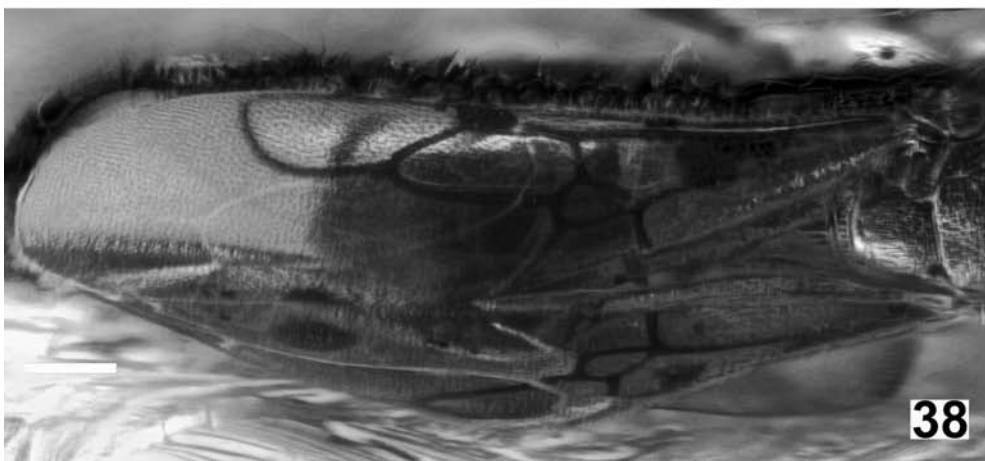
Figs. 33-35. *Lytropsenella kerneggeri* OHL. **33.** Habitus. **34.** Mesosoma in dorsal view. **35.** Left forewing in dorsal view. (Scale bar = 300 μ m).



36



37



38

Figs. 36-38. *Lytopsenella kerneggeri* OHL (Rovno amber) k-7923, new material. **36.** Habitus. **37.** Head in dorsal view. **38.** Left forewing in dorsal view. (Scale bar = 300 μ m).

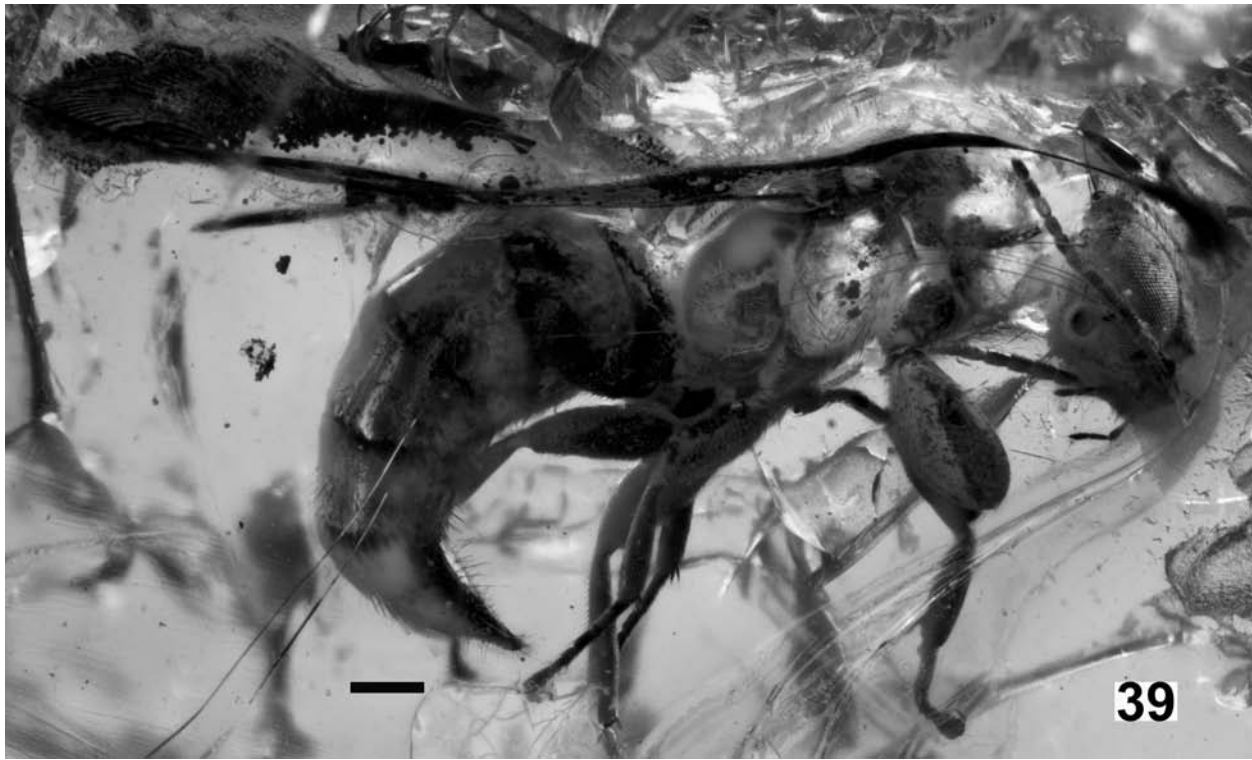


Fig. 39. *Lytopsenella kerneggeri* OHL (Rovno amber) k-3553, new material. **39.** Habitus. (Scale bar = 300 μ m).

