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The *Leptopilina* Förster, 1869 of the Western Palearctic, and an updated list of the world species (Hymenoptera, Figitidae, Eucoilinae)

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Abstract

The genus *Leptopilina* comprises species of parasitoid wasps that primarily attack early instar larvae of drosophilid species, some of which are well-known agricultural or nuisance pests. To unravel host-parasitoid interactions and to use parasitoids effectively in biological control, the correct taxonomic assignment is of crucial importance.

In the course of the German Barcode of Life III: Dark Taxa (GBOL III: Dark Taxa) project, we assembled specimens of all seven species of *Leptopilina* of the Western Palearctic. Using *CO1* barcode sequence analyses and morphological examination allows us to evaluate species limits in an integrative approach, to provide extended species diagnoses as well as an updated key to the species of the Western Palearctic.

This work also summarizes current knowledge on Western Palearctic *Leptopilina* species, including their distribution, population parameters, habitats, flight periods, and hosts. We provide the first country records of three *Leptopilina* species for Belgium, including the non-native *L. japonica*, propose two species level synonymies and move one Western Palearctic species out of *Leptopilina*.

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Finally, to facilitate taxonomic research on *Leptopilina* in lesser-known regions, we provide a list of non-Western Palearctic species, including the moving of 13 species into *Leptopilina*. These changes also result in two new generic synonymies.

In conclusion, Western Palearctic *Leptopilina* can be clearly diagnosed both morphologically and molecularly. Comparable ease of identification and cultivation, as well as the economic interest in potent biological control agents against drosophilid pests make them ideal organisms for basic and applied research.

Keywords

Biological control, CO1 barcode, identification key, integrative taxonomy

Introduction

Leptopilina Förster, 1869 is a genus within the cynipoid family Figitidae. It comprises primary solitary koinobiont larval-pupal endoparastoids of Drosophilidae with a varying degree of host-specialization (Carton et al. 1986). As some *Leptopilina* species and their respective hosts are easy to rear under artificial conditions (e.g. *Drosophila melanogaster* Meigen, 1830), they have been used for decades in laboratory and field studies. In his revision of the genus *Leptopilina* in 1980, Nordlander stated that *Leptopilina heterotoma* (Thomson, 1862) "has been intensively studied […] during the last 30 years" (Nordlander 1980). Just as its main host, *D. melanogaster*, *Leptopilina heterotoma* serves as a model organism to address ethological, ecological, evolutionary, microbiological or physiological questions (Quicray et al. 2023).

Recently, a considerable amount of research has been dedicated to *Leptopilina japonica* Novković & Kimura, 2011, because it is a natural enemy of the invasive spotted wing drosophila, *Drosophila suzukii* (Matsumura, 1931). *Leptopilina japonica* has established adventive populations, outside its native range in East Asia, in a number of European and North American countries (Abram et al. 2020; Puppato et al. 2020; Beers et al. 2022; Martin et al. 2023; Rousse et al. 2023; Gariepy et al. 2024; Rossi-Stacconi et al. 2025). A main difficulty for pest management researchers is distinguishing *L. japonica* from closely related congeneric species that cannot develop *D. suzukii*, especially *L. heterotoma*.

Morphological diagnostic information to separate the Western Palearctic species of *Leptopilina*, including the introduced *L. japonica*, is scattered (Nordlander 1980; Van Alphen et al. 1991; Martin et al. 2023). Additionally, *CO1* barcode depositories such as BOLD (Ratnasingham and Hebert 2007) contain several mOTUs (BINs (Ratnasingham and Hebert 2013)) of *Leptopilina* spp., which are composed of misidentified specimens (accessed 24th June 2025). This impedes unambiguous identification of some *Leptopilina* species both by morphology and *CO1* barcodes. A database, dedicated to *Drosophila* Fallén, 1823 parasitoids (DROP) was established in 2021 (Lue et al. 2021) that aims to provide high quality genetic sequence data backed with morphologically evaluated voucher specimens. Many, but not all of the currently described species of *Leptopilina* are represented in the current version 1.3 (http://doi.org/10.5281/zenodo.4519656).

By integrating morphological and molecular (*CO1* barcode) data from 91 Western Palearctic *Leptopilina* specimens, complemented by morphological analysis of additional material, we characterise the constituent species. Based on these diagnoses, we provide an updated identification key to the *Leptopilina* species occurring in the Western Palearctic.

The biology and distribution of the genus *Leptopilina* is comparably well-studied, but the information has not been summarized for the Western Palearctic taxa since Nordlander (1980), while some species and numerous studies have been added later. Based on a comprehensive literature review, we summarized the known distribution, population parameters, habitat, flight period and host records. This can help to check for plausibility of identification and will help to point out new discoveries and thus further stimulate research on *Leptopilina*. Given the geographic spread of *L. japonica*, possible intra-guild effects (such as competition for hosts) with native *Leptopilina* are of special interest, so we added all previously reported parasitoid-host relationships as well as parasitoid wasp community compositions of the Western Parlearctic *Leptopilina* in supplementary tables.

Finally, we compiled lists of the non-Western Palearctic species of *Leptopilina* grouped by zoogeographic region, including taxonomic changes where we studied type specimens within the past two decades. Together with the characterisation of the Western Palearctic species, this work will facilitate research on *Leptopilina* worldwide and be of use for taxon experts and applied researchers alike.

Material and methods

Institutional abbreviations

If available, we use the institutional codens as listed in the Insects and Spider Collections of the World Website (Evenhuis 2025, accessed 11th April 2025) and followed common practice otherwise:

AMNH	American Museum of Natural History, New York, USA;
BPBM	Bernice P. Bishop Museum, Hawaii, Honolulu, USA;
CCDB	Canadian Center for DNA Barcoding;
HNHM	Hungarian Natural History Museum, Budapest, Hungary;
JKI	Julius Kühn Institute, Institute for Biological Control, Dossenheim, Germany;
MNCN	Museo Nacional de Ciencias Naturales, Madrid, Spain;
MNHN	Muséum National d‘Histoire Naturelle, Paris, France;
MHNG	Muséum d’Histoire Naturelle, Genève, Switzerland;
MZH	Finnish Museum of Natural History, Helsinki, Finland;
MZLS	Museé Zoologique, Lausanne, Switzerland;
MZLU	Zoological Museum of the Lund University, Lund, Sweden;
NHMO	Zoological Museum of the Oslo University, Oslo, Sweden;

NHRS	Natural History Museum of Sweden, Stockholm, Sweden;
NINA	Norwegian Institute for Nature Research, Trondheim, Norway;
NMBE	Naturhistorisches Museum, Bern, Switzerland;
NMPC	National Museum (Natural History), Prague, Czech Republic;
OLML	Oberösterreichisches Landesmuseum, Linz, Austria;
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany;
USNM	National Museum of Natural History, Washington DC, USA;
ZFMK	Leibniz Institute for the Analysis of Biodiversity Change, Museum Koenig Bonn, Germany (formerly Zoologisches Forschungsmuseum "Alexander Koenig");
ZIN	Russian Academy of Sciences, Zoological Institute, St. Petersburg, Russia;
ZMHB	Museum für Naturkunde, Berlin, Germany;
coll GN	Göran Nordlander's collection at Swedish University of Agricultural Sciences, Uppsala, Sweden;
coll MF	Private collection of Mattias Forshage;
coll MK	Private collection of Martti Koponen;
coll MS	Private collection of Michael Sporrong.

Morphological examination and imaging

We assembled the Western Palearctic specimens during the German Barcode of Life III: Dark Taxa project (listed in Suppl. material 1). For preparation, mounting and examination, we used a Leica M205 C stereomicroscope (Leica Camera AG, Germany).

A material examined section for the respective species is not included in the treatments but put in Appendix 1 within this document instead, in order to increase readability of the treatments. Respective information can also be found in Suppl. material 1 (.xlsx file).

The images for the figure plates and key illustrations are focus-stacked composite images produced using a Keyence VHX-7100 digital microscope (Keyence Corporation, Japan).

DNA sequencing and molecular species delimitation

For the specimens with ZFMK-TIS ID, we performed non-destructive full-body DNA extractions at ZFMK. The mtDNA barcode region of the *CO1* gene was amplified by using the LCO1490-JJ forward and HCO2198-JJ reverse primer (Astrin and Stüben 2008) and the PCR protocol as described in Müller et al. (2024). We added five sequences of *L. japonica*, that were published prior to this study (Martin et al. 2023, BOLD dataset "DS-LJAP").

For specimens with the NOFIG ID, DNA was extracted from a leg following standard protocols for insect tissue at CCDB. PCR was performed with the LepF1 forward and LepR1 reverse primer (Hebert et al. 2004). Sanger sequencing was done at the CCDB.

The DNA of specimens with HM1 ID was extracted non-destructively at the ZFMK using HotSHOT extractions (Truett et al. 2000) by adding 25 µl alkaline lysis buffer to the specimen. After incubation at 70 °C for 30 minutes, 25 µl of neutralising solution were added and 1 µl of the extract was used in the PCR. The sample was further processed using LCO1490-JJ and HCO2198-JJ primers (Astrin and Stüben 2008) with individual tags attached. We sequenced the amplicon pool using MinION technology (Oxford Nanopore Technologies plc, UK) as described in Vasilita et al. (2024).

The sequences of both reads were assembled to a consensus sequence in Geneious Prime v.2022.1.1 (Dotmatics). We kept and used those sequences for downstream analyses if they fulfilled the GBOL gold standard (i.e. consensus sequences have 1. ≥ 500 base pairs sequence length, 2. a high-quality BIN assignment, and 3. ≤ 1% disagreements and ambiguities, see Jafari et al. (2023) for more details). We aligned the sequences using the built-in MUSCLE alignment algorithm with a maximum of eight iterations (Edgar 2004) in Geneious. The sequence IDs of all specimens used for the molecular work are cited in Suppl. material 2.

Using IQ-TREE v2.2.2.6 (Minh et al. 2020), we reconstructed a maximum likelihood tree and calculated ultrafast bootstrap support with 1000 replicates (Hoang et al. 2018) together with an SH-aLRT fast branch test (Guindon et al. 2010) with 1000 replicates, without further specifications. For species delimitation, the ASAP species delimitation algorithm (via https://bioinfo.mnhn.fr/abi/public/asap/, default settings, accessed 23rd January 2025; Puillandre et al. 2021) and the Clustering function of Species Identifier v.1.6.2 (Meier et al. 2006) set to a 3% threshold (further called SpID 3%) were applied to our alignment, and multirate PTP (further called mPTP, Kapli et al. 2017) via a web server (https://mptp.h-its.org/#/tree, default settings, accessed 23rd January 2025) was applied to the tree file that was previously rooted with an outgroup sequence (*Rhoptromeris heptoma* (Hartig, 1840), BOLD-ID: NOFIG1495-17) in Figtree v1.4.4 (Rambaut 2018). The species delimitation illustration was then composed in Inkscape v.1.3 (Inkscape project) by combining the tree and the species delimitation results.

