

First record of the *Sulia glaesaria* Simutnik, 2015 (Hymenoptera, Chalcidoidea, Encyrtidae) from Rovno amber

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Abstract

Sulia glaesaria Simutnik, 2015 (Chalcidoidea, Encyrtidae), originally described from late Eocene Danish amber, is reported in coeval Rovno amber. A revised diagnosis of this genus is provided based on the new specimen and high-resolution photomicrographs of the holotype. Some character states, such as a short radicle, clypeus with long lateral margins, the presence of a strigil and basitarsal comb, spur vein of the hind wing, costal cell of hind wing along entire marginal vein with single line of long setae, and almost vertical syntergum with abruptly reflexed extension apically are reported in this species for the first time.

Keywords

Acropleural sulcus, acropleuron, Danish amber, Eocene, fossil Encyrtidae, syntergum

Introduction

Our research on several amber collections shows that the Encyrtidae is one of the most widespread families of Chalcidoidea in Eocene ambers (Simutnik 2001, 2002, 2007, 2015a, 2020; Simutnik and Perkovsky 2017, 2018a, b, c, 2020; Simutnik et al. 2014, 2021) along with Mymaridae, Aphelinidae and Trichogrammatidae. Most extant families of Chalcidoidea, including Tanaostigmatidae s.s., are, however, still unknown from the late Eocene. The large and distinctive chalcidoid wasp *Leptoomus janzeni* Gibson, 2008 from Baltic amber was previously attributed to Tanaostigmatidae s.l. along with the extant genus *Cynipencyrtus* Ishii, (1928) (Gibson 2008, 2009), but Heraty et al. (2013) subsequently treated *Cynipencyrtus* as its own family, Cynipencyrtidae Trjapitzin, 1973. A second, well preserved female specimen of *L. janzeni* was then reported from Rovno amber by Simutnik et al. (2020a). Some of its character states, in particular a bare and flat prepectus, suggest that a separate family should likely also be established for *Leptoomus*.

Sulia glaesaria Simutnik, 2015 was described from late Eocene Danish amber (Simutnik 2015b) and recently discovered in Rovno amber. Using a Leica Z16 APO stereomicroscope allowed revision of the diagnosis of this extinct genus.

The earliest known Encyrtidae include one female and four males ascribed to five different genera from middle Eocene Sakhalinian amber (Simutnik 2014, 2015b, 2020; Simutnik et al. 2021). They differ significantly from modern and late Eocene European amber encyrtids.

Material and methods

Ukrainian Rovno amber (33.9–37.8 Mya) is coeval with Baltic and Danish ambers from which *L. janzeni* and *S. glaesaria* were described.

The localities and composition of the Rovno amber fauna were recently characterized in a series of reviews by Perkovsky et al. (2010), Perkovsky (2018), Martynova et al. (2019) and Mitov et al. (2021). Including new Pristocerinae and Epyrinae (Bethyilidae) (Colombo et al. 2021a, b), *Formica* (Formicidae) (Radchenko et al. 2021) and the species reported here, 141 species of Hymenoptera are now known from Rovno amber, with 66 (47%) in common with Baltic amber.

Nearly all studied Rovno amber inclusions from Rovno were collected from Klesov and the Horyn River Basin (Perkovsky et al. 2010; Perkovsky 2017; Kirichenko-Babko et al. 2021; Sukhomlyn et al. 2021; Mitov et al. 2021 and references therein) except those of new collections from the former Vladimirets and Zarechnoye districts of the Rovno region and Manevichi district of the Volyn region (basins of Styr, Veselukha and Stokhod rivers). These new collections (mostly from Kuchotskaya Volya, Voronki and Velyki Telkovich) reveal dozens new species of hymenopterans, isopterans, blattodeans, hemipterans, coleopterans, trichopterans, neuropterans and raphidiopterans (listed in Tshernyshev and Perkovsky (2021), with additions in Legalov et al. (2019,

2021), Gifka et al. (2021), Melnitsky et al. (2021), Jałoszyński and Perkovsky (2021), Golub et al. (2021) as well as species previously recorded from Baltic amber (Perkovsky and Olmi 2018; Martynova et al. 2019; Mamontov et al. 2020; Simutnik et al. 2020) or Baltic and Bitterfeld ambers (Radchenko and Perkovsky 2018, 2020).

Danish amber is much understudied (Nadein et al. 2016). Its Hymenoptera was briefly reviewed by Simutnik et al. (2021). *Sulia glaesaria* is the first of four Danish encyrtid genera (Simutnik 2015b; Simutnik and Perkovsky 2017, 2018a, b; Simutnik et al. 2020b, 2021) shared with another amber. Only two *Dolichoderus* (Formicidae) species were previously known exclusively from Rovno and Danish amber, and *Fallomyrma transversa* Dlussky et Radchenko – from Rovno, Bitterfeld and Danish amber (Perkovsky 2018).

The amber piece containing the new specimen of *S. glaesaria* was found near the village of Voronki in the Vladimirets District (basin of Styr River), Rovno Region, Ukraine. It is housed in the collection of the Schmalhausen Institute of Zoology of the National Academy of Sciences of Ukraine, Kiev (SIZK). Danish amber containing the holotype is reddish and not very transparent. The sample from Rovno amber is yellow and clear (Fig. 1A). The Rovno amber specimen is distinguished by a darker coloration of the body, antennae, legs, wing venation, and by having slightly infusate, brownish, rather than hyaline forewings with narrow darkening ventral marginal vein and parastigma, although this may be an artefact of differing amber preservation. It is smaller (1.7 mm vs 1.9 mm of holotype) but no differences were found in the proportions of its body parts.

The condition of the Rovno specimen changed over time since it was initially studied, in one month (7.03.2021–13.04.2021) the air layer spreading over almost the entire mesoscutum (Fig. 5A, B), though since then until 7.07.2021 the extent of the air layer has not changed.

Photographs were taken using Leica Z16 APO stereomicroscope equipped with a Leica DFC 450 camera and processed with LAS Core and Adobe Photoshop software (brightness and contrast only).

Terminology and abbreviations follow Sharkov (1985), Gibson (1997), and Heraty et al. (2013). For the emended diagnosis, we used the characters listed by Noyes and Hayat (1994) in which the character states were polarized through comparison with those of the Tanaostigmatidae; diagnosis of Tanaostigmatidae by Gibson (1989); the detailed analysis of the morphology of *L. janzeni* and comparison it with that of *Cynipencyrtus* Ishii, 1928 (Cynipencyrtidae), Encyrtidae, Eupelmidae, and Tanaostigmatidae (Gibson 2008); and lists of synapomorphies for the Chalcidoidea families of the clade E given by Heraty et al. (2013).

The following abbreviations are used in the text and plates of illustrations: **ac** = acropleuron; **acs** = acropleural sulcus; **ae** = arched elevation of Mt6; **btc** = basitarsal comb; **c** = cercus; **cers** = cercal setae; **cly** = clypeus; **cs** = covering setae of the linea calva; **cuf** = cubital fold; **F1, F2, etc.** = funicular segments 1, 2, etc.; **hyp** = hypopygium; **lc** = linea calva; **LOL** = minimum distance between the anterior ocellus and a posterior ocellus; **ls** = line of setae along marginal vein of hind wing; **mpps** = multiporous

plate sensilla; **Mt1, Mt2, etc.** = metasomal terga, numbering starts from petiole (Mt1); **OOL** = minimum distance between an eye margin and the adjacent posterior ocellus; **OCL** = minimum distance between a posterior ocellus and the occipital margin; **opo** = outer plates of ovipositor; **pl3** = metapleuron; **POL** = minimum distance between the posterior ocelli; **pre** = prepectus; **r** = radicle; **sp** = spiracle; **spf** = spur fold; **spv** = spur vein; **st** = strigil; **syn** = syntergum; **v1+v2** = ovipositor stylet; **v3** = ovipositor sheath.

SIZK = I. I. Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine (Kyiv); **ZMUC** = Zoological Museum of the University of Copenhagen.

Results

Taxonomy

Chalcidoidea Latreille, 1817

Family Encyrtidae Walker, 1837

Genus *Sulia* Simutnik, 2015

Type species. *Sulia glaesaria* Simutnik, 2015 (Simutnik 2015b, 2020).

Material examined. *Holotype*, ZMUC, 5–1–1961, ♀, Børge Mortensen, Danish amber, late Eocene. The inclusion is in a reddish and not very transparent piece of amber in a shape of an almost rectangular parallelepiped (ca. 6 × 5 × 4 mm) (Fig. 1A). All body parts are preserved. Syninclusions absent.

