

RESEARCH PAPER

# A new species of the genus *Eurystylops* (Strepsiptera: Stylopidae) rediscovered after more than 100 years from *Rophites* bees (Hymenoptera: Halictidae)

Daniel BENDA<sup>1,2,3</sup> & Jakub STRAKA<sup>2</sup>)

<sup>1</sup>) Department of Entomology, National Museum of the Czech Republic, Prague, Cirkusová 1740, CZ-193 00 Praha – Horní Počernice, Czech Republic

<sup>2</sup>) Department of Zoology, Faculty of Science, Charles University, Prague, Viničná 7, CZ-128 43, Praha 2, Czech Republic;  
e-mail: jakub.straka@aculeataresearch.cz

<sup>3</sup>) Corresponding author: e-mail: benda.daniel@email.cz, ORCID: 0000-0002-5729-0411

Accepted:  
17<sup>th</sup> March 2025

Published online:  
3<sup>rd</sup> June 2025

**Abstract.** A new species of Strepsiptera of the genus *Eurystylops* Bohart, 1943 (Stylopidae) from the Western Palearctic Region is described based on the female cephalothorax. *Eurystylops ogloblini* sp. nov. represents the first species described from the host bee of the genus *Rophites* Spinola, 1808. We have found *Rophites clypealis* Schwammberger, 1976, *R. hartmanni* Friese, 1902 and *R. quinquespinosus* Spinola, 1808 to be hosts of this species. We summarize all known data on the distribution of the genus *Eurystylops* in the Western Palearctic Region which suggest a recent decline of these rare parasites. We consider their rarity to be a direct consequence of the threat to their hosts, which are oligolectic bees. We also provide the first evidence of the existence of males in the genus *Eurystylops* based on an empty male puparium, which was noticed more than 100 years ago in *R. quinquespinosus*. A detailed redescription of the female cephalothorax of *Eurystylops oenipontana* Hofeneder, 1949 is provided. *Eurystylops oenipontana* is recorded from the Czech Republic for the first time.

**Key words.** Strepsiptera, bee parasite, bees, cephalothorax, host, morphology, taxonomy, Hymenoptera, *Anthophila*, *Rophites*, *Dufourea*, Palearctic Region

**Zoobank:** <http://zoobank.org/urn:lsid:zoobank.org:pub:541ECA0E-F17F-4A18-9C1E-1737B7A13C1B>

© 2025 The Authors. This work is licensed under the Creative Commons Attribution-NonCommercial-NoDerivs 3.0 Licence.

## Introduction

Stylopidae are insect endoparasites of bees from four families: Mellitidae, Andrenidae, Colletidae, and Halictidae (COOK 2019). They belong to Stylopida, a clade containing more than 97% of species of the order (POHL & BEUTEL 2008). Stylopidae and its sister taxon Xenidae are the groups with the highest degree of specialization in Strepsiptera. The origin of this clade (Stylopidae + Xenidae) dates back to the time after the Cretaceous-Tertiary (K-T) extinction event approximately 60 million years ago (McMAHON et al. 2011). The age of Stylopidae is not exactly known because molecular phylogenetic work on this group is still lacking. An important evolutionary novelty, as found in the monophyletic group consisting of the sister families Xenidae and Stylopidae, is the phoresy of the primary larvae that attach themselves to foraging bees and wasps. This is likely a key to the relative success

of these families representing the most diverse lineage in Strepsiptera (POHL & BEUTEL 2008). Species in Stylopidae are all parasites of bees. An important evolutionary shift is the loss of the jumping capacity in the primary larvae, which is replaced by phoretic behaviour (POHL 2000).

The first species of *Eurystylops* Bohart, 1943 was described under the name *Pseudostylops desertorum* from *Dufourea boregoensis* (Michener, 1937) in the monography of Strepsiptera published by BOHART (1941). However, *Pseudostylops* Bohart, 1941 was preoccupied by a genus of fossil mammals, which caused the genus to be renamed as *Eurystylops* (BOHART 1943, COOK 2019). Later, four species of *Eurystylops* were described from host bees of the genera *Dufourea* Lepeletier, 1841 and *Conanthalictus* Cockerell, 1901 from the USA and Central Europe (BOHART 1943, HOFENEDER 1949, KINZELBACH 1971, BOHART & IRWIN 1978). For most species, only the female is known; only first-instar larvae of *Eurystylops desertorum* have



been described (BOHART 1941). Support for the existence of males has never been provided for the genus *Eurystylops*.

Although strepsipterans of the genus *Eurystylops* were formally described in 1941, data on their parasitised hosts had been reported much earlier. The first record of stylopised *Dufourea* Lepeletier, 1841 from Europe was noted by BLÜETHGEN (1919) from Germany but without any specific locality (KINZELBACH 1978). BOHART (1941) also noted the record of stylopised *Dufourea* (as *Halictoides* Nylander, 1848) from Austria (Innsbruck) collected by H. Friese but without mentioning the citation and year of collection. The species was finally described by HOFENEDER (1949) from *Dufourea dentiventris* (Nylander, 1848) and *D. inermis* (Nylander, 1848) as *Eurystylops oenipontana* Hofeneder, 1949. A summary of information known to date, especially on hosts and distribution, was provided by KINZELBACH (1978).

No species of Strepsiptera has hitherto been described from bees of the genus *Rophites* Spinola, 1808, even though records of parasitism have been documented in the literature and museum collections for over a hundred years. The first published record of stylopised *Rophites* was provided by Ulrich (1930) who reported the stylopisation of *R. quinquespinosus* Spinola, 1808 from central Europe. Later, HOFENEDER (1939) mentioned stylopised *R. hartmanni* Friese, 1902 from Turkey. Additional records of stylopised *R. quinquespinosus* and *R. hartmanni* in Central Europe were also provided by SZÉKESSY (1959).

In this study, we present the description of a new *Eurystylops* species from *Rophites* based on the female cephalothorax, and also a redescription of *E. oenipontana*. We also present evidence of the existence of males in the genus *Eurystylops* based on an empty male puparium in *R. quinquespinosus* and support that this specimen was already examined by Alexander A. Ogloblin in the early 1920s.

## Material and methods

**Depository of examined specimens.** For this study, speci-

mens from the following institutions and private collections were analysed:

EEC	Eidgenössische Technische Hochschule Zürich, Entomological Collection (Zurich, Switzerland);
HNHM	Hungarian Natural History Museum, Budapest, Hungary;
JSPC	Jakub Straka's personal collection, Prague, Czech Republic;
MMBC	Moravian Museum, Brno, Czech Republic;
NMPC	National Museum of the Czech Republic, Prague, Czech Republic.

The newly described species was labelled as follows: "HOLOTYPE ♀, name of taxon, Benda & Straka, sp. nov." on a red card; yellow cards were used for paratypes. Exact label data are cited only for the holotype. Separate lines on the labels are indicated with a slash "/", and separate labels are indicated with a double slash "//".

**Morphological studies.** All host individuals (except for the one with an empty male puparium) were first relaxed in water vapour and then immediately dissected. The endoparasitic females were removed from the host's body. Females used for morphological study were cleared using a mixture of lysis buffer ATL and proteinase K (Qiagen) heated to 56 °C. The lysis procedure took several hours or overnight. The cleared specimen was cleaned several times in distilled water and then stored in a vial with 96% ethanol. The female cephalothorax was air-dried or dried by using absolute ethanol and hexamethyldisilazane (HMDS method) (HERATY 1998) to prevent the cuticle from collapsing during the drying process. The female body was separated from the cephalothorax before drying. After this step, the dried cephalothoraces were glued onto card mounting points which were pinned afterwards. The width and length of the female cephalothorax and the female head capsule were measured using a Leica S9D stereo microscope with a calibrated ocular micrometre. The length of the cephalothorax was measured from the apex of the clypeal lobe to the constriction of the abdominal segment I; the cephalothorax width is the maximum distance between its lateral margins.

The general habitus of the parasitised host specimen



Fig. 1. Holotype (female) of *Eurystylops ogloblini* sp. nov. inside the host bee *Rophites quinquespinosus* Spinola, 1808: A – lateral view; B – detail of host abdomen with the female cephalothorax under the 4<sup>th</sup> tergite.

and the host gaster with protruding strepsipteran females and an empty male puparium were documented. For the documentation of the original colouration of the female cephalothorax and for the documentation of minute structures, a Canon EOS 70D camera attached to an Olympus BX40 microscope was used. The microscope was equipped with lateral lights and a diffuser. Zerene Stacker (Zerene Systems LLC, Richland, USA) was used to process stacks of images with different focus.

The dried cephalothorax glued to a card point was mounted on a specimen holder by adhesive carbon tabs. The specimen was not sputter coated with gold. SEM images were taken using a Hitachi S-3700N environmental electron microscope (Hitachi, Tokio, Japan) at the Department of Palaeontology, National Museum of the Czech Republic. All images were processed and arranged into plates with Adobe Photoshop® CS5 (Adobe System Incorporated, San Jose, USA) software. CorelDraw® X8 (CorelDraw Corporation, Ottawa, ON, Canada) was used for the lettering of the plates.

**Terminology and description style.** The terminology used for the female cephalothorax is adopted from BENDA et al. (2022a, 2022b, 2024a), LÖWE et al. (2016), and KINZELBACH (1971). New appropriate terminology was developed for morphological characters without specific

designation. Cephalothorax is described in morphological orientation in figures, although their functional orientation in the host's body is inverted. Abbreviations: ♀ – female, EMP – empty male puparium.

## Results

### *Eurystylops ogloblini* sp. nov.

(Figs 1–5)

**Type locality.** Czech Republic: Southern Moravia, Horní Bojanovice env.

**Type material.** HOLOTYPE: ♀ (NMPC), cephalothorax on triangular mounting card: "CZECH REPUBLIC, Mor. / mer., Horní Bojanovice / 222 m, pan traps / 48.942386, 16.808153 / M. Štrobl lgt., 03.07.2022".

