ISSN 1804-6487 (online) - 0374-1036 (print)

www.aemnp.eu

RESEARCH PAPER

# Two Palaearctic species of *Orthonevra* (Diptera: Syrphidae) under the name *O. brevicornis*

Robert ŻÓRALSKI<sup>1)</sup>, Frank VAN DE MEUTTER<sup>2)</sup>, Ximo MENGUAL<sup>3)</sup> & Piotr GADAWSKI<sup>4)</sup>

- 1) Norwida 9, 84-240 Reda, Poland; e-mail: robert@insects.pl; ORCID: 0000-0001-6017-2144
- <sup>2)</sup> Research Institute for Nature and Forests (INBO), Achterheide 16, 3980 Tessenderlo, Belgium; e-mail: frank.vandemeutter@gmail.com; ORCID: 0000-0002-9850-1860
- <sup>3)</sup> Museum Koenig Bonn, Leibniz-Institut zur Analyse des Biodiversitätswandels, Adenauerallee 127, 53113 Bonn, Germany; e-mail: x.mengual@leibniz-lib.de; ORCID: 0000-0002-6185-9404
- <sup>4)</sup>University of Lodz, Department of Invertebrate Zoology and Hydrobiology, Banacha 12/16, 90-237 Łódź, Poland; e-mail: piotr.gadawski@biol.uni.lodz.pl; ORCID: 0000-0001-9334-1960

Accepted: 19th June 2024

Published online: 1st October 2024

**Abstract.** During studying European material of *Orthonevra* Macquart, 1829 the presence of two widespread species so far interpreted as Orthonevra brevicornis (Loew, 1843) has been discovered. One species occurs from Central Europe into Transcaucasia and agrees with the taxon O. brevicornis of LOEW (1843). The second species, O. atlantica Żóralski & Van de Meutter sp. nov., has its main distribution range in the Atlantic parts of Europe and is described here. We provide a redescription of O. brevicornis and designate a neotype from the type locality (Poland, Posen [= Poznań] vicinity). The most important characters for distinguishing males of these two closely related species are in the structures of the terminalia. A diagnosis and identification key to European black-legged Orthonevra species is given as well as new sequences of the cytochrome c oxidase subunit I (COI) of mitochondrial DNA (mtDNA), also known as DNA barcodes, for most of the species of this group. Some new information and changes to the known ranges of Orthonevra species are provided as a result of this revisionary work: O. frontalis (Loew, 1843) is removed from the list of species occurring in Poland; O. gemmula Violovitsh, 1979 is confirmed from Hungary; O. incisa (Loew, 1843) is confirmed from its locus typicus (Poland, Posen vicinity); and O. montana Vujić, 1999 is reported from Poland and Austria for the first time and confirmed for Germany. An explanation for some previous records published as O. plumbago (Loew, 1840) is also given.

**Key words.** Diptera, Syrphidae, flower flies, hoverflies, COI, distribution, DNA barcode, identification key, new species, Europe, Palaearctic Region

**Zoobank:** http://zoobank.org/urn:lsid:zoobank.org:pub:320B3110-5FB6-4561-926A-8140627D1A51 © 2024 The Authors. This work is licensed under the Creative Commons Attribution-NonCommercial-NoDerivs 3.0 Licence.

### Introduction

Hoverflies of the genus *Orthonevra* Macquart, 1829 belong to the tribe Brachyopini (Chrysogasterini of some authors, e.g. MAIBACH et al. 1994) and are associated with streams, flushes, wet woodland and wetlands (MAIBACH et al. 1994, SPEIGHT 2017). They are small black flies with metallic, often greenish lustre and are characterised by the concave or flat face with protruding mouth edge and usually have a recessive M<sub>1</sub> crossvein (with the intersection between veins M<sub>1</sub> and R<sub>4+5</sub> closer to the wing base than the most apical corner of the radial cell r<sub>4+5</sub>). Females of *Orthonevra* have abdominal segments 6–8 strongly sclerotised and telescoped (VOCKEROTH & THOMPSON 1987). Larvae

of those *Orthonevra* species whose natural history is known live in organically enriched mud and in wetlands among dead plant material, and larvae of all *Orthonevra* species are probably aquatic or semi-aquatic (MAIBACH et al. 1994).

Worldwide 47 species of the genus *Orthonevra* are found in all biogeographical realms except for Australia (EVENHUIS & PAPE 2022). In Europe, according to the current state of knowledge, 17 species are present, including 16 species listed in the latest European summaries (VUJIĆ et al. 2022, REVERTÉ et al. 2023), plus the poorly known *O. fumipennis* (Loew, 1843) described from the Greek Kos island [= Stanchio] (LOEW 1843).



MAIBACH et al. (1994) split *Orthonevra* into two species groups: the *nobilis*-group, with completely black legs and swollen frons in the males, and the *elegans*-group, with bicoloured legs and males with nearly flat frons. Species of the black-legged *nobilis*-group are, particularly, morphologically very similar and difficult to determine with hitherto available keys. This difficulty was partly resolved by RICARTE et al. (2022) in their revision of the Iberian Brachyopini through the redescription of female lectotypes for *O. incisa* (Loew, 1843) and *O. plumbago* (Loew, 1840), the introduction of some new diagnostic characters and an updated identification key to the Iberian members (including two North-European species) of the *nobilis*-group.

The aim of this study is to make the next step in revising the European *Orthonevra*, by presenting morphological and genetic evidence and geographical distribution of two Palaearctic species so far recognized under the name *Orthonevra brevicornis* (Loew, 1843). In addition, we also aim to extend our knowledge of the genetic characterization among European *Orthonevra* species based on mitochondrial DNA sequences.

### Material and methods

**Morphology.** The material studied is deposited in the following institutes or private collections, referred to in the text using abbreviations:

Collection of Frank Van de Meutter, Tessenderlo, Belgium;

Department of Biology and Ecology, Faculty of Sciences,

	F
	University of Novi Sad, Serbia;
JMGB	Collection of Jonas Mortelmans, Ghent, Belgium;
JVAB	Collection of Jan Versigghel, Aalter, Belgium;
LMJC	Collection of Libor Mazánek, Jívová, Czech Republic;
LMMP	Collection of Łukasz Mielczarek, Miękinia, Poland;
MZLS	Musée zoologique de Lausanne, Lausanne, Switzerland;
MZPW	Museum and Institute of Zoology, Polish Academy of Sci-
	ences, Warsaw, Poland;
PTPP	Collection of Paweł Trzciński, Poznań, Poland;
RBINS	Royal Belgian Institute of Natural Sciences, Brussels, Bel-
	gium;
RMMU	Collection of Roger Morris, Mitcham, United Kingdom;
RMNH	Naturalis Biodiversity Center, Leiden, the Netherlands;
RZRP	Collection of Robert Żóralski, Reda, Poland;
SBHN	Collection of Sander Bot, Haren, the Netherlands;
SFKU	Collection of Steven Falk, Kenilworth, United Kingdom;
SIZK	Schmalhausen Institute of Zoology, National Academy of
	Sciences of Ukraine, Kyiv, Ukraine;
USMB	Upper Silesian Museum in Bytom, Poland;
WORB	Collection of Wout Opdekamp, Rochefort, Belgium;
WSBN	Collection of Wouter van Steenis, Breukelen, the Nether-
	lands;

### Other abbreviations:

XLSF

ZFMK

FM Frank Van de Meutter RZ Robert Żóralski

Morphological terminology follows Cumming & Wood (2017). As such we used the terms *postpedicel*, *phallus* and *postgonite* that are used in most other dipteran families instead of *basoflagellomere*, *aedeagus* and *superior lobe* (of hypandrium) that are often used for

Collection of Xavier Lair, Sournia, France;

Museum für Naturkunde, Berlin, Germany.

Museum Koenig, LIB, Bonn, Germany;

Syrphidae. A recently published glossary for adult Syrphidae (VAN STEENIS et al. 2023) promotes the same terminology changes. For size proportions of the postpedicel, terminology "length, width" (not "length, height") was used for consistency with other publications on Diptera, including those recently published for *Orthonevra*. The term *surstylus* is used to refer to the apical clasping lobes of the epandrium and is equivalent to the term *gonostylus* as used in the gonostylar hypothesis of the origin of male terminalia in Eremoneura (ZATWARNICKI 1996).

The choice of an individual to designate the holotype was driven by the best possible condition (including excellent preparation of terminalia) among all the individuals optimally representing the new species, as needed to best express and visualise the diagnostic features distinguishing it from other taxa. The selection of an individual for neotype designation for O. brevicornis was driven by the same reason, but only among specimens caught at the locus typicus. For the type and other important specimens, we provide the original labels verbatim within double quotation marks ("") and we use a double slash (//) to indicate separate lines within a label. The term *allotype* used on the label of one of the female specimens of O. atlantica is an opinionated indication of which female among all the paratypes optimally represents the opposite sex to the holotype and is recommended for future direct comparisons of females. It has no name-bearing function, as stated in Recommendation 72A of the ICZN (1999). For the same practical purpose, we have indicated which female specimen is our opinionated optimal voucher of O. brevicornis, calling it "voucher specimen" on the label, in accordance with the suggestion of SAN-TIAGO-BLAY et al. (2008) and Recommendation 72F of the ICZN. Where an individual of *O. atlantica* sp. nov. was previously published as O. brevicornis, we cite the publication in the material section along with the note "as O. brevicornis".

A Leica M205A stereomicroscope with a Leica DCF 495 camera were used to take pictures of representative specimens for further drawing, and with a Sony NEX-3N photo camera to take layered pictures of the male terminalia. Drawings were made by hand using the drawing pad connected to the computer with Gimp 2.10.14, based on photographs. As for the male terminalia drawings, only strong setae were drawn, but not hairs. Colour characters are described from dry pinned specimens. For descriptions, measurement on one or more ("n") of the studied specimens were taken as follows using micrometer in an eyepiece grid: body length from the antennal sockets to the tip of abdomen, postpedicel length between the tips of postpedicel and pedicel, postpedicel width at its maximum, upper face width was measured just below the antennal sockets, lower face width just above the tip of mouth edge.

During the construction of the map, when both species occurred at the same localities, their positions were slightly shifted latitudinally to make dots visible.

**DNA barcoding.** One or two legs of selected specimens were used for DNA extraction. Extractions were carried out using the DNeasy Blood and Tissue Kit (Qiagen Inc., Santa Clara, CA, USA) following the manufacturer's protocol at ZFMK (Germany), and CHELEX method at the University of Lodz (UniLodz) (Poland) (Casquet et al. 2012). Entire specimens or remnants of specimens from which legs were dissected were preserved and labelled as DNA voucher specimens for the purpose of morphological studies and deposited in the authors' or above-mentioned collections. For the specimens processed at ZFMK, the COI barcode region was amplified using the forward primer LCO1-1490 (5'-GCTCAACAAATCATAAAGATATTGG-3'; FOLMER et al. 1994) and the reverse primer COI-Dipt-2183R (5'-CCAAAAAATCARAATARRTGYTG-3'; GIBSON et al. 2011), also known as COI-780R. PCR amplification protocols were the same as described in Rozo-Lopez & MENGUAL (2015). For the specimens processed at the University of Lodz, the COI barcode region was amplified using the forward primer LCO JJ (5'-CHACWAAYCA-TAAAGATATYGG-3'; ASTRIN & STÜBEN 2008) and the reverse primer HCO JJ (5'-AWACTTCVGGRTGVCCA-AARAATCA-3'; ASTRIN & STÜBEN 2008).

Following the amplification, 1.5% agarose gels were used to visualise the PCR product. PCR products were cleaned using the commercially available QIAquick PCR Purification Kit (Qiagen) at ZMFK and Exonuclease/BAP Fast AP at UniLodz. Sequencing reactions were carried out by Macrogen Inc.: bidirectional sequencing reactions were carried out for ZFMK specimens and one direction (forward) for individuals processed at UniLodz. Chromatograms were edited in Geneious Prime ver. 2022.1.1 (Biomatters Ltd). All new sequences were submitted to GenBank via BOLD (www.boldsystems.org). GenBank accession numbers are listed for each sequenced specimen in Fig. 10. All sequences used in the present study are also publicly available in the BOLD dataset DS-ORTNEV (dx.doi.org/10.5883/DS-ORTNEV), except for the entire mitochondrial genome of O. geniculata (Meigen, 1830) that can be accessed in GenBank (GenBank accession number MT410796).

Bidirectional sequencing reported sequences of 658 bp, while unidirectional sequencing resulted in shorter final sequences of 573 bp in length. Thus, we trimmed our sequences to obtain an alignment of 573 bp to analyse them further. A distance-based Neighbour-Joining (NJ) analysis was done using the Jukes-Cantor Model as implemented in Geneious Prime. In addition to our new sequences, we downloaded all the available public sequences of European Orthonevra from BOLD (accessed on 17 Aug 2023) and we included only the BOLD sequences with more than 500 nucleotides in our NJ analysis. The DNA barcode of Chrysogaster solstitialis (Fallén, 1817) (GenBank Accession number MN622074) was constrained as the root for the NJ tree to facilitate the visualisation. Bootstrap support values (BS) were estimated from 1000 replicates directly from Geneious Prime. The NJ tree (Fig. 10) was drawn with the aid of FigTree ver. 1.3.1 (RAMBAUT 2018) and Adobe Illustrator 27.7.