Wings. – Macropterous. Tegula without setae. Forewing with 1M cell present, closed, subtriangulate. 1R1 cell of forewing present, 1R1 cell 1.0 x 2R1 cell. C cell widening distally. 2R1 cell closed, 0.23 x LFW. M vein straight. Rsa slightly diagonal to anterior margin of forewing. Rsb straight. Distal margin of Rsc convex, ending gently toward anterior margin of forewing. RS+M vein 1.0 x Rsa. M vein 2.5 x Rsa. Cua vein 2.5 x Rsa. Stigma expanded, rectangular, distal stigmal margin truncate. Claws bifid, curved. Metasoma. – 3.0 x longer than wide.

Description of male: Allotype, male, body length 1.7 mm, LFW 1.1 mm.

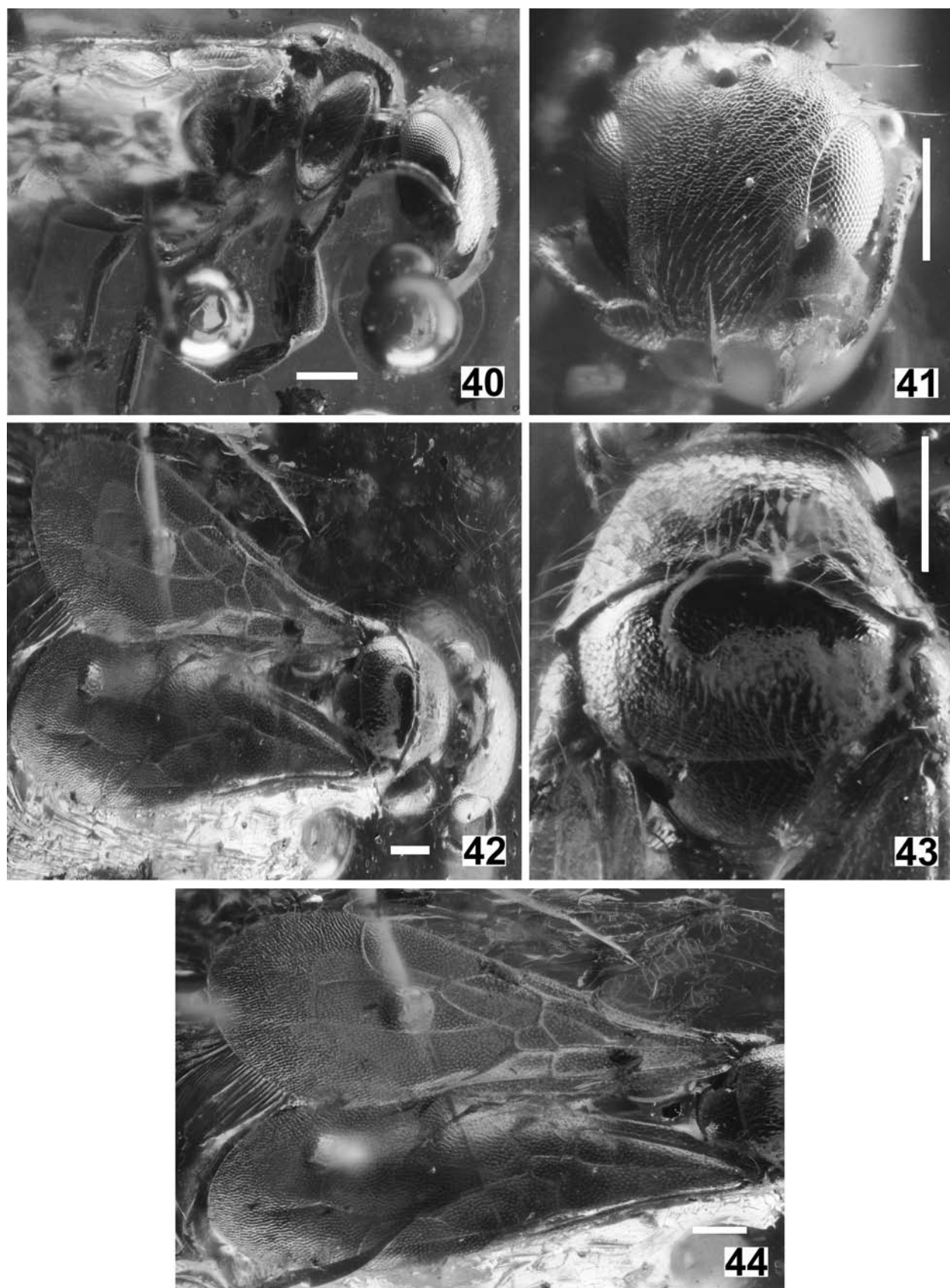
Head. – Head subquadrate in dorsal view, longer than wide. Clypeus with median clypeal lobe angulate. First five antennal segments in ratio of about 7:2:2:2:2. Eye not gibbous, small, ≤ 0.5 x LH, glabrous. Ocelli large, > 0.30 x WOT, 0.33 x WOT. HE 0.4 x LH. WH 0.8 x LH. WF 0.6 x WH. WF 1.2 x HE. OOL 3.3 x WOT. VOL 0.7 x HE. Vertex crest 8.0 x DAO. DAO 0.1 x WF. Distance between posterior ocelli 3.0 x DAO. Ocellar triangle compact. Anterior ocellus not surpassing imaginary top eye line. Vertex crest convex. Mesosoma. – Pronotal disc coriaceous, 0.3 x as long as wide, very short, anterior corner rounded, anterior margin slightly convex, posterior margin slightly concave medially; shorter than the mesoscutum. Mesoscutum 0.4 x as long as

wide, coriaceous. Notaulus absent. Scutellum with scutellar fovea elliptical, narrowed. Propodeal disc with median longitudinal carina incomplete.