New material: SIZK, no. L-139, 1♀, vicinities of Voronki village, Vladimirets District, Rovno Region, Ukraine; Rovno amber; late Eocene. The inclusion is in a yellow and clear piece of amber in a shape of triangular prism (ca. 20 × 16 × 15 × 7 mm) (Fig. 4A). All body parts are preserved. Syninclusions are absent.

Diagnosis (emended). Body robust, barrel-shaped; clypeus setose, with long lateral margins and sharp ventrolateral angles; scape with apicoventral depression; funicle cylindrical; dorsoapical part of mesopleuron with convex differentiated region ventral to tegula delineated by sulcus; linea calva without filum spinosum, but with well-developed line of long setae along basal margin of dorsal surface; costal cell of hind wing with single line of long setae along the entire marginal vein; spur vein or fold originating from the marginal venation of the hind wing present but visible only at some angles; strigil and basitarsal comb present; gaster barrel-shaped, syntergum rather vertical with abruptly reflexed extension apically; cerci only slightly advanced toward gastral base; apex of hypopygium far from reaching apex of gaster; outer plates of ovipositor narrow, crescent-shaped in lateral view.

Redescription. Female. Largest known fossil encyrtid, body length 1.7–1.9 mm, not flattened, robust, barrel-shaped.

Coloration. Head and body black, but appear silvery where surrounded by thin layer of air (only in these places a shallow reticular sculpture visible, Figs 2C, 3B, 4B, D, E, 5A, B, D). Scape black with lighter apex (holotype) or completely black (Rovno

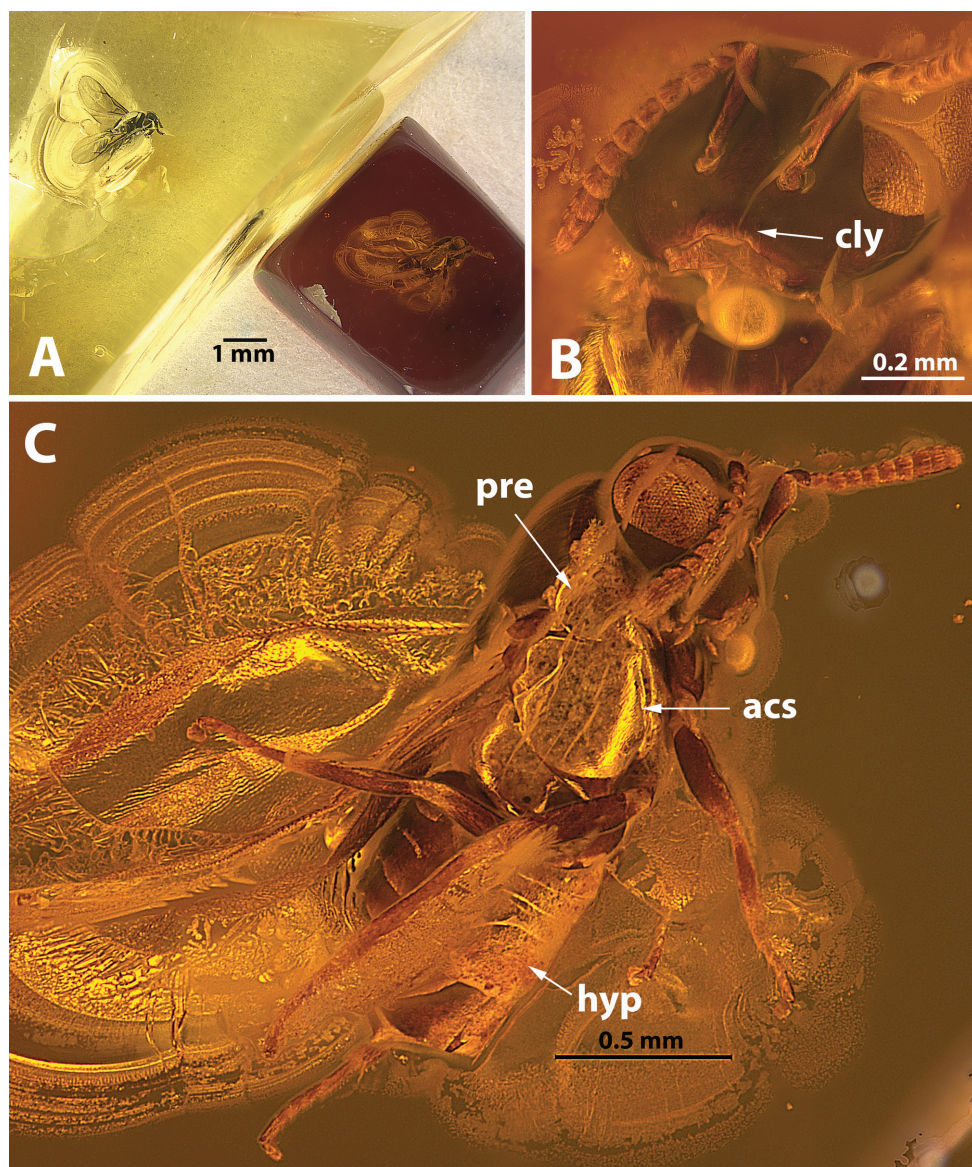


Figure 1. *Sulia glaesaria*, females **A** pieces of amber containing the inclusions: holotype in Danish amber, deposited in ZMUK (red) and new specimen from Rovno amber, deposited in SIZK (yellow) **B** head, holotype, ventrofrontal **C** habitus, holotype, right lateral (acs – acroleural sulcus, cly – clypeus; hyp – hypopygium, pre – prepectus).

specimen); pedicel black; all segments of funicle from pale yellow (holotype) to entirely black (Rovno specimen); tegulae dark, legs of holotype lighter than those of Rovno specimen. Differences in color most likely an artefact of preservation.

Head. Lenticular, as wide as thorax, broader than long, frontovertex curved to posterior ocelli; broadly rounded in frontal view, not vaulted above eyes; eyes bare, without

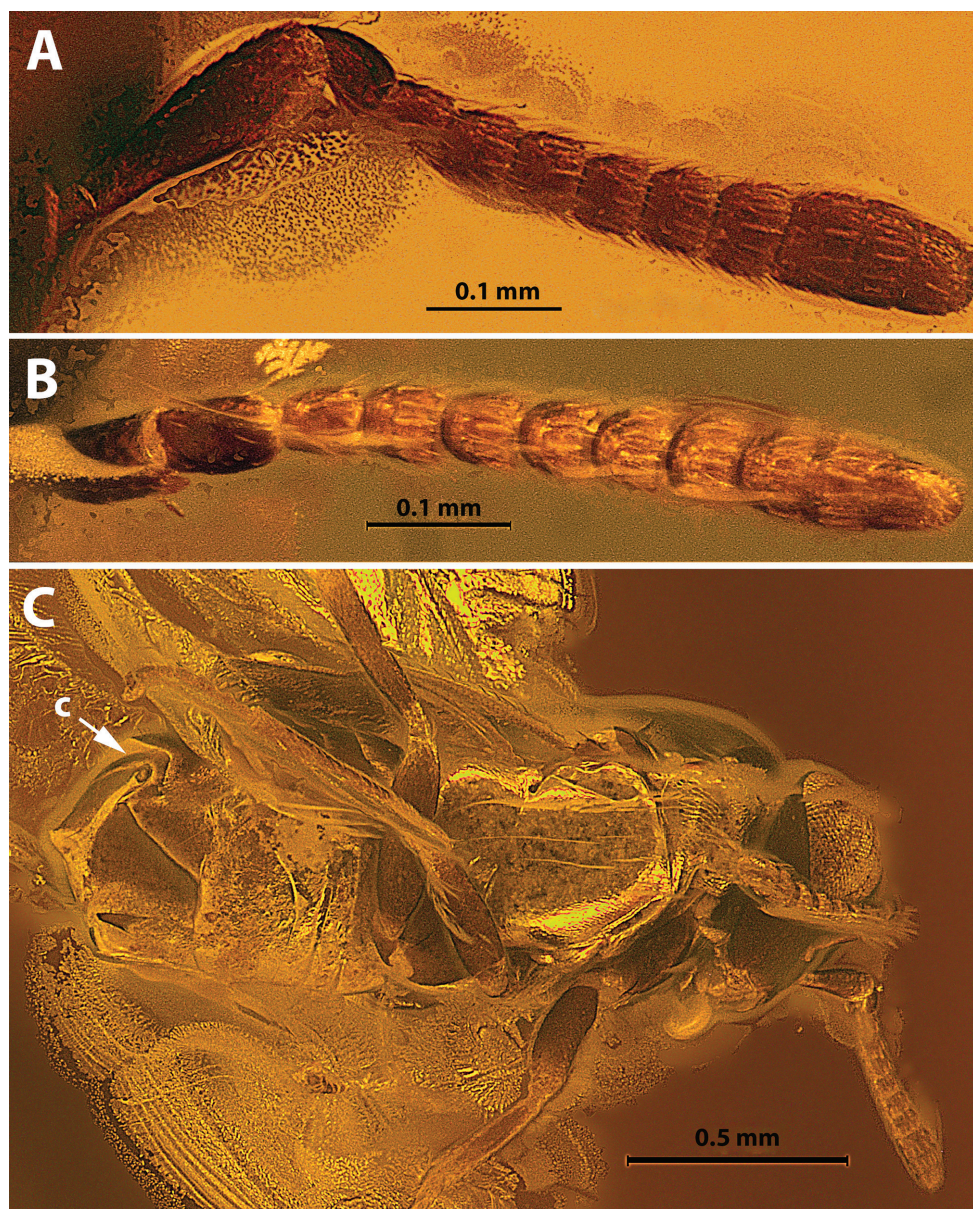


Figure 2. *S. glaesaria*, female, holotype **A** antenna lateral **B** antenna dorsal **C** habitus, right posterolateral (c – cercus).