### **Results**

### **Taxonomy**

Family Syrphidae Latreille, 1802 Genus *Orthonevra* Macquart, 1829

Orthonevra atlantica Żóralski & Van de Meutter, sp. nov. (Figs 1A–B, 2A–B, 3A, 4A, 5A–C, 7A–E)

**Type material.** HOLOTYPE: ∂ (Figs 1A, 2B, 4A, 5A, 5B, 5C, 7A), labelled "20159 // Polska CF16 // Kartoszyno // on Crataegus spp. // 3 VI 2021 // R. Żóralski leg." and with our red holotype label "HOLOTYPE & // Orthonevra atlantica // Żóralski & Van de Meutter, 2024". Deposited in ZMHB. Paratypes: 61 ♂♂ 14 ♀♀, all bearing our yellow paratype label: BELGIUM: Liège, univ. Sart Tilman, 1979, 1 👌, leg. A. Pauly (RBINS); Oud-Heverlee, 28.iv.1999, 1 & (Fig. 7E), leg. FM (FMTB); Engsbergen, Achterheide, 22.v.2011, 1 3, leg. FM (FMTB); Assent, Papenbroek, 5.–19.iv.2012, 1 3, Malaise trap, leg. FM (FMTB); Torgny, reservaat, 10.iv.2015, 1 &, leg. FM (FMTB); Halma, Route Napoleon B, 8.iv.2017, 1  $\circlearrowleft$ , leg. FM (FMTB); Froidfontaine, Tanton, 6.v.2017, 1  $\circlearrowleft$ , leg. FM (FMTB); Teuven, Bos, 2.v.2018, 1  $\circlearrowleft$ , leg. FM (FMTB); Bertrix, Rue de Muno, 22.iv.2019, 1 $\circlearrowleft$ , leg. FM (FMTB); Buzenol, Montauban, 29.v.2020, 2 33 (GenBank acc. no. OR859731), leg. FM (FMTB); Ovifat, Reinhardstein, 9.v.2021, 1 3 (GenBank acc. no. OR859711), leg. FM (FMTB); Bertrix, Rue de Muno, 16.iv.2022, 1 & (GenBank acc. no. OR859697), leg. FM (RBINS). CZECH REPUBLIC: Jívová, u Dómského lesa, 540 m, on flowering Crataegus sp., 27.v.2017, 5 33, leg. L. Mazánek (3 👌 🖒 LMJC, 2 👌 🖒 RZRP), 28.v.2017, 1 🖒, leg. L. Mazánek (LMJC). **GERMANY:** Prov. Brandenbg., [no date], 1  $\circlearrowleft$  (ZMHB, ex. coll. Mehr); Niedersachsen, Harz-Südrand Hirseteich, 1 km NW Walkenried, 19.v.2002, 2 33, leg. Stuke (ZFMK); Niedersachsen, Harz, Oberaue Zwischen Breitenbach und Unterzorge, 31.v.2003, 1 &, leg. Stuke (ZFMK); Schleswig-Holstein, Kreis Ostholstein, Glinde südlich Schonwalde am Bungsberg, 54.1773N 10.7536E, 27.v.2016, Malaise trap, 1 ♀ (GenBank acc. no. OR859649), leg. GBOL-team, ZFMK-TIS-2608557 (ZFMK); Schleswig-Holstein, Kreis Ostholstein, Erlenbruch am Masselberg bei Schwienkuhl, 54.2342N 10.9154E, 3.vi.2016, Malaise trap, 1  $\c \bigcirc$ (GenBank acc. no. OR859696), leg. GBOL-team, ZFMK-TIS-2608415 (ZFMK). **NETHERLANDS:** GE − Beek, Smorenhoek, 1.v.2009, 1  $\Diamond$ , leg. W. van Steenis (WSBN); ZH – Nieuwkoopse Plassen, kano aanlegplaats, 14.v.2017, 1 ♂, leg. W. van Steenis (WSBN). **POLAND:** ♀ (Figs 1B, 7B) labelled "22154 // Polska CF16 // Kartoszyno // on Crataegus spp. // 4 VI 2022 // R. Żóralski leg." and with our yellow paratype label "PARATYPE (ALLOTYPE) ♀ // Orthonevra atlantica // Żóralski & Van de Meutter, 2024"; caught in copula with a male paratype, on the same Crataegus sp. as the holotype, but in the following year; it is on the same pin as the male paratype and deposited in ZMHB; Niemcza [= Nimpsch Schles. Duda; O. plumbago Lw.], 6.v.1908, 1 3 (ZMHB, ex coll. O. Duda); Puszczykowskie Góry, XT29, 8.v.2008, 1 ♂ 1 ♀, in copula, leg. P. Trzciński (PTPP); Trzcielińskie Bagno, XT19, 1.–10.v.2008, 2 33, Moericke trap, leg. P. Trzciński (RZRP); Trzcielińskie Bagno, 24.iv.2010, 3 ♂♂, leg. P. Trzciński (PTPP); Jarosławiec, XT29, 19.v.2011, 1 ♂, leg. P. Trzciński (PTPP); Kartoszyno, CF16 (all leg. RZ), 30.v.2021, on Apiaceae near the stream, 1  $\circlearrowleft$  (Figs 2A, 3A) (MZPW), 3.vi.2021, 2  $\circlearrowleft$   $\circlearrowleft$ on Crataegus sp. (RZRP), 3.vi.2021, 1 ♂ on Crataegus sp. (ZFMK), 5.vi.2021, 3  $\stackrel{\wedge}{\circ}$   $\stackrel{\wedge}{\circ}$  1  $\stackrel{\hookrightarrow}{\circ}$  on *Crataegus* sp. (RZRP), 22.v.2022, 2  $\stackrel{\hookrightarrow}{\circ}$  (Gen-Bank acc. no. OR859735, OR859692), in riparian forest near the stream (RZRP), 27.v.2022, 2 ♂♂ (GenBank acc. no. OR859707, OR859656) on Crataegus sp. (RZRP), 4.vi.2022, 1 d caught "in copula" with allotype and deposited in ZMHB, 4.vi.2022, 2 ♂♂ 2 ♀♀ on Crataegus sp., leg. RZ (RZRP), 1  $\circlearrowleft$  1  $\circlearrowleft$  on *Crataegus* sp. (ZFMK), 28.v.2023, 4  $\circlearrowleft$   $\circlearrowleft$  (GenBank acc. no. OR859675, OR859668, OR859677), 1 ♀ (GenBank acc. no. OR859730) on Crataegus sp. (RZRP), 29.v.2023, 3  $\mbox{2}\mbox{3}$  (GenBank acc. no. OR859712) on Crataegus sp. (RZRP), 3.vi.2023, 2 ♀♀ (GenBank acc. no. OR859695, OR859679) in riparian forest (RZRP); Stawiska ad. Miękinia, CA95, 10.iv.–5.v.2022, 2 & A, Malaise trap, leg. Ł. Mielczarek (LMMP); Słowiński National Park, O.O. Smołdzino, distr. 129 (old railway embankment), 16.v.2022, 1  $\circlearrowleft$ , on *Pyrus* sp., leg. RZ (RZRP); Żegocin, marshy alder forest, XT96, 30.iv.2023, 1  $\circlearrowleft$ , leg. P. Żurawlew (RZRP).

SERBIA: Tara, Manastir Rača, 43.9166667N 19.535E, 28.iv.2012, 1  $\circlearrowleft$ , leg. Vujić A., Radenković S., Likov L. (FSUNS). SPAIN: Cortes de la Frontera, 15.iv.2023, 1  $\circlearrowleft$ , leg. FM (FMTB); Capileira, 17.iv.2023, 1  $\circlearrowleft$ , leg. FM (FMTB); Lugros, rio Alhama, 19.iv.2023, 1  $\circlearrowleft$  (GenBank acc. no. PP214180) (Fig. 7D), leg. FM (FMTB); Sierra Nevada, vic. of Monachil, 1650 m a.s.l., near forest stream in *Pinus-Quercus* mountain belt, 37.13N 3.44W, 1  $\circlearrowleft$ , 24.iv.2023, leg. Popov G. (SIZK).

Additional material studied. 70 ♂♂ 24 ♀♀. BELGIUM: Bonheiden, Dorstveld, 8.v.1999, 1 ♀, leg. FM (FMTB); Diepenbeek, De Maten 8, 29.v.2002, 1  $\stackrel{\frown}{\circ}$ , leg. FM (FMTB); Tessenderlo, Engsbergen, Achterheide, 1.v.2011, 1 ♀, leg. FM (FMTB); Assent, Papenbroek, 5.–19.iv.2012, 1 ♂, Malaise trap, leg. FM (FMTB); Holsbeek, Dunbergbroek, 2.v.-2.vi.2012, 2 ♀♀, Malaise trap, leg. FM (FMTB); Torgny, Réserve Naturelle Raymond Mayné, 10.iv.2015, 1 ♀, leg. FM (FMTB); Ovifat, Reinhardstein, 5.vi.2015, 1  $\c \bigcirc$  , leg. FM (FMTB); Oudenaarde, Bos t'Ename, 6.v.2015, 2 ♀♀, leg. FM (FMTB); Meeuwen-Gruitrode, Itterbeek Eetsevelderbeek, 4.v.2016, 1 ♀, leg. FM (FMTB); Lavacherie, Rue St. Ode, 30.iv.2017, 1 ♀, leg. FM (FMTB); Awenne, Rue de Souvenir, 10.v.2017, 1 ♀, leg. FM (FMTB); Champlon, Barrière de Champlon, 25.v.2017, 1 3, leg. FM (FMTB); Léglise, 24.iv.2021, 1 ♀, leg. FM (FMTB); Rossignol, Rue de Hageai, 24.iv.2021, 1 & (GenBank acc. no. OR859705), leg. FM (FMTB). CZECH REPUBLIC: Bílý Potok, nature reserve Nad koupalištěm, 430 m, wetland, 22.v.2003, 1  $\circlearrowleft$ , leg. J. Preisler (LMJC) (Mazánek et al. 2009, as O. brevicornis); Mníšek u Liberce env., 400 m, meadow, 24.v.2003, 3 & d, leg. J. Preisler (LMJC) (MAZÁNEK et al. 2009, as O. brevicornis); Jizerské hory Mts, Nature reserve Meandry Smědé, pond Dubák env., wetland, alder, Malaise trap, 19.v.–31.v.2005, 3 ♂♂ 3 ♀♀, leg. J. Preisler & P. Vonička (LMJC) (Mazánek et al. 2009, as O. brevicornis); Jívová, u Dómského lesa, 540 m, on flowering Crataegus sp., 27.v.2017, 4 ♀♀, leg. L. Mazánek (2  $\mathcal{Q}$  LMJC, 2  $\mathcal{Q}$  RZRP), 28.v.2017, 3  $\mathcal{Q}$ , leg. L. Mazánek (LMJC). Sedm Dvorů, Bystřice valley, 510 m, sweeping on flowering Salix sp., 10.v.2021, 1 3, leg. L. Mazánek (LMJC); Krkonošský NP, Vítkovice, 650 m, on flowering Crataegus sp., 8.vi.2022, 1 3, leg. L. Mazánek (LMJC). **DENMARK:** Langaa, Dania: EJN, 2.vi.1987, 1 3, leg. J.A.W. Lucas (RMNH). FRANCE: Savigny, la Prairie, 23.iv.2010, 1 3, leg. X. Lair (XLSF); Ducey-les-Chéris, Bois d'Ardennes, 15.v.2008, 1 ♂, leg. X. Lair (XLSF). **GERMANY:** Langballigau, Schleswig-Holstein/ Nordangeln, 6.v.1972, 1 &, leg. C. Claussen (ZFMK); Langballigau, 8.vi.1976, 1 &, 10.vi.1976, 3 & d, leg. C. Claussen (ZFMK); 25 km S Oldenburg, Ahlornerteiche, 10.v.1980, 1 3, W. Barkemeyer (ZFMK); Langballigautal, Schleswig-Holstein/E of Flensburg, 14.v.1983, 1 3, leg. J.A.W. Lucas (ZFMK); Flensburg, Schleswig-Holstein, Roikier See, 21.vi.1987, 1 3, 22.vi.1987, 2 33, leg. J.A.W. Lucas (ZFMK); LK Uelzen, Großes Bruch bei Altenebstorf, 22.v.1991, 3 ♂♂, 17.vi.1991, 1 Å, 6.v.1995, 2 ÅÅ, 25.v.1997, 3 ÅÅ, 7.v.1998, 2 ÅÅ, leg. D. Wolff (ZFMK); LK Uelzen, Galgenberg bei Grünhagen, Nordhang Quelliger Laubmischwald, 29.v.1991, 1 &, v.1997, 1 &, leg. D. Wolff (ZFMK); LK Uelzen, Niehof bei Veersen Erlen-Eschenwald, 18.v.1992, 4 33, leg. D. Wolff (ZFMK); Insmühlen Umgebung, Lüneburger Heide, 7.v.1994, 2 ನೆನ, 10.v.1994, 4 ನೆನ, leg. J.-H. Stuke (ZFMK); LK Uelzen, im Sieken bei Westerweyhe quelliger Erlenwald, 12.v.1994, 1 3, leg. D. Wolff (ZFMK); Darmstadt, Messel Buchenwald, 2.v.1995, 1 3, leg. M. Hauser (ZFMK); LK Uelzen, Eitzener Bruch bei Eitzen, 9.v.1998, 1 ♂, leg. D. Wolff (ZFMK); LK Stade, Surbrook b. Fredenbeck, 14.v.1998, 3 3 3, leg. D. Wolff (ZFMK); Zorge, Neue Teich near Zorge, Harz, Niedersachsen, 18.v.2002, 1 ♂, leg. W. van Steenis (WSBN); Harz-Südrand, Hirseteich, 1 km NW Walkenried, 19.v.2002, 5 33, leg. J.-H. Stuke (ZFMK); Harz-Südrand, Oberaue zwischen Breitenbach und Unterzorge, 31.v.2003, 1 ∂, leg. J.-H. Stuke (ZFMK); Markhausen, Niedersachsen, Emsland, Markatal SW Markhausen, 1.v.2005, 1 3, leg. J.-H. Stuke (ZFMK). **POLAND:** Żegocin, marshy alder forest, XT96, 7.v.2023, 1 ♀, leg. P. Żurawlew (RZRP). SWITZERLAND: Chevroux, 8.–15.v.2020 (Malaise trap), 1 Å, leg. Association de la Grande Cariçaie, Nina Perret-Gentil (MZLS). UNITED KINGDOM: Sutton, Sutton Park, 18.v.1997, 1 3, leg. S. Falk (SFKU); Lewes, Mount Caburn, 17.iv.2005, 1 ♂, leg. S. Falk (SFKU); Birdford-on-Avon, Marsh Farm, 14.vi.2014, 1 ♂, leg. S. Falk (SFKU); Hampshire, Ashford Hangers, 30.v.1987, 1  $\circlearrowleft$ , leg. R. B. Hastings (RMMU); West Norfolk, East Walton Common SSSI, 18.v.2007, 1 3, 19.v.2007, 1 3, leg. R. Morris (RMMU); East Suffolk, Walberswick, 2.v.1990, 1 &, leg. R. Morris (RMMU).