For the molecular characterisation of species (see species treatments), we analysed the distance matrix from the alignment provided in Geneious to determine maximum intraspecific distances and minimum interspecific distances, stating the number of contained sequences and the name of the closest species in parentheses respectively. The consensus sequence was generated by aligning the sequences of each species separately using the MUSCLE algorithm (Edgar 2004) in Geneious. For the molecular characterisation we only used the sequences of those specimens that we also studied morphologically, i.e. those listed in Suppl. material 2.

In addition to the morphological identifications, we used the DROP database (Lue et al. 2021) for molecularly matching our sequences with the database sequences.

The *CO1* barcode sequences with the ZFMK-TIS ID can be accessed via bolgermany.de (German Barcode of Life Consortium 2011), DROP (Lue et al. 2021) and boldsystems.org (Ratnasingham and Hebert 2007, dataset DOI: dx.doi.org/10.5883/DS-GB3LEPTO). The latter two additionally contain the sequences with NOFIG- and HM1 IDs.

Summary of biological data and distribution records

Biological and geographical data was assembled from available published data as well as from notes collected from label data in museum collections for a continuous period over the past decades by MF. How the information was compiled, varies between the (sub-)sections and is outlined below.

The biology sections of the species treatments contain summarized information on a) habitat (biotic and abiotic factors allowing a species to occur), b) flight period (adult activity period), c) host (host species that the parasitoid wasp species is able to develop in), and d) population parameters (various life history and ecological traits).

For a) habitat and b) flight period, we used a synthesising approach. A backbone of information was gathered, combining the information given in Nordlander (1980) and van Alphen et al. (1991) with label data from two major collecting efforts: The Swedish Malaise Trap Project (identified specimens in the NHRS) (Karlsson et al. 2020) and the German Barcode of Life project (specimens in the ZFMK and partnering institutes, listed in Suppl. material 1 and Appendix 1). Additional information was extracted from several papers (Vet and Hoeven 1984; Vet and van Alphen 1985; Driessen et al. 1990; Kimura 2015; Lue et al. 2016; Abram et al. 2022; Martin et al. 2023; Rossi-Stacconi et al. 2025), specimens available in NHRS and coll MF, and in some cases from notes from other museum collections visited by or sent on loan to MF during the past 25 years, though such notes were usually focused on other specific questions or other genera (useful data for this study was nevertheless retrieved at least from MHNG, MZH, MZLS, MZLU, NHMG, NHRS, NMBE, OLML, coll MK, coll MS). All this heterogenous data was summarised into broad patterns and broader habitat classes, and we do not give specific references in the taxon treatments for these categories.

The sources for c) hosts and d) population parameters are cited in the conventional way in the taxon treatments. Host records were divided into *in situ* records and those exclusively coming from *ex situ* observations. We also differentiated between hosts that are present in the Western Palearctic and those absent. We considered hosts to be absent in the Western Palearctic, if they are not included in any of the recent checklists or faunistic studies from the region (Bächli et al. 2004; Kahanpää 2014; Bächli 2021, 2023, 2024; Özbek Çatal et al. 2021; Kettani et al. 2022; Gornostaev et al. 2023, 2024). We use the terms "taken from" (puparium of host was extracted from substrate *in situ*, so host species and substrate are known) and "reared from" (waps attacked hosts *ex situ*) to differentiate the degrees of host record quality. Additionally, we use "emerged from", for *in situ* observations, where only the substrate is known, but host puparia were not extracted and thus the host species is speculative at best.

The distribution records were compiled from the same data source types as outlined for a) habitat and b) flight period of the biology sections; from a combination of literature and database searches and museum label data information. The backbone for the distribution records is provided by the Fauna Europaea database (Ronquist and Forshage 2004, currently offline), which was in its turn based on Nordlander (1980) as well as a compilation of all available literature records (to the extent they were considered meaningful), and data from a few important collections (coll GN, coll MS, MZLU). Several checklists of local national faunas have been considered, both printed papers (like Forshage et al. 2017) and online resources. Particularly useful in that respect has been the BOLD database (molecular records become useful even if the uploader has not been able to make a species-level identification). To facilitate readability, we summarized the distribution data within the taxon treatments, but give a more comprehensive listing per species in Suppl. material 5. Conventional citations for distribution records within the treatments are only given for *L. japonica* due to its concurrent spreading.

In the listing in Suppl. material 5, we noted the first country record for every species, respectively. If the first record was not previously published, we give the name of the collection that hosts the voucher specimen instead. The designation of "new country records" has been reserved for such records that are based on a collecting associated with the projects GBOL I-III (i.e. if a specimen listed in Supp. material 1 is being the first of a species in its country of origin). Other country records may not have been published before but can hardly meaningfully be claimed as "new records" when very little previous effort has been made to make national inventories or even national checklists, to identify available museum material, or to scrutinise available records from collections.

Though not included in the taxon treatments, we summarised the parasitoid wasp community of the Western Palearctic *Leptopilina* in Suppl. material 4. We considered a parasitoid species to be in community with *Leptopilina*, if it was collected and reared or emerged together from a (baiting) substrate together with *Leptopilina*. Parasitoid species which share the same host species, but have never been recorded together in field data were excluded. Records are treated as non-Western Palearctic, if the community of a *Leptopilina* species and another parasitoid was exclusively recorded outside of the Western Palearctic.

Results

Sequencing and molecular species delimitation

We analyzed a total of 91 sequences of five morphologically distinct species. The three species delimitation algorithms applied here recognise the same five clusters as distinct species. These clusters match the morphological identifications of the species *Leptopilina clavipes* (Hartig, 1841), *L. fimbriata* (Kieffer, 1901), *L. heterotoma*, *L. japonica*, and *L. longipes* (Hartig, 1841) (Fig. 1). The other two Western Palearctic species did not successfully produce barcode sequences (in the case of the rare *L. australis* (Belizin, 1966)), or were not attempted (in the case of *L. boulardi* (Barbotin, Carton & Kelner-Pillault, 1979)). While there is a multitude of sequences available for *L. boulardi* on BOLD, no *CO1* barcode sequence information is currently available for *L. australis*. The former species was not included in the analysis as we did not study the corresponding specimens morphologically.

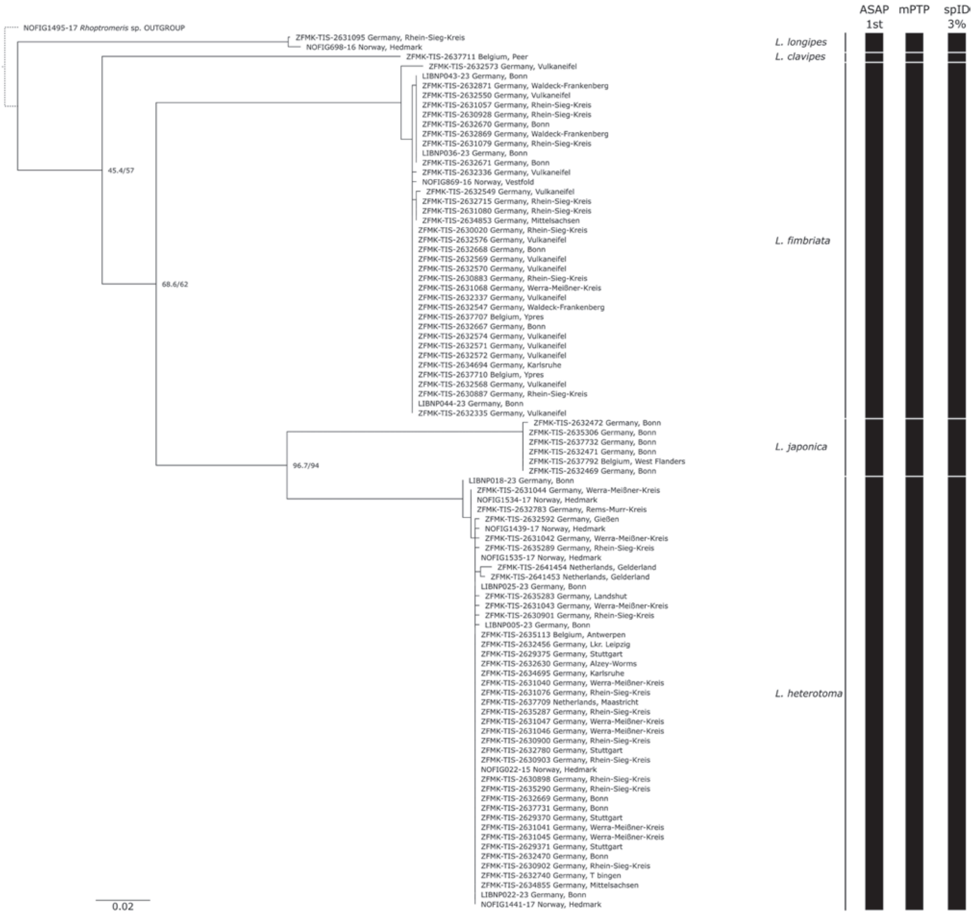

Figure 1. Maximum likelihood tree based on *CO1* barcode data, constructed with IQ Tree. The results of the species delimitation analyses are summarised on the right. The sequence clusters are named according to the results of our integrative taxonomy approach (see corresponding treatments). The dotted line is connecting the outgroup, *Rhoptromeris heptoma*, to the remaining tree and is not to scale. SH-aLRT- (first value) and Ultrafast-bootstrap-support (second value) are shown on the nodes.

Taxonomic section

Class Insecta
Order Hymenoptera
Superfamily Cynipoidea Billberg, 1820
Family Figitidae Hartig, 1840
Subfamily Eucoilinae Thomson, 1862

Genus *Leptopilina* Förster, 1869

Type species. *Leptopilina longipes* (Hartig, 1841).

Diagnosis. *Leptopilina* species are recognized from other cynipoid wasps by having a mesoscutellar plate (as do all members of the Eucoilinae subfamily), the dorsally broadly interrupted to almost absent hairy ring of the metasoma (dorsally shortly interrupted, absent, or complete in other eucoiline genera) in combination with the postpetiolar rim (absent in most genera, e.g. *Ganaspis* Förster, 1869 and *Hexacola* Förster, 1869, present in *Cothonaspis* Hartig, 1840, Diglyphosematini, and Zaeucoilini; these usually lack a hairy ring). Female specimens have 13 antennomeres, while male specimens have 15. In males, the second flagellomere (F2) is curved and somewhat irregular (unlike in several other groups of Eucoilinae, where the first flagellomere (F1) is irregular).