Host: *Rophites quinquespinosus*. PARATYPES: **AZERBAIJAN:** 1 ♀ (JSPC), Altiaghach env., Altiaghaj NP, 11.vi.2012, swept, M. Volf lgt., host: *Rophites chypealis*. **GREECE:** 1 ♀ (JSPC), Thessalia prov., Ossá Mt., 8.viii.2010, swept, J. Halada lgt., host: *Rophites hartmanni*. **SLOVAKIA:** 1 ♀ (MMBC), Štúrovo, Svodín, 27.vii.1961, swept, E. Staněk lgt., host: *R. quinquespinosus*; 2 ♀♀ (NMPC), Fiľakovo env., 13.vii.1938, swept, V. Zavadil lgt., host: *R. quinquespinosus*. **TURKEY:** 12 ♀♀ (NMPC), Kahramanmaraş prov., Budaklı env., 1934 m, 37.655694, 37.041111, 5.vii.2011, swept, J. Straka lgt., host: *Rophites chypealis*.

**Other material.** **CZECH REPUBLIC: BOHEMIA:** 1 EMP (NMPC), Jilové u Prahy env., 16.vii.1906, Holík lgt., host: *R. quinquespinosus*.

**Diagnosis of female cephalothorax.** Differing from *Eurystylops oenipontana* mainly in size and shape of cephalothorax. Size of cephalothorax larger in *E. ogloblini*



Fig. 2. Empty male puparium of *Eurystylops ogloblini* sp. nov. inside the host bee *Rophites quinquespinosus* Spinola, 1808: A – lateral view; B – detail of host abdomen with empty puparium under the 4<sup>th</sup> tergite; C–E – labels.

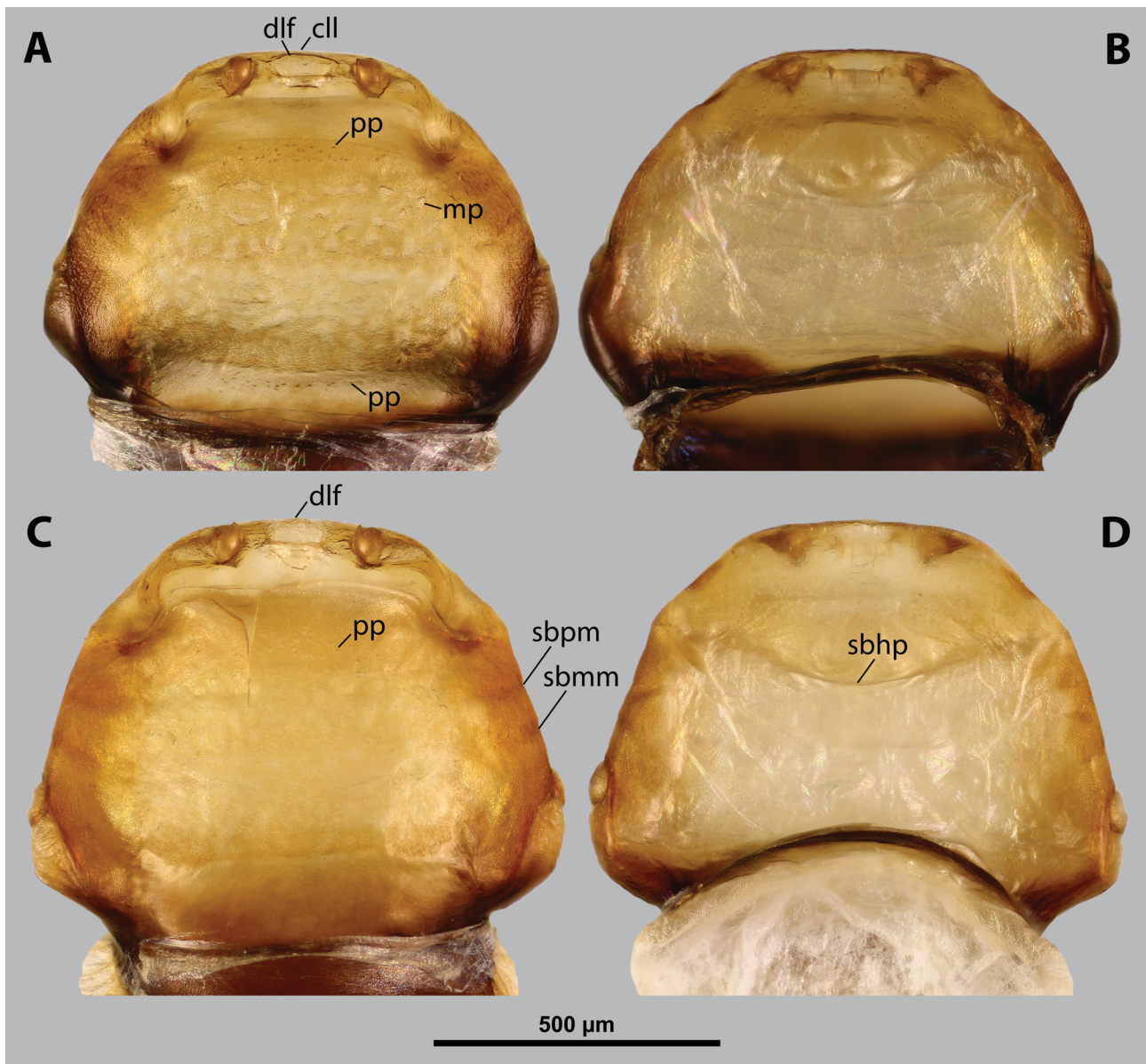


Fig. 3. *Eurystylops ogloblini* sp. nov., females, detail of cephalothorax: A – detail of ventral side of cephalothorax (holotype); B – detail of dorsal side of cephalothorax (holotype); C – detail of ventral side of cephalothorax (paratype); D – detail of dorsal side of cephalothorax (paratype). Abbreviations: cll – clypeal lobe, dlf – dorsal labral field of labral area, mp – membranous patch of cuticle, pp – pigmented papillae, sbhp – segmental border between head and prothorax, sbmm – segmental border between mesothorax and metathorax, sbpm – segmental border between prothorax and mesothorax.

(length 0.92–0.96 mm, width 0.72–0.80 mm) in comparison with *E. oenipontana* (length 0.50–0.58 mm, width 0.64–0.73 mm). Lateral part of abdominal segment I below spiracles rounded, not forming spiracular corner as in *E. oenipontana* (sc, Fig. 7A). Head of *E. ogloblini* shorter than cephalothorax: length proportion of head/cephalothorax 0.30 but 0.36–0.40 in *E. oenipontana*. Cuticle of prothorax (prosternum) uniformly pale orange in *E. ogloblini*, completely reticulate, posteriorly with transversal group of pigmented papillae (pp, Fig. 3A); *E. oenipontana* in contrast only rarely with thoracic papillae. Very variable membranous patches of cuticle present on mesosternum and anterior part of metasternum in *E. ogloblini* (mp, Fig. 3A), but completely absent in *E. oenipontana*.

Features visible on SEM images: Clypeal region of *E. ogloblini* not well delimited from labral area (sbcl, Fig. 4C), and labral area distinctly constricting clypeal area or

even overlapping it and protruding from head capsule (dlf; Figs 3A, C). In contrast, clypeal region well delimited from labral area in *E. oenipontana* (sbcl, Fig. 8C), and labral area well visible in ventral view, not constricting clypeal area. Mandibular tooth small in *E. ogloblini* (mdt, Fig. 5A), but conspicuously large in *E. oenipontana* (mdt, Fig. 8C).

**Description of female cephalothorax. Shape and colouration.** Cephalothorax (holotype) length 0.72 mm, width 0.92 mm. Shape slightly variable but always wider than long, length 0.92–0.96 mm, width 0.72–0.80 mm. Flattened in cross-section, semi-elliptic. Anterior head margin not protruding from cephalothorax capsule. Thorax distinctly widening posteriorly. Pro-mesothoracic and meso-metathoracic segmental border very slightly constricted laterally, indistinct in some specimens (sbpm, sbmm; Fig. 3C). Colouration from pale yellow to dark brown. Cephalothorax with conspicuous colour pattern with abdominal part