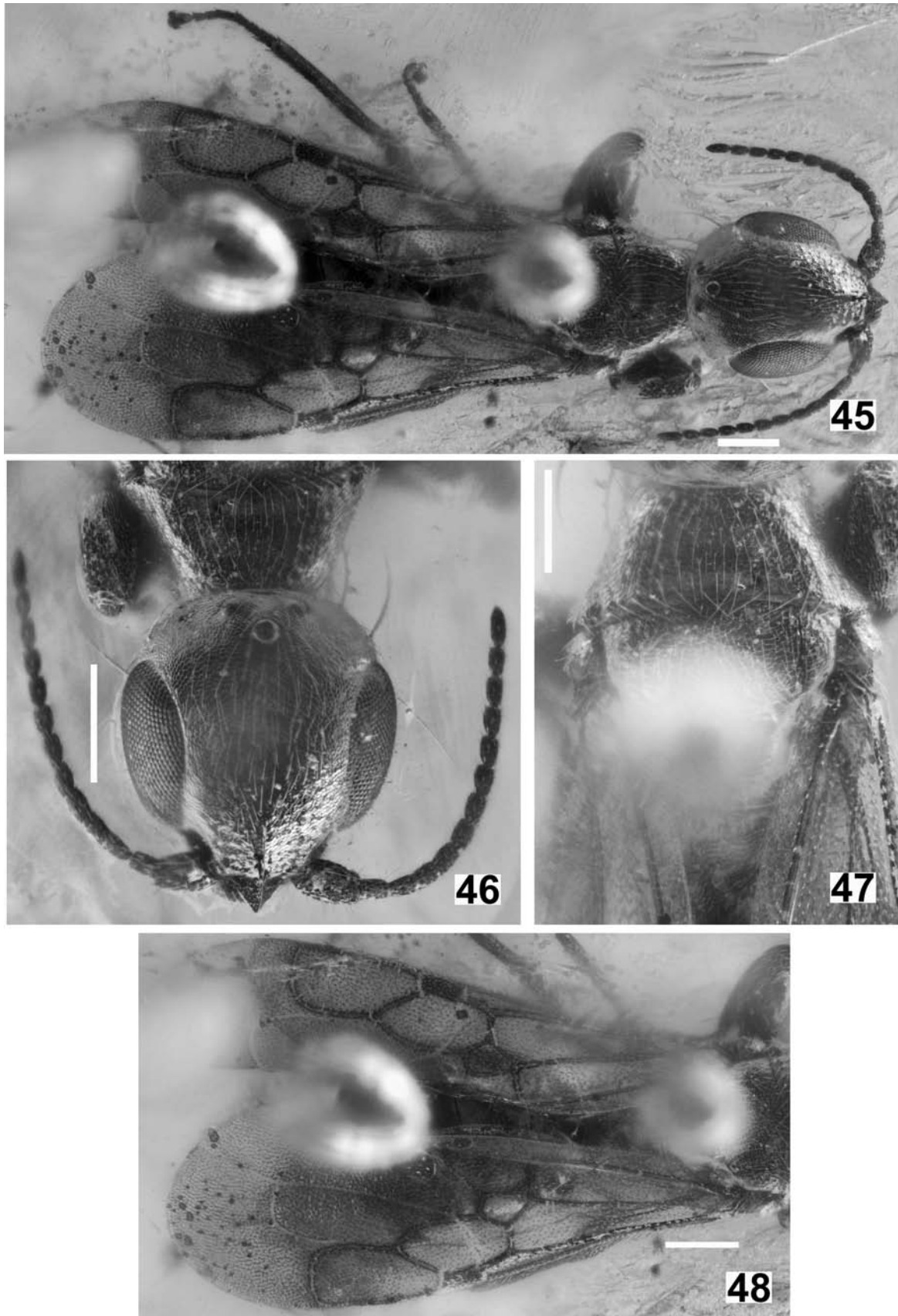
Wings. – Macropterous. Tegula without setae. Forewing with 1M cell present, closed, subquadrate. 1R1 cell present, 1R1 cell 0.88 x 2R1 cell. C cell widening distally. 2R1 cell closed, 0.28 x LFW. M vein straight. Rsa slightly diagonal to anterior margin of forewing. Rsb straight. Distal margin of Rsc convex, ending gently toward anterior margin of forewing. RS+M vein 1.0 x Rsa. M vein 1.5 x Rsa. Cua vein 2.0 x Rsa. Rsa slightly inclined toward tegula. Stigma expanded, rectangular, distal stigmal margin truncate. Claws bifid, curved.