**Diagnosis.** A black *Orthonevra* (Figs 1A–B) with metallic reflections, completely black legs, shiny sternite I and suboval postpedicel (1.1-1.25 times as long as wide, sometimes slightly angular at tip regardless of sex) and largely black with orange-brown basoventral area. Males of O. atlantica sp. nov. are best distinguished from other Orthonevra by morphological characters of the terminalia. The characteristic shape of the surstylus, wide in the basal half of its length, then abruptly narrowing into a curved tip (Fig. 5A), is a diagnostic character shared only with two other west Palaearctic species: O. brevicornis and the North-African endemic of the high Atlas O. bouazzai Kassebeer, 1999. Males of O. atlantica sp. nov. are easily distinguishable from these two species by further characters of the terminalia: O. brevicornis has several significant differences in the shape of the phallus, the postgonites and the posteroventral process of the surstylus (for details see species descriptions and compare Figs 4A and 5A-C with Figs 4B and 5D–F). *Orthonevra bouazzai* differs from *O*. atlantica sp. nov. in the shape of the postgonites with a slender anterodorsal tip and three denticles on its posterodorsal margin (Figs 10-11 in KASSEBEER 1999). Males of O. atlantica sp. nov. are also distinguishable by non--genital characters: from O. brevicornis mainly by having black hairs on the scutum and on the vertex (yellow in O. brevicornis) and from O. bouazzai (both sexes) by having a shorter and partly orange-brown postpedicel (elongated and black in O. bouazzai). Females of O. atlantica sp. nov. have an unmodified tergite V without a keel or incision, a shiny sternite I and a partly orange short postpedicel — a set of characters that differentiates them from the females of all other European Orthonevra species except for the females of *O. brevicornis*. Characters to distinguish females of O. atlantica sp. nov. and O. brevicornis are subtle and influenced by individual variability. The colour of the postpedicel of O. atlantica sp. nov. is black with a restricted orange-brown area basoventrally, whereas the orange-brown area extends more to the tip in O. brevicornis with the dark areas often being brown instead of black. A subtle but generally good indicative feature is found in the wing venation: if we draw an imaginary line between the vein junctions  $M_1/M_2$  and  $C/R_{2+3}$ , the junction  $M_1/R_{4+5}$ is located usually at the wing base side of this line in O. atlantica sp. nov. (Figs 7A, 7B), whilst in O. brevicornis it is usually situated on the line or at the wing tip side (Figs 7F, 7G). It is worth noting that similar characteristic was proposed to distinguish between O. arcana Ricarte & Nedeljković, 2022 and *O. incisa* by RICARTE et al. (2022). In addition, O. atlantica sp. nov. is on average sturdier than O. brevicornis and has a slightly wider face (but face width is rather variable), the body hue is (especially in fresh specimens) pitch black to dark olive green in O. atlantica sp. nov., whereas the colour of O. brevicornis is more dark grey to grey-blue. The colour of the wing venation is on average darker in O. atlantica sp. nov. All the above indicative characters of females also apply to males. Females of one species belonging to another genus, Lejogaster metallina (Fabricius, 1777), have been found originally partially misidentified as O. brevicornis in one of

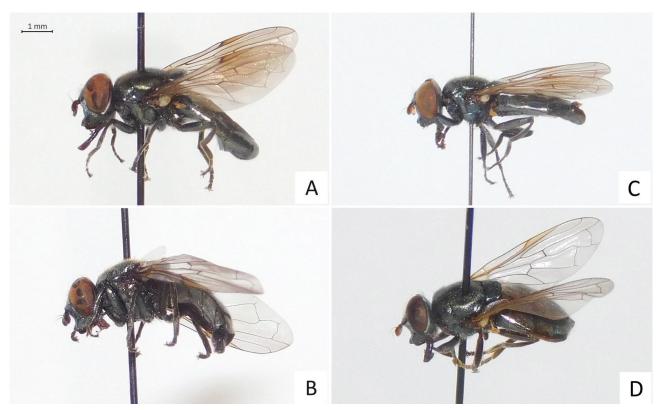


Fig. 1. Overall appearance, lateral view. A – *Orthonevra atlantica* sp. nov., male, holotype; B – *O. atlantica* sp. nov., female, paratype; C – *O. brevicornis* (Loew, 1843), male, neotype; D – *O. brevicornis*, female.

the very old collections (ŻÓRALSKI 2023), so they can also be confused with females of O. atlantica sp. nov. Despite similar overall appearance, the wing vein  $M_1$  in the females of L. metallina is, however, processive (non-recessive) and their mouthparts are strongly protruding.

**Description.** *Male.* Body length 5.6-7.0 mm (n = 34; average = 6.3 mm; median = 6.5 mm; holotype = 6.5 mm), black with metallic reflections (Fig. 1A).

Head. Eyes bare. Antennae (Fig. 3A): scape black; pedicel black with a few white hairs ventrally that are as long as segment width and with a few shorter black hairs dorsally; postpedicel slightly longer than wide (length to width ratio  $1.1-1.25\times$ ), slightly angular at tip, bicoloured: overall black but with orange-brown area ventrally near its base. Sensory pit present on outer side. Arista black, twice as long as postpedicel. Face (Fig. 2A) broad (holotype: upper face width 0.95 mm; lower face width 1.25 mm), slightly wider than half width of head, shiny black, with diverging eye margins. Upper and lateral part of face with wrinkled texture, central part above mouth protrusion with smooth, bare surface. All facial hairs white to yellow, covering part of face, largely missing in central area. Central symmetrical trapezium-shaped area of white pilosity just below antennal sockets connected to triangular areas of white pilosity near eyes. Facial hairs shorter near mouth. Face below antennal sockets in profile (Fig. 2B) almost straight but varies between individuals from completely straight to slightly convex. Mouth edge in profile protruding far beyond antennal sockets, covered with yellowish to light brown hairs. Frons prominent, shiny, punctuated,

covered with yellowish hairs with some hairs in middle black. Vertex shiny, punctuated, with long black-brown hairs bent forward. Ocelli forming equilateral triangle. Occiput with band of white pilosity along eyes.

Thorax. Scutum black with metallic, densely punctuated cover. Covered with short erect hairs of equal length, with a few longer hairs. Majority of hairs on scutum black (best seen in posterior view), exceptionally (two specimens from Belgium) all white. Four darker, gold-brown shiny, longitudinal vittae appear where this cover has less dense or absent punctation. Scutellum metallic black, covered with yellowish hairs, with rim along posterior margin and with row of hairs at margin, some slightly bent towards midline, shorter than half length of scutellum. Anterior anepisternum shiny, without hairs, except for very short hairs on its posterior dorsal part. Posterior anepisternum shiny, covered with long hairs, except for its bare anteroventral part. Hair patches on upper and lower katepisternum widely separated.

Wings transparent but slightly darkened and completely covered with microtrichia. Venation black. Vein  $\rm M_1$  bent in middle, recessive through location of junction  $\rm M_1/R_{4+5}$  in wing topology towards wing base, as illustrated on Fig. 7A; varying between individuals as on Figs 7C–E. Pterostigma light brown with dark brown basal area. Halteres yellow-grey.

Legs. All legs shiny metallic black. Femora slightly swollen, two times maximum width of tibia. Tibia covered with short adpressed white hairs, fore and mid femora covered with upstanding longer whitish hairs on posterior

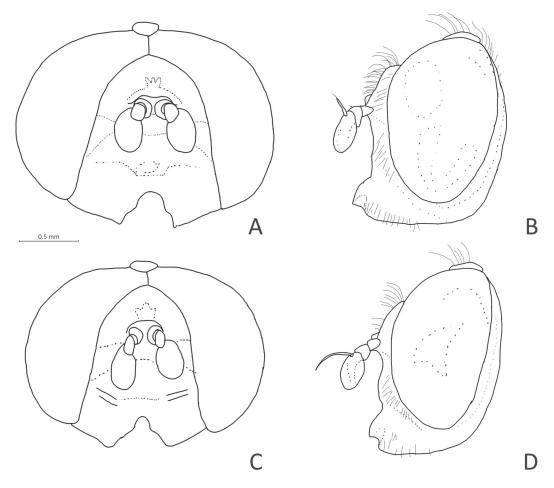


Fig. 2. Male, head, anterior and lateral view. A - Orthonevra atlantica sp. nov., paratype; B - O. atlantica sp. nov., holotype; C, D - O. brevicornis (Loew, 1843), neotype.

side, longest hairs on posteroventral side, some more than 3/4 of femora width. Hind femora with short hairs, less than half femur width. Ventral side of hind femora covered with short adpressed black bristles. Ventral side of all tarsomeres of middle legs covered with short adpressed black bristles. First tarsomeres of middle legs with four longitudinal rows of these bristles, inner rows located close to each other. Middle tibiae with some black bristles at top. Claws orange at base, black at tip.

Abdomen oval, black. Dull and lightly pollinose in central areas, shiny olive-golden metallic on sides of all tergites. Dull area on tergite IV forms triangular (rarely slightly trapezoid), backwards directed vitta, covering around 50% of tergite. Shiny parts of tergites covered with white adpressed hair, directed towards sides of tergites. Dull central area covered with shorter and much sparser hairs. Sternites covered with white hairs: sternite I shiny with sparse hairs restricted to median part; sternite II with erect and long hairs; sternites III and IV with shorter and inclined hairs, pointing backwards or to centre of sternite.

Terminalia. Surstylus very wide in basal half with broadest section in middle part and with top abruptly narrowing into curved tip (Figs 5A–C). Posteroventral process of surstyli rudimentary (Fig. 5B). Phallus, in anterior view (Fig. 5C), shaped as broad cylindrical, concave cavity. In lateral view (Fig. 5A), with rather long, slender ante-

rodorsal hook-shaped appendix and small anteroventral appendix. Beneath these third delicate, long, recurving, bristle-like process of phallus, extending far outside genital capsule from beyond anteroventral edge of postgonites. Postgonites with quadrate tip posterodorsally, extending beyond tip of phallus. Each postgonite with small denticle on its anterior edge and with single strong seta beneath. Hook-shaped anteroventral extension of postgonite, found in *O. brevicornis*, is missing (Fig. 5B).

Female. Body length 5.9-7.0 mm (n = 12; average = 6.6 mm; median = 6.6 mm). Resembling male (Fig. 1B) except for the following: eyes dichoptic; frons with five (sometime six) deep and distinct lateral furrows, abdomen broader, face in lateral view more concave, hairs on scutum all white to light brown (no black hairs) and hairs on vertex pale (single black might appear). Tergite V with shallowly curved posterior margin and without keel or incision in middle. The same variability in wing topology and postpedicel length to width ratio as reported for males. Biology and behaviour. Males of this species have been observed sitting next to water-filled tracks in deciduous forest with wood and leaf debris and along the muddy margins of small forest streams. Most individuals from Poland (locus typicus) were caught on a solitary hawthorn shrub close to a spring-fed marshy area with alder carr and in direct vicinity of small streams with clean and cold water.

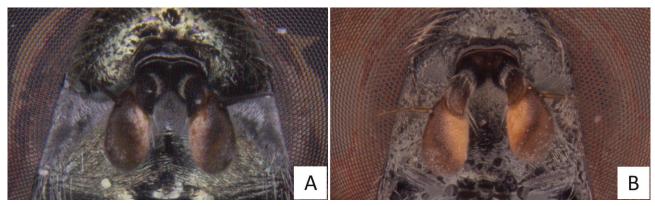


Fig. 3. Postpedicel coloration. A - Orthonevra atlantica sp. nov., male, paratype; B - O. brevicornis (Loew, 1843), male, neotype.



Fig. 4. Male terminalia, lateral view. A - Orthonevra atlantica sp. nov., holotype; B - O. brevicornis (Loew, 1843), neotype.

Elsewhere, this species is found mostly close to small and shaded rivulets in deciduous forest, or in deciduous forests with seepages. In Southern Europe it becomes increasingly montane (up to 1720 m a.s.l.), though less so in areas with high rainfall.

**Etymology.** From the Latin *atlanticus*, meaning "of or near the Atlantic Ocean", referring to the main compact biogeographical region of occurrence of this species in Europe, as opposed to the similar *O. brevicornis* that is nearly absent in these areas.

**Distribution.** Species with a mainly Atlantic distribution (Fig. 8) with its strongholds along the Central European Atlantic coast and in Great Britain, extending east to the Baltic coast and south-west parts of Poland, and south into the Iberian Peninsula. Scarcer and more isolated records appear out of the Atlantic zone. The range of *O. atlantica* sp. nov. is very similar to the range of two other Brachyopini species, i.e., *Melanogaster hirtella* (Loew, 1843) and *Chrysogaster virescens* Loew, 1854, also explicitly referred to or presented as "Atlantic" species (Speight 2017).

**Molecular data.** A total of 16 specimens of *O. atlantica* sp. nov. from Belgium, Poland and Spain were successfully sequenced for this study. Additionally, we downloaded

another sequence from BOLD and two more sequences from GBOL belonging to specimens previously identified as *O. brevicornis* coming from England and Germany, respectively. In our NJ tree we recover all sequences of *O. atlantica* sp. nov. and *O. brevicornis* together, forming a cluster with high support (BS = 100%). All sequences of our new species cluster together with high support (BS = 100%), except for one Belgian specimen (GenBank accession number OR859705) and a Spanish individual (PP214180) (Fig. 10). The COI sequences of *O. atlantica* sp. nov. show an uncorrected intraspecific pairwise distance between 0.0 and 0.014 (or a difference between 0.0 and 1.4%).