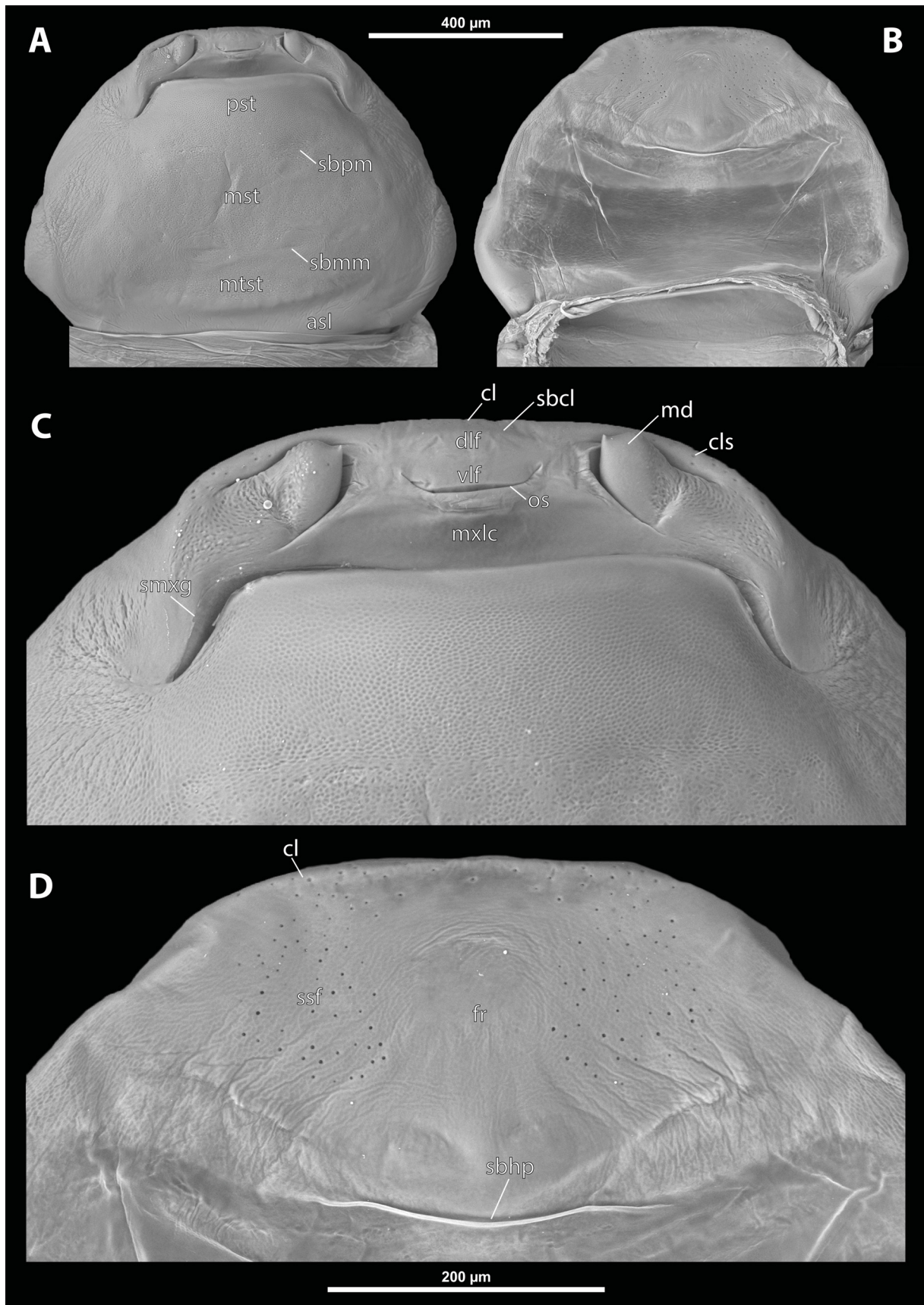


Fig. 4. *Eurystylops ogloblini* sp. nov., holotype, female, detail of cephalothorax (SEM): A – ventral side of cephalothorax; B – dorsal side of cephalothorax; C – detail of anterior part of cephalothorax (ventral side); D – detail of anterior part of cephalothorax (dorsal side). Abbreviations: asI – abdominal segment I, cl – clypeus, cls – clypeal sensillum, dlf – dorsal labral field of labral area, fr – frontal region, md – mandible, mst – mesosternum, mtst – metasternum, mxlc – maxillolabial complex, os – mouth opening, pst – prosternum (prosternal extension), sbcl – segmental border between clypeus and labrum, sbhp – segmental border between head and prothorax, sbmm – segmental border between mesothorax and metathorax, sbpm – segmental border between prothorax and mesothorax, smxg – submaxillary groove, ssf – supraantennal sensillary field, vlf – ventral labral field of labral area.

of cephalothorax darker than anterior part.

**Head capsule.** Length of head about one third of cephalothorax. Length proportion of head/cephalothorax 0.30 including lateral cephalic extension. Width of birth opening 0.46 (0.46–0.56) mm. Head colouration predominantly pale, without dark colouration. Clypeal region not well delimited from labral area (sbcl, Fig. 4C), labral area significantly constricting clypeal area (holotype), in some specimens even overlapping clypeal area and protruding from head capsule (dlf; Figs 3A, C). Apical margin of clypeal area blunt, not forming protruding clypeal lobe (cll, Fig. 3A). Clypeal surface smooth, with distinctly visible sensilla present and more or less evenly scattered (cls, Fig. 4C). Cuticle of frontal region slightly wrinkled, reticulated (fr, Fig. 4D). Segmental border between head and prothorax indicated by distinct suture on dorsal side (sbhp; Figs 3D, 4D). Head and prothorax distinctly separated by birth opening ventromedially, and laterally by indistinct suture as in *Stylops* (LÖWE et al. 2016).

**Supraantennal sensillary field** slightly wrinkled, reticulated, with distinctly recognisable sensilla. Not delimited by furrow medially, border not recognisable. Clypeal area not clearly delimited from supraantennal sensillary field, clypeal sensilla hardly distinguishable from sensilla of supraantennal sensillary field (ssf, cl; Fig. 4D).

**Antenna.** Vestiges of antennae absent.

**Labrum.** Ventral field elliptic, not protruding. Dorsal field elongated, slightly arcuate, protuberant, ~5–6× (5× in holotype) wider than long in midline (dlf, Fig. 4C). Border between dorsal and ventral labral field not well delimited. Setae of dorsal field present or absent (in holotype). Dorsal field overlapping clypeal area from ventral side in some specimens.

**Mandible** anteromedially directed at angle of 30–35° (35° in holotype) and slightly protruding from mandibular capsule (md, Fig. 4C). Mandibular bulge more or less distinctly raised, with several indistinct sensilla. Cuticle wrinkled laterally, completely smooth medially (Fig. 5A).

Tooth small, narrow, pointed apically (mdt, Fig. 5A).

**Maxilla** completely absent and fused with labial area, forming maxillolabial complex (mxlc, Fig. 2C). Surface of maxillolabial complex completely smooth. Maxillary base fused, part of maxillolabial complex. Vestige of maxillary palp absent. Submaxillary groove present, produced posterolaterally, curved along birth opening (smxg, Fig. 4C).

**Labium.** Labial area indistinct, only delimited anteriorly by mouth opening and posteriorly by birth opening. Laterally completely fused with maxillae, without visible borders. Surface completely smooth.

**Mouth opening.** medially straight, laterally arcuate, area around mouth opening slightly lighter in colour (os, Fig. 4C).

**Thorax.** Pro-mesothoracic and meso-metathoracic borders indistinct on ventral side, borders laterally more visible (sbpm, sbmm; Fig. 3C), medially separated by indistinct impressions (sbpm, sbmm; Fig. 4A). Distinct change in cuticular sculpture visible on pro-mesothoracic borders, but meso-metathoracic borders nearly invisible on SEM micrographs and colour photo (pst, mst, mtst; Fig. 4A). On dorsal side, pro-mesothoracic and meso-metathoracic borders indistinct, almost unrecognisable. Border between metathorax and abdomen indicated by change in cuticular surface structure (asl, Fig. 4A). Cuticle of prothorax (prosternum) uniformly pale orange, completely reticulate, posteriorly with transverse group of more strongly pigmented papillae. Pigmented papillae well visible in holotype (pp, Fig. 3A), in some specimen indistinctly visible (Fig. 3C). Anterior edge of prosternal extension not distinctly translucent. In ventral view, mesosternum reticulated, lateral parts also wrinkled. Metasternum completely reticulated, surface extending laterally, almost reaching abdominal spiracles. Membranous patches of cuticle presented on mesosternum and anterior part of metasternum, variable in shape, distinct in holotype (mp, Fig. 3A) but in some specimen not well visible (Fig. 3C). Pigmented papillae present posteriorly on metasternum. Prothorax, mesothorax

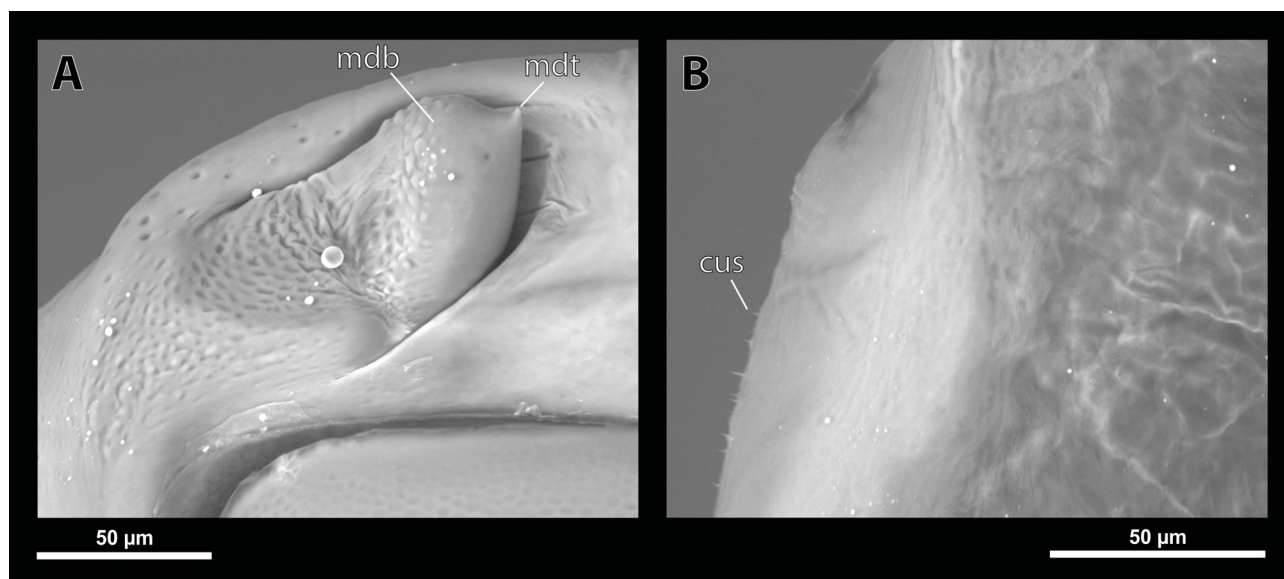


Fig. 5. *Eurystylops ogloblini* sp. nov., female, detail of cephalothorax (SEM): A – detail of mandible; B – detail of lateral part of abdominal segment I with spiracle. Abbreviations: cus – cuticular spine, mdb – mandibular bulge, mdt – mandibular tooth.

and metathorax almost completely fused dorsally, with indistinct borders. Surface smooth or slightly wrinkled, translucent in comparison with head capsule on dorsal side (Figs 3B, D).