Metasoma. – 2.4 x longer than wide.

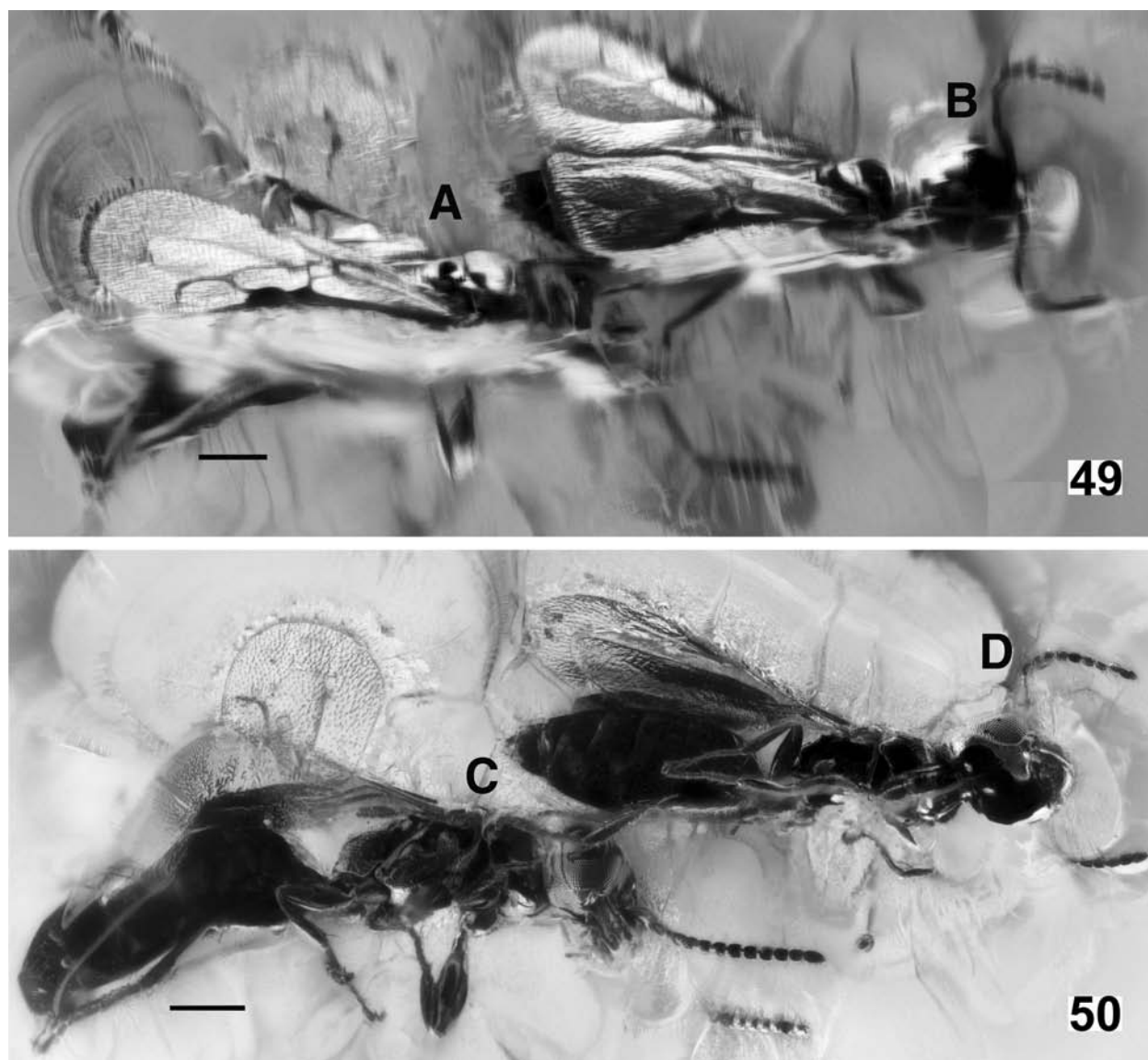
Remarks: This species is similar to *Lytopsenella kerneggeri* OHL (Figs. 30–32) in having the notauli absent, the propodeal disc with the median longitudinal carina present but incomplete, the C cell widening distally, and the second section of the Rs vein (Rsb) straight. However, *Lytopsenella maritima* RAMOS & AZEVEDO sp. nov. has a median clypeal lobe with the median carina angulate in profile and the vertex crest convex and lacking long bristly hairs, whereas *L. kerneggeri* OHL has a median clypeal lobe with the median carina strongly arched in profile and the vertex crest straight and bearing a series of long bristly hairs.



Figs. 40-44. *Lytopsenella kerneggeri* OHL (Baltic amber) PAH 964/129, new material. **40.** Habitus. **41.** Head in dorsal view. **42.** Mesosoma in dorsal view. **43.** Mesosoma in dorsal view. **44.** Left and Right forewings in dorsal view. (Scale bar = 300 μm).