visible microtrichia, inner orbits parallel over much of height but ventrally divergent (Figs 1B, 3C, 5D); frontovertex broader than long, minimum distance between eyes about $0.4\times$ head width; ocelli normal in size, forming about 100° angle; OOL about equal to posterior ocellar diameter (Figs 3C, 5B); OOL:POL:LOL:OCL about 1.5:6:3.5:0.8; occipital margin sharp; eye reaching occipital margin; antennal scrobe deep, not extended

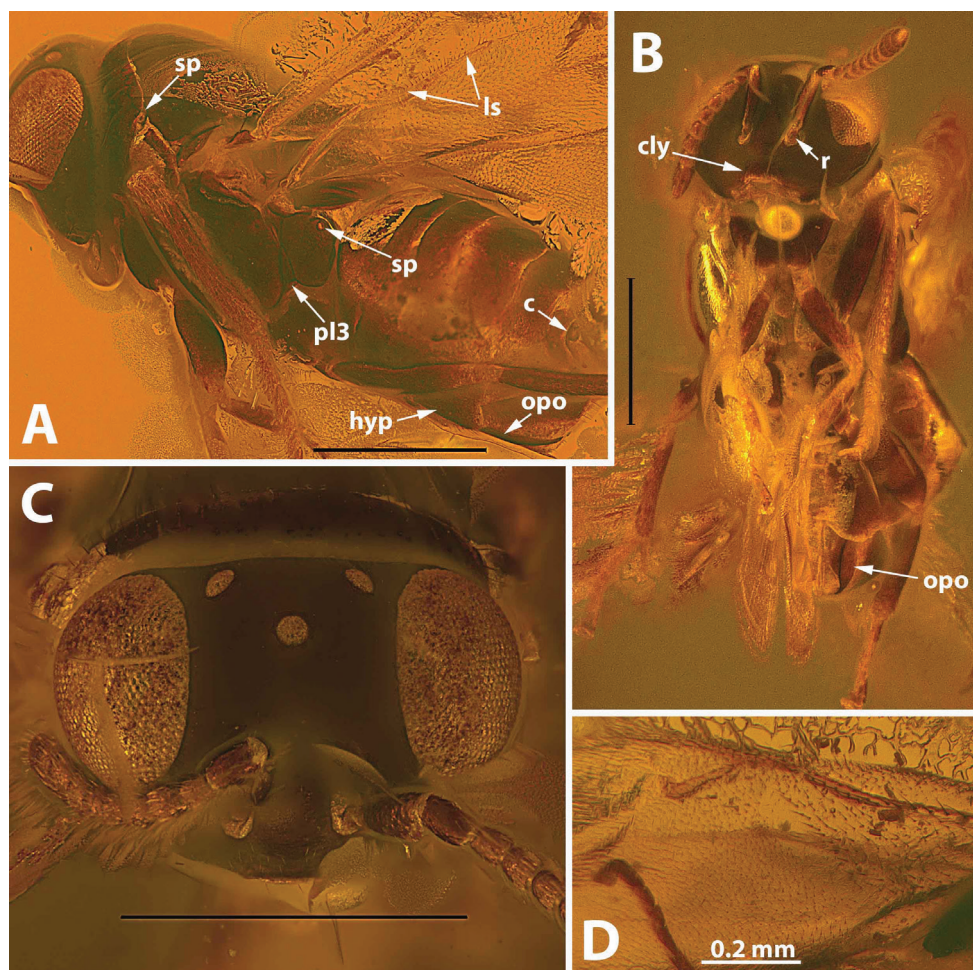


Figure 3. *S. glaesaria*, female, holotype **A** habitus, left lateral **B** habitus, ventral **C** head, frontal **D** forewing venation (cly – clypeus, hyp – hypopygium, ls – line of setae, opo – outer plates of ovipositor, pl3 – metapleuron, r – radicle, sp – spiracle) number of mandibular teeth not visible; maxillary palpi 4-segmented; labial palpi 3-segmented (Fig. 5D). Scale bars: 0.5 mm (**A–C**).

to anterior ocellus, in dorsal view anterior ocellus at equal distance from occiput margin and from margin of scrobal depression; interantennal projection small but visible in lateral view (Figs 1C, 2C); toruli located at level of lower margin of eyes (Figs 1B, 5D); distance between toruli equal to distance between lower margin of torulus and oral margin, about twice width of torulus, about $0.3\times$ length of malar space; malar space with complete malar sulcus (Fig. 5D), slightly shorter than height of eye, about equal to width of mouth; clypeus widely emarginated with long lateral margins, about twice as broad as long, with sharp ventrolateral angles, and with row of setae (Figs 1B, 5D); mandibles wide (Figs 1B, 5D),

Antenna. Geniculate, 11-segmented, without differentiated anelli, with 6 funicular segments and with 3-segmented clava; radicle short, about $2\text{--}2.5\times$ as long as broad