External and genital morphology of the Belgian male from Rossignol (GenBank acc. no. OR859705) was carefully studied several times and by different people (FM and XM), and we confirm that it belongs to *O. atlantica* sp. nov.. The terminalia are still attached to the male body (they were extended and rotated, but not detached), assuring that terminalia were not swapped with other individuals. We, thus, exclude the possibility of a morphological misidentification of this individual. During the molecular laboratory steps, in the 96-well plate where this specimen was included, all its neighbour wells contained either other genera or species, or

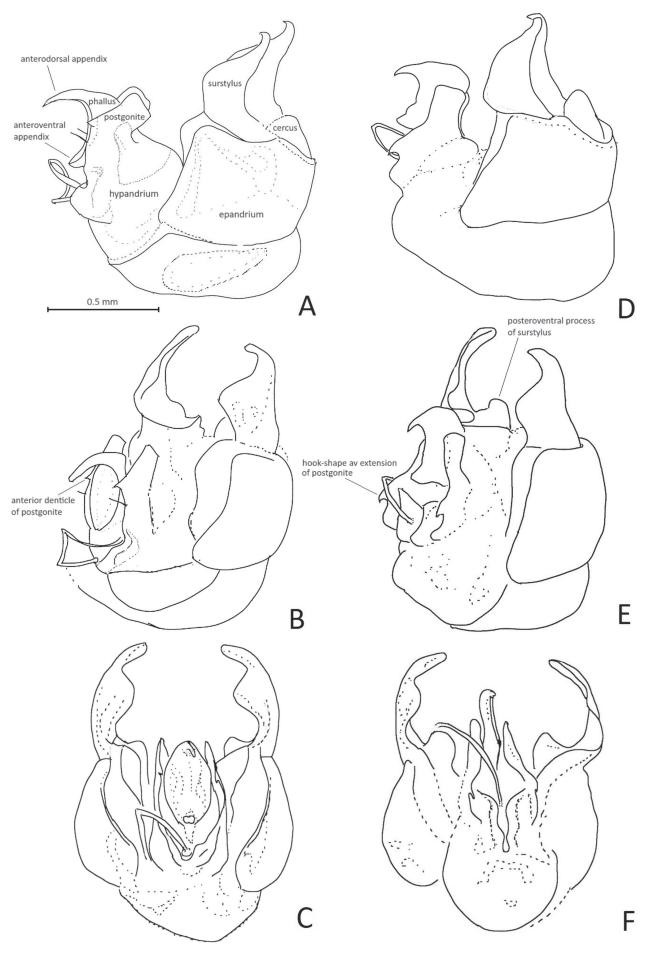


Fig. 5. Male terminalia. A, B, C – Orthonevra atlantica sp. nov., holotype, Poland, Kartoszyno; D, E, F – O. brevicornis (Loew, 1843), Poland, Jeleń.

individuals of O. atlantica sp. nov. This makes a material switch between a specimen of O. brevicornis into the well corresponding to the Belgian male very unlikely. We are confident that there was no error made in the laboratory. A second attempt to re-sequence this Belgian fly failed. The fact that this specimen shares the COI haplotype with another individual of O. brevicornis was not expected, as the differences in external morphology and genitalia are clear and stable, but it is not uncommon in Syrphidae that two different species share the same COI haplotype (see Discussion). Moreover, the placement of the Spanish specimen of O. atlantica sp. nov. from Lugros (GenBank acc. no. PP214180) in the NJ tree between the two clusters of O. atlantica sp. nov. and O. brevicornis (without high support value), whereas it agrees morphologically completely with the concept of O. atlantica sp. nov., and the low interspecific variability between these two species reinforces the results from our study, so we can conclude that both species cannot be unmistakably characterised using DNA barcodes.

### Orthonevra brevicornis (Loew, 1843)

(Figs 1C-D, 2C-D, 3B, 4B, 5D-F, 6A-C, 7F-J, 9B, 9C)

Chrysogaster brevicornis Loew, 1843: 269 (description of a male, drawings of the postpedicel, face profile and wing). Type locality: Poland, Posen [= Poznań].

Chrysogaster brevicornis: BECKER (1921): 14 (in part: Schlesien/Sobten (Poland) and Berlin (Germany) are O. brevicornis; but Gastein (Austria) are O. tristis and O. montana; Schlesien/Wölfelsfall (Poland) is O. montana; Schweiz (= Switzerland) are O. tristis); BAŃKOWSKA (1963): 147–148 (short description in the key, drawings of wing and postpedicel).

Orthoneura brevicornis (Loew, 1843): LOEW (1857): 7 (description of a female, in part: Meseritz [= Międzyrzecz], Poland); SACK (1930): 23 (in part, short description in the key); STACKELBERG (1970): 54–55 (short description in the key and drawing of male terminalia).

Type material. NEOTYPE: ♂ (Figs 1C, 2C–D, 3B, 4B, 6A, 7F), labelled: "Poland XT 19 // Wielkopolski Nat. Park // 52°18'25"N 16°40'14"E // "Trzcielińskie Bagno" // 10 / V / 2006 // P. Trzciński leg." and with our red neotype designation label "NEOTYPE ♂ // Chrystogaster brevicornis Loew, 1843 // design. R. Żóralski & F. Van de Meutter, 2024". Matches type locality and all characters of original description by LOEW (1843), deposited in ZMHB.

Additional material studied. Voucher specimens. GERMANY: Frankfurt am Main ["Frankf. a/M. // Coll. H. Loew // 12930 // Typus (red label) // Orthoneura brevicornis m // NOT A TYPE locality mism. R. Żóralski, 2023"], 1  $\circlearrowleft$  (Figs 7H, 9B, 9C) (ZMHB, ex coll. H. Loew). POLAND: 1 ♀ (Figs 1D, 7G), labelled "Poland XT 19 // Wielkopolski Nat. Park // 52°18'25"N 16°40'14"E // "Trzcielińskie Bagno" // 10 / V / 2006 // P. Trzciński leg." and "VOUCHER SPECIMEN  $\buildrel P$  // Orthoneura brevicornis (Loew, 1843) // det. R. Żóralski // & F. Van de Meutter, 2024", intentionally designated voucher specimen to unambiguously reflect characters of opposite sex of the neotype, matches all characters of original description of female (LOEW 1857), caught together with neotype, deposited in ZMHB; 2 & d, bearing our label "VOUCHER SPECIMEN ∂ // Orthonevra brevicornis (Loew, 1843) // det. R. Żóralski // & F. Van de Meutter, 2024": Jeleń, 4.v.1986, 1 & (Figs 5D, 5E, 5F, 6B, 7I), leg. B. Soszyński (USMB); Mrzezino, near Reda river [CF35], 29.iv.2019, 1 👌 (Fig. 6C) (GenBank acc. no. OR859720), leg. RZ (MZPW). GEORGIA: Dviri, 12.v.2022, 1 3 (Fig. 6J), leg. FM (RBINS).

Other specimens. 229  $\lozenge\lozenge$  96  $\lozenge$  9. CZECH REPUBLIC: Veltrusy-Obora, deciduous forest, 7.v.1985, 1  $\lozenge$ , leg. Barták (ZFMK). GERMANY: Berlin [= Berlin; Berlin 55949.], 15.v.1906, 1  $\lozenge$  (ZMHB, ex. coll. T. Becker); Berlin [= Berlin; Orth. brevicornis Lw.; det. Oldenberg; Berlin 55949.], 25.v.1906, 1  $\lozenge$  (ZMHB, ex. coll. T. Becker). Berlin, Schildhorn, vi.1948, 1  $\lozenge$  (ZMHB, ex. coll. A. Riedel). GREECE: Grevena, 505 m,

40.015N 21.395E, 8.v.2022, 1 ♂ (GenBank acc. no. OR859727), leg. FM (FMTB). HUNGARY: Hild, date unknown, 1 &, leg. Thalhammer (ZFMK). POLAND: Ślęża Mtn. [= Zobten 12310], 3.v, (ZMHB, ex coll. T. Becker). Niemcza [= Nimpsch Schles. Duda; O. plumbago Lw.], 14.v.1908, 1  $\Diamond$  1  $\Diamond$ , 17.v.1908, 1  $\Diamond$ , 23.v.1908, 3  $\Diamond$   $\Diamond$ , 26.v.1908, 1  $\Diamond$ , 13.vi.1910, 1 ♀, 14.v.1912, 1 ♂ 1 ♀, (ZMHB, ex coll. O. Duda); Jędrzejów, oddz. 210, 3.v.1954, 1 ♀, on Padus avium, leg. J. Karczewski (MZPW) (Trojano-WA-BAŃKOWSKA 1959, BAŃKOWSKA 1961, as O. frontalis); Zdziar-Łopatki ad. Staroźreby, alder carr near Płonka river, DD33, 17.v.1971, 1 ♂ 2 ♀♀, leg. J. K. Kowalczyk (RZRP); Aleksandrów Łódzki, 1.v.1973, 1 ♀, leg. B. Soszyński (RZRP); Rogów ad Łódź, 27.v.1975, 1 3, leg. B. Soszyński (RZRP); Świętokrzyski National Park: Święty Krzyż, 2.vi.1979, 1 ♀, leg. J. K. Kowalczyk (RZRP) (Żóralski et al. 2017); Teofilów, DC40, 1.v.1983, 1 ♀, leg. B. Soszyński (RZRP); Spalski Landscape Park: Konewka, DC41, 19.v.1985, 1  $\stackrel{\bigcirc}{\downarrow}$ , leg. B. Soszyński (RZRP), 13.v.2017, 1  $\stackrel{\bigcirc}{\downarrow}$ , leg. M. Soszyński (RZRP); Łagiewnicki Forest: Marianka, 4.v.1995, 1 📮 leg. B. Soszyński (RZRP); Biebrza National Park: Sztabin, 17.v.2003, 1 ∂, leg. Wanat M. (RZRP); Wiry, XT19, 15.v.2004, 1 ∂, leg. P. Trzciński (PTPP); Biebrza National Park: Grobla Honczarowska, 8.vi.2006, 1 ♀, Malaise trap, leg. J. Sawoniewicz (RZRP); Trzcielińskie Bagno [XT19], 1.–10.v.2008, 192 ♂♂ (GenBank acc. no. OR859703, OR859667, OR859676, OR859690, OR859714, OR859726, OR859728, OR859700, OR859693), 54  $\circlearrowleft$ , Moericke traps (part of it: 125  $\circlearrowleft$  and 13  $\circlearrowleft$  continued to be stored in alcohol), leg. P. Trzciński (PTPP, RZRP), 1.-10.v.2008, 2 ♂♂ 1 ♀, Moericke traps, leg. P. Trzciński (ZFMK), 1.–10.v.2008, 1 ♂ 1 ♀, Moericke traps, leg. P. Trzciński (SBHN), 14.v.2008, 1 ♂, leg. P. Trzciński (PTPP), 23.v.2008, 1 💍, leg. P. Trzciński (PTPP), 24.iv.2010, 5 ♂♂4♀♀, leg. P. Trzciński (PTPP); Oleśnickie Jodły, CC64, 24.iv.2009, 1 ♀, leg. B. Soszyński (RZRP); Kuzki ad Włoszczowa, 3.v.2012, 1 ♂, leg. Ł. Mielczarek (LMMP); Spalski Landscape Park: Spała, DC41, 24.iv.2015, 1 Å, leg. RZ (RZRP) (WITEK et al. 2015). Spalski Landscape Park: Ceteń, DC50, 4.iv.2014, 1  $\circlearrowleft$ , leg. M. Soszyński (RZRP), 22.iv.2014, 1  $\circlearrowleft$ , leg. Ł. Mielczarek (LMMP), 27. iv. 2015, 1  $\stackrel{\frown}{+}$ , leg. B. Soszyński (RZRP) (WITEK et al. 2015), 27.iv.2015, 1 Å, leg. RZ (RZRP) (WITEK et al. 2015), 27.iv.2015, 1 ♂ 1 ♀, leg. P. Trzciński (PTPP) (WITEK et al. 2015), 9.v.2015, 1 ♀, leg. M. Soszyński (RZRP), 25.v.2015, 1  $\circlearrowleft$ , leg. Ł. Mielczarek (LMMP); Suwalski Landscape Park: Sidorówka, 22.v.2015, 1 ♀, leg. Ł. Mielczarek (LMMP); Karniowce ad Trzebinia, 19.vi.2015, 1 &, leg. Ł. Mielczarek (LMMP); Krynica Morska, 7.v.2016, 1 &, leg. Ł. Mielczarek (LMMP); Nowa Wieś near Maniówka river, 24.v.2016, 1 ♀, leg. RZ (RZRP) (Żóralski et al. 2016); Wiatrołuża III, peatbog, 24.v.2016, 1  $\circlearrowleft$ , leg. Ł. Mielczarek (LMMP) (Żóralski et al. 2016); Gdańsk-Oliwa: Kwietna Street near the Oliva stream, 1.vi.2016, 1 ♀, leg. RZ (RZRP); Gibała near Drwęca river, 13.v.2017, 1 ♂, leg. RZ (RZRP); Zaskalskie-Bodnarówka, 24.vi.2017, 1 ♀, leg. Ł. Mielczarek (LMMP); Lisówki ad Stęszew, XT19, 22.v.2018, 1 ♂, leg. P. Trzciński (PTPP); Szumny Zdrój ad Górzno, DD19, 27.iv.2019, 1 🖒, leg. Ł. Mielczarek (LMMP); Gdynia-Leszczynki near Chylonka stream, 14.v.2019, 1 ♀, leg. RZ (RZRP); Włoszczowa "klekot", vi.2019, 2 ♀♀, Malaise trap, leg. Ł. Mielczarek (LMMP); Kartoszyno, CF16, 30.v.2021, 1 ♂ (GenBank acc. no. OR859651), on *Crataegus* sp., leg. RZ (RZRP), 24.vi.2023, 2 ♀♀ (GenBank acc. no. OR859686), leg. RZ (RZRP); Zakrzewska Osada, XV61, 20.vi.2022, 1 ♀, leg. & coll. D. Tarnawski. GEORGIA: Dviri, 10.v.2022, 1 3, leg. FM (FMTB); Dviri, 12.v.2023, 2 ∂∂ 1 ♀, leg. W. Opdekamp (WORB). **SWITZERLAND:** Chevroux, 8.–15.v.2020 (Malaise trap), 1 ♂, leg. Association de la Grande Cariçaie, Nina Perret-Gentil (MZLS).

**Diagnosis.** See notes on *O. brevicornis* within diagnosis of *O. atlantica*.

**Redescription.** *Male.* Body length 5.0-6.4 mm (n = 45; average = 5.9 mm; median = 5.9 mm; neotype = 5.9 mm), overall black to grey (Fig. 1C).

Head. Eyes bare. Antennae (Fig. 3B): scape black; pedicel dark-brown with a few white hairs ventrally that are as long as segment width and with a few shorter black hairs dorsally; postpedicel slightly longer than wide (length to width ratio 1.1–1.3×), not angular at tip, bicoloured: basoventral orange area extending over more than half of postpedicel and rest dark-brown. Sensory pit present on

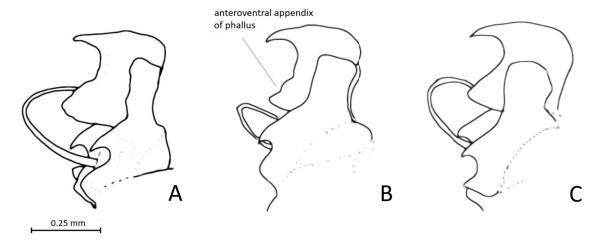


Fig. 6. Variation in the shape of the anteroventral flat appendix of phallus of *O. brevicornis* (Loew, 1843). A – Poland, Poznań vicinity, neotype; B – Poland, Jeleń; C – Poland, Mrzezino.

outer side. Arista brown, twice as long as postpedicel. Face (Fig. 2C) in most cases relatively narrow (neotype: upper face width 0.75 mm, lower face width 1 mm), less than half width of head, dull grey with diverging eye margins. Face with wrinkled texture, central part above mouth protrusion often with small, bare surface. Central symmetrical trapezoid area of dense white pilosity just below antennal sockets connected to triangular areas of white pilosity near eyes. All facial hairs white to yellow, covering part of face, largely missing in central area. Facial hairs shorter near mouth. In side view (Fig. 2D), facial profile slightly convex in middle, but varies between individuals between slightly convex to straight. Mouth edge protruding only slightly beyond antennal sockets. From not prominent, dull grey, punctuated, covered with white to yellowish hairs. Vertex dull grey, punctuated, with long yellowish hairs slightly bent forward. Ocelli forming almost equilateral triangle. Occiput with band of white pilosity along eyes.