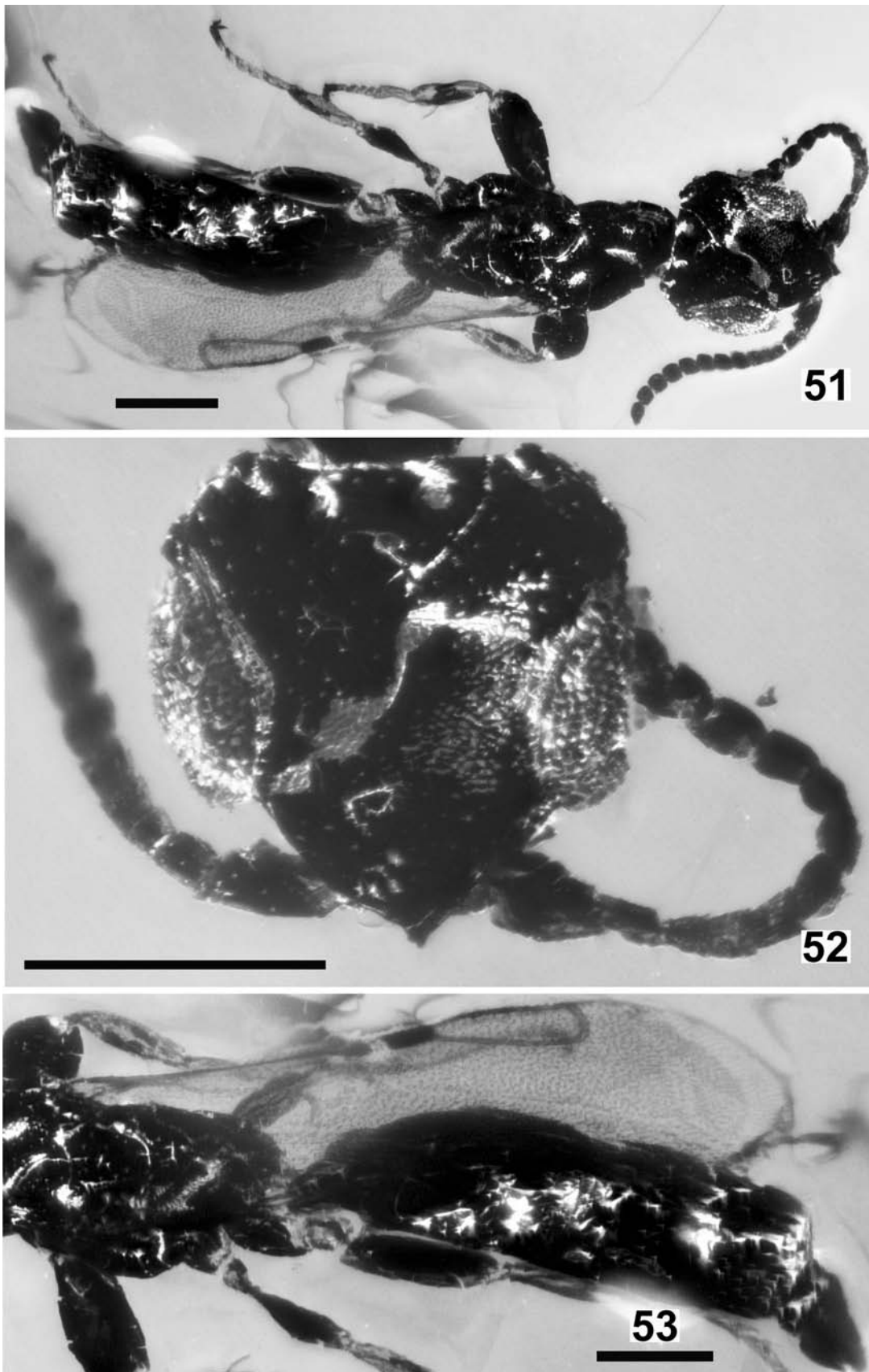
Figs. 45-48. *Lytopsenella baltica* RAMOS & AZEVEDO sp. nov. **45.** Body in dorsal view. **46.** Head in dorsal view. **47.** Mesosoma in dorsal view. **48.** Left and Right forewings in dorsal view. (Scale bar = 300 μ m).



Figs. 49-50. *Lytopsenella maritima* RAMOS & AZEVEDO sp. nov. **49.** A. Body length in dorsal view of female (holotype). **B.** Body length in dorsal view of male (allotype). **50.** **C.** Body in ventral view of female (holotype). **D.** Body in ventral view of male (allotype). (Scale bar = 300 μ m).

The fossil record of Bethylinae has hitherto included only female specimens. However, both male and female specimens of *L. maritima* RAMOS & AZEVEDO sp. nov. are known. Thus, this report constitutes the first record of sexual association in fossil species of Bethylinae. The sexual dimorphism is weak in this species, and the specimens share several features indicating that they are conspecific. The male and female specimens have the vertex crest convex, the pronotal disc short, the mesoscutum lacking notauli, the propodeal disc with the median longitudinal carina present but incomplete, the prostigma large and trapezoidal, the

Rsb of the forewing straight, the *Rsc* of the forewing convex and tapering gently toward the anterior margin of forewing, and the *RS+M* vein equal to the first section of the *Rs* vein (*Rsa*). The main differences between the male and female specimens are that the females are slightly larger than the males, the *M* and *Cu* veins of the forewing are longer in females, and the *1M* cell is triangulate in females but quadrate in males. Considering this evidence, we are convinced that these specimens represent conspecific female and male *L. maritima* RAMOS & AZEVEDO sp. nov.