**Abdominal segment I and spiracles.** Sclerotised abdominal part of abdominal segment I smooth dorsally, slightly wrinkled on ventral side. Colouration varies from dark brown, contrasting to pale metathorax (in holotype), to pale orange in some other specimens. Borders between smooth abdominal segment I and reticulated or wrinkled metathorax well recognisable on ventral side, in dorsal view distinct laterally but indistinct medially. Spiracles located on posterior half of cephalothorax, not elevated, with anterolateral orientation. Cuticular spines present on lateral region of abdominal segment I (cus, Fig. 5B). Lateral part of abdominal segment I below spiracles rounded, not forming spiracular corner.

**Male and primary larvae.** Unknown.

**Etymology.** Named in honour of Alexander A. Ogloblin, an expert of Strepsiptera and Hymenoptera, who worked several years in the National Museum in Prague and significantly contributed to the development of the collections of our Department of Entomology.

**Hosts.** *Rophites clypealis* Schwammerberger, 1976; *R. hartmanni* Friese, 1902 and *R. quinquespinosus* Spinola, 1808.

**Phylogenetic relationships.** Related to *Eurystylops oenipontana* Hofeneder, 1949 (Benda & Straka unpubl.)

**Distribution.** Western Palaearctic (Fig. 10).

**Note.** A host specimen with an empty male puparium (EMP) is the only evidence of the existence of a male in the genus *Eurystylops*. This specimen was studied by A. A. Ogloblin and was labelled as “? *Rophitostylops* n. gen.” (Fig. 2E). We also examined the collection of V. Székessy deposited in HNHM. Although the records of stylipised *Rophites quinquespinosus* and *R. hartmanni* were published by SZÉKESSY (1959), the material is missing in the collection. There is a note in his list of species in the collection that the material is lost and could thus not be described (KINZELBACH 1978).

### *Eurystylops oenipontana* Hofeneder, 1949

(Figs 6–9)

*Eurystylops oenipontana* Hofeneder, 1949: 119 (original description, syntypes in Friese collection, their current location unknown).

**Material examined.** CZECH REPUBLIC: 1 ♀ (JSPC), Malé Březno env., České středohoří Protected Landscape Area, 16.vii.2006, swept, J. Batelka lgt., host: *Dufourea dentiventris*; 1 ♀ (NMPC), Arnultovice env., 9.vii.1940, swept, K. Špaček lgt., host: *D. dentiventris*; 1 ♀ (NMPC), Praha env., Radotín, 30.vi.1964, swept, B. Tkalců lgt., host: *D. dentiventris*; 1 ♀ (NMPC), Strančice env., vii.1960, swept, V. Kočmíd lgt., host: *D. dentiventris*; 1 ♀ (NMPC), Vrané nad Vltavou env., vii.1954, swept, V. Kočmíd lgt., host: *D. dentiventris*; 1 ♀ (NMPC), Vitín env., České středohoří PLA, 10.vii.1921, collector unknown, host: *D. dentiventris*; 1 ♀ (NMPC), Polička env., Františky, 24.vii. (without year), swept, L. Duda lgt., host: *D. dentiventris*; 1 ♀ (NMPC), Všenory env., 27.vii.1912, swept, O. Šustera lgt., host: *D. dentiventris*; 3 ♀♀ (NMPC), Malá Skála env., without date, swept, J. Obenberger lgt., host: *D. dentiventris*; 1 ♀ (NMPC), Káraný nad Labem env., without date, swept, J. Obenberger lgt., host: *Dufourea inermis*; 2 ♀♀ (NMPC), Přebuz env., Přebuz moorland, 12.viii.2011, P. Kment lgt., host: *D. dentiventris*; 6 ♀♀ (JSPC), Přebuz env., Přebuz moorland, 21.vii.2021, J. Straka lgt., host: *D. dentiventris*. SWITZERLAND: 1 ♀ (EEC), Haldenstein, 8.viii.1997, swept, A. Müller

lgt., host: *D. inermis*; 1 ♀ (JSPC), Leuk env., 8.vii.2008, combined trap, Y. Chittaro lgt., host: *D. dentiventris*.

**Diagnosis of female cephalothorax.** See diagnosis of the female cephalothorax of *Eurystylops ogloblini* sp. nov.

**Redescription of female cephalothorax. Shape and colouration.** Cephalothorax variable but always wider than long, length 0.50–0.58 mm, width 0.64–0.73 mm. Flattened in cross-section, semi-elliptic. Anterior head margin not protruding from cephalothoracic capsule or only very slightly. Thorax slightly (Fig. 7C) or distinctly (Fig. 7A) widening posteriorly. Pro-mesothoracic and meso-metathoracic segmental border not constricted laterally, border unrecognizable. Colouration from pale yellow to dark brown. Cephalothorax with conspicuous colour pattern with posterolateral parts darker than anterior part.

**Head capsule.** Length of head slightly more than one third of cephalothorax. Length proportion of head/cephalothorax 0.36–0.40 including lateral cephalic extension. Width of birth opening 0.36–0.42 mm. Head predominantly pale, without dark areas. Clypeal region well delimited from labral area (sbcl, Fig. 8C); labral area well visible from ventral side, not constricting clypeal area. Apical margin of clypeal area blunt or forming slightly protruding clypeal lobe (cll, Fig. 7C). Clypeal surface smooth with distinctly visible sensilla present on clypeal surface, more or less evenly scattered (cls, Fig. 8C). Cuticle of frontal region distinctly wrinkled horizontally (fr, Fig. 4D). Segmental border between head and prothorax indicated by distinct suture on dorsal side (sbhp; Figs 7B, 8D). Head and prothorax distinctly separated by birth opening ventromedially, and laterally by unrecognisable suture as in *Stylops* (LÖWE et al. 2016).

**Supraantennal sensillary field** smooth, with distinctly recognisable sensilla. Not delimited by furrow medially, without recognisable border. Clypeal area not clearly delimited from supraantennal sensillary field, clypeal sensilla hardly distinguishable from sensilla of supraantennal sensillary field (ssf, cl; Fig. 4D). Some sensilla also dispersed medially between both sensillary fields (ssf, Fig. 4D).

**Antenna.** Vestiges of antennae absent.

**Labrum.** Ventral field elliptic, not protruding. Dorsal field elongated, slightly arcuate, flat, not protuberant, ~ 5–6× wider than long in midline (dlf, Fig. 8C). Border between dorsal and ventral labral field well delimited. Dorsal field with several setae, not overlapping clypeal area.

**Mandible** anteromedially directed at angle of 35–45°, not protruding from mandibular capsule (md, Fig. 8C). Mandibular bulge more or less distinctly raised, sensilla not visible. Cuticle wrinkled laterally, completely smooth medially (Fig. 5A). Mandibular tooth conspicuously large, narrow, pointed apically (mdt, Fig. 8C).

**Maxilla** completely absent as individual structure, fused with labial area, both forming maxillolabial complex (mxlc, Fig. 8C). Surface of maxillolabial complex completely smooth. Maxillary base fused, part of maxillolabial complex. Vestige of maxillary palp absent. Submaxillary groove present, produced posterolaterally, curved along birth opening (smxg, Fig. 8C).