Thorax. Scutum dull grey with metallic, densely punctuated cover. Covered with short erect hairs of equal length. All hairs on scutum white, exceptionally (two specimens from Georgia) with a few black hairs. Four darker longitudinal vittae where this cover is less dense or punctation is absent, best visible from anterodorsal side. Scutellum dull grey and slightly lighter than scutum, covered with white hairs, with rim on its posterior margin and with row of hairs along its hind rim, some slightly bent towards midline, shorter than half length of scutellum. Anterior anepisternum shiny, without hairs, except for very short pilosity on its posterior dorsal part. Posterior anepisternum shiny, covered with long hairs, except for its bare anteroventral part. Hair patches on upper and lower katepisternum widely separated.

Wings transparent and with microtrichia all over; rarely with brown cloud in centre. Venation between dark brown and black, but not pitch black. Vein  $M_1$  with its anterior end almost perpendicular to  $R_{4+5}$ , non-recessive because of location of junction  $M_1/R_{4+5}$  in wing topology as illustrated on Fig. 7F; much varying between individuals as on Figs

7H–J. In almost all cases, if line is drawn between vein junctions  $M_1/M_2$  and  $C/R_{2+3}$ , then junction  $M_1/R_{4+5}$  is located very close to it, usually a bit to wing tip (Figs 7F, 7G), but never much to wing base as it is the case in *O. atlantica* sp. nov. (Figs 7A, 7B). Rarely crossvein  $M_1$  more deeply curved (Fig. 7I) or even wavy, according to the observed rule that the narrower wing cell  $r_{4+5}$  is, the more bent vein  $M_1$  is. Very rarely specimens have extra drop swelling on vein  $M_1$  on one or two wings, or extra denticles on vein  $M_2$  on two wings. Pterostigma light brown with brown anterior margin. Halteres yellow-grey.

Legs. All legs black, usually with shade of grey. Femora slightly swollen, two times maximum tibia width. Tibia covered with short adpressed white hairs, fore and mid femora covered with upstanding longer whitish hairs on the posterior side, longest hairs on posteroventral side (some more than 3/4th of the width of the femora), hind femora with short hairs (less than half femur width). Ventral side of hind femora and ventral side of all tarsomeres of middle legs covered with short adpressed black bristles. First tarsomeres of middle legs with four longitudinal rows of these bristles, inner rows located close to each other. Claws orange at base, black on top.

Abdomen oval, grey. Dull and lightly pollinose in central areas, shiny grey metallic on sides of all tergites. Shiny parts of tergites covered with white erect or adpressed hairs, mostly directed towards posterior edge of tergites. Dull central area covered with shorter and much sparser hairs. Sternites covered with white hairs: sternite I shiny with sparse hairs, but lateral parts hairless; sternite II with erect and long hairs; sternites III and IV with shorter and inclined hairs, pointing backwards or to centre of sternite.

Terminalia. Phallus, in anterior view (Fig. 5F) laterally flattened. In lateral view (Figs 5D, 6A–C), with relatively short and broad anterodorsal hook-shaped appendix and prominent flat anteroventral appendix. Some individual variation in shape of flat anteroventral appendix of phallus was observed, as illustrated on Fig. 6. Delicate, long and bristle-like process of phallus present. Postgonites not

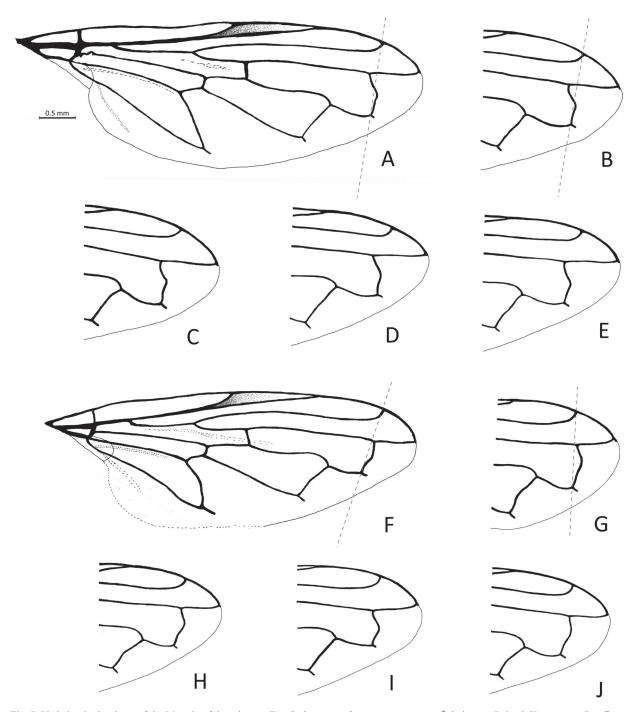


Fig. 7. Variation in the shape of the  $M_1$  vein of the wing.  $A-E-Orthonevra\ atlantica$  sp. nov.:  $A-\mathcal{J}$ , holotype, Poland, Kartoszyno;  $B-\mathcal{Q}$ , paratype (allotype), Poland, Kartoszyno;  $C-\mathcal{J}$ , paratype, Poland, Kartoszyno;  $D-\mathcal{J}$ , paratype, Spain;  $E-\mathcal{J}$ , paratype, Belgium.  $F-J-Orthonevra\ brevicornis$  (Loew, 1843):  $F-\mathcal{J}$ , neotype, Poland, Poznań vicinity;  $G-\mathcal{Q}$ , voucher specimen, Poland, Poznań vicinity;  $G-\mathcal{Q}$ , Germany, Frankfurt am Main;  $G-\mathcal{Q}$ , Poland, Jeleń;  $G-\mathcal{Q}$ , Georgia, Dviri.

extending beyond tip of phallus, with visible hook-shaped extension anteroventrally (Fig. 5E), and without small denticle on anterior edge found in *O. atlantica* sp. nov. Posteroventral process of surstyli present (Fig. 5E).

**Female.** Body length 5.2–6.8 mm (n = 23; average = 6.2 mm; median = 6.3 mm). Resembling male (Fig. 1D), except for the following: eyes dichoptic; frons with 5 lateral furrows, abdomen larger, face in lateral view more concave. Tergite V with shallowly curved posterior margin and without keel or incision in middle. The same variation in wing topology and postpedicel length/width ratio as

reported for males is observed in females.

Biology and behaviour. Adults have been found sitting on vegetation near marshland or feeding on flowers with a preference for shrubs and trees (maples *Acer* spp., willows *Salix* spp., rowans *Sorbus* spp.) but also on low flowers. The area where this species occurs in very large numbers near Poznań (*locus typicus*) is the "Trzcielińskie Bagno" [= Trzcielińskie Marsh], a protected area within the Wielkopolska National Park, where many species of Stratiomyidae were also found (Trzciński 2007), including *Actina chalybea* Meigen, 1804 in its north edge of

the range, and endangered *Stratiomys cenisia* Meigen, 1822, *Oxycera nigricornis* Olivier, 1822 and *O. trilineata* (Linnaeus, 1767). The swamp is a remnant of a former post-glacial lake fed by the waters of the small river Samica Stęszewska, surrounded by a thicket of willows and reeds, and the floodplain of the river has a variable water level, probably creating favourable conditions for the development of the larvae. Over 250 adults of both sexes of *O. brevicornis* were collected there using Moericke traps in hard-to-reach thickets of flowering willows in the first days of May 2008, and this species was dominant in Syrphidae material. Other findings, documented in the material section, are generally sporadic and associated with the immediate proximity of wetlands.

**Distribution.** Mainly distributed over Central and Eastern Europe (Fig. 8) and further east into Russia and Transcaucasia. Most records come from Poland (locus typicus) but the species is also confirmed from eastern Germany, Ukraine (Fig. 21 in Prokhorov et al. 2023 shows the typical male terminalia), Russia (Fig. 12 in STACKELBERG 1953 shows the typical male terminalia; present in European parts of Russia and western Siberia), the Czech Republic, Hungary, northern Greece, the Republic of Georgia and few, isolated locations in Western Europe: in the Netherlands and Switzerland. Unverified records of O. brevicornis sensu lato that would fit into the known distribution come from Romania (BRĂDESCU 1991), Turkey (Tóth 2013) and Austria (Heimburg et al. 2022). Reports of O. brevicornis from Iran (SHAKERYARI et al. 2012) and Morocco (Sahib et al. 2020) belong to different species, and the presence of O. brevicornis in these countries needs reassessment. Previous reports of the species from Japan were extensively commented on by ICHIGE (2006) as referring to another species; the slender surstyli and highly asymmetric postgonites in male, as well as the deep incision in the 5th sternite in female, as described and shown for O. brevicornis in Ohishi (2011), are clearly not conspecific with O. brevicornis, but close to O. incisa.

**Molecular data.** We were successful in sequencing 14 specimens of *O. brevicornis* from Poland, Georgia and Greece. In our NJ tree all DNA barcodes of *O. brevicornis* cluster with sequences of *O. atlantica* sp. nov. with high support (BS = 100%), but there is no support for grouping sequences of *O. brevicornis* alone (Fig. 10). The COI sequences of *O. brevicornis* have an uncorrected intraspecific pairwise distance between 0.0 and 0.0035 (or a difference between 0.0 and 0.35%).

**Notes on types.** Loew (1843) described the species *Chrysogaster brevicornis* based on two male specimens from Posen [= Poznań] in Poland (Loew 1843, Peck 1988). The original type locality was specified based on two independent statements in the Loew's publication:

"Professor Dr. H. Loew in <u>Posen.</u> (...) Ich besitze von dieser Art zwei ganz übereinstimmende <u>hier</u> gefangene Männchen [= I have two identical males of this species caught here.]" Further in the paper, after expanding on the species Chrysogaster nobilis Fall., Chrysogaster plumbago Loew and Chrysogaster brevicornis nov. sp., and before describing Chrysogaster frontalis nov. sp. and Chrysogaster plumbago

gaster fumipennis nov. sp., he wrote: "Zu den bereits beschriebenen drei schwarzbeinigen Arten der zweiten Abtheilung von Chrysogaster, die in der Umgegend Posens vorkommen, treten nur noch zwei, dem südlichen Europa und benachbarten Kleinasien angehörige Arten hinzu, (...) [= To the three black-legged species of the second chapter of Chrysogaster already described, that occur in the vicinity of Poznań, two other species are added now, occurring in southern Europe and neighbouring Asia Minor, (...)]"

Only one specimen of O. brevicornis of the collection of Hermann Loew was logged into the ZMHB register book of accessions (Fig. 9D) to the collection from 1858–1884 (under registration no. 12930). This specimen is still present (Figs 9B, 9C). Loew's first handwritten label under the specimen reads "Frank. a/M" [= Frankfurt am Main], a German city located 630 km west from the type locality. Loew's second handwritten label reads "Orthoneura brevicornis m.", with "m." meaning "mihi" or "mein", to explicitly indicate the species was described by himself, as in Loew (1857). Note that Loew uses "Orthoneura" instead of the original "Chrysogaster" as the genus name. The name Orthoneura (wrong spelling of Orthonevra Macquart) became widely accepted by authors only after the publications of WALKER (1851) and RONDANI (1857) and became finally also accepted by LOEW (1857) but was not used by Loew (1843) when describing Chrysogaster brevicornis. In conclusion, both the location and deduced timing of this specimen do not match with the type series. The specimen clearly comes from Loew's collection, but it is not one of the two original syntypes. Below the two above-mentioned labels is a red label with "Type" typed on it. Ziegler et al. (2020) clarify that specimens of the Loew collection only have two original handwritten labels and that all other labels were added later by museum workers. In this case, the specimen was clearly misinterpreted as a syntype and the type indication is false. Article 72.4 of the Code explicitly allows to take any evidence into account, published or unpublished, when determining which specimens belong to the type series. In this case the documented doubts, especially the mismatch in locality, do not allow designation of the mentioned specimen as the lectotype according to the Article 74.5 of the ICZN (1999). Type material of O. brevicornis was actively searched for by authors. Careful analysis of the collections of ZMHB (main collection and all supplementary drawers) and MZPW did not result in finding Loew's specimens that could be considered syntypes. Thus, the type series is considered lost or destroyed, and a neotype male specimen from a locality close to the original type locality (Poland, close vicinity of Posen) is hereby designated for the purpose of stabilisation of the taxonomic nomenclature and for stabilisation of the type locality of a nominal taxon. It must be noted, that the terminalia of Loew's specimen (from Frankfurt am Main, the one rejected to be a syntype) were extracted and examined by the first author in 2023 and is the same as the terminalia of the neotype being here designated. The shape of the terminalia is also consistent with the drawing of the terminalia of O. brevicornis published by Stackelberg (1953, 1970) and further reproduced by other authors: VAN

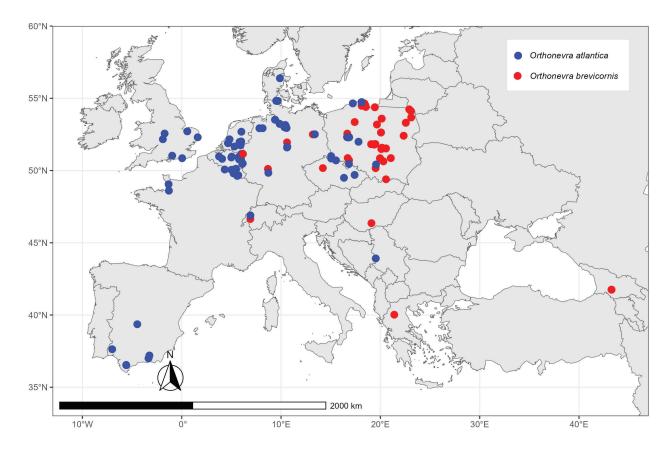


Fig. 8. Verified distribution of Orthonevra atlantica sp. nov. and O. brevicornis (Loew, 1843).

DER GOOT (1981), BRĂDESCU (1991), and ICHIGE (2006).