Figs. 51-53. *Sierola rovniana* RAMOS & AZEVEDO sp. nov. **51.** Body length in dorsal view. **52.** Head in dorsal view. **53.** Right forewing and Metasoma in dorsal view. (Scale bar = 300 μ m)

Genus *Sierola* CAMERON, 1881

Type species: *Sierola testaceipes* CAMERON, by monotypy.

Sierola rovniana RAMOS & AZEVEDO sp. nov.

Figs. 51-53

Etymology: The specific epithet *rovniana* is in allusion to the Rovno region of the Ukraine.

Material examined: Holotype. Ukraine, Klesov, Rovno amber, 1 female, n° K-24208 (SIZK).

Occurrence: Rovno amber, Ukraine, Upper Eocene.

Diagnosis: Clypeus with median clypeal lobe angulate. Median clypeal lobe with median carina. Anterior ocellus surpassing imaginary top eye line. Vertex crest straight. Notaulus present. Forewing with first medial cell closed, and nebulous. 1R1 cell absent. C cell evenly narrow. 2R1 cell closed, and subtriangulate. Distal margin of Rsc ending abruptly toward anterior margin of forewing. R cell formed by nebulous veins. 1Cu cell formed by nebulous veins. 1M cell formed by nebulous veins.

Description: Holotype, female, body length 2.0 mm, LFW 1.2 mm.

Head. – Head subtriangular in dorsal view, as long as wide. Clypeus with median clypeal lobe angulate, with median carina. First five antennal segments in ratio of about 9:3:3:3:3. Eye not gibbous, glabrous. Ocelli small, $\leq 0.30 \times \text{WOT}$, $0.2 \times \text{WOT}$. HE $0.5 \times \text{LH}$. WH $1.0 \times \text{LH}$. WF $0.5 \times \text{WH}$. WF $1.0 \times \text{HE}$. OOL $1.4 \times \text{WOT}$. VOL $0.33 \times \text{HE}$. Vertex crest $5.0 \times \text{DAO}$. DAO $0.1 \times \text{WF}$. Distance between posterior ocelli $5.0 \times \text{DAO}$. Ocellar triangle not compact. Anterior ocellus surpassing imaginary top eye line. Vertex crest straight.

Mesosoma. – Pronotal disc coriaceous, $0.66 \times$ as long as wide, posterior margin slightly concave medially. Mesoscutum $0.5 \times$ as long as wide, coriaceous. Notaulus present, convergent posteriorly. Scutellum with scutellar fovea elliptical, wide. Prosternum expanded, excavated medially, excavation complete.

Wings. – Macropterous. Tegula without setae. Forewing with 1M cell present, closed, but nebulous. 1R1 cell absent. C cell evenly narrow. 2R1 cell closed, subtriangulate, $0.21 \times \text{LFW}$. R cell formed by nebulous veins. 1Cu cell formed by nebulous veins. 1M cell formed by nebulous veins. Distal margin Rsc ending abruptly toward anterior margin of forewing. Stigma not expanded, rectangular, distal stigmal margin truncate.

Legs. – Profemur $2.2 \times$ longer than wide. Claws bifid, curved.

Metasoma. – $2.4 \times$ longer than wide.

Male unknown.

Remarks: This species is similar to *Sierola hastata* SORG, 1988 in having 13 antennomeres and the 2R1 cell closed and subtriangulate. However, *Sierola rovniana* RAMOS & AZEVEDO sp. nov. has the distal margin of Rsc ending

abruptly toward the anterior margin of the forewing and the R, 1Cu, and 1M cells formed by nebulous veins, whereas *S. hastata* SORG has the distal margin of Rsc tapering gently toward the anterior margin of the forewing and the R, 1Cu, and 1M cells formed by tubular veins.

4. Discussion

No other fossil locality is comparable with Baltic amber in terms of diversity, and its amber inclusions are undoubtedly among those most widely known by lay people. However, Rovno amber has long been considered poor in inclusions, even compared to Belarusian amber (ZHERIKHIN & ESKOV 1999). Today, the Rovno and Belarusian ambers are considered identical, re-deposited over a territory encompassing parts of both countries (PERKOVSKY et al. 2007, 2010).

Rovno amber is chemically identical to Baltic amber, and both are considered roughly contemporaneous, dating from the Late Eocene (PERKOVSKY et al. 2007). However, Oise amber is autochthonous and substantially differs from Baltic amber in age (earliest Eocene, 53 My), chemical composition, and origin (NEL et al. 1999).

In general, fossil evidence is necessary to accurately understand the character combinations found in living species. Thus, the material analyzed here may allow us to further study the evolution of the characters preserved in the Bethylinae specimens.

Lytopsenella KIEFFER includes four fossil species from Baltic amber (Upper Eocene): *L. crastina*, *L. setigera*, and *L. simplex*, described by BRUES (1923), and *L. kerneggeri*, described by OHL (1995) (Figs. 33-44). Thus, *Lytopsenella* is the genus of Bethylinae with the largest number of described fossil species. The known distribution and taxonomic variation of *L. kerneggeri* OHL are here expanded: this species is recorded for the first time from Rovno amber. *Lytopsenella* closely resembles *Eupsenella*, mainly differing in having the 2R1 cell clearly longer. In *Lytopsenella*, the 1R1 cell of the forewing is always significantly shorter than the 2R1 cell; in *Eupsenella*, the 1R1 cell is equal to or longer than the 2R1 cell.