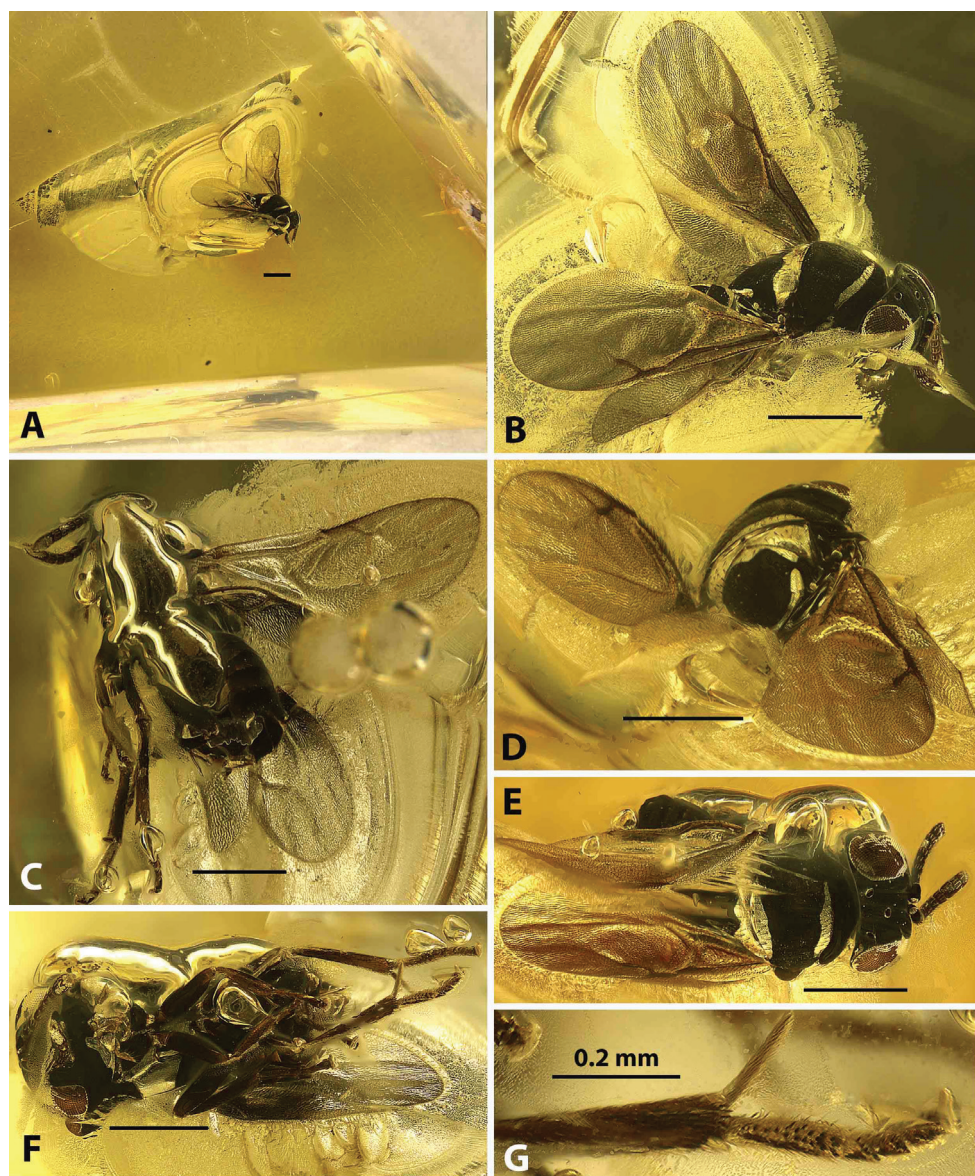


Figure 4. *S. glaesaria*, female, new Rovno specimen **A** general view in piece of amber **B** dorsolateral **C** lateral **D** posterodorsal **E** dorsal **F** ventral **G** apex of mid leg. Scale bars: 0.5 mm (**A–F**).

(Fig. 1B); scape with apicoventral depression (Figs 2A, 3C), $2.7\times$ as long as broad, widest at apex, flattened; pedicel conical, slightly shorter than first two funicular segments combined, longer than any segment of funicle; funicle cylindrical, F1–F3 longer than broad, F4–F6 almost square; all segments of funicle and clava with mps; clava as long as F4–F6 combined, without oblique truncation (Fig. 2A, B).

Mesosoma. Pronotum almost vertical, but in dorsal view with very narrow transverse dorsal surface (Figs 1A, 3A, C), without medial line; mesoscutum not

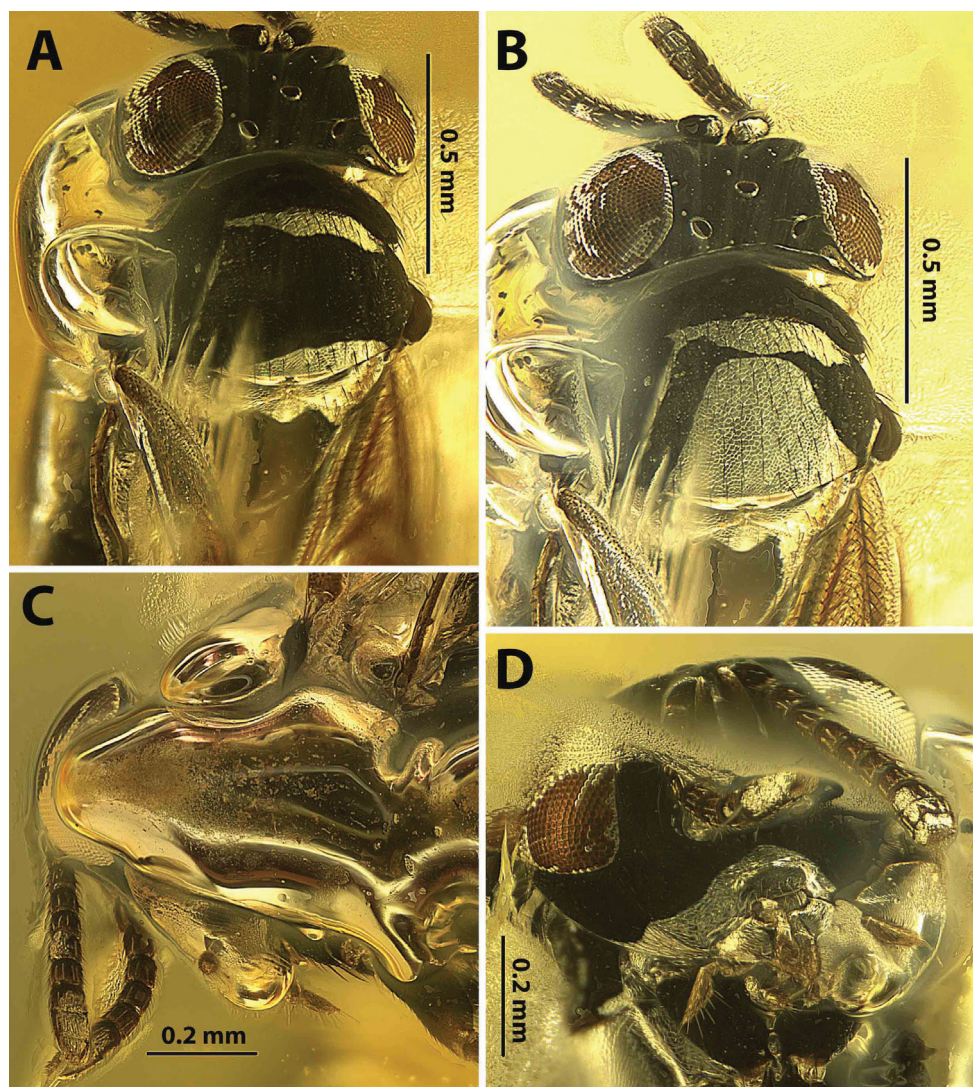


Figure 5. *S. glaesaria*, female, Rovno specimen **A** head, mesosoma, dorsal **B** head, mesosoma with layer of air spread over mesoscutum, dorsal **C** head, antennae lateral **D** head, clypeus, mandibles, frontal.

conspicuously wider than pronotum, broader than long, polygonally reticulate with sparse punctures, with posterior edge transverse, straight; mesoscutum articulated with scutellar-axillar complex only laterally, with edges of sclerites narrowly separated medially (Rovno specimen Figs 4D, 5A, B), connected by slender, delineated anterior portion of scutellar-axillar complex; mesothoracic spiracle open, not concealed beneath pronotum (Fig. 3A); notauli absent, axillae transverse-triangular with antero-medial angles contiguous (Figs 4D, 5B); scutellum as broad as long, slightly convex, sculptured as mesoscutum and clothed in long, stout, black setae; prepectus large, bare, flat, with anterior margin not extend anterior to mesothoracic spiracle, posterior

margin extended to base of tegula (Figs 1C, 2C, 3A); acropleuron convex, bare, with longitudinal reticulate sculpture, short, in lateral view its length equal to height (Figs 1C, 2C, 3C), with distinct acropleural sulcus (Figs 1C, 2C) extended anteriorly from above base of mesocoxa toward posteroventral angle of prepectus; dorsoapical part of mesopleuron with small, convex differentiated region ventral to tegula, also delineated by distinct sulcus (Figs 1C, 2C, 3A), visible in holotype only; metapleuron triangular, narrow, without visible setation (Fig. 3A: pl3); propodeum bare, with large, polygonally reticulate lateral parts, and circular spiracle (Fig. 3A); mid coxa inserted level with mid line of mesopleuron (Fig. 2C), in ventral view with mesosternum transverse-rectangular and abutting bases of coxae, without a membranous area anterior to each coxal base; mesotarsal pegs arranged only along anteroventral margin of tarsus and coxae cannot rotate anteriorly out of their fossae (Fig. 4F).

Wings. Fully developed. Fore wing with basal cell uniformly setose; costal cell broad; submarginal vein with single line of long setae, parastigma with two lines of shorter setae; cubital vein present as non-pigmented but distinct fold (Fig. 7B, cuf); linea calva almost entire, closed posteriorly by only one seta along cubital fold, without filum spinosum, but with well-developed line of long setae along basal margin of dorsal surface (Figs 3D, 7A, B: cs); parastigma only slightly widened, hyaline break (unpigmented area) present (Fig. 7B, C); marginal vein long, about 5 times as long as broad; stigmal vein slightly longer than marginal, with long narrow uncus and uncal sensilla; postmarginal vein twice as long as stigmal vein, enlarged seta marking apex of postmarginal vein of fore wing absent; setae of marginal fringe short. Hind wing relatively narrow; submarginal and marginal veins swollen, submarginal vein with single line of setae; costal cell narrow, membrane of cell along entire marginal vein with single line of long setae (Figs 3A, 6C, 7F, E: ls); spur vein originating from marginal venation present as differentiated hyaline (holotype) or pigmented (Rovno specimen Figs 6C: spf; 7C–E: spv) process or fold (visible only at some angles); apex of marginal vein with 3 hamuli.