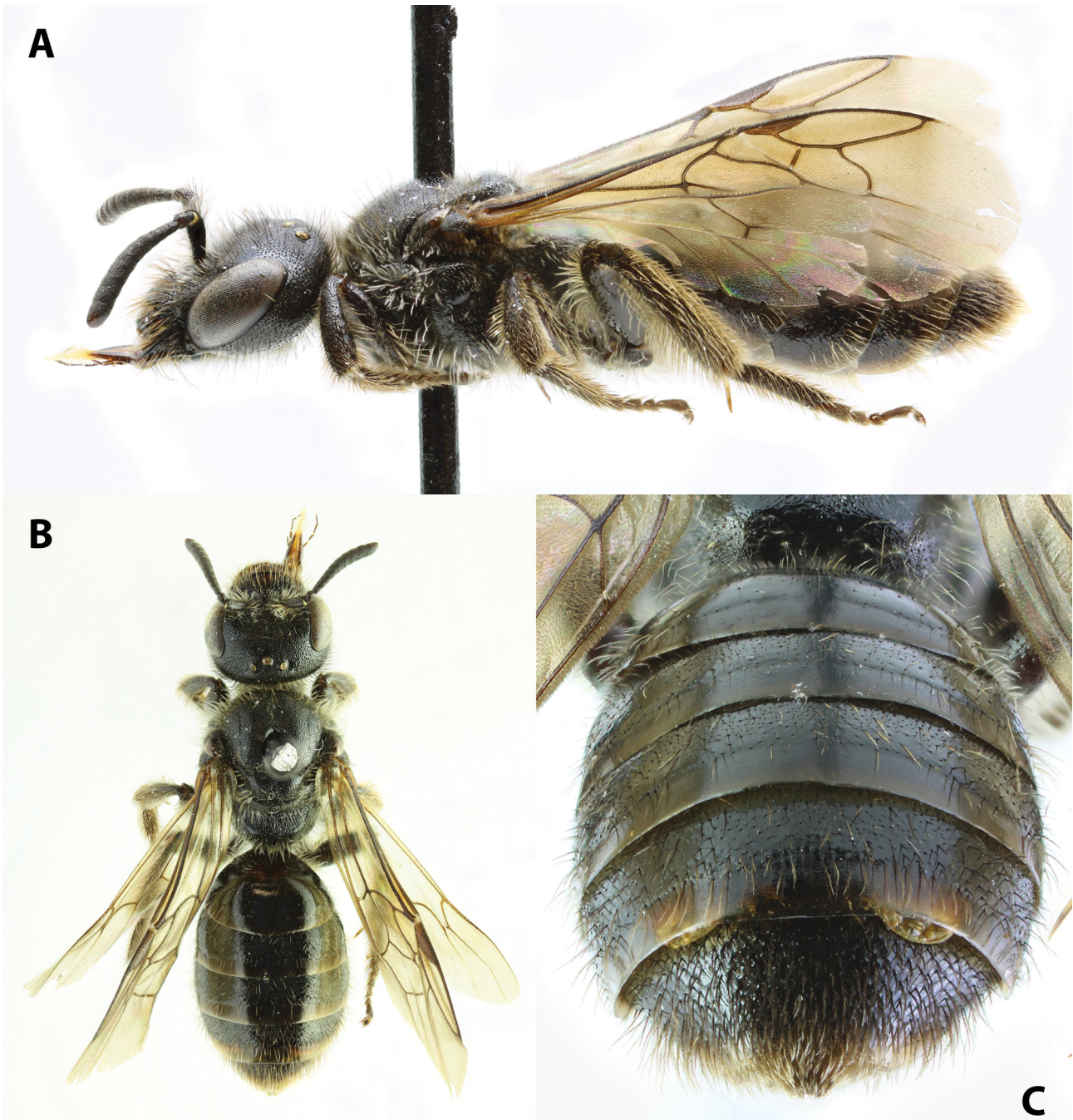


Fig. 6. Females of *Eurystylops oenipontana* Hofeneder, 1949 inside the host bee *Dufourea dentiventris* (Nylander, 1848): A – lateral view; B – dorsal view; C – detail of host abdomen with two female cephalothoraces under the 4<sup>th</sup> tergite.

**Labium.** Labial area indistinct, only delimited anteriorly by mouth opening and posteriorly by birth opening. Laterally completely fused with maxillae, without visible borders. Surface completely smooth.

**Mouth opening** medially straight or concave, laterally arcuate, area around mouth opening slightly lighter in colour (os, Fig. 8C).

**Thorax.** Pro-mesothoracic and meso-metathoracic borders indistinct on ventral side, hardly recognisable on colour photos, but more distinct on SEM image (sbpm, sbmm; Fig. 8A), medially separated by indistinct impressions. Change in cuticular sculpture on pro-mesothoracic borders and meso-metathoracic borders hardly visible on SEM and colour images (pst, mst, mtst; Fig. 8A). Pro-meso-

thoracic and meso-metathoracic borders indistinct dorsally, almost unrecognisable. Border between metathorax and abdomen recognisable as change in cuticular surface structure (asI, Fig. 8A). Cuticle of prothorax (prosternum) uniformly pale orange, completely reticulated, posteriorly without transverse group of pigmented papillae. Rarely some papillae present on prosternum but scattered, not regularly arranged. Anterior part of prosternal extension not conspicuously translucent, only outermost edge slightly transparent. Mesosternum reticulated ventrally, lateral parts mostly smooth. Metasternum completely reticulated, surface nearly reaching abdominal spiracles laterally. Membranous patches of cuticle completely absent on mesosternum and anterior part of metasternum. Pigmented

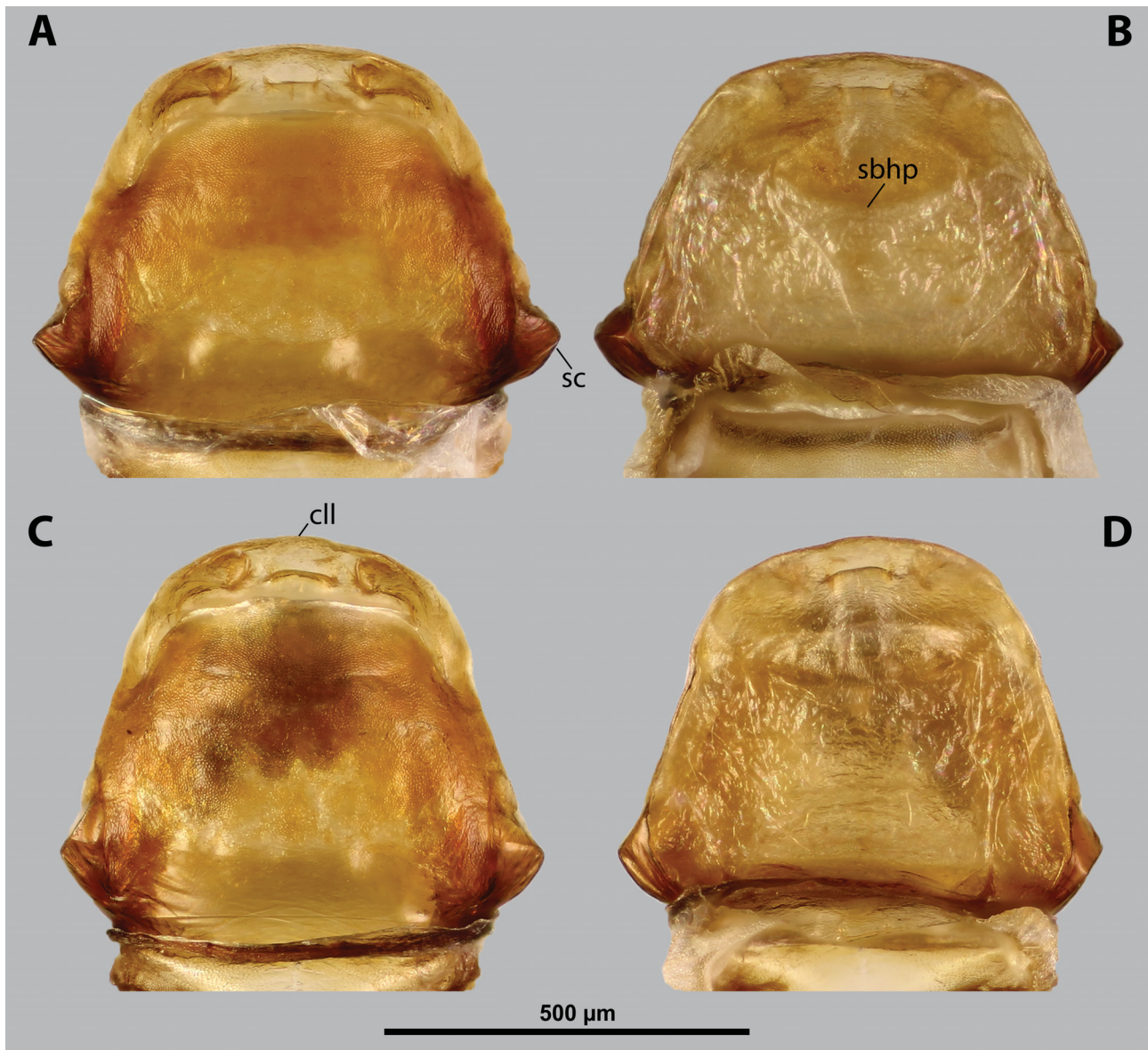


Fig. 7. *Eurystylops oenipontana* Hofeneder, 1949, females, detail of cephalothorax: A – detail of ventral side of cephalothorax (1<sup>st</sup> specimen); B – detail of dorsal side of cephalothorax (1<sup>st</sup> specimen); C – detail of ventral side of cephalothorax (2<sup>nd</sup> specimen); D – detail of dorsal side of cephalothorax (2<sup>nd</sup> specimen). Abbreviations: cfl – clypeal lobe, sbhp – segmental border between head and prothorax, sc – spiracular corner.

papillae lacking posteriorly on metasternum. Prothorax, mesothorax and metathorax completely fused dorsally, but indistinct borders recognisable. Surface smooth or slightly wrinkled, dorsally translucent in comparison with head capsule (Figs 7B, D).

**Abdominal segment I and spiracles.** Sclerotised abdominal part of abdominal segment I smooth on dorsal side, slightly wrinkled ventrally. Colouration of abdominal segment I variable from dark brown, in contrast to pale metathorax, to pale orange in some specimens. Borders between smooth abdominal segment I and reticulated or wrinkled metathorax well recognisable in ventral view, dorsally distinct laterally but indistinct medially. Spiracles located on posterior third of cephalothorax, not elevated, with anterolateral orientation. No distinct cuticular spines present on lateral region of abdominal segment I. Lateral part of abdominal segment I below spiracles forming distinct spiracular corner (sc, Fig. 7A).

**Male and primary larvae.** Unknown.

**Hosts.** *Dufourea dentiventris* (Nylander, 1848), *D. inermis* (Nylander, 1848).

**Phylogenetic relationships.** Related to *Eurystylops ogloblini* sp. nov. (Benda & Straka unpubl.).

**Distribution.** Central Europe: Austria (HOFENEDER 1949), Czech Republic (this study), Germany (KINZELBACH 1971), Switzerland (HOFENEDER 1949) (Fig. 11).