Leptopilina species can have their hairy ring reduced and species of Diglyphosematini, Zaeucoilini or *Cothonaspis* can developed an unusually distinct hairy ring. In these cases, *Leptopilina* can be differentiated from the Diglyphosematini and Zaeucoilini by having a regularly wide pronotum without distinct shoulders (very broad pronotum with distinct shoulders in Diglyphosematini and Zaeucoilini). Additionally, the male F1 is modified in Diglyphosematini and Zaeucoilini and the metasoma is roundish, not longer than high in Diglyphosematini and Zaeucoilini (more elongate in *Leptopilina*). In comparison to *Cothonaspis*, *Leptopilina* species have a much less elongate appearance, especially the mesosoma is less elongate in *Leptopilina*, with a mesoscutum about as long as wide (clearly longer than wide in *Cothonaspis*), and the propodeal area is much more setose in *Leptopilina* (hardly any seta in *Cothonaspis*).

Remarks. A more extensive diagnosis can be found in Lue et al. (2016).

The name *Leptopilina* was not frequently used after its original description by Förster (1869). Kieffer, who was generally circumscribing taxa by a minimal set of *a priori* chosen diagnostic characters and did not study types, collected a somewhat haphazard assembly of species under the name *Leptopilina* in his Cynipoidea world monograph (von Dalla-Torre and Kieffer 1910). His concept of the genus was of limited use, so that for 70 years, only a single species was described in it. Later, Nordlander revisited eucoiline classification based on type studies and phylogenetic concerns. His type studies showed that some of the species, which had been described by 19th century authors and that he could not immediately associate with a genus name, were not currently classified in a meaningful way. The genus name *Leptopilina* was not in use by these authors, despite being available since Förster (1869). And it turned out that two slightly better known yet misclassified species belonged there (*L. heterotoma* and *L. boulardi*, then known as *Pseudeucoila bochei* Weld, 1944 and *Cothonaspis boulardi* Barbotin, Carton & Kelner-Pillault, 1979 respectively). Thus, it is from Nordlander's revival of the genus (1980) that the modern sense and use of the name originates.

Leptopilina is currently classified as belonging to the tribe Eucoilini together with the type genus *Eucoila* Westwood, 1833, the genera *Afrodontaspis* Weld, 1962, *Bothrochacis* Cameron, 1904, *Linaspis* Lin, 1988, *Linoeucoila* Lin, 1988, *Maacynips* Yoshimoto, 1963, *Quasimodoana* Forshage, Nordlander & Ronquist, 2008, and the far more common *Trybliographa* Förster, 1869 (Buffington et al. 2020). The Eucoilini as currently defined seemed monophyletic only in the analyses of Fontal-Cazalla et al. (2002)

(morphological characters) and Forshage et al. (2008) (European taxa only, morphological characters), while already the first combined analysis using molecular and morphological data (Buffington et al. 2007) resulted in a more problematic topology with the Eucoilini as a paraphyletic grade leading up to Trichoplastini, and some other genera complicating the picture further. An additional difficulty is that some of these genera are much more poorly known than *Leptopilina* and not necessarily well circumscribed (such as *Maacynips* and *Leptolamina* Yoshimoto, 1962). Recent analyses (Blaimer et al. 2020; Guinet et al. 2025, and unpublished results) have retained a problematic picture with a non-monophyletic Eucoilini, but the taxon sampling has not been broad enough and the results not stable enough to suggest a new improved classification with monophyletic and recognisable tribes, so this task remains to be undertaken.

Leptopilina novicia Belizin, 1964 was described from Armenia so it is a Western Palearctic species, but it does not belong in *Leptopilina* and is here formally moved to *Hexacola* resulting in the comb. nov. *Hexacola novicia* (Belizin, 1964), as was suggested in the now offline Fauna Europaea database (Ronquist and Forshage 2004). The type is held at ZIN and was studied by GN and MF.

Body size varies greatly within species in *Leptopilina* (as is common in parasitoids), and is something like 1.0–2.2 mm across the genus (not considering occasional rare aberrant specimens that are even smaller or larger). For those species of which we have studied numerous specimens, the average body size falls in either the higher or lower part of this range. Deviations from the average usually peak around the opposite end with a more or less distinct gap between the average and the deviant group of specimens. For this reason, we give body size mainly in relative terms in the species diagnoses of these species.

Leptopilina australis (Belizin, 1966)

Rhoptromeris australis Belizin, 1966: 87.

Diagnosis. *Leptopilina australis* is a relatively small species (1.3–1.4 mm ♀ body length in a small number of measured females) with somewhat slender appearance and a relatively short antenna (Fig. 2A).

The species is unique in the combination of the mesoscutum having rows of setae mediolaterally (Fig. 11A, susceptible to damage), a state shared with *L. clavipes* (mesoscutum glabrous in other species), and the short metapleural ridge 1 (Fig. 2D, see Fig. 9A for an overview on the metapleural ridges 1–3). The short ridge is shared with *L. fimbriata*, but in other species it is either absent (*L. boulardi*) or at least half the length of the metapleuron.

The metapleural ridge 2 is shorter than half the length of the metapleuron, albeit longer than ridge 1 (Fig. 2D). The ridge 2 is equally long in *L. boulardi*, *L. clavipes* and *L. fimbriata* but at least half the length of the metapleuron in the other species.

A setal patch on the base of the hind coxa is present (Fig. 2D), in contrast to *L. japonica* and *L. boulardi*, where there are at most a few singular setae that are not arranged in a patch.

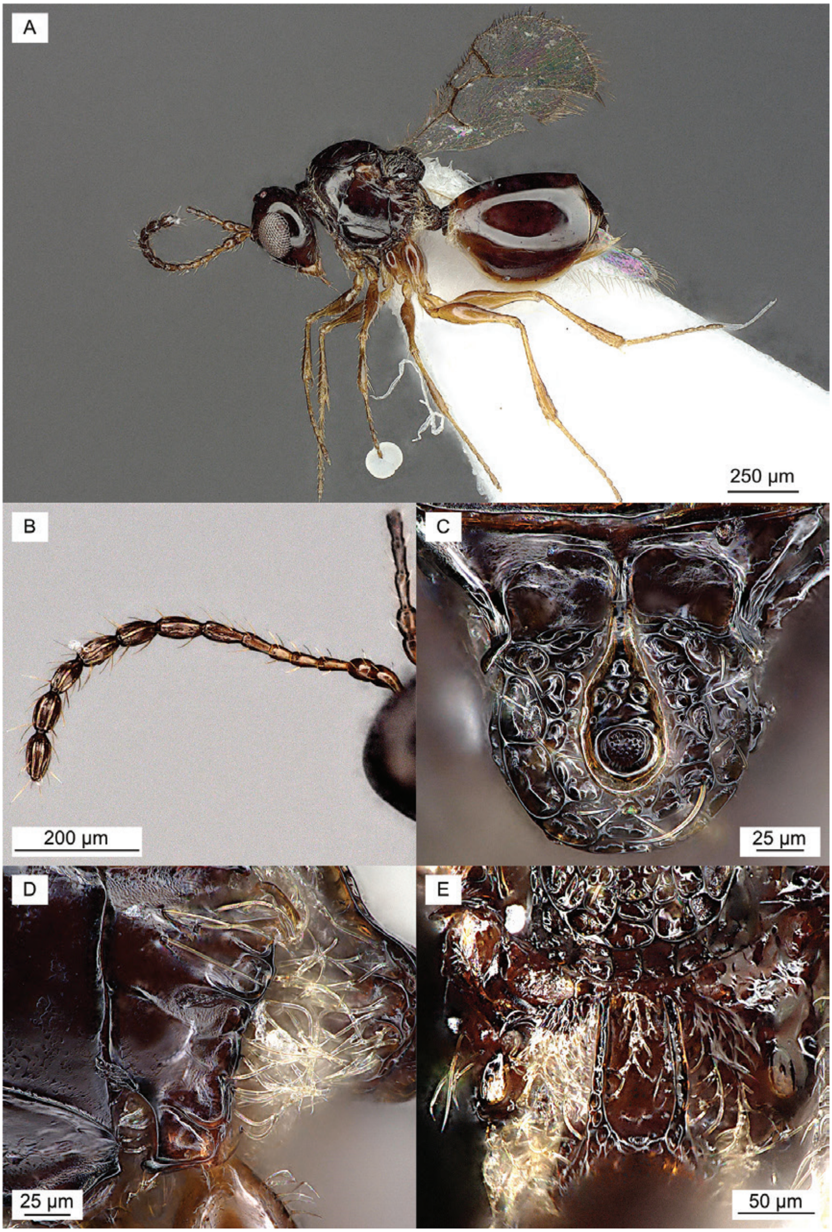

Figure 2. Female specimen of *L. australis* (ZFMK-TIS-2637706) **A** lateral habitus **B** left antenna **C** dorsal view on mesoscutellum **D** lateral view on metapleuron and base of metacoxa **E** posterior view on mesoscutellum and propodeum.

Biology. ***Habitat.*** Occurs in parks and forests, mainly in nemoral deciduous forest, with decaying plant material and fungal fruiting bodies. In one study, the species emerged from *Drosophila* spp. developing in the petioles of *Heracleum mantegazzianum* Sommier & Levier (giant hogweed). Additionally, it shows attraction to

Phallus impudicus L. (common stinkhorn), but was never recovered from it *in situ*. Not attracted to fermenting fruit. Rarely collected in Malaise traps or by sweep netting.

Flight period. July to September.

Host. Mainly *Drosophila limbata* Roser, 1840 and other species within the *Drosophila quinaria* species group (van Alphen et al. 1991; Eijs and van Alphen 1999).

Ex situ reared from *Drosophila kuntzei* Duda, 1924 and *Scaptomyza pallida* (Zetterstedt, 1847), and to a lesser degree from *Drosophila transversa* Fallén, 1823 (van Alphen et al. 1991). Not reared from *D. busckii* Coquillett, 1901, *D. immigrans* Sturtevant, 1921, *D. phalerata* Meigen, 1830, *D. subobscura* Collin, 1936, and *Lordiphosa fenestrarum* Fallén, 1823, despite sharing the ecological niche with the suitable hosts (van Alphen et al. 1991).

Population parameters. Primarily thelytokous with occasional development of males, observed after *ex situ* diapause by van Alphen et al. (1991).