Legs. Relatively short, stout; all coxae large, with polygonal reticulate sculpture (only visible under layer of air, Figs 4D, 5B); protibia with long, curved, bifurcate calcar, with strong, straight, socketed seta and three stout setae along anteroapical margin (Fig. 6A); strigil and basitarsal comb present (Fig. 6A); tarsi 5-segmented; mesotibia with thick mesotibial spur, about as long as mesobasitarsus (Figs 4G, 6B), and with row of pegs along anteroapical edge (Fig. 4G); ventral surface of mesobasitarsus and each next tarsomere with row of setae and irregular pattern of pegs along anteroventral edge (Fig. 6B); metatibia with two spurs.

Gaster. Sculpture of gaster not visible, apical margins of Mt2–Mt5 straight, parallel; Mt6 with a small arched elevation medially (Figs 8B–D, 9A: ae); Mt7 U-like between cerci, almost vertical in both specimens but, perhaps, is an artefact of preservation resulting from metasoma being abnormally inflated due to decomposition effects; Mt8, Mt9 fused as syntergum; syntergum also almost vertical except for abruptly reflexed extension apically (Figs 1A, 2C, 4C, 8A–D, 9A), setose and with two longer setae apicolaterally; cercus with long straight setae (Fig. 9A: cers), cerci only slightly

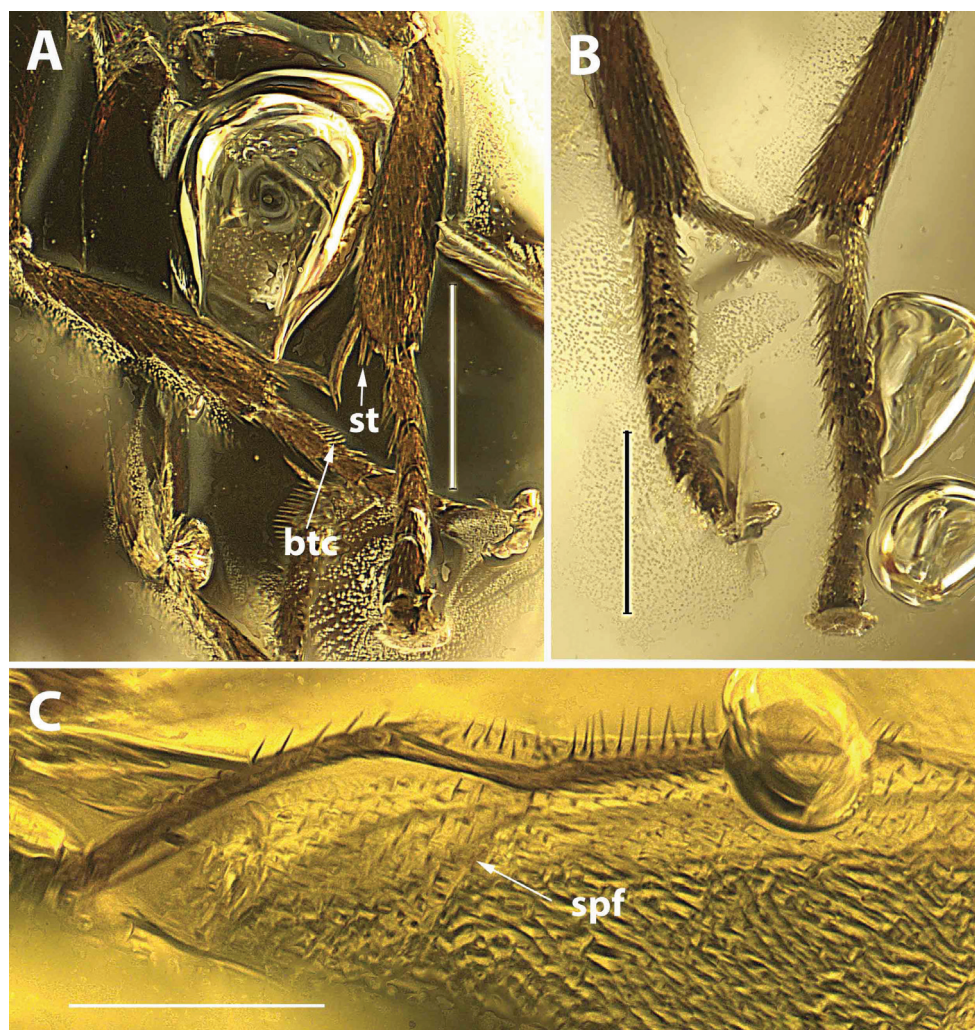


Figure 6. *S. glaesaria*, female, Rovno specimen **A** front legs, ventral **B** apices of mid legs **C** venation of hind wing. (btc – basitarsal comb, spf – spur fold, st – strigil). Scale bars: 0.2 mm.

advanced toward gastral base (Figs 2C, 8A–D), but gaster with elongate membranous band posterior to each cercus (Fig. 8A–C) differentiating dorsal surface of syntergum from slender lateral portion recurved around cercus; paratergites not visible; apex of hypopygium far from reaching apex of gaster (Figs 1C, 2C, 8A–C: hyp); ovipositor not extended beyond apex of ultimate tergum; only apical parts of ovipositor sheaths visible in ventrolateral and posterior views (Figs 8D, 9A: v3); membranous bands posterior to cerci subdivide the dorsal surface of syntergum from narrow, crescent-shaped in lateral view outer plates of ovipositor (Figs 3A, B, 8A, C, D, 9A: opo).

Male. Unknown.

Genus composition. Type species only.

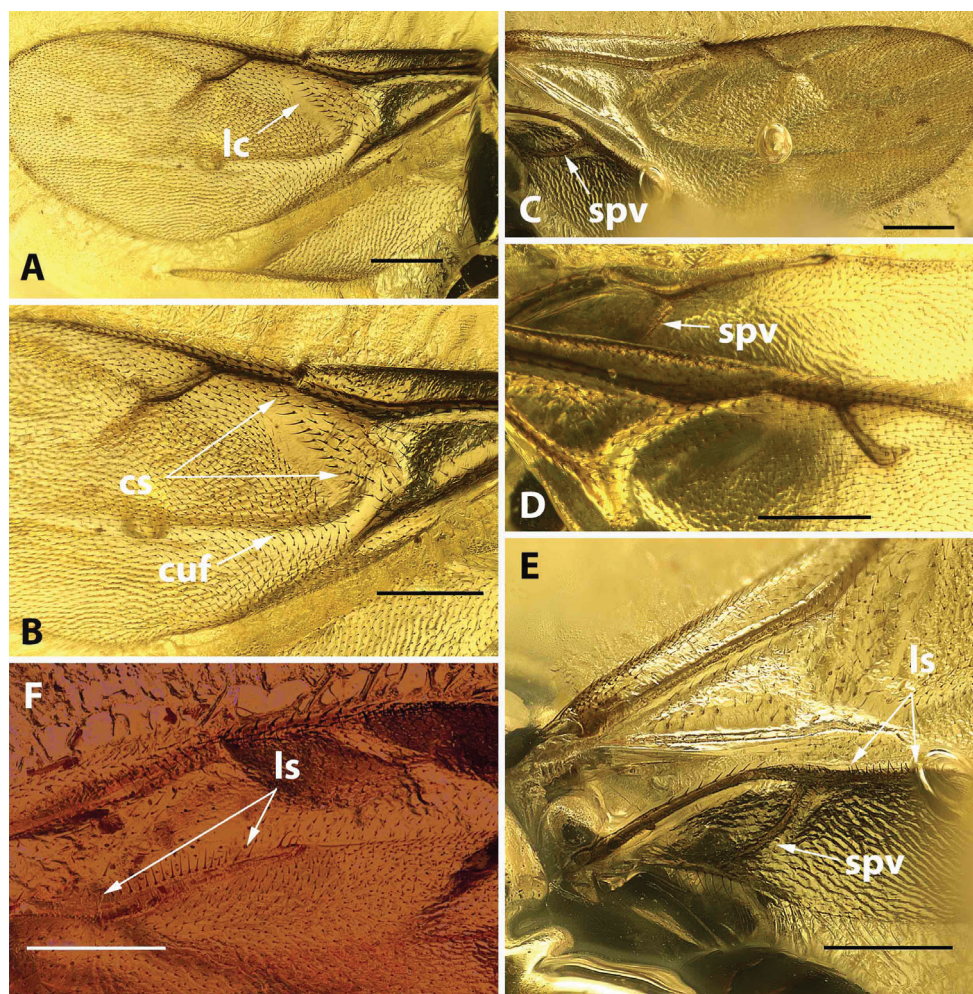


Figure 7. *S. glaesaria*, females, wings **A–E** Rovno specimen **F** holotype from Danish amber **A** left pair of wings dorsal **B** forewing venation, dorsal **C** left pair of wings, ventral **D** right pair of wings, venation, dorsal **E** left pair of wings, hind wing venation, ventral **F** wings venation, ventral. (cs – covering setae, cuf – cubital fold, lc – linea calva, ls – line of setae, spv – spur vein). Scale bars: 0.2 mm.