### Discussion

A conspicuous female autapomorphy of Stylopodia, i.e. Strepsiptera excl. Mengenillidae, is the secondary tagmosis with development of cephalothorax, the anterior part of the body that contains the head, thorax and first abdominal segment (POHL & BEUTEL 2008). This derived feature is present in the entire Stylopiformia including Stylopidae. This complex structural transformation and simplification is closely linked to the permanent endoparasitic lifestyle of

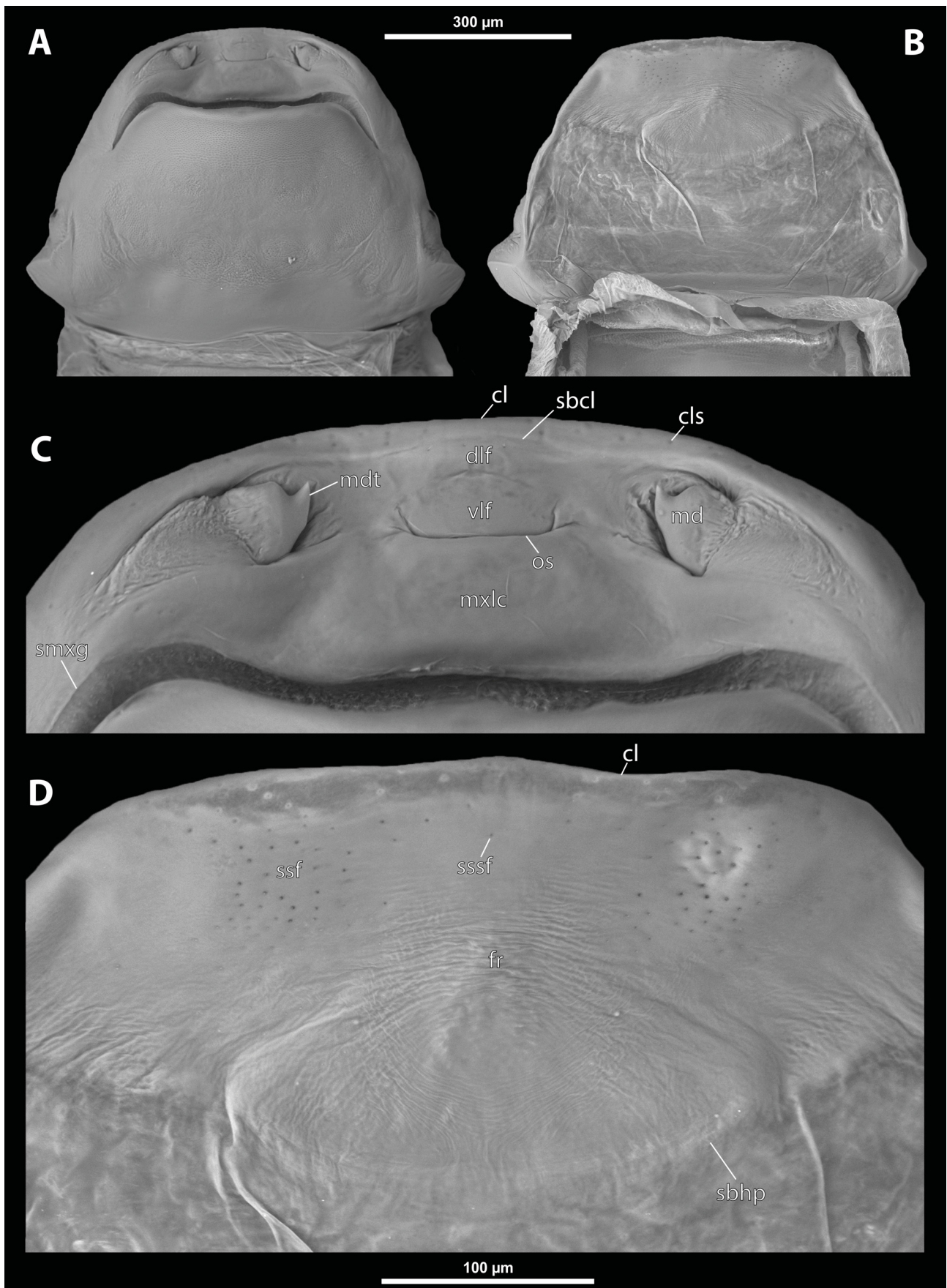


Fig. 8. *Eurystylops oenipontana* Hofeneder, 1949, female, detail of cephalothorax (SEM): A – ventral side of cephalothorax; B – dorsal side of cephalothorax; C – detail of anterior part of cephalothorax (ventral side); D – detail of anterior part of cephalothorax (dorsal side). Abbreviations: cl – clypeus, cls – clypeal sensillum, dlf – dorsal labral field of labral area, fr – frontal region, md – mandible, mdt – mandibular tooth, mxlc – maxillolabial complex, os – mouth opening, sbcl – segmental border between clypeus and labrum, sbhp – segmental border between head and prothorax, smxg – submaxillary groove, ssf – supraantennal sensillary field, sssf – sensillum of supraantennal sensillary field, vlf – ventral labral field of labral area.

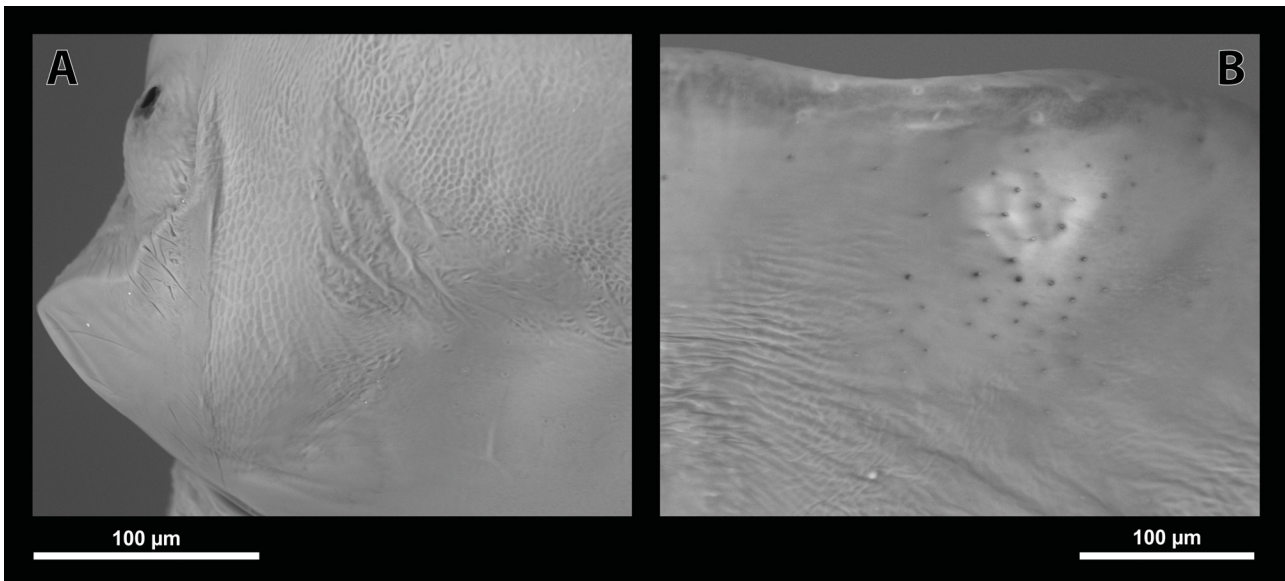


Fig. 9. *Eurystylops oenipontana* Hofeneder, 1949, female, detail of cephalothorax (SEM): A – lateral part of abdominal segment I with spiracular corner below spiracles, ventral view; B – detail of anterior part of cephalothorax with supraantennal sensillary field, dorsal view.

females, which are also characterised by the far-reaching or complete reduction of the antennae, mouthparts, compound eyes and legs (KINZELBACH 1971, POHL & BEUTEL 2008). Unexpectedly, the simplified female cephalothorax exhibits a number of characters that can be easily used to identify genera and species (BENDA et al. 2023, 2024b).

A conspicuous autapomorphy of Stylopiformia is the birth opening, a structure which allows easier mating (PEINERT et al. 2016, JANDAUSCH et al. 2022, 2023) and in which the primary larvae are released viviparously (POHL & BEUTEL 2005, 2008). This structure is absent in Corioxenidae, the sister taxon of Stylopiformia (POHL & BEUTEL 2005, 2008). Morphologically, the birth opening is an area between the head and thorax and its function is correlated with the rupture of the membranous cuticle of this region (KINZELBACH 1971). On the ventral side, the birth opening continues laterally as a suture, which is very variable within the clade Xenidae + Stylopidae. In *Eurystylops* the suture is not recognisable, as in many other genera of Stylopidae, such as *Stylops* Kirby, 1802 (LÖWE et al. 2016), *Halictoxenos* Pierce, 1908 (STRAKA et al. 2006), *Hylecthrus* Saunders, 1850 and *Chrysostylops* Benda & Straka, 2024 (BENDA et al. 2024a). In contrast, the lateral suture is clearly recognisable in most genera of Xenidae (BENDA et al. 2022a). A completely different situation occurs in genera *Paragioxenos* Ogloblin, 1923 (Xenidae) and *Rozenia* Straka, Jůzová & Batelka, 2014 (Stylopidae): the head and prothorax are completely separated by the birth opening on the ventral side (STRAKA et al. 2014, BENDA et al. 2022a). The maxilla is completely fused with the labial area in *Eurystylops*, both forming a maxillolabial complex. This is common in most of the genera of Stylopidae (HOFENEDER 1949, STRAKA et al. 2014, LÖWE et al. 2016, BENDA et al. 2024a) but is still unconfirmed in *Crawfordia* Pierce, 1908 (KINZELBACH 1970). In contrast, the shape of the maxilla is highly variable in Xenidae, with a conspicuous protuberance in several genera (BENDA et al. 2022a).

The description of a new species of *Eurystylops* from

the Western Palearctic is not a surprise. As we have mentioned, records of stylopised *Rophites* have already been provided by ULRICH (1930), HOFENEDER (1939) and SZÉKESY (1959). In fact, the species was noticed by A. A. Ogloblin in the early 1920s for the first time, who considered the strepsipterans from *Rophites quinquespinosus* to be a species of a new genus. For understandable reasons, he did not describe the species and genus based only on the empty male puparium inside a single bee specimen. At that time, female or male specimens were not available. However, ULRICH (1930) presented information on stylopisation of *Rophites* from western Ukraine (Lviv and Poltava), also referring to communication with A. A. Ogloblin and J. Noskiewicz. This material should have been at the disposal of A. A. Ogloblin as it was collected by his brother (ULRICH 1930), and he was also in contact with J. Noskiewicz and worked on his material (OGLOBLIN 1925). Possibly, a misunderstanding occurred between Ogloblin and Ulrich. It is conceivable that Ulrich's statement referred to *Crawfordia labiata* Ogloblin, 1924 and its host *Panurginus labiatus* (Eversmann, 1852), as Ogloblin described *Crawfordia* based on material from Lviv and Poltava. A description of *Eurystylops* from *Rophites* was possibly also planned by V. Székessy, but his material was lost (KINZELBACH 1978), what we also confirmed by our search in the collection of the HNHM. The complex situation that unfolded in the 20<sup>th</sup> century therefore caused that *Eurystylops* parasitising *Rophites* was described a hundred years after its discovery.