A female was described by Loew (1857) under the name *Orthoneura brevicornis* based on an unspecified number of specimens from Meseritz [= Międzyrzecz] (Poland) with Loew making a note that he also had specimens collected in Florence (Italy) in his collection. None of these female specimens were donated by H. Loew to the ZMHB, nor are present elsewhere to our knowledge. Female specimen(s) used for the description are considered lost or destroyed. A voucher female specimen caught together with the neotype and matching the original description will be deposited in a well-curated accessible collection (ZMHB) together with the neotype.

# Notes on other European *Orthonevra* species with black legs

Because of the omnipresence of misidentified black-legged *Orthonevra* in collections, our revision of collection material for this study resulted in new knowledge on the distribution of several other *Orthonevra* species.

*Orthonevra arcana* is present in Belgium, as published in a dedicated article (VAN DE MEUTTER et al. 2024).

Orthonevra frontalis (Loew, 1843) is removed from the list of species of Poland. The record in Trojanowa-Bańkowska (1959) and Bańkowska (1961) concerns O. brevicornis, confirmed by checking the specimen in the collection. Karl (1935) published O. frontalis records from north Poland which were depicted by Bańkowska

(1963, 1967) (drawings of head and abdomen based on the 3 female specimens from Karl's collection) under the name *O. plumbago*. These drawings clearly indicate *O. erythrogona* (Malm, 1863) specimens, confirmed by checking the collection. The record of *O. plumbago* from Bulgaria and drawing of its wing (BAŃKOWSKA 1967) concerns *O. frontalis* and was also confirmed by checking the collection.

Orthonevra gemmula Violovitsh, 1979 is confirmed to occur in Hungary. New records are reported from: Hortobágyi N.P., Puszta, 3./4. Juni 1980, 1 ♂, leg. H. Wendt (ZMHB). Distribution of that species was recently compiled in VAN STEENIS et al. (2021).

Orthonevra incisa is confirmed from its locus typicus (Poland, Posen vicinity). New records are reported from: Trzcielińskie Bagno [XT19], 1.−10.v.2008, 2 ♂ 1 ♀, Moericke trap, leg. et coll. P. Trzciński. The location with the highest abundance of this species in Poland is the swamp forests of the Biebrza National Park (Żóralski & Bystrowski in prep.). A very old female specimen of O. incisa, presumably from Germany, is present in the collection of ZMHB: "Berol. Gerst. [handwriting; = Berolinensis (Berlin), leg. A. Gerstaecker] // 6337 [printed] // "violaceus Meig. ?" [handwriting] // Orthonevra brevicornis LOEW det. D. Wolff, 1990 [handwriting]". Distribution of that species is available in VAN STEENIS et al. (2021).

Orthonevra montana Vujić, 1999, known so far from the Balkans (Vujić 1999, van Steenis et al. 2021), south Germany (DOCZKAL et al. 2002), the Czech Republic

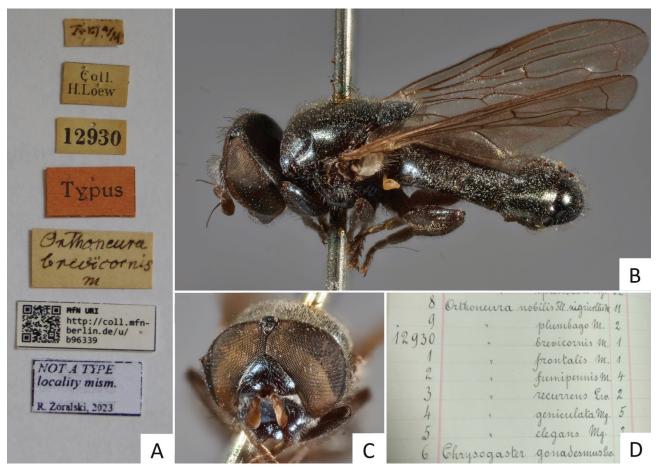


Fig. 9. Orthonevra brevicornis (Loew, 1843), voucher specimen, ♂, Germany, Frankfurt am Main. A – labels; B – lateral view; C – head; D – part of ZMHB register book of accessions to the collection 1858–1884.

and Slovakia (MAZÁNEK et al. 2009), is now confirmed as a new species to Poland and Austria. New records for Austria were reported from: Gastein, 1 ♂, 18.iv.(19)07, *O. brevicornis* det. Oldenberg, var. schwarz, Gastein 55944 (ZMHB, ex coll. T. Becker) (Becker 1921); for Poland from: "Wölfelsfall 20/6 13468." [= Międzygórze, Silesia], 1 ♀, vi.[19]20 (ZMHB, ex coll. Becker), Reinerz [= Duszniki-Zdrój], 1 ♂, vi.[19]28, *Orth. brevicornis* Lw., det. M.P. Riedel (ZMHB, ex coll. Riedel); and for Germany: Oberbayrn, TOL, Ob. Isar Tal zw. Wallgau u. Vorderiss, 830m, 16.vi.2002, 1 ♂, leg. B.J. Sinclair (as *O.* cf. *tristis*) (ZFMK).

Orthonevra plumbago. We have found out by checking the collections that the male specimen labelled "POLONIA DB35 // rez. Piskorzeniec // Distr. Piotrków Tr. // 23.04.1994 // B. Soszyński leg.", coll. LMMP, published as O. plumbago from Poland (250 km from locus typicus) in Soszyński (1995) and the male specimen published as O. plumbago from Mongolia in Bańkowska (1968), coll. MZPW, represent the same species. They have identical terminalia, consistent with the drawings and description (incl. postpedicel 1.3 length-width ratio) of O. varga Violovitsh, 1979 from Tuva in Russia, but whether the female lectotype of O. plumbago, as redescribed in RICARTE et al. (2022), is conspecific with these male specimens from Poland and Mongolia cannot be decided with certainty. Information in the key and rudimentary drawing of the male terminalia

of O. plumbago in STACKELBERG (1953, 1970) and also information in the key and drawings of O. plumbago in VIOLOVITSH (1979), refer to yet another Siberian species; having a length-width ratio for the postpedicel of 1.5–2.0, these cannot be conspecific with the female lectotype of O. plumbago. The mentioned record from Siberia in VIOLOVIT-SH (1979) cannot be verified (BARKALOV & MUTIN 2018). Records of O. plumbago in Becker (1921), as checked with the collection, concern O. subincisa Violovitsh, 1979 (1  $\circlearrowleft$  from Russia: "10 26 // Baikalen 54561 // Orthoneura plumbago Lw. // det. Becker", in coll. ZMHB) and O. tristis  $(1 \circlearrowleft \text{ and } 2 \circlearrowleft \circlearrowleft \text{ from France, Dauphiné, "Lautaret // 56938",}$ in coll. ZMHB), with the latter record, of "O. plumbago from France", being previously considered unverifiable (SPEIGHT & CASTELLA 2011). Information and male terminalia drawing of another specimen from France identified as O. plumbago in Speight & Castella (2011) is interpreted (VAN DE MEUTTER et al. 2024) to refer to O. arcana. The record of O. plumbago from Poland in Bańkowska (1995) concerns Lejogaster metallina.

### **DNA** barcoding

A total of 112 DNA barcodes representing 15 nominal *Orthonevra* species were analysed in the present study. We were able to newly sequence 61 *Orthonevra* specimens, to add 23 sequences from specimens of the projects German Barcode of Life (GBOL; https://gbol.bolgermany.de/en/

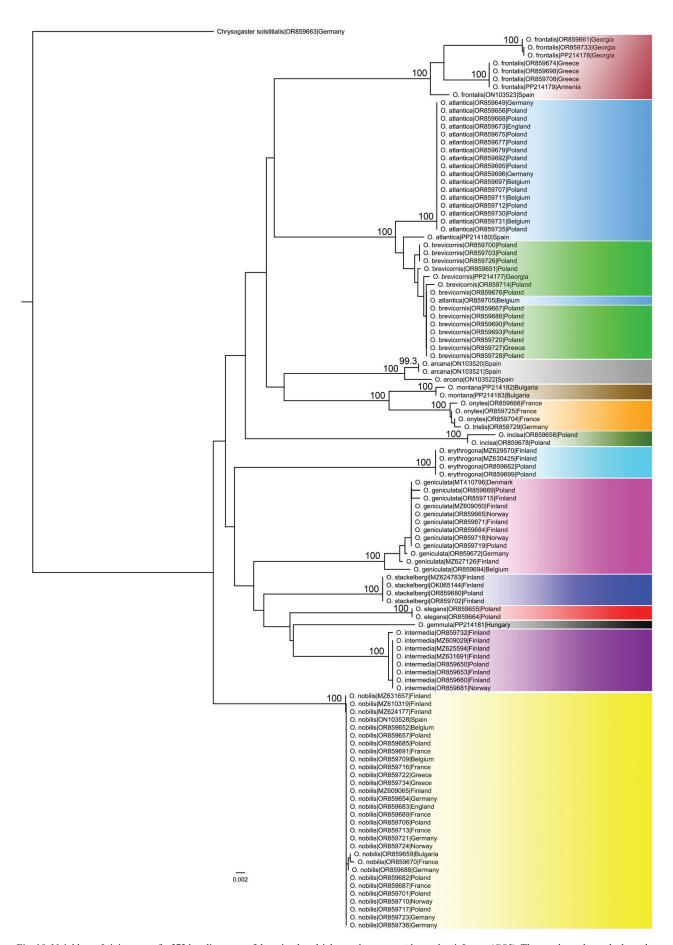


Fig. 10. Neighbour-Joining tree of a 573 bp alignment of the mitochondrial  $cytochrome\ c\ oxidase$  subunit I gene (COI). The numbers above the branches are bootstrap values >80% based on 1000 replicates. For each sequence and separated by a |, the name of the species, the GenBank accession number and the country of origin of the specimen are given.

german-barcode-of-life-2/) and Caucasus Barcode of Life (CaBOL; https://ggbc.eu/), and to download 28 sequences from BOLD (https://www.boldsystems.org/) and GenBank (https://www.ncbi.nlm.nih.gov/genbank/), including the mitochondrial genome of O. geniculata (accession number MT410796). For all studied Orthonevra species, individuals of the same species are resolved together with high bootstrap support values (BS = 100%), except for the pair O. atlantica sp. nov. and O. brevicornis. Individuals identified by morphology as O. onytes (Séguy, 1961) and O. *tristis* (Loew, 1871) were resolved together (BS = 100%). For all the included species in our analysis, the intraspecific variability is very low for the studied species (less than 1.5%), except for O. frontalis (Loew, 1843) that has an intraspecific variability of 0.0–2.64%. On the contrary, the interspecific variability is much higher (usually more than 4%), except for the pair O. atlantica sp. nov. and O. brevicornis (0.0-1.57%), and for the pair O. montana and O. onytes/O. tristis (2.27–2.62%).

Three downloaded sequences of specimens previously identified as *O. brevicornis* (i.e., GenBank accession numbers OR859673 [England], OR859696 [Germany], and OR859649 [Germany]) cluster with our new species, *O. atlantica* sp. nov. For the two German specimens a new morphological study was possible, and we corroborate that they belong to *O. atlantica* sp. nov. A new identity assessment for the English specimen was not possible, although we believe that it also belongs to *O. atlantica* sp. nov. based on the study of English specimens from the same area (see the listed paratypes of our new species from the United Kingdom). In addition, we were able to determine a previously unidentified specimen from Bulgaria (OR859659) as *O. nobilis* (Fallén, 1817) based on the sequence clustering.

# Key to the European *Orthonevra* species with black legs

1 Legs entirely black, or (in some specimens of O. erythrogona) only knees yellowish. ...... 2 Legs in large part orange or brown. ...... Other European Orthonevra: O. elegans (Wiedemann, 1822), *O. gemmula* Violovitsh, 1979, *O.* geniculata (Meigen, 1830), O. intermedia Lundbeck, 1916 and *O. stackelbergi* Thompson & Torp, 1982 2 Postpedicel short, less than 1.3 times as long as wide. Postpedicel elongated, more than 1.3 times as long as wide. ..... 8 3 Postpedicel orange-brown in part. ..... 4 4 Sternite I shiny, not contrasting with sternites II-IV; female: tergite V without incision in the middle; male terminalia: surstyli broadened in basal half (Fig. 5A). .... 5 Sternite I heavily pollinose, contrasting with shiny sternites II-IV; female: tergite V with incision; male terminalia: surstyli slender. ...... 6 5 Postpedicel black with a restricted orange-brown area basoventrally (Fig. 3A); wing vein M, recessive (Figs 7A, 7B); slightly larger and more pitch black species;

- wing venation usually pitch black; males: scutum at least with some black hairs on central disc (best seen in posterior view), often extensively black haired; vertex with black hairs; male terminalia: phallus in shape of broad cylindrical cavity (Fig. 5C) with anterodorsal hook-shaped appendix in lateral view long and slender (Fig. 5A), postgonites with quadrate tip posterodorsally, extending beyond tip of phallus (Fig. 5A) and without hook-shaped extension anteroventrally (Fig. 5B); mostly in Western Europe.
- 6 Body with longer hairs (RICARTE et al. 2022: fig. 4); wing vein M<sub>1</sub> recessive; eye without or with very short scattered hairs; katepisternum with third patch of hairs below dorsal patch in such way that dorsal and ventral patches might be connected or almost so; hind femur with black, sometimes spiny, black hairs ventrally; male terminalia: postognites slightly asymmetric, bearing a spur on inner side (RICARTE et al. 2022: fig. 7); Western Europe.
- Body with shorter hairs (RICARTE et al. 2022: fig. 11); wing vein M<sub>1</sub> less or non-recessive; eye virtually bare; katepisternum with two separate patches of hairs, one dorsal and another ventral; hind femur entirely white pilose, at most with some scattered black hairs ventrally; male terminalia: postgonites extremely asymmetric and twisted (RICARTE et al. 2022: fig. 14, STACKELBERG 1953: fig. 13); Central Europe, Asia. ......