Biology. Unknown.

Comments. The **radicle** of many recent encyrtids is very long, four times or more as long as broad. This character state is included in lists of synapomorphies of extant Encyrtidae by Heraty et al. 2013, but there are many exceptions, among both extant Encyrtinae and Tetracneminae. The radicle of all known fossil Encyrtidae, including *S. glaesaria*, is also no more than twice as long as broad.

The **forewing venation** of *S. glaesaria* is typical for fossil Encyrtidae. In modern encyrtids, the most similar venation of the forewings occurs, e.g., in the genera *Savzdargia* Trjapitzin, 1979, *Ericydnus* Walker, 1837, *Mira* Schellenberg, 1803, and *Moraviella* Hoffer, 1954 (Tetracneminae). All veins are long, including the

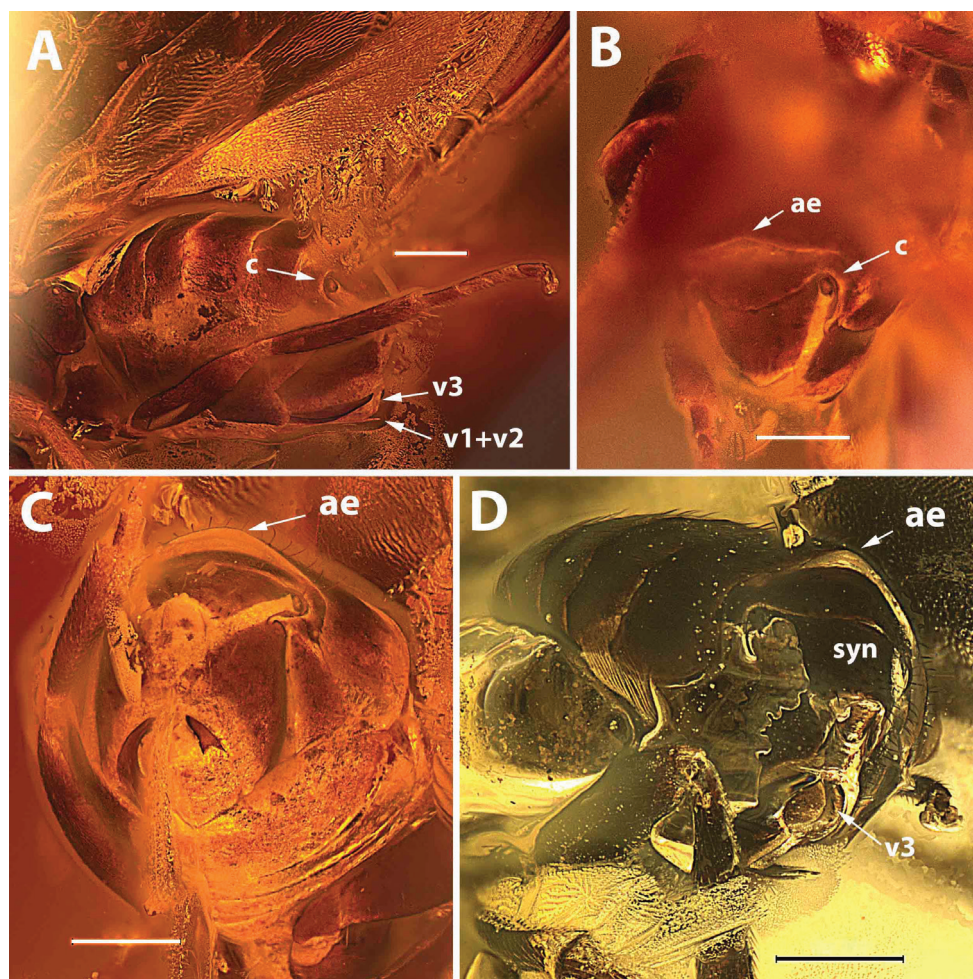


Figure 8. *S. glaesaria*, females, metasoma **A–C** holotype **D** Rovno specimen **A** lateral **B** dorsal **C** posteroventral **D** posterolateral. (ae – arched elevation of Mt6, c – cercus, syn – syntergum, v1+v2 – ovipositor stylet, v3 – ovipositor sheath). Scale bars: 0.2 mm.

marginal. The linea calva has a line of long setae along its basal margin (Fig. 7B: cs), **covering setae** sensu Sharkov (1985). When the wings are folded, the anterior margin of one abuts this row of setae. This structure is present in most extant Encyrtinae, some extant Tetracneminae, and in all known earliest, middle Eocene encyrtids. Late Eocene encyrtids have been reported both with and without covering setae (Simutnik 2020).

In the hind wing of *S. glaesaria*, the costal cell has a membrane with a single **line of long setae** along the entire marginal vein as in Tanaostigmatidae. A similar character state is rarely present in extant Encyrtidae, e.g., in *Exoristobia* Ashmead, 1904. The fossil *E. sugonjaevi* also has this line of setae, but it differs from *S. glaesaria* by the hypopygium extending past the apex of horizontal syntergum.

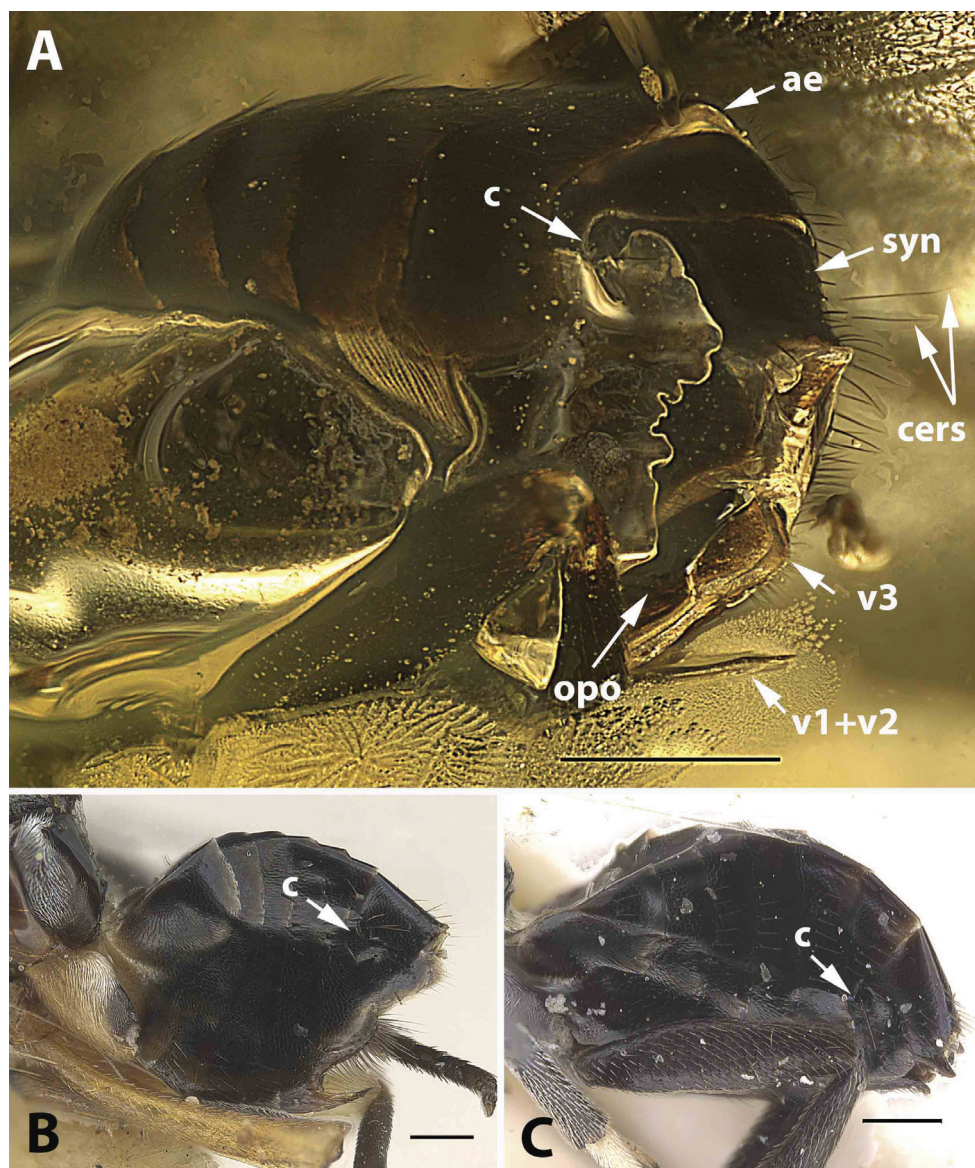


Figure 9. Metasoma, lateral **A** *S. glaesaria*, female, Rovno specimen **B, C** *Prionomastix morio* (Dalman, 1820) **B** female **C** male. (ae – arched elevation of Mt6, c – cercus, cers – cercal setae, syn – syntergum, v1+v2 – ovipositor stylet, v3 – ovipositor sheath). Scale bars: 0.2 mm.