Very interesting structures on the cephalothorax of the female of *E. ogloblini* are membranous patches of the cuticle on the mesosternum and on the anterior part of the metasternum. Interestingly, in the related species *E. oenipontana* as well as in Xenidae, no signs of membranous patches were described in earlier works (BENDA et al. 2022a). The work of KINZELBACH (1971) suggested that these membranous patches could be related to orifices of Nasonow's glands, but further investigation, especially based on microtome sections, is required (LÖWE et al.

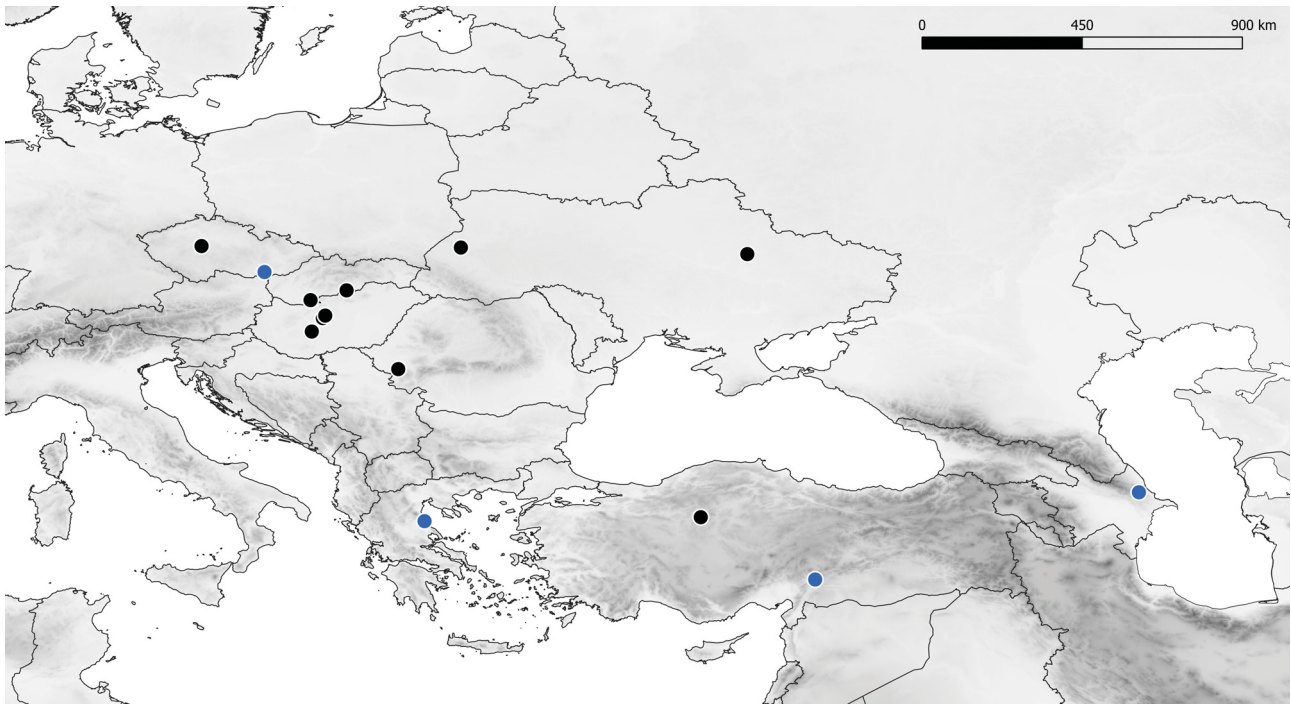


Fig. 10. Distribution of *Eurystylops ogloblini* sp. nov. Black spots indicate findings up to the year 2000, blue spots indicate findings from 2000 to the present. Historical records are adopted from KINZELBACH (1978).

2016). In SEM micrographs, we found no evidence of perforations of the cuticle of the cephalothorax in either *Eurystylops* species.

The phylogenetic position of *Eurystylops* is unclarified. Although KINZELBACH (1971) assumed a relationship with *Halictoxenos*, a phylogenomic study is still required for a well-supported placement. The biogeographical history of the genus *Eurystylops* would also be interesting, as it is Holarctic, with a likely dispersal event between North

America and Europe. Its geographical origin also remains unclear, due to the lack of a robust molecular phylogeny for Stylopidae. To date, four species have been described from the Nearctic and two species from the Palearctic Region (Table 1). However, the current diversity may be underestimated, as about 70 species of the genus *Dufourea* occur in the Nearctic and about 60 species in the Palearctic (MICHENER 2007). We also expect a greater diversity of the genus *Eurystylops* in the Nearctic, as many more genera

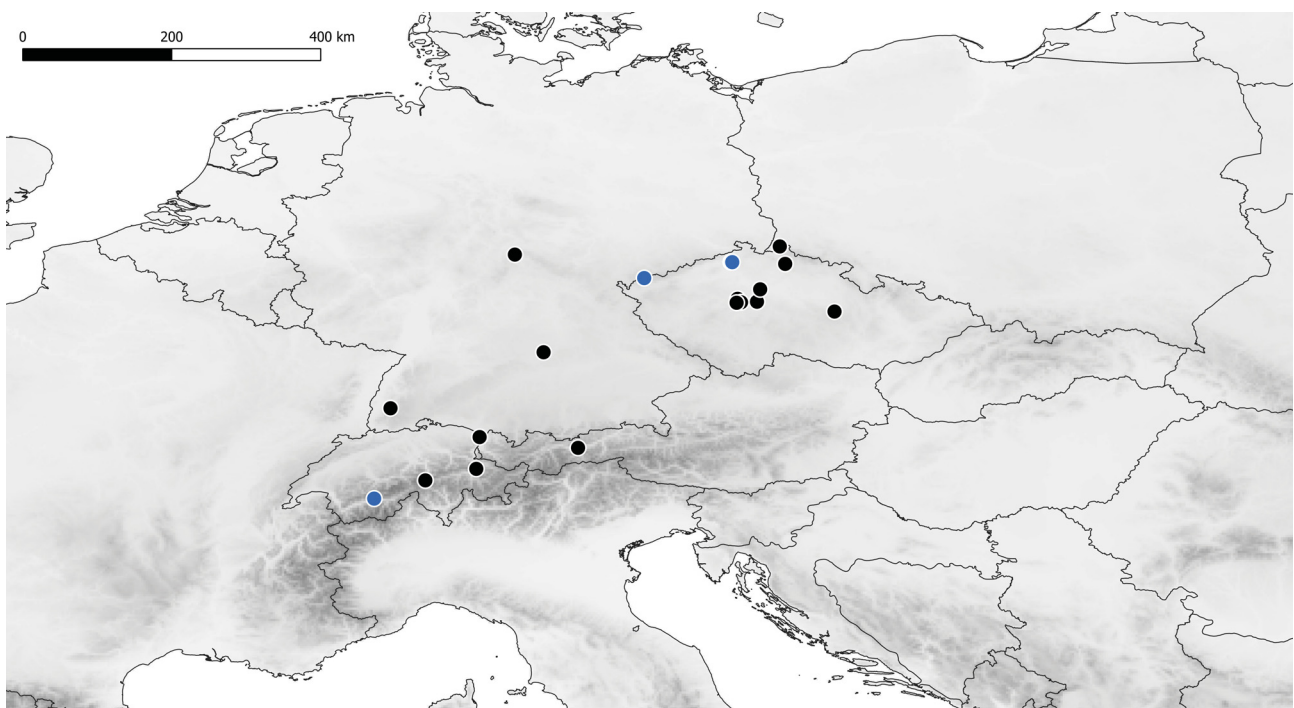


Fig. 11. Distribution of *Eurystylops oenipontana* Hofeneder, 1949. Black spots indicate findings up to the year 2000, blue spots indicate findings from 2000 to the present. Historical records are adopted from KINZELBACH (1978).

Table 1. Overview of six currently valid species of *Eurystylops* Bohart, 1943 with general information on their distribution and hosts.

Species	Distribution	Hosts
<i>Eurystylops conanthalicti</i> Kinzelbach, 1971	USA (California)	<i>Conanthalictus</i> sp.
<i>Eurystylops desertorum</i> (Bohart, 1941)	USA (California)	<i>Dufourea boregoensis</i> (Michener, 1937)
<i>Eurystylops oenipontana</i> Hofeneder, 1949	Central Europe	<i>Dufourea dentiventris</i> (Nylander, 1848); <i>Dufourea inermis</i> (Nylander, 1848)
<i>Eurystylops ogloblini</i> sp. nov.	Western Palaearct	<i>Rophites clypealis</i> Schwammberger, 1976; <i>Rophites hartmanni</i> Friese, 1902; <i>Rophites quinquespinosus</i> Spinola, 1808
<i>Eurystylops sierrensis</i> Bohart, 1978	USA (California)	<i>Dufourea trochantera</i> Bohart, 1948
<i>Eurystylops tetonensis</i> Bohart, 1943	USA (Wyoming)	<i>Dufourea maura</i> (Cresson, 1878)

of Rophitinae occur there (MICHENER 2007).