...... *O. arcana* Ricarte & Nedeljković, 2022

- Hairs on central disc of mesoscutum usually predominantly black; slightly smaller species; wing vein M<sub>1</sub> less recessive (Vujić 1999: fig. 31); male terminalia: anterodorsal appendix of phallus in lateral view shorter, hook-shaped; postgonites shorter and broader (Vujić 1999: fig. 36). The Alps, east to Sudetes, Carpathian and Balkan Mts. .......................... O. montana Vujić, 1999
- 8 Postpedicel narrow, bar-shaped, rectangular (LOEW 1843: fig. 10; Bańkowska 1963: fig. 451); sternite I pollinose; male terminalia: postgonites enlarged,

in lateral view extending far beyond tip of phallus (Vujić 1999: fig. 25). Southern Europe. ..... 9 Postpedicel more than 3× as long as wide. ..... 10 Postpedicel more than or about  $2\times$  as long as wide, tapering towards apex, with pointed tip. ...... 11 Postpedicel less than 1.5× as long as wide, rounded at tip. Male unknown. ....... O. plumbago (Loew, 1840) 11 Postpedicel partly orange; legs black; female: tergite IV with denticle; male terminalia: anterodorsal appendix of phallus in lateral view like duck head (STACKEL-BERG 1953: fig. 17.4; VIOLOVITSH 1979: fig. 1; VUJIĆ Postpedicel black; knees usually slightly lightened; female: tergite IV without denticle; male terminalia: anterodorsal appendix of phallus in lateral view like snake (STACKELBERG 1953: fig. 3.3), phallus extremely long (Violovitsh 1979: fig. 6). ..... 

#### **Discussion**

The first two authors independently discovered the presence of a new species in Europe, which is similar to O. brevicornis. After exchanging notes and photographs, it appeared that the established interpretation of O. brevicornis in their own regions, Central and Western Europe respectively, was different. The analysis of more material revealed the presence of two widespread European species hidden under the name O. brevicornis, one in the east, O. brevicornis (Loew, 1843), and another in the west, O. atlantica sp. nov.. Males of O. atlantica sp. nov. and O. brevicornis are differentiated by several characters of the terminalia, as documented in the description sections of this study, and these characters are stable for both species across a large set of studied material. The only significant variability noticed in the male terminalia is the shape of the anteroventral flat appendix of the phallus (Figs 6A–C), as observed among individuals of *O. brevicornis* series.

Both species have a broad geographical distribution in Europe (O. atlantica sp. nov. in the west and O. brevicornis in the east), with a wide contact zone from eastern Poland to western Germany, where both species can co-occur. Based on the current knowledge, O. atlantica sp. nov. occurs mainly in the Atlantic Europe south of Scandinavia, including the UK, Iberia, and countries in mainland Western Europe, with gradually more localized occurrences further east in Central Europe, reaching Poland, the Czech Republic and Serbia. The main area of occurrence of O. brevicornis is Central and Eastern Europe, from central Poland east and south to Georgia and Greece, with only single isolated populations found in the Netherlands and Switzerland, marking the western edge of its range. This pattern of two closely related species occurring in Eastern and Western Europe is found in another Orthonevra species pair in Europe (O. tristis in the west and O. montana in the east) and is common in European fauna and flora (AUDISIO et al. 2009, SZCZEPAŃSKI 2023). The most common hypothesis is that during glacial maxima ancestral species were forced into different isolated southern refugia, and after following independent evolutionary trajectories, recolonized more northern latitudes later, causing the geographic pattern we see today. *Orthonevra atlantica* sp. nov. and *O. brevicornis* are currently common from sea level altitudes to low mountains in Central Europe, whereas in Southern Europe they are more local and often restricted to mountains.

These two species are part of a larger group of morphologically very similar species with black legs, for whose reliable determination we recommend the study of the male terminalia. The examination of the ZMHB, MZPW and ZFMK collections revealed that almost all male specimens of this genus do not have opened (nor otherwise visible) genital capsules, so that their identification was based on external morphology alone. It is therefore no surprise that we found many erroneous records and we advise to be cautious with old literature mentions. Male terminalia extraction and careful examination of all specimens labelled or morphologically resembling O. brevicornis (including specimens ex coll. Loew, Becker, Riedel, Duda and Bańkowska) confirmed that many specimens were confused with other species, especially with O. tristis and O. montana. As an example, some of the specimens in the Becker collection (ZMHB) have a label "var. tristis" or "var. Schwarz". The reason for this is that Becker, at some point of his study on Syrphidae, interpreted tristis as a darker form of brevicornis. The literal citation from BECKER (1921) is:

"Ursprünglich hatte auch ich in meiner Sammlung Chrysogaster tristis und Orthoneura brevicornis getrennt behandelt; nachdem ich aber brevicornis zu Chrysogaster herübergenommen und eine genaue Vergleichung mit der Bestimmungstabelle einsetzte, fielen beide Arten zusammen; ein nochmaliger Vergleich beider Originalbeschreibungen ergab keinerlei Verschiedenheit; tristis Lw. ist eine etwas dunklere Varietät. [= Originally, I also treated Chrysogaster tristis and Orthoneura brevicornis separately in my collection; but after I took brevicornis over to Chrysogaster and made an exact comparison with the table of identification, both species fell together; a repeated comparison of both original descriptions showed no difference; tristis Lw is a slightly darker variety.]"

The mentioned statement was made, however, without the study of terminalia in males, as was common those days and as testified by the unopened genital capsules of his specimens. The terminalia of these specimens were checked and confirmed to be specific with *O. tristis sensu* VUJIĆ (1999) and much different from those of *O. brevicornis* and *O. atlantica* sp. nov., so Becker's note on synonymy is not valid.

DNA barcoding helps to identify the *Orthonevra* species that we studied. For the majority of the species there is a "barcode gap" in our data set, i.e., the intraspecific sequence variability does not overlap with the interspecific sequence variability (MEIER et al. 2008). The use of DNA barcodes, however, is not conclusive to separate

O. atlantica sp. nov. and O. brevicornis, as we were not able to unequivocally characterise our new species genetically using COI sequences. COI haplotype sharing among different species is not rare in hoverflies and it has been reported for several genera (Locke & Skevington 2013, Haarto & Stähls 2014, Jordaens et al. 2015, Young et al. 2016, Nedeljković et al. 2018, van Steenis et al. 2020, Dietz et al. 2023). The presence of the barcode gap depends on the data set and the statistics used (Čandek & Kuntner 2015) and its absence challenges the universal use of the DNA barcoding alone for species identification. Paraphyly and polyphyly seems common in mitochondrial gene trees due to the same natural history of the mitochondrion, incomplete lineage sorting, imperfect phylogenetic reconstructions, and other reasons (Funk & Omland 2003).

Some taxonomic challenges in European Orthonevra remain unsolved, for instance a likely synonymy of O. onytes (Séguy, 1961) with O. tristis, as already pointed out by RICARTE et al. (2022) and indicated also in our study by the molecular data obtained. Further, Orthonevra auritarsis Brădescu, 1992 and O. shusteri Brădescu, 1993, both described from Romania, do also need clarification. So far, both have been known from single specimens that resemble O. gemmula (VAN STEENIS et al. 2021) and O. frontalis, respectively. In addition, we need more evidence, ideally from Poland (locus typicus) and eastern neighbouring countries, to unambiguously state a possible synonymy of O. varga (female morphology is unknown) with O. plumbago (described based on female morphology and with no male in the type series). Only the combination of external adult morphological characters with the characters of the male terminalia and DNA barcodes will help to elucidate the taxonomy of the remaining problematic European species of Orthonevra.

### Acknowledgements

The authors would like to express their gratitude to P. Trzciński for sharing his material for analysis, neotype designation and publishing. We also thank S. Bot, S. Falk, L. Fisler, X. Lair, Ł. Mielczarek, R. Morris, J. Mortelmans, W. Opdekamp, G. Popov, A. Ricarte, M. Soszyński, W. van Steenis, D. Tarnawski, J. Versigghel, A. Vujić and P. Żurawlew for sharing their material (and photographs), J. Pohl for help regarding ZMHB materials, W. Dekoninck for help regarding the RBINS collection, P. Ciliberti for help with accessing the RMNH collection, D. Szymroszczyk regarding MZPW collection, M. Zakrzewska for the help with making layered photographs of the male terminalia, D. Yanega and N. Evenhuis for taxonomical consultations. We thank Jana Thormann (ZFMK) for her help in the molecular lab to obtain the sequences. Special thanks to L. Mazánek and one anonymous reviewer for their very valuable comments and corrections to the manuscript, as well as to the journal's editorial staff. The CaBOL (grant number 01DK20014A) and GBOL (grant number FKZ 01LI1101) projects on which this study is partly based were funded by the German Federal Ministry of Education and Research.

### References

- ASTRIN J. J. & STÜBEN P. E. 2008: Phylogeny in cryptic weevils: molecules, morphology and new genera of western Palaearctic Cryptorhynchinae (Coleoptera: Curculionidae). *Invertebrate Systematics* 22: 503–522.
- AUDISIO P., BRUSTEL H., CARPANETO G. M., COLETTI G., MAN-CINI E., TRIZZINO M., ANTONINI G. & DE BIASE A. 2009: Data on molecular taxonomy and genetic diversification of the European Hermit beetles, a species-complex of endangered insects (Coleoptera: Scarabaeidae, Cetoniinae, *Osmoderma*). *Journal of Zoological Systematics and Evolutionary Research* 47: 88–95.
- BANKOWSKA R. 1961: Studia nad muchówkami z rodziny Syrphidae (Diptera) Doliny Nidy. (Studies on the family Syrphidae (Diptera) in the Nida Valley). *Fragmenta Faunistica* **9 (13)**: 153–201 (in Polish, with Russian and English summary).
- BAŃKOWSKA R. 1963: Klucze do oznaczania owadów Polski. Część XXVII. Muchówki Diptera, zeszyt 34 Syrphidae. [Key to the identification of Polish Insects. Nr. 42 part 28, Diptera. fascicle 34: Syrphidae.] PWN Warszawa, 236 pp (in Polish).
- BANKOWSKA R. 1967: Matériaux pour l'étude des Syrphides (Diptera) de Bulgarie. *Fragmenta Faunistica* **13 (21)**: 345–389.
- BAŃKOWSKA R. 1968: Materialien zur Kenntnis der Syrphidae, Conopidae, und Stratiomyidae (Diptera) der Mongolei und der angrenzenden Gebiete. Fragmenta Faunistica 15 (17): 33–44.
- BAŃKOWSKA R. 1995: Fauna Syrphidae (Diptera) Puszczy Białowieskiej. (Syrphidae (Diptera) of Puszcza Białowieska). Fragmenta Faunistica 37 (21): 451–483 (in Polish, with English abstract and summary).
- BARKALOV A. V. & MUTIN V. A. 2018: Checklist of the hover-flies (Diptera, Syrphidae) of Russia. *Euroasian Entomological Journal* 17 (6): 466–510.
- BECKER T. 1921: Neue Dipteren meiner Sammlung. Mitteilungen aus dem Zoologischen Museum in Berlin 10 (1): 1–93.
- BRĂDESCU V. 1991: Les Syrphides de Roumanie (Diptera, Syrphidae). Clé de détermination et répartition. *Travaux du Muséum d'Histoire naturelle "Grigore Antipa"* **33**: 7–83.
- ČANDEK K. & KUNTNER M. 2015: DNA barcoding gap: reliable species identification over morphological and geographical scales. *Molecular Ecology Resources* 15: 268–277.
- CASQUET J., THEBAUD C. & GILLESPIE R. G. 2012: Chelex without boiling, a rapid and easy technique to obtain stable amplifiable DNA from small amounts of ethanol-stored spiders. *Molecular Ecology Resources* 12 (1): 136–141.
- CUMMING J. & WOOD D. M. 2017: Adult morphology and terminology. Pp. 89–133. In: KIRK-SPRIGGS A. H. & SINCLAIR B. J. (eds.): Manual of Afrotropical Diptera. Vol. 1. Introductory chapters and keys to Diptera families. South African National Biodiversity Institute, Pretoria, 425 pp.
- DIETZ L., EBERLE J., MAYER C., KUKOWKA S., BOHACZ C., BAUR H., ESPELAND M., HUBER B. A., HUTTER C., MENGUAL X., PETERS R. S., VENCES M., WESENER T., WILLMOTT K., MISOF B., NIEHUIS O. & AHRENS D. 2023: Standardized nuclear markers improve and homogenize species delimitation in Metazoa. *Methods in Ecology and Evolution* 14 (2): 543–555.
- DOCZKAL D., CLAUSSEN C. & SSYMANK A. 2002: First supplement and corrections to the checklist of the hoverflies of Germany (Diptera, Syrphidae). *Volucella* 6: 167–173.
- EVENHUIS N. L. & PAPE T. 2021: Systema Dipterorum, Version 3.11 October 2023. Available on-line: http://diptera.org/
- FOLMER O., BLACK M., HOEH W., LUTZ R. & VRIJENHOEK R. 1994: DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294–299.
- FUNK D. J. & OMLAND K. E. 2003: Species-level paraphyly and polyphyly: frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annual Review of Ecology, Evolution,* and Systematics 34: 397–423.
- GIBSON J. F., KELSO S., JACKSON M. D., KITS J. H., MIRANDA G. F. G. & SKEVINGTON J. H. 2011: Diptera-specific PCR-amplification primers of use in molecular phylogenetic research. *Annals of the Entomological Society of America* 104: 976–997.