A **spur vein** or fold originating from the marginal venation of the hind wing is visible in *S. glaesaria* (Fig. 7C–E: spv) similar to that found in Tanaostigmatidae, *Lep-toomus*, some Pteromalidae, and Eupelmidae (Simutnik et al. 2020a). In *S. glaesaria*, however, the spur vein is present rather as a fold, visible only at some angles.

The both specimens of *S. glaesaria* have almost **vertical syntergum** (Figs 2A, 9A). Perhaps, it is an artefact of preservation resulting from metasoma being abnormally

inflated due to decomposition effect. But, abruptly reflexed extension at the apex of syntergum (Figs 2A, 9A) indicates that it can actually be somewhat vertical in living specimens. The almost vertical syntergum is very rare in extant Encyrtidae. A similar structure is known, e.g., in *Prionomastix* Mayr, 1876 (Encyrtinae) (Fig. 9B, C), and *S. glaesaria* shares this character with many of members of Tanaostigmatidae.

The taxonomic position of the *Sulia* is retain unplaced within the Encyrtidae. Its biology is also unknown. Nevertheless, a large size of *S. glaesaria*, its barrel-shaped habitus, short and high acropleuron, structure of protibial apex, presence of spur vein and line of long setae along the entire marginal vein of hind wings, and supposedly almost vertical syntergum somewhat resemble those of members of Tanaostigmatidae and may indicate convergent adaptation to the plant galling.

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References

- Colombo WD, Gobbi FT, Perkovsky EE, Azevedo CO (2021a) Synopsis of the fossil Pritocercinae (Hymenoptera, Bethyridae), with description of two new genera and species from Burmese, Taimyr, Baltic and Rovno ambers. *Historical Biology* 33(9): 1736–1752. <https://doi.org/10.1080/08912963.2020.1733551>
- Colombo WD, Perkovsky EE, Waichert C, Azevedo CO (2021b) Synopsis of the fossil flat wasps Epyrinae (Hymenoptera, Bethyridae), with description of three new genera and 10 new species. *Journal of Systematic Palaeontology* 19(1): 39–89. <https://doi.org/10.1080/14772019.2021.1882593>
- Gibson GAP (1989) Phylogeny and classification of Eupelmidae, with a revision of the world genera of Calosotinae and Metapelmatinae (Hymenoptera: Chalcidoidea). *Memoirs of the Entomological Society of Canada* 149: 1–121. <https://doi.org/10.4039/entm121149fv>
- Gibson GAP (1997) Chapter 2, Morphology and terminology. In: Gibson GAP, Huber JT, Woolley JB (Eds) *Annotated keys to the genera of Nearctic Chalcidoidea* (Hymenoptera). NRC Research Press, Ottawa, 16–45. [794 pp.]
- Gibson GAP (2008) Description of *Leptoomus janzeni*, n. gen. and n. sp. (Hymenoptera: Chalcidoidea) from Baltic amber, and discussion of its relationships and classification relative to Eupelmidae, Tanaostigmatidae and Encyrtidae. *Zootaxa* 1730: 1–26. <https://doi.org/10.11646/zootaxa.1730.1.1>

- Gibson GAP (2009) Description of three new genera and four new species of Neanastatinae (Hymenoptera, Eupelmidae) from Baltic amber, with discussion of their relationships to extant taxa. In: Johnson N (Ed.) Advances in the systematics of Hymenoptera. Festschrift in honour of Lubomír Masner. ZooKeys 20: 175–214. <https://doi.org/10.3897/zookeys.20.161>
- Gilka W, Harbach RE, Perkovsky EE (2021) Mosquitoes (Diptera: Culicidae) in Eocene amber from the Rovno region, Ukraine. Zootaxa 5016(2): 257–270. <https://doi.org/10.11646/zootaxa.5016.2.6>
- Golub VB, Perkovsky EE, Vasilenko DV (2021) A new fossil species of the genus *Parasinalda* Heiss & Golub (Hemiptera: Heteroptera: Tingidae) from Upper Eocene Rovno amber. Zootaxa 5027(2): 290–296. <https://doi.org/10.11646/zootaxa.5027.2.9>
- Heraty JM, Burks RA, Cruaud A, Gibson GA, Liljeblad J, Munro J, Rasplus JY, Delvare G, Janšta P, Gumovsky A, Huber JT, Woolley JB, Krogmann L, Heydon S, Polaszek A, Schmidt S, Darling DC, Gates MW, Mottern J, Murray E, Dal Molin A, Triapitsyn S, Baur H, Pinto JD, van Noort S, George J, Yoder M (2013) A phylogenetic analysis of the megadiverse Chalcidoidea (Hymenoptera). Cladistics 29: 466–542. <https://doi.org/10.1111/cla.12006>
- Jałoszyński P, Perkovsky EE (2016) Diversity of Scydmaeninae (Coleoptera: Staphylinidae) in Upper Eocene Rovno amber. Zootaxa 4157(1): 1–85. <https://doi.org/10.11646/zootaxa.4157.1.1>
- Jałoszyński P, Perkovsky EE (2021) A new bizarre species of *Euconnus* (*Cladoconnus*) in Upper Eocene Rovno amber (Coleoptera: Staphylinidae: Scydmaeninae). Zootaxa 5004(2): 395–400. <https://doi.org/10.11646/zootaxa.5004.2.8>
- Kirichenko-Babko M, Perkovsky EE, Vasilenko DV (2021) A new genus and species of Lebiini (Coleoptera: Carabidae) from late Eocene Rovno amber. Historical Biology. <https://doi.org/10.1080/08912963.2021.1924701>
- Legalov AA, Nazarenko VYu, Perkovsky EE (2019) New weevils (Coleoptera: Curculionidae) from Rovno amber. Paleontological Journal 53(10): 1045–1059. <https://doi.org/10.1134/S0031030119100101>
- Legalov AA, Nazarenko VYu, Vasilenko DV, Perkovsky EE (2021) *Ceutorhynchus* Germar (Coleoptera, Curculionidae) as proxy for Eocene core Brassicaceae: first record of the genus from Rovno amber. Journal of Paleontology. <https://doi.org/10.1017/jpa.2021.82>
- Mamontov YuS, Atwood JJ, Perkovsky EE, Ignatov MS (2020) Hepatics from Rovno amber (Ukraine): *Frullania pycnoclada* and a new species, *F. vanae*. The Bryologist 123(3): 421–430. <https://doi.org/10.1639/0007-2745-123.3.421>
- Martynova KV, Perkovsky EE, Olmi M, Vasilenko DV (2019) New records of Upper Eocene chrysidoid wasps (Hymenoptera: Chrysidoidea) from basins of Styr and Stokhod rivers (Rovno amber). Paleontological Journal 53(10): 998–1023. <https://doi.org/10.1134/S0031030119100125>
- Melnitsky SI, Ivanov VD, Perkovsky EE (2021) A new species of *Plectrocnemia* (Trichoptera: Polycentropodidae) from Rovno amber. Zootaxa 5006(1): 106–109. <https://doi.org/10.11646/zootaxa.5016.2.5>
- Mitov PG, Perkovsky EE, Dunlop JA (2021) Harvestmen (Arachnida: Opiliones) in Eocene Rovno amber (Ukraine). Zootaxa 4984: 43–72. <https://doi.org/10.11646/zootaxa.4984.1.6>
- Nadein KS, Perkovsky EE, Moseyko AG (2016) New Late Eocene Chrysomelidae (Insecta: Coleoptera) from Baltic, Rovno and Danish ambers. Papers in Palaeontology 2: 117–137. <https://doi.org/10.1002/spp2.1034>