Although the distribution ranges of the two European *Eurystylops* species are certainly underestimated, the currently available data strongly suggest that they are under threat in Europe. *Eurystylops* individuals can easily escape attention by hiding under the abdominal tergites of species of *Dufourea* and *Rophites*. Nevertheless, the threat to the host bees of these genera is probably mainly responsible for the rarity of the parasites. All hosts of *E. ogloblini* and *E. oenipontana* (Table 1) are listed in different threat categories in the European and local Red Lists of bees: *Rophites clypealis* (Data Deficient), *R. hartmanni* (DD), *R. quinquespinosus* (Near Threatened), *Dufourea dentiventris* (NT), *Dufourea inermis* (NT) (NIETO et al. 2014). At the local level, the hosts are even more endangered or extinct, as the Red List of Threatened Species of the Czech Republic shows: *Rophites hartmanni* (DD) *Dufourea dentiventris* (Endangered) and *Dufourea inermis* (regionally extinct) (HEJDA et al. 2017). One of the reasons for the vulnerability of the host bees is their specialisation on specific flowers (they are all oligolectic) (BOGUSCH et al. 2020). The reason for the threat to *E. oenipontana* is a far-reaching disappearance of its host species from the lowlands. According to data from museum collections, hosts of the genus *Dufourea* were previously also common in the lowlands, where they were probably typical bees of the extensive cultural landscape. However, today they have almost completely disappeared from the typical agricultural landscape and mostly survive in the mountains or foothills. *Eurystylops oenipontana* only survives at higher altitudes where *Dufourea* populations are still abundant, such as in the Alps or the Ore Mountains (Fig. 11).

### Acknowledgements

We would like to thank all colleagues who provided material for this study, namely Martin Štrobl, Michal Perlík, Jan Batelka and Martin Volf. This project was supported by the Ministry of Culture of the Czech Republic (DKRVO 2024–2028/5.I.b, National Museum of the Czech Republic, 00023272). The authors declare no conflict of interests.

### References

BENDA D., PARSLow B. A., LEIJS R. & STRAKA J. 2024a: New insect family for Australia: *Chrysostylops australiensis* Benda & Straka, gen. et sp. nov. (Strepsiptera: Stylopidae) described from

- Chrysocolletes aureus* Leijs & Hogendoorn, 2021 (Hymenoptera: Colletidae). *Austral Entomology* **63**: 360–368.
- BENDA D., POHL H., BEUTEL R. & STRAKA J. 2024b: Solitary folded-winged wasps of the genus *Zethus* Fabricius (Vespidae, Zethinae) parasitised by two new species of Strepsiptera on different continents. *Journal of Hymenoptera Research* **97**: 721–739.
- BENDA D., POHL H., NAKASE Y., BEUTEL R. & STRAKA J. 2022a: A generic classification of Xenidae (Strepsiptera) based on the morphology of the female cephalothorax and male cephalotheca with a preliminary checklist of species. *ZooKeys* **1093**: 1–134.
- BENDA D., POHL H., BEUTEL R. & STRAKA J. 2022b: Two new species of *Xenos* (Strepsiptera: Xenidae), parasites of social wasps of the genus *Mischocyttarus* (Hymenoptera: Vespidae) in the New World. *Acta Entomologica Musei Nationalis Pragae* **62**: 1–11.
- BENDA D., POHL H., NAKASE Y., BEUTEL R. & STRAKA J. 2023: A new species of the genus *Paraxenos* Saunders, 1872 (Strepsiptera: Xenidae) from *Bembix* digger wasps (Hymenoptera: Bembicidae) and a redescription of *Paraxenos hungaricus* (Székessy, 1955). *European Journal of Taxonomy* **885**: 134–155.
- BLÜTHGEN P. 1919: Zur Kenntnis der Bienenfauna Nordthüringens. *Mitteilungen aus der Entomologischen Gesellschaft zu Halle (Saale)* **12**: 19–36.
- BOGUSCH P., BLÁHOVÁ E. & HORÁK J. 2020: Pollen specialists are more endangered than non-specialised bees even though they collect pollen on flowers of non-endangered plants. *Arthropod-Plant Interactions* **14**: 759–769.
- BOHART R. M. 1941: A revision of the Strepsiptera with special reference to the species of North America. *University of California Publications in Entomology* **7**: 91–160.
- BOHART R. M. 1943: A new generic name in Strepsiptera and descriptions of a new species (Strepsiptera, Stylopidae). *Bulletin of the Brooklyn Entomological Society* **38**: 12–13.
- BOHART R. M. & IRWIN M. E. 1978: A study of stylopisation in the bee genus *Dufourea*. *Pan-Pacific Entomologist* **54**: 98–102.
- COOK J. L. 2019: Annotated catalog of the order Strepsiptera of the World. *Transactions of the American Entomological Society* **145**: 121–267.
- HEJDA R., FARKAČ J. & CHOBOT K. (eds.) 2017: Červený seznam ohrožených druhů České republiky. Bezobratlí (Red list of threatened species of the Czech Republic. Invertebrates). *Příroda* **36**: 1–612.
- HERATY J. M. 1998: Hexamethylsilazane: A chemical alternative for drying insects. *Entomological News* **109**: 369–374.
- HOFENEDER K. 1939: Über zwei neue Strepsipteren aus *Andrena similis* F. Smith und *Halictus malachurus* Kirby. *Veröffentlichungen aus dem Deutschen Kolonial- und Übersee-Museum in Bremen* **2**: 181–200.
- HOFENEDER K. 1949: Über einige Strepsipteren. *Brotéria* **18**: 109–122.
- JANDAUSCH K., MICHELS J., KOVALEV A., GORB S. N., VAN DE KAMP T., BEUTEL R. G., NIEHUIS O. & POHL H. 2022: Have female twisted-wing parasites (Insecta: Strepsiptera) evolved tolerance traits as response to traumatic penetration? *PeerJ* **10** (e136655): 1–26.
- JANDAUSCH K., VAN DE KAMP T., BEUTEL R. G., NIEHUIS O. & POHL H. 2023: ‘Stab, chase me, mate with me, seduce me’: how widespread is traumatic insemination in Strepsiptera? *Biological Journal of the Linnean Society* **140**: 206–223.
- KINZELBACH R. 1970: Ein neues Strepsipteron aus den Atlasländern, *Crawfordia warnckeii* n. sp. (Insecta: Strepsiptera: Stylopidae). *Mit-*

- teilungen der Deutschen Entomologischen Gesellschaft **29**: 29–31.
- KINZELBACH R. 1971: *Morphologische Befunde an Fächerflüglern und ihre phylogenetische Bedeutung (Insecta: Strepsiptera)*. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, 256 pp.
- KINZELBACH R. 1978: *Fächerflügler (Strepsiptera)*. Gustav Fischer, Jena, 166 pp.
- LÖWE S., BEUTEL R. G. & POHL H. 2016: The female cephalothorax of *Stylops ovinae* Noskiewicz & Poluszyński, 1928 (Strepsiptera: Stylopidae). *Arthropod Systematics and Phylogeny* **74**: 65–81.
- McMAHON D. P., HAYWARD A. & KATHIRITHAMBY J. 2011: The first molecular phylogeny of Strepsiptera (Insecta) reveals an early burst of molecular evolution correlated with the transition to endoparasitism. *PLoS One* **6** (e21206): 1–10.
- MICHENER C. D. 2007: *The bees of the world*. 2nd ed. The Johns Hopkins University Press, 992 pp.
- NIETO A., ROBERTS S. P., KEMP J., RASMONT P., KUHLMANN M., GARCÍA CRIADO M., BIESMEIJER J. C., BOGUSCH P., DATHE H. H., DE LA RÚA P., DE MEULEMEESTER T., DEHON M., DEWULF A., ORTIZ-SÁNCHEZ F. J., LHOMME P., PAULY A., POTTS S. G., PRAZ C., QUARANTA M., RADCHENKO V. G., SCHEUCHL E., SMIT J., STRAKA J., TERZO M., TOMOZII B., WINDOW J. & MICHEZ D. 2014: *European red list of bees*. Publication Office of the European Union, Luxembourg, 84 pp.
- OGLOBLIN A. A. 1925: New and little known Strepsiptera from Poland. *Polskie Pismo Entomologiczne* **3**: 113–122.
- PEINERT M., WIPFLER B., JETSCHKE G., KLEINTEICH T., GORB S. N., BEUTEL R. G. & POHL H. 2016: Traumatic insemination and female counter-adaptation in Strepsiptera (Insecta). *Scientific Reports* **6** (25052): 1–10.
- POHL H. 2000: Die Primärlarven der Fächerflügler – evolutive Trends (Insecta, Strepsiptera). *Kaupia* **10**: 1–144.
- POHL H. & BEUTEL R. G. 2005: The phylogeny of Strepsiptera (Hexapoda). *Cladistics* **21**: 328–374.
- POHL H. & BEUTEL R. G. 2008: The evolution of Strepsiptera (Hexapoda). *Zoology* **111**: 318–338.
- STRAKA J., BATELKA J. & MALENOVSKÝ I. 2006: Genus *Halictoxenos* Pierce, 1908 (Strepsiptera: Stylopidae) in the Czech Republic and Slovakia. *Acta Musei Moraviae, Scientiae Biologicae* **91** (1–2): 69–82.
- STRAKA J., JÚZOVÁ K. & BATELKA J. 2014: A new genus of Strepsiptera, *Rozenia* gen. n. (Stylopidae), a parasite of bee genera *Acamptopoeum* and *Calliopsis* (Andrenidae, Panurginae, Calliopsini). *ZooKeys* **442**: 31–49.
- SZÉKESY V. 1959: Die Strepsipteren-Sammlung des Ungarischen Naturwissenschaftlichen Museums in Budapest. *Annales Historico-Naturales Musei Nationalis Hungarici* **51**: 301–337.
- ULRICH W. 1930: *Ordnung: Fächerflügler, Strepsiptera Kirby (1813). Die Tierwelt Mitteleuropas*. Queller und Meyer, Leipzig, 26 pp.