Distribution. Western Palearctic but sparsely distributed, possibly spreading towards northwest but slowly and still uncommon. Armenia (locus typicus of *Rhoptromeris australis*), Belgium (new record), Denmark, the Netherlands and Slovenia.

Remarks. Originally described in the genus *Rhoptromeris* Förster, 1869 but moved to *Leptopilina* Förster, 1869 by Nordlander and Grijpma (1991).

We did not successfully sequence any specimen of *L. australis*. At present, barcode sequence information is available neither on BOLD nor on DROP.

Leptopilina boulardi (Barbotin, Carton & Kelner-Pillault, 1979)

Charips mahensis Kieffer, 1911: 312 – secondary junior homonym in *Leptopilina* of *Erisphagia mahensis* Kieffer, 1911.

Cothonaspis (*Cothonaspis*) *boulardi* Barbotin, Carton & Kelner-Pillault, 1979: 20–26.

Diagnosis. *Leptopilina boulardi* is a small to medium-sized species (up to 1.5 mm ♀ body length) with a stout appearance and relatively short appendages (Fig. 3A).

The species is unique by its smooth metapleuron, having at most a short ridge 2 and the other ridges absent (Fig. 3D). In all other species, the three ridges are at least somewhat developed. Also, the propodeal carinae are diverging to a varying degree in the posterior half of the propodeum (Fig. 3E). Other species have their propodeal carinae running uniformly straight or outwardly curved from the anterior to the posterior margin of the propodeum.

The sculpture on the dorsal surface of the mesoscutellum is striate. The striae are radiating from the base of the mesoscutellar plate (Fig. 3C) and the posterior surface is areolate. The sculpture of *L. heterotoma* is similar, though the striae are more dispersed elong the entire length of the mesoscutellar plate and the posterior surface is foveate-reticulate. In other species, the mesoscutellum is sculptured entirely foveate-reticulate. Just as in *L. japonica*, the setal patch on the base of the metacoxa of *L. boulardi* is absent. There are at most a few singular setae (Fig. 3D).

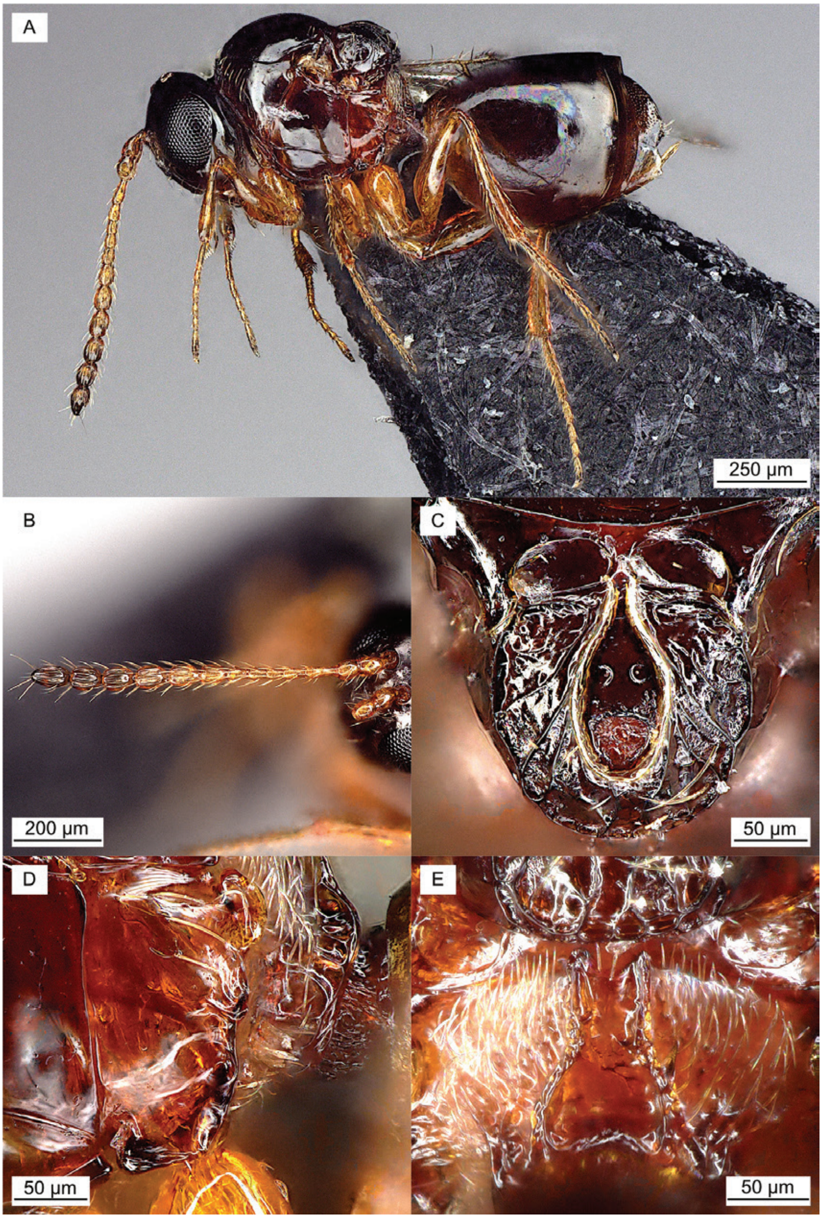

Figure 3. Female specimen of *L. boulardi* (ZFMK-HYM-00039733) **A** lateral habitus **B** left antenna **C** dorsal view on mesoscutellum **D** lateral view on metapleuron and base of metacoxa **E** posterior view on mesoscutellum and propodeum.

The forewing is usually relatively small with a narrow, elongate marginal cell, but can be different and is thereby not sufficient as a diagnostic character.

Biology. ***Habitat.*** Occurs in forests and orchards.

Flight period. At least June to October, mainly July to August, in European data. Clearly able to breed around the year in warm climates, as it is present also in winter months in Macaronesia and North Africa. In data from the USA, there seems to be a distinct spring generation in May, also, there is a record from January in Florida.

Hosts. Specialist of fruit-inhabiting *Drosophila*; emerged from *D. melanogaster* and *D. simulans* Sturtevant, 1919 in fermenting fruits (Nordlander 1980; Vet and van Alphen 1985; van Alphen and Vet 1986; Fleury et al. 2009). Attacks *D. suzukii*, but is not able to develop in this host (Chabert et al. 2012) and is not suitable for application in biological control (Gonzalez-Cabrera et al. 2019).

Ex situ: Reared from *D. virilis* Sturtevant, 1916 and the non-Western Palearctic species *D. erecta* Tsacas & Lachaise, 1974, *D. eugracilis* Bock & Wheeler, 1972, *D. mauritiana* Tsacas & David, 1974, *D. pseudoobscura* Frolova & Astaurov, 1929, *D. sechellia* Tsacas & Bächli, 1981, *D. teissieri* Tsacas, 1971; in some cases, with very high encapsulation rates (Schlenke et al. 2007).

Population parameters. Relative abundance in summer is parallel to *D. simulans* (Fleury et al. 2004; Mazzetto et al. 2016). French populations of *L. boulardi* were fully pro-ovigenic and developed at temperatures between 20–28 °C *ex situ* (Moiroux et al. 2013). Thermal reaction and life history parameters are adapted to macrohabitat and less to geographic range, indicating an adaption to the habitat-specific host range (Moiroux et al. 2013). No *Wolbachia* Hertig, 1936 symbionts were detected in examined populations (Vavre et al. 2009; Wachi et al. 2015).

Distribution. Cosmopolitan species; in Western Palearctic with a center in the Mediterranean region and not extending far north: found in the Canary Islands, France, Greece, Iran, Italy, Madeira, Portugal, Serbia, Spain, Switzerland, Tunisia and Turkey. Also present in the Afrotropics: Democratic Republic of the Congo, Republic of the Congo, Gambia, Ivory Coast, Kenya, Madagascar, Seychelles (locus typicus of *Charips mahensis*), South Africa, Zambia and Zimbabwe; in North America: Canada and USA (east and west); South America: Argentina, Brazil, Guadeloupe (locus typicus of *Cothonaspis boulardi*), and Mexico; and in Australia and Vanuatu. We have not seen records from tropical Asia, but the species is probably also present there.

Remarks. Originally described as *Charips mahensis* Kieffer, 1911, the name became a secondary homonym with *Erisphagia mahensis* Kieffer, 1911 when both species were moved into *Leptopilina* by Nordlander (1980). The junior synonym name *Leptopilina boulardi* (Barbotin, Carton & Kelner-Pillault, 1979) was available and became the valid name of this species, whereas it is the other species, originally *Erisphagia mahensis* Kieffer, 1911 which is now *Leptopilina mahensis* (Kieffer, 1911).

The species was diagnosed and redescribed in Lue et al. (2016) and Nordlander (1980) describes and illustrates some of the morphological variation regarding the propodeal carinae in different *L. boulardi* strains.

We obtained specimens from a laboratory population late during the project and did not see the necessity to sequence the species ourselves because many records identified as *L. boulardi* by hymenopterist experts are already available in GenBank, BOLD and DROP and represent a singular BIN (BOLD:ACB7933, note that one likely erroneously associated specimen image does not show a *Leptopilina boulardi* but an aculeate wasp, accessed 27th June 2025). An unambigous identification of the species with *CO1* barcode data or morphology is comparably unproblematic. We neither included sequences from external sources into the dataset for the species delimitation, nor utilised them for the molecular characterisation of *L. boulardi* because we only included those sequences in the analyses which we could examine morphologically ourselves.

***Leptopilina clavipes* (Hartig, 1841)**

Cothonaspis clavipes Hartig, 1841: 357.

Diagnosis. *Leptopilina clavipes* is a size-variable species with relatively short appendages (Fig. 4A).

The species has a unique mesoscutellum which is not subdivided into a dorsal and posterior surface by a circumscutellar carina or varying sculpture dorsally and posteriorly (Fig. 4E). In other species, there is a more or less clear division by the circumscutellar carina and different sculpture dorsally and posteriorly.

The mesoscutum has rows of setae mediolaterally, just as in the smaller *L. australis* (Fig. 11A, susceptible to damage). None of the other species exhibit these rows of setae.

The metapleural ridge 1 reaches to about half the length of the metapleuron (Fig. 4D), as in *L. longipes*. The other species either possess a longer ridge 1 (*L. japonica* and *L. heterotoma*), a shorter (*L. australis* and *L. fimbriata*), or an absent one (*L. boulardi*).

The metapleural ridge 2 is shorter than half the length of the metapleuron (Fig. 4D) as in *L. australis*, *L. boulardi* and *L. fimbriata*. In all other species, ridge 2 is at least half the length of the metapleuron.

Molecular characterisation.