In most species of Bethylinae, the veins are tubular. However, *Sierola rovniana* RAMOS & AZEVEDO sp. nov. (Figs. 51, 53) exhibits a novel pattern. In this species, the R, 1Cu, and 1M cells are wholly formed by nebulous veins. The only cell in the forewing formed by tubular veins is the 2R1 cell, whereas in *Sierola hastata* SORG, 1988, for example, the R, 1Cu, and 1M cells are formed by tubular veins. This peculiarity of *S. rovniana* RAMOS & AZEVEDO sp. nov. is new for this genus.

Several aspects of *Eupsenella* are notable. The fossil *Eupsenella* species analyzed here closely resemble the living species, although the 2R1 cell appears consistently longer in the fossil species.

WESTWOOD (1874) cited five to six apical mandibular teeth in the original description of the genus, but all living species have four apical mandibular teeth (see RAMOS & AZEVEDO 2012). This condition also appears in *E. aulax* RAMOS & AZEVEDO sp. nov. (Figs. 5, 10) and *E. rossica* RAMOS & AZEVEDO sp. nov. (Fig. 20). However, it was not possible to count the exact number of apical teeth in *E. klesoviana* RAMOS & AZEVEDO sp. nov. and *E. yantarnica* RAMOS & AZEVEDO sp. nov. because the mandible was not clearly discernible.

The pronotal disc is usually simple in *Eupsenella*. However, a novel pattern occurs in *E. aulax* RAMOS & AZEVEDO sp. nov. (Figs. 5-6, 9). This species has a peculiar deep transverse furrow near the posterior margin. This character is completely new for *Eupsenella*.

According to RAMOS & AZEVEDO (2012), the prosternum is clearly expanded in *Eupsenella*. This character appears in all fossil *Eupsenella* species analyzed here, including *Eupsenella eocenica* (DE PLOËG & NEL, 2004) comb. nov. (Fig. 2).

In extant *Eupsenella* species the notauli are always evenly narrow. However, a novel pattern appears in *Eupsenella yantarnica* RAMOS & AZEVEDO sp. nov. (Figs. 24, 27), which has the notauli strongly widened posterad.

Characters related to wing venation are especially useful for delimiting living and fossil *Eupsenella* species. No new pattern was found in this study. Notably, however, the 2R1 cell of the forewing is never longer than the 1R1 cell in extant *Eupsenella* species; at most, the 2R1 cell is equal to the 1R1 cell. All fossil *Eupsenella* species described here have the 2R1 cell as long as the 1R1 cell, corroborating the proposed pattern for *Eupsenella*.

Regarding the geographical distribution of the genus, extant *Eupsenella* species are restricted to Australia, except for *E. insulana* GORDH & HARRIS, 1996, which also occurs in New Zealand. Thus, the distribution of *Eupsenella* has hitherto been confined to the Australian region. However, we here describe two new species from Ukraine, *E. aulax* RAMOS & AZEVEDO sp. nov. (Figs. 5-9) and *E. klesoviana* RAMOS & AZEVEDO sp. nov. (Rovno amber) (Figs. 13-16), and two new species from Russia, *E. rossica* RAMOS & AZEVEDO sp. nov. (Figs. 17-22) and *E. yantarnica* RAMOS & AZEVEDO sp. nov. (Baltic amber) (Figs. 23-27). Thus, this genus had a much wider geographical distribution in the

past. This information demonstrates that *Eupsenella* species were present outside the Australian region between 36 and 37 My. *Eupsenella* thus provides a further example of a group whose contemporary distribution is southern ("Gondwanan") but that is present in the fossil record of northern continents, indicating a formerly global distribution (ESKOV 2002).

However, extant species of the genus *Goniozus* FÖRSTER are present worldwide, recorded from the Oriental, Neotropical, Nearctic, Palaearctic, Afrotropical, and Australian regions. According to LIM & LEE (2012), *Goniozus* comprises approximately 170 species. However, only two fossil species have been described previously: *Goniozus contractus* (BRUES, 1933) from Baltic amber (Eocene) and *Goniozus respectus* SORG, 1988 from Dominican amber (Miocene). Here, a third fossil *Goniozus* species is described: *G. definitus* RAMOS & AZEVEDO sp. nov. (figs. 28-32) from Baltic amber.

Wing venation is also important for delimiting modern and fossil *Goniozus* species. Species of this genus can have the 1M cell (areolet) of the forewing either closed or open (see POLASZEK & KROMBEIN 1994). In *G. definitus* RAMOS & AZEVEDO sp. nov., *G. contractus*, and *G. respectus*, the forewing 1M cell is closed. This character occurs in most *Goniozus* species. In several species, however, the areolet is incomplete; only the upper part is preserved as a 'stub' arising from the *Rsa* vein. This character occurs, for example, in *G. floridanus* (ASHMEAD).