- Noyes JS, Hayat M (1994) Oriental mealybug parasitoids of the Anagyrini (Hymenoptera: Encyrtidae). CAB International, Wallingford, Oxon, [viii+] 554 pp.
- Perkovsky EE (2016) Tropical and Holarctic ants in Late Eocene ambers. *Vestnik zoologii* 50(2): 111–122. <https://doi.org/10.1515/vzoo-2016-0014>
- Perkovsky EE (2017) Rovno amber caddisflies (Insecta, Trichoptera) from different localities, with information about three new sites. *Vestnik zoologii* 51(1): 15–22. <https://doi.org/10.1515/vzoo-2017-0003>
- Perkovsky EE (2018) Only a half of species of Hymenoptera in Rovno amber is common with Baltic amber. *Vestnik zoologii* 52(5): 353–360. <https://doi.org/10.2478/vzoo-2018-0037>
- Perkovsky EE, Olmi M (2018) Discovery of the first pincer wasp (Hymenoptera, Dryinidae) from Rovno amber. *Zootaxa* 4457(2): 296–304. <https://doi.org/10.11646/zootaxa.4457.2.5>
- Perkovsky EE, Zosimovich VYu, Vlaskin AP (2010) Rovno amber. In: Penney D (Ed.) *Biodiversity of Fossils in Amber from the Major World Deposits*. Siri Sciences Press, Manchester, 116–136.
- Peters R, Niehui O, Gunkel S, Bläser M, Mayer C, Podsiadlowski L, Kozlov A, Donath A, van Noort S, Liu Sh, Zhou X, Misof B, Heraty J, Krogmann L (2018) Transcriptome sequence-based phylogeny of chalcidoid wasps (Hymenoptera: Chalcidoidea) reveals a history of rapid radiations, convergence, and evolutionary success. *Molecular Phylogenetics and Evolution* 120: 286–296. <https://doi.org/10.1016/j.ympev.2017.12.005>
- Radchenko AG, Perkovsky EE (2018) First record of fossil ant species *Eocenomyrma rugosotriata* (Mayr) (Hymenoptera: Formicidae) from the Rovno amber. *Russian Entomological Journal* 27(3): 285–288. <https://doi.org/10.15298/rusentj.27.3.08>
- Radchenko AG, Perkovsky EE (2020) New records of the fossil ant genus *Prionomyrmex* Mayr (Hymenoptera, Formicidae, Myrmeciinae) from Late Eocene European ambers. *Paleontologicheskii Zhurnal* 2020(6): 60–67. [In Russian] [Translated: *Paleontological Journal* 54(6): 617–626] <https://doi.org/10.1134/S0031030120060088>
- Sharkov AV (1985) Encyrtids (Hymenoptera, Chalcidoidea, Encyrtidae) of the southern Far East of the USSR [dissertation]. Extended Abstract of Cand. Sci. (Biol.). Leningrad. [in Russian]
- Simutnik SA (2001) A find of encyrtid (Hymenoptera, Chalcidoidea, Encyrtidae) in the late Eocene Rovno amber. *Vestnik Zoologii* 35(6): 81–84. [in Russian]
- Simutnik SA (2002) A new genus of encyrtid wasps (Hymenoptera, Chalcidoidea, Encyrtidae) from the late Eocene Rovno amber (Ukraine). *Vestnik Zoologii* 36(4): 99–102. [in Russian]
- Simutnik SA (2007) Fossil Encyrtidae (Hymenoptera: Chalcidoidea) from the Rovno amber. *Izvestiya Kharkovskogo Entomologicheskogo Obshchestva* 15(1–2): 137–141. [in Russian]
- Simutnik SA (2014) First record of Encyrtidae (Hymenoptera, Chalcidoidea) from the Sakhalin Amber. *Paleontologicheskii Zhurnal* 2014(6): 46–49. [In Russian] [Translated: *Paleontological Journal* 48(6): 621–623] <https://doi.org/10.1134/S0031030114060124>
- Simutnik SA (2015a) A new fossil genus of Encyrtidae (Hymenoptera: Chalcidoidea) from late Eocene Danish amber. *Russian Entomological Journal* 24(1): 73–75. <https://doi.org/10.15298/rusentj.24.1.07>
- Simutnik SA (2015b) Description of two new monotypical genera of encyrtid wasps (Hymenoptera, Chalcidoidea: Encyrtidae), based on males from the middle Eocene Sakhalin amber. *Entomological Review* 95(7): 937–940. <https://doi.org/10.1134/S0013873815070118>

- Simutnik SA (2020) The earliest Encyrtidae (Hymenoptera, Chalcidoidea). Historical Biology. <https://doi.org/10.1080/08912963.2020.1835887>
- Simutnik SA, Perkovsky EE (2017) *Protocopidosoma* gen. nov. (Hymenoptera, Chalcidoidea, Encyrtidae) from the late Eocene Danish amber. Paleontologicheskii Zhurnal 2017(3): 64–65. [In Russian] [Translated: Paleontological Journal 51(3): 288–290] <https://doi.org/10.1134/S0031030117030108>
- Simutnik SA, Perkovsky EE (2018a) *Dencyrtus* gen. nov. (Hymenoptera, Chalcidoidea, Encyrtidae) from the late Eocene Danish amber. Paleontologicheskii Zhurnal 2018(3): 67–68. [In Russian] [Translated: Paleontological Journal 52(3): 290–293] <https://doi.org/10.1134/S0031030118030139>
- Simutnik SA, Perkovsky EE (2018b) *Trjapitzion* Simutnik, gen. n. (Hymenoptera, Chalcidoidea: Encyrtidae), a new genus of encyrtid wasps from the late Eocene Rovno amber. Entomological Review 98(8): 1152–1156. <https://doi.org/10.1134/S0013873818080225>
- Simutnik SA, Perkovsky EE (2018c) *Archaeocercus* gen. nov. (Hymenoptera, Chalcidoidea, Encyrtidae) from late Eocene Rovno amber. Zootaxa 4441(3): 543–548. <https://doi.org/10.1080/08912963.2020.1835887>
- Simutnik SA, Perkovsky EE (2020) *Ektopicercus* Simutnik gen. nov. (Hymenoptera, Chalcidoidea, Encyrtidae) from late Eocene Rovno amber. Palaeoentomology 3(4): 342–346. <https://doi.org/10.11646/palaeoentomology.3.4.3>
- Simutnik SA, Perkovsky EE, Gumovsky AV (2014) Review of the Late Eocene Encyrtidae (Hymenoptera, Chalcidoidea) with a description of the first fossil genus with filum spinosum. Paleontologicheskii Zhurnal 2014(1): 65–74. [In Russian] [Translated: Paleontological Journal 48(1): 65–73] <https://doi.org/10.1134/S0031030114010122>
- Simutnik SA, Perkovsky EE, Vasilenko DV (2020a) First record of *Leptoomus janzeni* Gibson (Hymenoptera, Chalcidoidea) from Rovno amber. Journal of Hymenoptera Research 80: 137–145. <https://doi.org/10.3897/jhr.80.58882>
- Simutnik SA, Perkovsky EE, Vasilenko DV (2020b) *Efesus trufanovi* Simutnik gen. et sp. n. (Hymenoptera: Chalcidoidea: Encyrtidae) from late Eocene Danish amber. Russian Entomological Journal 29(3): 298–302. <https://doi.org/10.15298/rusentj.29.3.10>
- Simutnik SA, Perkovsky EE, Vasilenko DV (2021) *Sakhalinencyrtus leleji* Simutnik gen. et sp. nov. of earliest Encyrtidae (Hymenoptera, Chalcidoidea) from Sakhalinian amber. Journal of Hymenoptera Research 84: 361–372. <https://doi.org/10.3897/jhr.84.66367>
- Sukhomlyn MM, Heluta VP, Perkovsky EE, Ignatov MS, Vasilenko DV (2021) First record of a fungus of Mycocaliciaceae from Rovno amber (Ukraine). Paleontologicheskii Zhurnal 2021(6): 98–103. [In Russian] [Translated: Paleontological Journal 55(6): 684–690]
- Trjapitzin VA (1989) Parasitic Hymenoptera of the fam. Encyrtidae of Palaearctics. Opredeliteli po faune SSSR izdavaemiye Zoologicheskim institutom AN SSSR 158: 1–489. [In Russian]
- Tshernyshev SE, Perkovsky EE (2021) *Protomauroania mikhailovi* – a new species of malachite beetles (Coleoptera, Dasytidae) in Rovno amber. Zootaxa 5006(1): 189–194. <https://doi.org/10.11646/zootaxa.5006.1.20>
- Zhang J, Lindsey ARI, Peters RS, Heraty JM, Hopper KR, Werren JH, Martinson EO, Woolley JB, Yoder MJ, Krogmann L (2020) Conflicting signal in transcriptomic markers leads to a poorly resolved backbone phylogeny of chalcidoid wasps. Systematic Entomology 45(4): 783–802. <https://doi.org/10.1111/syen.12427>