Maximum intraspecific barcode-distance: -% (1).

Minimum interspecific barcode-distance: 14.3% (*L. longipes*).

CO1 barcode sequence: 658 bp.

5’-TTTAATATATTTTATATTTGGAATTTGGTCAGGGATAGTAGGAGCAAGATTAAGAATAATTATTCGATTAGAGTTAGGAACTCCTGGGCAGTTAATTAATAATGACCAGATTTATAATTCTATAGTGACTGTTCATGCTTTTGTTATAATTTTTTTTATAGTTATGCCTATTATAGTAGGAGGATTTGGTAATTATTTAGTTCCTTTAATAGTTACAGTTCCTGATATGGCTTTTCCTCGTTTAAATAATATGAGATTATGACTTTTATTTCCTTCTTTAATTTTAATGTTAGCTAGTATATTTATTGATCAAGGAGCAGGAACTGGGTGAACTGTGTATCCTCCTCTTTCTTTAAGTGTAAGGCATCCTGGAGTAGCTGTAGATTTAATTATTTTTTCTTTACATTTAAGAGGGGTTTCATCAATTTTAGGGTCTATTAATTTTATTTCTACAATTTTTAATATTCGTCCATTGTTAATAGGGATAGATAAAATTACTTTATTTTTATGATCTATTTTTTTAACAACTATTTTATTATTACTTTCTTTACCTGTATTAGCAGGAGGGATTACAATATTATTATTTGACCGTAATTTAAATACTTCTTTTTATGATCCAGTTGGGGGTGGGGATCCAATTTTGTATCAACATTTATTT-3’.

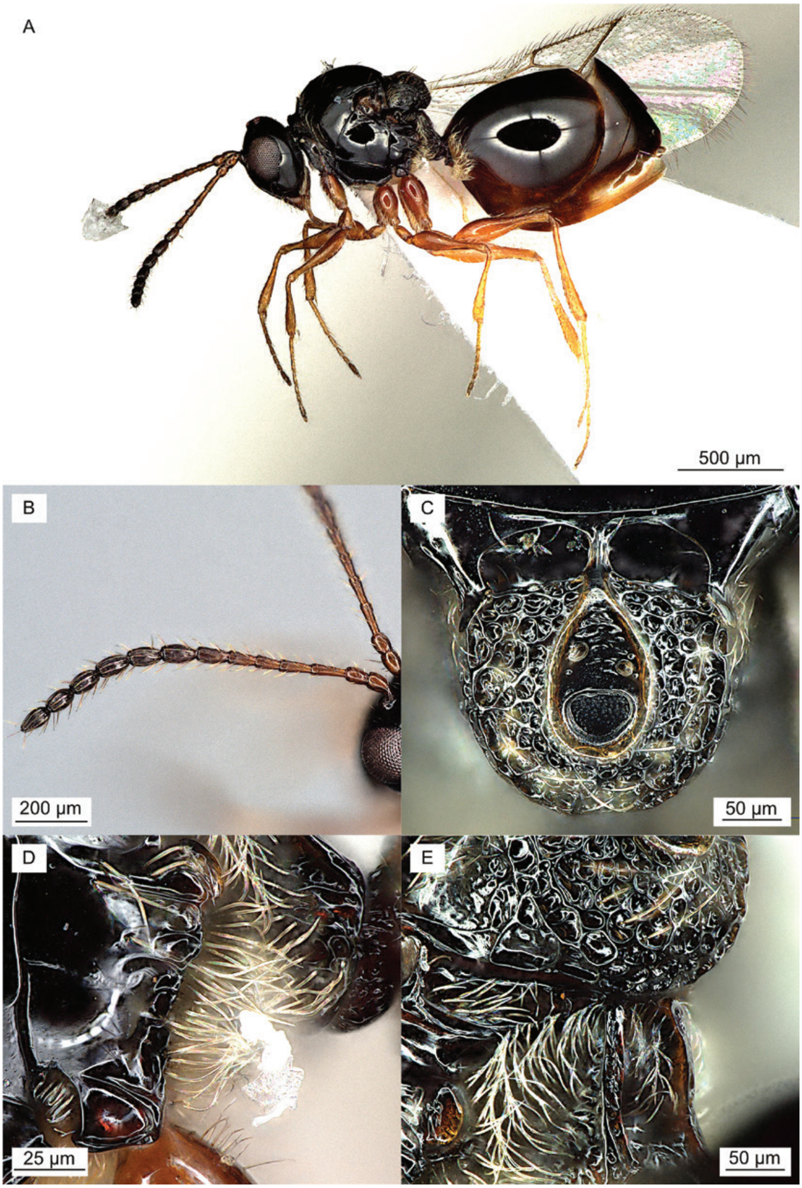

Figure 4. Female specimen of *L. clavipes* (ZFMK-TIS-2637711) **A** lateral habitus **B** left antenna **C** dorsal view on mesoscutellum **D** lateral view on metapleuron and base of metacoxa **E** posterolateral view on mesoscutellum and propodeum.

Biology. ***Habitat.*** Occurs in forests (coniferous and deciduous), open meadows and pastures, if they are more or less damp and contain mushrooms and decaying plant material (e.g. beech forest, spruce plantation, oak grove, railway bank between pastures, alpine meadow, wet mowing meadow). Emerged from decaying mushrooms: *Amanita phalloides* (Vaill. ex Fr.) Link, 1833 (death cap), *Imleria badia* (Fr.) Vizzini, 2014 (bay bolete, reported as *Boletus badius* (Fr.) Fr., 1832), *Phallus impudicus*, *Russula cyanoxantha* (Schaeff.) Fr., 1863 (variegated russula), *Megacollybia platyphylla* (Pers.) Kotl. & Pouzar, 1972 (whitelaced shank, reported as *Tricholomopsis platyphylla* (Pers.) Singer, 1939), also from decaying petioles of *Heracleum mantegazzianum*. Rarely collected in Malaise traps or by sweep netting.

Flight period. May to November, seemingly earlier in southern Europe (May to October, most abundant in June and July) than in northern Europe (July to November, most abundant in August).

Hosts. Fungivorous Drosophilidae of the *Drosophila quinaria* species group. Mostly taken from *D. phalerata* (Vet 1983; van Alphen and Vet 1986; Driessen et al. 1990), also from *D. subobscura*, *D. kuntzei* and *D. transversa* (Driessen et al. 1990).

Ex situ: Reared from *Scaptomyza pallida* (Eijs and van Alphen 1999) and with lower success rates from *Drosophila melanogaster* (Pannebakker et al. 2008).

Population parameters. Host and habitat overlap with *L. australis* and *L. longipes* (Nordlander 1980; van Alphen et al. 1991; Lue et al. 2016), also *L. heterotoma* (Driessen et al. 1990). Mean developmental time in the field: 50 days, with the males taking 2.7 days longer; entering diapause mid-July in the Netherlands which indicates discrete generations (Driessen et al. 1990). Thelytokous with occasional development of males (Driessen et al. 1990; van Alphen et al. 1991), though there is geographic variation within Europe: Arrhenotokous populations are present in the south, which are not infested with *Wolbachia* (Pannebakker et al. 2004; Wachi et al. 2015).

Distribution. Possibly Holarctic: in Europe mainly in Northern and central parts, records from Austria, Belgium (new record), Czech Republic, Denmark, Estonia, Finland, Germany (locus typicus of *Cothonaspis clavipes*), the Netherlands, Norway, Spain, Sweden, and United Kingdom. Also present in eastern USA (and likely Canada, but none of the records confirmed), Japan, and Argentina.

Remarks. The species was diagnosed and redescribed in Lue et al. (2021).

We sequenced one specimen from one location of *L. clavipes*. On BOLD, four BINs include specimens identified as *L. clavipes*: BOLD:ACB6926, BOLD:ACB7032, BOLD:AEH2594 and BOLD:AEH2595. Our sequence falls inside the BIN BOLD:ACB7032. Inside this BIN are two additional specimens identified as *L. clavipes*, one of which was identified by Chia-Hua Lue who is the first author of the Nearctic *Leptopilina* revision (Lue et al. 2016). BOLD:ACB6926 contains eight specimens in total. They are identified as *Leptopilina maia* Lue & Buffington, 2016 (2), *L.* sp. (1), *L.* sp. 3 (4) and *L. clavipes* (1). The BIN matches sequences of *L. maia* in the DROP database. The BINs BOLD:AEH2594 and BOLD:AEH2595 are represented by several specimens that are collected in either the US or Canada. It is likely that these specimens are misidentified as *L. clavipes* and represent one or two different species, possibly belonging to some undescribed Nearctic species near *L. clavipes* available in collections (MF personal observation).

Leptopilina fimbriata (Kieffer, 1901)

Erisphagia longipes Cameron, 1883: 371.
Eucoela (*Eucoela*) *fimbriata* Kieffer, 1901: 174.
Psilosema (*Erisphagia*) *xanthopum* Kieffer, 1904: 605.
Psilosema (*Erisphagia*) *filicorne* Kieffer, 1904: 606–607.
Psilosema longicornis Kieffer, 1907: 619.
Episoda dolichocera Hellén, 1960: 19–20.

Diagnosis. *Leptopilina fimbriata* is a small to medium-sized species (up to 1.6 mm ♀ body length) with slender appearance and remarkably long and filiform antennae in both sexes reaching more than 1.0 times the body length in females and more than 1.9 times the body length in males (Fig. 5A). The metasoma is significantly paler than head and mesosoma, a pattern similar as in *L. longipes*, but more distinct. Also, the legs are strikingly stramineous (Fig. 5A), while they are generally darker (brownish to reddish) in all other species.

Additionally, the mesoscutellar plate is usually notably circular and short in dorsal view (Fig. 5C), and elevated and strongly sloping posteriorly in lateral view (Fig. 5A). Other species possess either a rhombic (*L. heterotoma*) or drop-shaped (all other species), not notably short or elevated mesoscutellar plate, only slightly sloping posteriorly in *L. longipes*.

The metapleural ridge 1 is shorter than half the length of the metapleuron (Fig. 5D) as in *L. australis* and *L. clavipes*. In other species, ridge 1 is at least half as long as the metapleuron, if present at all. The metapleural ridge 2 is shorter than half the length of the metapleuron (Fig. 5D), as in *L. australis*, *L. boulardi*, and *L. clavipes*. In other species, ridge 2 is at least half as long as the metapleuron. The forewing is long with a narrow marginal cell. The forewing vein Rs is clearly longer than 2r, and the accessory veins (M, Rs+M CU1 and CU1a) are usually very distinct (Fig. 12B), while they are faint or absent in other species.