Considering that the types of most fossil species of Bethylinae have been lost, except those of *L. kerneggeri* and *E. eocenica* (see above), the present study is important because it confirms information previously available only in the literature.

Cenozoic ambers preserve 17 species in 5 genera of Bethylinae (Table 1). *Lytopsenella* and *Eupsenella*, the two genera with the most complete wing venation known in the subfamily, predominate, as expected for this ancient fauna. The material examined in the present study consists of 12 specimens representing as many as nine species and four genera. This small number of specimens per species suggests a comparatively high diversity and low abundance of bethyline wasps visiting amber trees. In our material, two species are known from two specimens each: *L. kerneggeri* and *L. maritima*. The two specimens of the former species come from two different kinds of amber (Baltic and Rovno), suggesting that the source areas of these two ambers were similar in their fauna despite their geographical separation (DLUSSKY & RASNITSYN 2009; PERKOVSKY et

Table 1. Valid species of fossil Bethylinae.

Taxon	Age	Amber	References
<i>Eupsenella aulax</i> RAMOS & AZEVEDO sp. nov.	Late Eocene	Rovno	This paper
<i>Eupsenella klesoviana</i> RAMOS & AZEVEDO sp. nov.	Late Eocene	Rovno	This paper
<i>Eupsenella eocenica</i> (DE PLOËG & NEL, 2004) comb. nov.	earliest Eocene	Oise	DE PLOËG & NEL (2004), this paper
<i>Eupsenella rossica</i> RAMOS & AZEVEDO sp. nov.	Late Eocene	Baltic	This paper
<i>Eupsenella yantarnica</i> RAMOS & AZEVEDO sp. nov.	Late Eocene	Baltic	This paper
<i>Goniozus contractus</i> (BRUES, 1933)	Late Eocene	Baltic	BRUES (1933)
<i>Goniozus respectus</i> SORG, 1988	Middle Miocene	Dominican	SORG (1988)
<i>Goniozus definitus</i> RAMOS & AZEVEDO sp. nov.	Late Eocene	Baltic	This paper
<i>Lytopsenella crastina</i> (BRUES, 1923)	Late Eocene	Baltic	BRUES (1933)
<i>Lytopsenella setigera</i> (BRUES, 1923)	Late Eocene	Baltic	BRUES (1933)
<i>Lytopsenella simplex</i> (BRUES, 1923)	Late Eocene	Baltic	BRUES (1933)
<i>Lytopsenella kerneggeri</i> OHL, 1995	Late Eocene	Baltic & Rovno	OHL (1995), this paper
<i>Lytopsenella baltica</i> RAMOS & AZEVEDO sp. nov.	Late Eocene	Baltic	This paper
<i>Lytopsenella maritima</i> RAMOS & AZEVEDO sp. nov.	Late Eocene	Baltic	This paper
<i>Prosierola submersa</i> BRUES, 1933	Late Eocene	Baltic	BRUES (1933)
<i>Sierola hastata</i> SORG, 1988	Late Eocene	Danish	SORG (1988)
<i>Sierola rovniana</i> RAMOS & AZEVEDO sp. nov.	Late Eocene	Rovno	This paper

al. 2010). The Cenozoic bethyline fauna was generally uniform across time and space, at least at the generic level: both older (Oise) and younger (Dominican) ambers, which are found at almost opposite points of the globe, reveal the same genera known from the Baltic and Rovno ambers (*Eupsenella* and *Goniozus*). Nevertheless, the generic composition of local amber assemblages displays non-trivial differences; for example, *Sierola* occurs in both the Rovno and Danish ambers but not in the much better-explored Baltic amber. A similar case has been reported for the ant genus *Fallomyrma* DLUSSKY & RADCHENKO, 2006 (PERKOVSKY & RASNITSYN 2013). This observation has been interpreted to indicate similarity between the environments and climatic conditions of the Rovno and Danish amber source areas in contrast to that of the Baltic amber (DLUSSKY & RASNITSYN 2009; PERKOVSKY 2011). The distribution of *Sierola* further supports this inference.

Our findings include other notable observations. For example, SORG (1988) considered Bethylinae to be basal within Bethylidae (excluding unplaced genera such as *Cretobethylellus*, some of which might be even more basal). However, all known genera of this sub-

family are still living; not one is extinct. This pattern is rather uncommon and suggests that more ancient and diverse assemblages of Bethylinae, including extinct genera, remain unknown.

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Addresses of the authors:

MAGNO S. RAMOS, CELSO O. AZEVEDO, Universidade Federal do Espírito Santo, Departamento de Biologia, Av. Marechal Campos 1468, Maruípe, 29.043-900 Vitória ES, Brazil, e-mails: magnosuprani@gmail.com; bethyridae@gmail.com

EVGENY E. PERKOVSKY, Schmalhausen Institute of Zoology of National Academy of Sciences of Ukraine, Khmel'nitsky 15, Kiev 01601, Ukraine; e-mail: perkovsky@fromru.com

ALEXANDER P. RASNITSYN, Borissiak Paleontological Institute, Russian Academy of Sciences, ul. Profsoyuznaya 123, 117868 Moscow, Russia, Natural History Museum, Cromwell Road, London SW7 5BD, UK; e-mail: rasnaa@mail.ru; e-mail: rasnaa@mail.ru