- GOOT V. S. VAN DER 1981: De Zweefvliegen van Noordwest-Europa en Europees Rusland, in het bijzonder van de Benelux. [Hoverflies of Northwestern Europe and European Russia, in particular the Benelux.] Koninklijke Nederlandse Natuurhistorische Vereniging, Amsterdam, 275 pp (in Dutch).
- HAARTO A. & STÅHLS G. 2014: When mtDNA COI is misleading: Congruent signal of ITS2 molecular marker and morphology for North European *Melanostoma* Schiner, 1860 (Diptera, Syrphidae). *ZooKeys* 431: 93–134.
- HEIMBURG H., DOCZKAL D. & HOLZINGER W. E. 2022: A checklist of the hoverflies (Diptera: Syrphidae) of Austria. *Zootaxa* **5115 (2)**: 151–209.
- ICHIGE K. 2006: Notes on the genus *Orthonevra* Macquart (Diptera, Syrphidae) in Japan (Part. 1). *Dipterist's Club of Japan "Hana Abu"* **22**: 18–24 (in Japanese).
- ICZN 1999: *International Code of Zoological Nomenclature*. 4<sup>th</sup> edition. International Trust for Zoological Nomenclature, London, 306 pp.
- JORDAENS K., GOERGEN G., VIRGILIO M., BACKELJAU T., VOKAER A. & DE MEYER M. 2015: DNA Barcoding to improve the taxonomy of the Afrotropical hoverflies (Insecta: Diptera: Syrphidae). PLoS ONE 10 (10) (e0140264): 1–15.
- KARL O. 1935: Die Fliegenfauna Pommerns. Diptera, Brachycera. Stettiner Entomologische Zeitung 96: 242–261.
- KASSEBEER C. F. 1999: Zur Kenntnis einiger Gattungen der Chrysogasterini in Marokko (Diptera: Syrphidae). Beiträge zur Schwebfliegenfauna Marokkos, IV. Entomologische Zeitschrift 109 (4): 155–164.
- LOCKE M. M. & SKEVINGTON J. H. 2013: Revision of Nearctic Dasysyrphus Enderlein (Diptera: Syrphidae). Zootaxa 3660 (1): 1–80.
- LOEW H. 1843: Bemerkungen über die bekannten europäischen Arten der Gattung Chrysogaster Meig. (Schluss.). Stettiner Entomologische Zeitung 4 (9): 258–281, 1 pl.
- LOEW H. 1857: Dipterologische Notizen. Wiener Entomologische Monatschrift 1: 1-10.
- MAIBACH A., GOELDLIN DE TIEFENAU P. & SPEIGHT M. C. D. 1994: Limites génériques et caractéristiques taxonomiques de plusieurs genres de la tribu des Chrysogasterini (Diptera: Syrphidae). I. Diagnoses génériques et description de Riponnensia gen. nov. Annales de la Société Entomologique de France 30: 217–247.
- MAZÁNEK L., VONIČKA P. & PREISLER J. 2009: Pestřenkovití (Diptera: Syrphidae) Jizerských hor a Frýdlantska. (Syrphidae (Diptera) of the Jizerské hory Mts and Frýdlant region (northern Bohemia, Czech Republic)). Sborník Severočeského Muzea, Přírodní Vědy 27: 3–46 (in Czech, with English abstract and summary).
- MEIER R., ZHANG G. & ALI F. 2008: The use of mean instead of smallest interspecific distances exaggerates the size of the "barcoding gap" and leads to misidentification. Systematic Biology 57: 809–813.
- NEDELJKOVIĆ Z., RICARTE A., ZORIĆ L. Š., ĐAN M., VIDAKOVIĆ D. O. & VUJIĆ A. 2018: The genus *Xanthogramma* Schiner, 1861 (Diptera: Syrphidae) in southeastern Europe, with description of two new species. *Canadian Entomologist* **150 (4)**: 440–464.
- OHISHI H. 2011: Orthonevra brevicornis (Loew) rediscovered from Japan (Diptera: Syrphidae). Dipterist's Club of Japan "Hana Abu" 11: 72–76 (in Japanese).
- PECK L. V. 1988: Syrphidae. Pp. 11–230. In: SOÓS A. & PAPP L. (eds.): Catalogue of Palaearctic Diptera. Vol. 8. Elsevier Science Publishers, Amsterdam & Akadémiai Kiadó, Budapest, 363 pp.
- PROKHOROV A. V., POPOV G. V., SHPARYK V. Y. & VASILYEVA Y. S. 2023: New records of hoverflies (Diptera, Syrphidae) from Ukraine. VI. *Zoodiversity* **57 (2)**: 125–142.
- RAMBAUT A. 2010: FigTree v1.3.1. Institute of Evolutionary Biology, University of Edinburgh, Edinburgh. http://tree.bio.ed.ac.uk/software/figtree/
- REVERTÉ S., MILIČIĆ M., AČANSKI J., ANDRIĆ A., ARACIL A., AUBERT M. et al. 2023: National records of 3000 European bee and hoverfly species: A contribution to pollinator conservation. *Insect Conservation and Diversity* **16 (6)**: 758–775.
- RICARTE A., NEDELJKOVIĆ Z., AGUADO-ARANDA P. & MAR-COS-GARCÍA M. Á. 2022: Assessing the diversity and systematics of Brachyopini hoverflies (Diptera: Syrphidae) in the Iberian Peninsula, including the descriptions of two new species. *Insects* 13 (648): 1–45.

- RONDANI C. 1857: Dipterologiae Italicae Prodromus. Vol: II. Species italicae ordinis Dipterorum in genera characteribus definita, ordinatim collectae, methodo analitica distinctae, et novis vel minus cognitis descriptis. Pars prima. Oestridae: Syrphidae: Conopidae. A. Stocchi, Parmae, 264 pp., 1 pl.
- ROZO-LOPEZ P. & MENGUAL X. 2015: Mosquito species (Diptera, Culicidae) in three ecosystems from the Colombian Andes: identification through DNA barcoding and adult morphology. *ZooKeys* 513: 39–64.
- SACK P. 1930: Schwebfliegen oder Syrphidae. Pp. 1–118. In: DAHL F. (ed.): Die Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Merkmalen und nach ihrer Lebensweise. Teil 20, Zweiflügler Order Diptera. IV: Syrphidae Conopidae. Gustav Fischer, Jena, 142 pp.
- SAHIB S., DRIAUACH O.& BELQAT B. 2020: New data on the hoverflies of Morocco (Diptera, Syrphidae) with faunistic and bibliographical inventories. *ZooKeys* 971: 59–103.
- SANTIAGO-BLAY J., RATCLIFFE B., KRELL F.-T. & ANDERSON R. 2008: Allotypes should be from the type series: a position paper for reinstating Recommendation 72A from the third edition of the Code that defines the term 'allotype'. *Bulletin of Zoological Nomenclature* **65 (4)**: 260–264.
- SHAKERYARI A., KHAGHANINIA S. & IRANI NEJAD K. H. 2012: Four species as new records of tribe Chrysogasterini (Diptera:Syrphidae) from Iran. *Munis Entomology and Zoology* 7: 385–390.
- SOSZYŃSKI B. 1995: Orthonevra plumbago (Loew, 1840) (Syrphidae, Diptera) z rezerwatu "Piskorzeniec" w Przedborskim Parku Krajobrazowym. [Orthonevra plumbago from the "Piskorzeniec" reserve in the Przedborski Landscape Park.] Biuletyn Entomologiczny 3/3: 3 (in Polish).
- SPEIGHT M. C. D. 2017: Species accounts of European Syrphidae, 2017. Syrph the Net, the database of European Syrphidae (Diptera), vol. 97. Syrph the Net publications, Dublin, 294 pp.
- SPEIGHT M. C. D. & CASTELLA E. 2011: Dix-neuf additions à la liste des Syrphidae (Diptera) de Haute-Savoie, incluant *Orthonevra plumbago* (Loew, 1840) et *Xanthogramma stackelbergi* Violovitsh, 1975, deux espèces nouvelles pour la France. *Entomo Helvetica* 4: 45–58.
- STACKELBERG A. A. 1953: Palearkticheskie vidy roda *Orthoneura* Macq. (Diptera, Syrphidae). [Palaearctic species of the genus *Orthonevra*]. *Entomologiceskoe Obozrenie* 33: 342–357 (in Russian).
- STACKELBERG A. A. 1970: Syrphidae Zhurchalki. Pp. 11–96. In: BEI-BIENKO G. Y. (ed.): Opredelitel' nasekomykh Evropeiskoi chasti SSSR. [Key to the Insects of the European part of USSR]. Vol. V. Part 2. Nauka, Leningrad, 943 pp (in Russian).
- SZCZEPAŃSKI W. T. 2023: A new species of *Dasypogon* (Diptera: Asilidae) from Central Europe. *Zootaxa* **5230** (3): 367–380.
- TÓTH S. 2013: Additional data to the hoverfly fauna of Turkey (Diptera: Syrphidae). *Natura Somogyiensis* 23: 239–254.
- TROJANOWA-BAŃKOWSKA R. 1959: Nowe dla Polski lub mniej znane gatunki z rodziny Syrphidae (Diptera). (New or little-known species of the family Syrphidae (Diptera) in Poland). Fragmenta Faunistica 8 (8): 137–157 (in Polish, with Russian and English summary).
- TRZCIŃSKI P. 2007: Stratiomyidae i Xylomyidae (Diptera) Wielkopolski. (Stratiomyidae and Xylomyidae (Diptera) of Wielkopolska Region). *Dipteron* 23: 38–44 (in Polish, with English abstract).
- VAN DE MEUTTER F., OPDEKAMP W., MORTELMANS J. & VER-SIGGHEL J. 2024: Orthonevra arcana Ricarte and Nedeljković, 2022 and Pelecocera caledonica (Collin, 1940) (Diptera: Syrphidae) new to the fauna of Belgium. Bulletin de la Société Royale Belge d'Entomologie 159 [2023]: 148–157.
- VAN STEENIS J., MIRANDA G. F. G., TOT T., MENGUAL X. & SKEVINGTON J. H. 2023: Glossary of morphological terminology of adult Syrphidae (Diptera): an update and extension. *Journaal van Syrphidae* **2 (4)**: 1–99.
- VAN STEENIS W., VAN STEENIS J. & VAN DER ENT L.-J. 2021: Orthonevra auritarsis: e.T149171237A149171239, Orthonevra gemmula [e.T149165215A149165225], Orthonevra incisa [e.T190431889A190432075], Orthonevra montana [e.T149165203A149165205], Orthonevra schusteri [e.T149171269A149171271]. In: The IUCN Red List of Threatened Species 2021. Available on-line: https://www.iucnredlist.org (Accessed on 14 April 2024.)

- VAN STEENIS J., VAN ZUIJEN M. P., RICARTE A., MARCOS-GAR-CÍA M. A., DOCZKAL D., SSYMANK A. & MENGUAL X. 2020: First records of *Chrysotoxum volaticum* Séguy, 1961 from Europe and *Platycheirus marokkanus* Kassebeer, 1998 from Spain (Diptera: Syrphidae) together with additional records of Spanish *Chrysotoxum* Meigen, 1803. *Bonn Zoological Bulletin* 69 (1): 141–155.
- VIOLOVITSH N. A. 1979: Obzor sibirskikh vidov roda Othoneura Macquart, 1829 (Diptera, Syrphidae). [Survey of Siberian species of the genus Orthonevra Macquart, 1829 (Diptera, Syrphidae)]. Pp. 48–63. In: CHEREPANOV A. I. (ed.): Chlenistonogie i gelminty. [Arthropods and helminths.]. Nauka, Novosibirsk, 135 pp (in Russian).
- VOCKEROTH J. R. & THOMPSON F. C. 1987: Syrphidae (Chapter 52).
  Pp. 713–743. In: McALPINE J. F., PETERSON B. V., SHEWELL G. E., TESKEY H. J., VOCKEROTH J. R. & WOOD D. M. (eds): Manual of Nearctic Diptera, Volume 2. Agriculture Canada Research Branch (Monograph. No. 28). Canadian Government Publishing Centre, Hull (Quebec), 1332 pp.
- VUJIĆ A. 1999: The tribe Chrysogasterini (Diptera: Syrphidae) in the Balkan Peninsula, with the description of three new cryptic species. *Studia Dipterologica* **6**: 405–423.
- VUJIĆ A., GILBERT F., FLINN G., ENGLEFIELD E., FERREIRA C. C., VARGA Z., EGGERT F., WOOLCOCK S., BÖHM M., MERGY R., SSYMANK A., VAN STEENIS W., ARACIL A., FÖLDESI R., GRKOVIĆ A., MAZANEK L, NEDELJKOVIĆ Z., PENNARDS G. W. A., PÉREZ C., RADENKOVIĆ S., RICARTE A., ROJO S., STÅHLS G., VAN DER ENT L.-J., VAN STEENIS J., BARKALOV A., CAMPOY A., JANKOVIĆ M., LIKOV L., LILLO I., MENGUAL X., MILIĆ D., MILIČIĆ M., NIELSEN T., POPOV G., ROMIG T., ŠEBIĆ A., SPEIGHT M., TOT T., VAN ECK A., VESELIĆ S., ANDRIC A., BOWLES P., DE GROOT M., MARCOS-GARCÍA M. A., HADRAVA J., LAIR X., MALIDŽAN S., NÈVE G., OBREHT VIDAKOVIC D., POPOV S., SMIT J. T., VAN DE MEUTTER F. & VELIČKOVIĆ N. 2022: Pollinators on the edge: our European hoverflies. The European Red List of Hoverflies. European Commission, Brussels, 96 pp.

- WALKER F. 1851: *Insecta Britannica, Diptera. Volume 1*. Reeve & Benham, London, 314 pp., 10 pls.
- WITEK A., MIELCZAREK Ł. E., SOSZYŃSKI B., ŻÓRALSKI R., TRCZIŃSKI P., MOCARSKI Z., KAŹMIERCZAK R. & TOFILSKI A. 2015: Sprawozdanie z V-tych Warsztatów Dipterologicznych PTE Syrphidae. [Report of the 5-th Dipterological Workshop of the Polish Entomological Society Syrphidae]. *Dipteron* 31: 77–81 (in Polish).
- YOUNG A. D., MARSHALL S. A. & SKEVINGTON J. H. 2016: Revision of *Platycheirus* Lepeletier and Serville (Diptera: Syrphidae) in the Nearctic north of Mexico. *Zootaxa* 4082 (1): 1–317.
- ZATWARNICKI T. 1996: A new reconstruction of the origin of eremoneuran hypopygium and its implications for classification (Insecta: Diptera). *Genus* 7: 103–175.
- ZIEGLER J., POHL J. & EVENHUIS N. L. 2020: Die Reise des Entomologen Hermann Loew nach Kleinasien in den Jahren 1841–1842. Beiträge zur Entomologie 70: 203–271.
- ŻÓRALSKI R. 2023: Lejogaster metallina (Fabricius, 1777) (Diptera: Syrphidae) w świetle 140 lat badan dipterologów polskich i pruskich. [Lejogaster metallina (Fabricius, 1777) (Diptera: Syrphidae) over 140 years of dipterological studies of Polish and Prussian entomologists.]. Dipteron 39 (5): 98–111 (in Polish, with English abstract and summary).
- ŻÓRALSKI R., KOWALCZYK J. K. & SOSZYŃSKI B. 2017: Syrphidae (Diptera) Świętokrzyskiego Parku Narodowego. (Hoverflies (Diptera) of the Świętokrzyski National Park). Dipteron 33: 55–76 (in Polish, with English abstract).
- ŻÓRALSKI R., MIELCZAREK Ł. E. & SOSZYŃSKI B. 2016: Sprawozdanie z VI Warsztatów Dipterologicznych Polskiego Towarzystwa Entomologicznego, Wigry, 2016. Przyczynek do poznania bzygowatych (Diptera: Syrphidae) Wigierskiego Parku Narodowego. [Report of the 6th Dipterological Workshop of the Polish Entomological Society, Wigry, 2016. Contribution to our knowledge of the hoverflies (Diptera: Syrphidae) of Wigry National Park]. Dipteron 32: 123–131 (in Polish, with English abstract).