Superficially, *L. fimbriata* is quite similar to *Ganaspis seticornis* Hellén, 1960. This is another eucoiline species from a genus potentially associated with *Drosophila* and the most slenderly built European species in that genus. However, these genera are not closely related. *Ganaspis* is having far more of a hairy ring, less of a petiolar rim, a long row of setae on the metacoxae, and modified F1 instead of F2 in the male antenna.

Molecular characterisation.

Maximum intraspecific barcode-distance: 1.4% (37).

Minimum interspecific barcode-distance: 13.0% (*L. japonica*).

Consensus barcode sequence: 658 bp.

5’-AGTTATATATTTTATTTTTGGGATTTGATCTGGGATAGTGGGGGCGAGATTGAGGATAATTATTCGTATAGAATTGGGGATACCGGGGCAGTTAATTAATAATGATCAAGTTTATAATACTATTGTTACGGCTCATGCATTTATTATAATTTTTTTTATAGTGATACCTATTATAGTTGGTGGGTTTGGGAACTATTTAATTCCTTTAATAATTACAGTTCCTGATATGGCGTTTCCTCGATTAAATAATATAAGATTATGACTTTTATTTCCTTCTTTATTTTTAATGTTAGCTAGAATATTTATTGATCAGGGGGCCGGGACAGGATGAACTGTTTATCCCCCTTTATCTTTAAGAATTGGGCATCCGGGGGTTTCTGTTGATTTAGTGATTTTTTCGTTACATTTAAGGGGGGTTTCTTC-

TATTTTGGGGTCAATTAATTTTATTTCTACTATTTTAAATGTTCGTCCAAATTTAATAATAATGGATAAAGTTACTTTATTTATTTGGTCTATTTTTTTAACAACTATTTTATTACTGTTATCTTTACCGGTATTAGCTGGGGGGATTACAATATTATTATTTGATCGTAATTTAAATACTTCTTTTTATGATCCTGTGGGAGGGGGGGATCCAATTTTGTATCAACATTTATTT-3'.

Biology. ***Habitat.*** Occurs in open and forested sites, as long as there is a layer of leaf litter, but preferrably in structure- and nutrient-rich and more or less damp habitats (e.g. lush garden, alluvial forest, spruce forest, beech forest, young aspen forest, open oak forest, abandoned meadow, shrubby meadow, open sandy pine forest, manure heap in open farmland, calcareous fen, reedbed). Emerged from decaying plant matter (e.g. beet leaves) and *Heracleum mantegazzianum*. Common in Malaise trap and sweep net samples.

Flight period. In Europe, from May to late September, but spring records are sparse and there is a peak in July and August. In Macaronesia also occurring throughout winter.

Hosts. Specialist which has only been found to parasitise *Scaptomyza pallida* (van Alphen and Vet 1986, no specifics mentioned on the methodology, but seemingly an *in situ* observation) and *Drosophila subobscura* (van Alphen & Vet pers comm. in Carton et al. 1986).

Distribution. Palearctic species. Present in Austria, Belgium, the Canary Islands, Czech Republic, Denmark, Estonia, Finland (locus typicus of *Episoda dolichocera*), France (locus typicus of *Eucoela fimbriata*, *Psilosema xanthopum*, *Psilosema filicorne* and *Psilosema longicornis*), Georgia, Germany, Greece, Italy, Lithuania, Madeira, the Netherlands, Norway, Poland, Portugal, Russia, Slovenia, Spain (locus typicus of *Erisphagia longipes*), Sweden, Switzerland, Ukraine, and the United Kingdom. Further East, the species was also recorded from Kyrgysztan and China (BOLD). The published record from the Afrotropical region (van Noort et al. 2015) may be a mistake and requires substantiation.

Remarks. The first available name for this species is *Erisphagia longipes* Cameron, 1883. However, after moving it to *Leptopilina*, it became a junior homonym of *L. longipes* (Hartig, 1841) (Nordlander, 1980). *Leptopilina fimbriata* (Kieffer, 1901), as the second-oldest name, thereby serves as the valid name.

We sequenced 37 specimens of *L. fimbriata* from 11 localities. On BOLD, this species is represented by a single BIN: "BOLD:ACO1262". Our *CO1* sequences are the first representatives of *L. fimbriata* in DROP.

Leptopilina heterotoma (Thomson, 1862)

Eucoila heterotoma Thomson, 1862: 403.
Ganaspis subnuda Kieffer, 1904: 6.
Ganaspis monilicornis Kieffer, 1904: 622–623.
Erisphagia philippinensis Kieffer, 1916: 282.
Pseudeucoila bochei Weld, 1944: 65–66.

Diagnosis. *Leptopilina heterotoma* is a size-variable species but on average large (frequently around 2 mm ♀ body length) with a robust appearance and medium-long antennae (Fig. 6A).

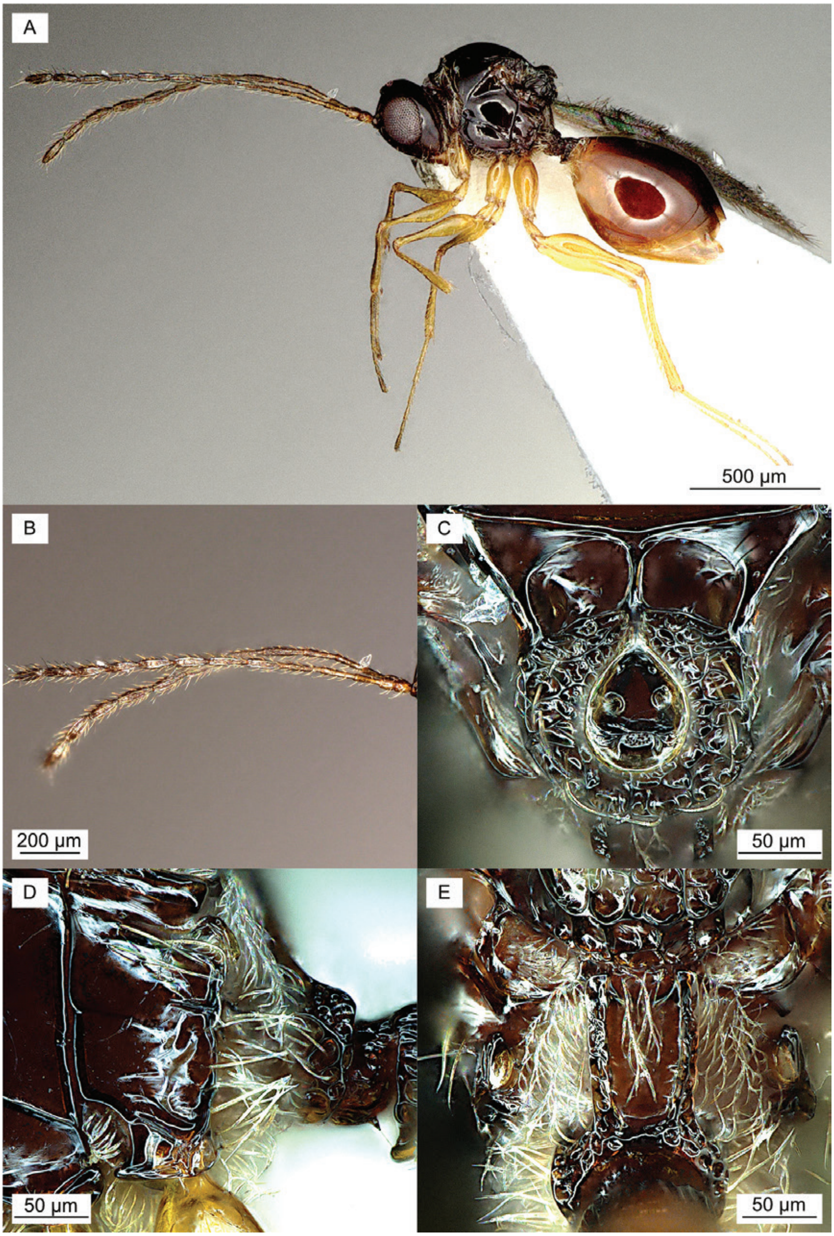

Figure 5. Female specimen of *L. fimbriata* (ZFMK-TIS-2630887) **A** lateral habitus **B** antennae **C** dorsal view on mesoscutellum **D** lateral view on metapleuron and base of metacoxa **E** posterior view on mesoscutellum and propodeum.

The species possesses a uniquely large mesoscutellar plate which is widest in its anterior half, making it rhombic in shape (Fig. 6C). However, the shape is varying slightly and can overlap with that of *L. japonica* and vice versa. The dorsal profile of the mesoscutellar plate usually appears s-shaped in *L. heterotoma* and is more evenly convex in *L. japonica*. The mesoscutellar plate is either more or less circular in *L. fimbriata* or less elongate drop-shaped in all other species.

The metapleural ridges 1 and 2 are reaching (or almost so) the anterior margin of the metapleuron (Fig. 6E), as in *L. japonica*. The ridges 1 and 2 of the other species, if present, reach at most to half the length of the metapleuron. The sculpture of the dorsal surface of the mesoscutellum is mediolaterally areolate. This is somewhat similar to the striae of *L. boulardi*, though the striae in *L. heterotoma* are more equally distributed along the mesoscutellar plate (Fig. 6C), while they are radiating from the base of the mesoscutellar plate in *L. boulardi*. The sculpture of all other species is usually foveate-reticulate. The base of the metacoxa has a setal patch (Fig. 6E), like most other species. Only *L. japonica* and *L. boulardi* have either no patch or at most a few singular setae.

L. heterotoma can be confused with small species of *Trybliographa*, which are similar and closely related but they have a full hairy ring and lack the petiolar rim.

Molecular characterisation.

Maximum intraspecific barcode-distance: 1.1% (45).

Minimum interspecific barcode-distance: 11.7% (*L. japonica*).

Consensus barcode sequence: 658 bp.

5’-TATTATATATTTTATATTTGGAATTTGATCAGGGATAGTAGGGGCAGGGTTAAGGTTGATTGTTCGGATAGAGTTAGGTATACCAGGTCAATTAATTAATAATGATCAAATTTATAATTCTATTGTTACTGCTCATGCATTTATTATAATTTTTTTTATAGTTATACCAATTATAGTTGGAGGATTTGGGAATTATTTAATTCCATTAATACTTACAGTTCCTGATATAGCATTTCCACGTTTAAATAATATAAGTTTATGACTTTTATTTCCTTCTATGATTTTAATATTAGCAAGAATAATAATTGACCAAGGGGCAGGAACAGGATGAACTGTTTACCCTCCTTTATCTCTTAGAGATAGACATCCTGGGGTTTCAACTGATTTAGTAATTTTTTCATTACATTTAAGGGGGGTATCTTCAATTTTAGGGTCTATTAATTTTATTTCAACAATTATTAATATACGACCTTATTTAATATCAATAGATAAAATTACATTATTTGTTTGAGCAATTTTTTTAACAACTATTCTTTTATTGTTATCATTACCTGTTTTAGCAGGAGGAATTACAATATTATTATTTGATCGAAATTTAAATACTTCTTTTTATGATCCTGTTGGAGGAGGAGATCCAATTTTGTATCAACATTTATTT-3’.

Biology. ***Habitat.*** Occurs in both open and forested habitats (nemoral forest, meadows, gardens, orchards), but mainly localities with an abundance of fruit. Most commonly emerging from decaying fruit, less frequently from decaying plant materials, fungi, and tree sap bleed. Common in Malaise trap and sweep net samples.

Flight period. April to October in Europe but common only in July and August. Occurring throughout winter in Macaronesia.

Hosts. Generalist with a wide host range, predominantly in fruit-inhabiting *Drosophila*: *Drosophila busckii*, *D. buzzatii* Patterson & Wheeler, 1942, *D. funebris* (Fabricius, 1787), *D. immigrans*, *D. kuntzei*, *D. melanogaster*, *D. obscura* Fallén, 1823,

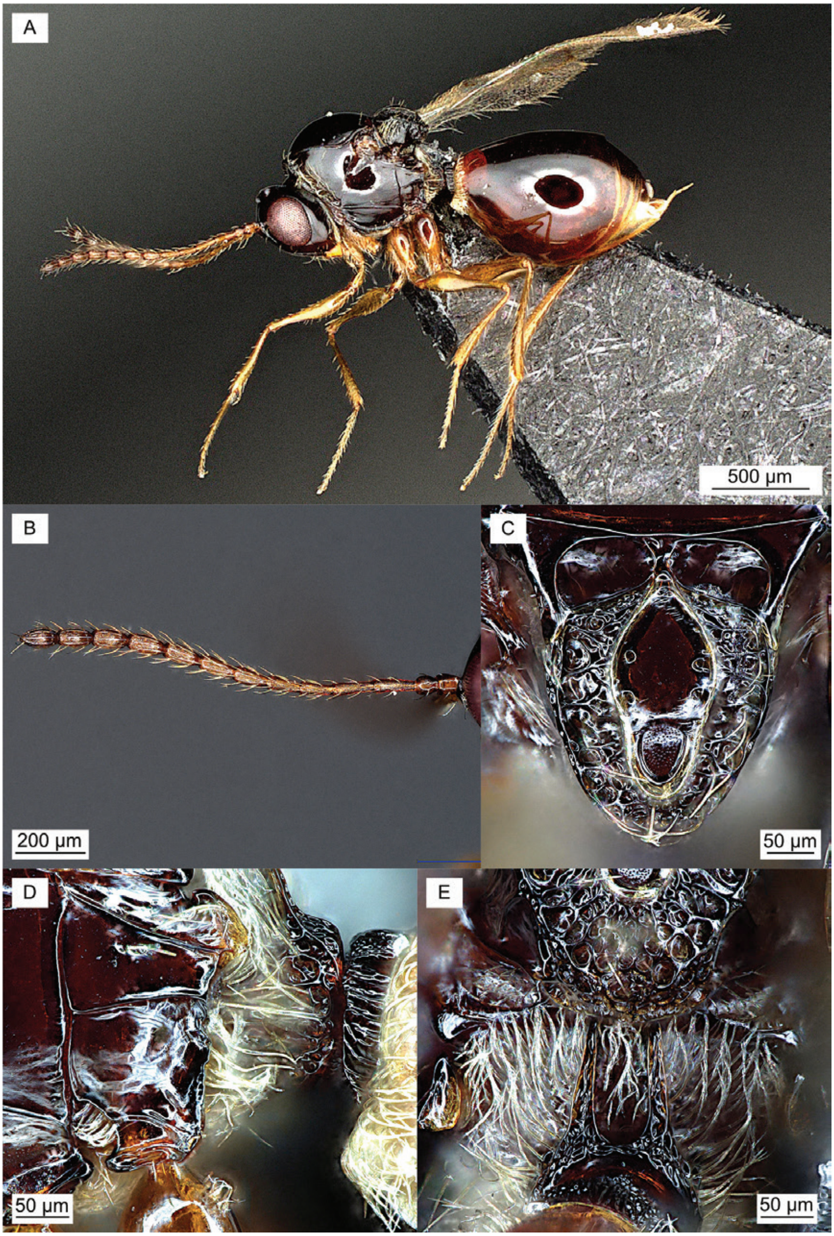

Figure 6. Female specimen of *L. heterotoma* (ZFMK-TIS-2629375) **A** lateral habitus **B** left antenna **C** dorsal view on mesoscutellum **D** lateral view on metapleuron and base of metacoxa **E** posterior view on mesoscutellum and propodeum.

D. phalerata, *D. simulans*, *D. subobscura*, additionally, there are several hosts that are not present in the Western Palearctic: *Drosophila americana* Spencer, 1938, *D. bocqueti* Tsacas & Lachaise, 1974, *D. malerkotliana* Parshad & Paika, 1965, *D. teissieri*, *D. yakuba* Burla, 1954 (rev. in Carton et al. 1986; Carton and Nappi 1991).

Also found in *D. limbata* in decaying plant materials (*Heracleum mantegazzianum*) (Vet and van Alphen 1985; van Alphen et al. 1991). Present in sap bleed of *Quercus robur* L. and *Acer pseudoplatanus* L., but not of *Hippophae rhamnoides* L. (Janssen et al. 1988). Low levels of parasitoidism in fungivorous hosts (*Phallus impudicus*, *Imleria badia*): *Drosophila immigrans*, *D. kuntzei*, *D. phalerata*, *D. picta* Zetterstedt, 1847 (Janssen et al. 1988; Driessen et al. 1990; Poolman Simons et al. 1992).

Ex situ: Reared from *D. bifasciata* Pomini, 1940 (Wachi et al. 2015), *D. hydei* Sturtevant, 1921 (Xie et al. 2010), *D. virilis*, and *Scaptomyza pallida* (Eijs and van Alphen 1999) and the non-Western Palearctic species *D. nigromaculata* Kikkawa & Peng, 1938, *D. orientacea* Grimaldi, James & Jaenike, 1992 (Wachi et al. 2015), *D. erecta*, *D. eugracilis*, *D. lutescens* Okada, 1975, *D. mauritiana*, *D. pseudoobscura*, *D. robusta* Sturtevant, 1916, *D. santomea* Lachaise & Harry, 2000, *D. sechellia*, *D. willistoni* Sturtevant, 1916, and *Zaprionus vittiger* Coquillett, 1901 (Schlenke et al. 2007).

No successful development in *D. suzukii* (Chabert et al. 2012), because eggs get hemocytically encapsulated (Poyet et al. 2013).

Population parameters. The most generalist *Leptopilina* species, predominant in northern France throughout the season and less frequent in the Mediterranean; it competes with *L. boulardi* where the geographical range overlaps and populations appear and peak before *L. boulardi* (Fleury et al. 2004, 2009; Mazzetto et al. 2016). Hosts are attacked at random, but superparasitoidism is avoided and increases with parasitoid density (van Alphen and Vet 1986). In cool temperate regions of Japan, female adults overwinter as a free-living adult while other stages and male adults die (Kimura 2019). It is pro-ovigenic (Vuarin et al. 2012) and infection with *Wolbachia* is possible (Vavre et al. 2009).

Distribution. Cosmopolitan species, widespread in the Western Palearctic: Austria, the Azores, Belgium, Bulgaria, the Canary Islands, Czech Republic, Finland, France (locus typicus of *Ganaspis monilicornis*), Germany, Greece, Ireland, Israel, Italy, Madeira, the Netherlands, Norway, Slovenia, Spain, Sweden (locus typicus of *Eucoila heterotoma*), Switzerland, Tunisia, Turkey, and the United Kingdom. In Eastern Palearctic: Japan; in North America: eastern USA (locus typicus of *Pseudeucoila bochei*), and Canada; in tropical Asia: the Philippines (locus typicus of *Erisphagia philippinensis*), in the Afrotropics: Democratic Republic of the Congo, Madagascar, and St Helena; and in Australia and Vanuatu.

Remarks. A comprehensive review on *L. heterotoma* was recently published by Quicray et al. (2023).

While Novković et al. (2011) found high intra-specific genetic differences between the *CO1*, *ITS1* and *ITS2* sequences of (a limited number of) Japanese specimens of *L. heterotoma* and specimens of a French laboratory strain, questioning whether they were the same species, we could not contribute to solving this issue as our material was exclusively from the Western Palearctic region.

We sequenced 45 specimens of *L. heterotoma* from 36 localities. The currently available sequences on BOLD represent a single BIN "BOLD:ACB8464". Three sequences in DROP (voucher IDs 339, 864 and 817) cluster close together with *L. heterotoma*, but show a high difference (> 6%) to the otherwise comparably homogenous *L. heterotoma* sequences, while two of them (339 and 864) are identified as *L. heterotoma* and the other one (817) as unidentified *Leptopilina*.

Leptopilina japonica Novković & Kimura, 2011

Leptopilina japonica japonica Novković & Kimura, 2011: 341–343.

Diagnosis. *Leptopilina japonica* is a large species (usually around 2 mm ♀ body length) with a robust appearance and medium-long antennae (Fig. 7A).

The species is, together with *L. boulardi*, characteristic in having at most a few singular setae on the base of the metacoxa instead of a distinct setal patch (Fig. 7D), which is typical for all other species. *Leptopilina japonica* differs from *L. boulardi* by the distinct metapleural ridges 1 and 2 that almost reach the anterior metapleural margin (Fig. 7D). The extension of the ridges 1 and 2 is shared with *L. heterotoma*, while all other species have significantly shorter or no ridges. The mesoscutellar plate is similar in shape to that of *L. heterotoma*, being more elongate than those of the other species, but *L. heterotoma* has a typically rhombic mesoscutellar plate, while it is more drop-shaped, being widest in the posterior half, in *L. japonica* (Fig. 7C). The shape is however rather variable and may overlap between the two species. The lateral view of the mesoscutellar plate usually appears s-shaped in *L. heterotoma* and is more evenly convex in *L. japonica*. The sculpture of the dorsal surface of the mesoscutellum is mediolaterally foveate-reticulate, as in most other species (Fig. 7C). Only *L. boulardi* and *L. heterotoma* are areolate instead. The mesoscutellar surface sometimes has additional concentric striae (as in Fig. 7C).

Molecular characterisation.

Maximum intraspecific barcode-distance: 0.6% (6).

Minimum interspecific barcode-distance: 11% (*L. heterotoma*).

Consensus barcode sequence: 658 bp.

5'-TGTAATGTATTTTGTTTTTGGTATTTGGTCTGGGATAGTGGGGGCTGGGTTAAGATTCCTTGTTCGTACAGAATTAGGGATACCTGGGCAGTTGATTAATAATGATCAAATTTATAATTCAATTGTAACTGCTCATGCTTTTGTTATAATTTTTTTTATAGTGATACCAATTATGGTTGGGGGGTTTGGCAATTATTTAGTACCATTAATATTAACTGTTCCTGACATAGCTTTCCCTCGATTGAATAATATAAGATTATGATTATTATTTCCTTCAATGATTTTAATGGTGGCAAGGATGATAATTGATCAAGGGGCAGGGACAGGGTGAACGGTTTATCCTCCTTTATCTTTAATAGATAGTCATCCTGGGGTTTCTACTGATTTAGTAATTTTTTCATTACATTTAAGAGGGGTATCTTCGATTTTAGGGTCAATTAATTTTATTTCTACTATTATTAATATACGTCCTTATTTAATAACAATAGATAAAATTACTTTATTTATTTGAGCTATTTTTTTTAACAACAATTCTTTTATTATTATCTTTACCTGTTTTAGCAGGGGGGATTACTATATTATTATTTGATCGTAATTTAAATACTTCTTTTTATGATCCTGTTGGAGGGGGGGACCCAATTTTGTATCAACATTTATTT-3'.

Biology. ***Habitat.*** Outside of the native range in East Asia, mostly found in orchards, parks, residential areas, and forests, if they contain suitable plants for *D. suzukii*, in the native range found in forests. Common in Malaise trap and sweep net samples.

Flight period. In Europe, from May to November, but most abundant in late summer.

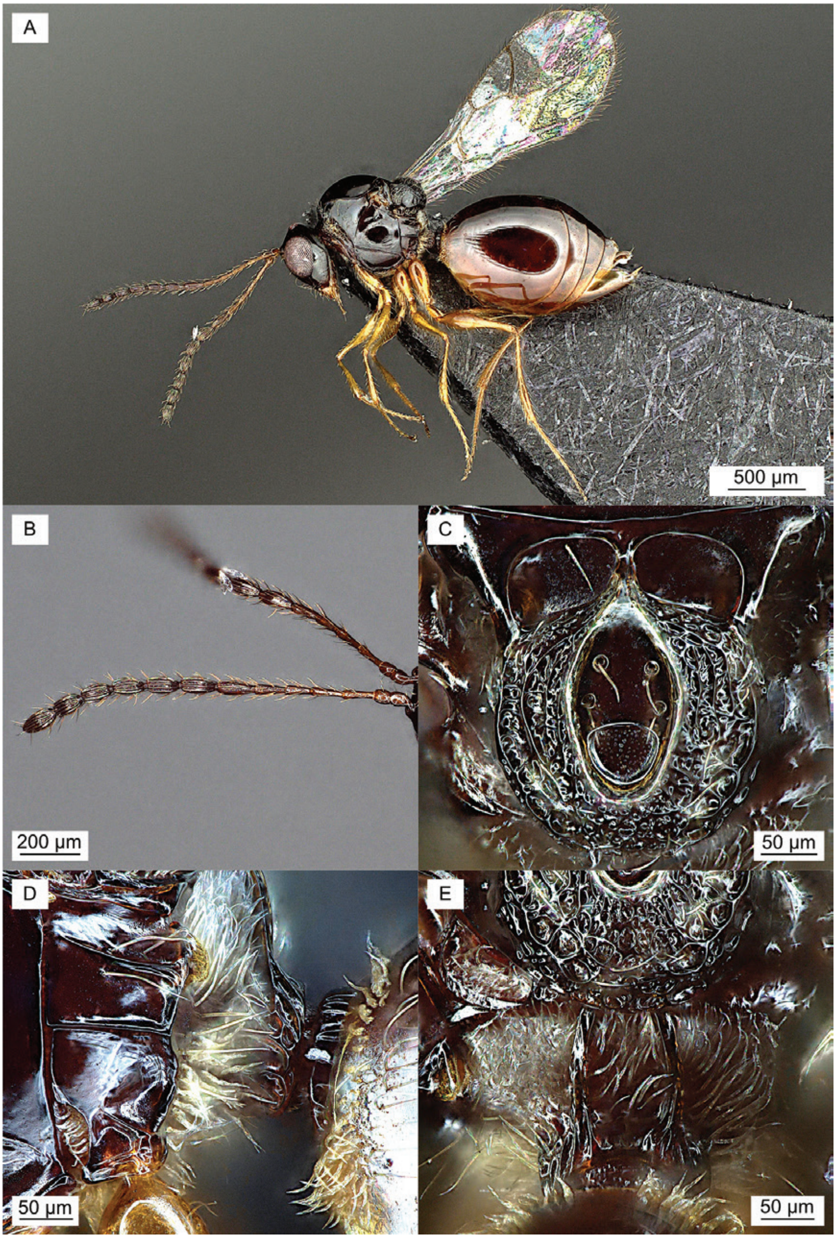

Figure 7. Female specimen of *L. japonica* (ZFMK-TIS-2632471) **A** lateral habitus **B** left antenna **C** dorsal view on mesoscutellum **D** lateral view on metapleuron and base of metacoxa **E** posterior view on mesoscutellum and propodeum.

Host. In the native range, *L. japonica* has been reared from *Drosophila suzukii* (Daane et al. 2016) and the non-Western Palearctic hosts *D. biauraria* Bock & Wheeler, 1972, and *D. rufa* Kikkawa & Peng, 1938 (Novković et al. 2011).

Ex situ, it has also been reared from *D. bifasciata*, *D. busckii*, *D. funebris*, *D. immigrans*, *D. melanogaster*, *D. simulans*, and *D. subobscura* (Novković et al. 2011; Kimura and Novković 2015; Girod et al. 2018a; Daane et al. 2021) and the non-Western Palearctic hosts *D. auraria* Peng, 1937, *D.* sp. aff. *bicornuta* Bock & Wheeler, 1972, *D. bipectinata* Duda, 1923, *D. bocki* Baimai, 1979, *D. lutescens*, *D. montana* Patterson & Wheeler, 1942, *D. orientacea*, *D. persimilis* Dobzhansky & Epling, 1944, *D. pseudoobscura*, *D. robusta*, *D. sulfurigaster* (Duda, 1923), *D. takahashii* Sturtevant, 1927, and *Hirtodrosophila duncani* (Sturtevant, 1918), but with very mixed success rates (Kimura and Novković 2015; Daane et al. 2021). Another three species were attacked with no parasitoid emergence (Kimura and Novković 2015). Parasitoidism success may depend on the geographic origin of parasitoid or host (Kimura and Novković 2015; Girod et al. 2018a).

Unlike native *Leptopilina* species from the Western Palearctic, *L. japonica* can overcome the immune response of *D. suzukii* (Chabert et al. 2012). While it has also been collected together with closely related *Drosophila*, *L. japonica* is associated with *D. suzukii* in the native ranges (Girod et al. 2018b; Matsuura et al. 2018) and in the non-native ranges. In North America, *in situ* parasitoidism of the *Drosophila obscura* species group and the *D. melanogaster* species group has been observed (Paul K. Abram personal communication). As a result of the close association with *D. suzukii* in the Western Palearctic, *L. japonica* has mostly been found in habitats with fruiting plants that host *D. suzukii* (Abram et al. 2022; Gariepy et al. 2024; Rossi-Stacconi et al. 2025).

Population parameters. Moderately pro-ovigenic (Wang et al. 2018), no *Wolbachia* infection is known (Wachi et al. 2015). Forming multiple generations per season (Rossi-Stacconi et al. 2025).

Distribution. Non-native species in the Western Palearctic, originally from East Asia. In Europe since 2019: present in Belgium (since 2022, new record), France (since 2022, Rousse et al. 2023), Germany (since 2021, Martin et al. 2023), Italy (since 2019, Puppato et al. 2020), Switzerland (since 2021, Rossi-Stacconi et al. 2025), and the United Kingdom (since 2024, Powell et al. 2025). In Asia present in China (Daane et al. 2016), Japan (Novković et al. 2011), and South Korea (Giorgini et al. 2019). It has spread to Canada since 2016 (Abram et al. 2020) and to the USA since 2020 (Beers et al. 2022). Records in 2023 and 2024 from Northern Germany in the state of Brandenburg represent the globally northernmost detections of this species so far (Rossi-Stacconi et al. 2025).

Remarks. A comprehensive review on *L. japonica* was recently published by Rossi-Stacconi et al. (2025).

In their original description, Novković & Kimura separated *L. japonica* into two subspecies: the subtropical *Leptopilina japonica formosana* Novković & Kimura, 2011, found in Taiwan, and the temperate *Leptopilina japonica japonica* Novković & Kimura, 2011, found in Japan (Novković et al. 2011; Murata et al. 2013). In accordance with the respective climatic preferences reported by Murata et al. (2013), populations in Europe and North America have been identified to belong to *L. j.*

japonica (Gariepy et al. 2024; Rossi-Stacconi et al. 2025). In this publication, we exlusively refer to *L. j. japonica* when we write *L. japonica*. Novković et al. (2011) describe the separation of the subspecies as challenging, as the described diagnostic differences consist only of the darker antenna and a narrower and elongated mesoscutellar plate of *L. j. formosana* compared to *L. j. japonica*. However, the subspecies are in need of taxonomic re-evaluation and will likely be elevated to species-rank based on genetic and morphological data (Ionela-Madalina Viciriuc and Matthew L. Buffington pers. comm.).

The data provided here contain two hitherto unpublished records of *L. japonica* collected in 2022, one from Bonn (Germany, ZFMK-TIS-2637732) and the other collected in Ypres (Belgium, ZFMK-TIS-2637792). The latter represents a new country record and is, together with the recently published record from the United Kingdom (Powell et al. 2025), another indicator of the rapid spread of *L. japonica* within Europe.

The absence of the setal patch on the metacoxal base is a previously unrecognised character that is consistent in both males and females throughout our material and that from the Nearctic (Matt Buffington and Paul K. Abram pers. Comm.). This character, only shared with the otherwise quite distinct *L. boulardi*, facilitates the diagnosis of *L. japonica* substantially.

We sequenced six specimens of *L. japonica* from two localities. On BOLD, sequences of 499 specimens are recorded, forming three BINs. Our sequences are assigned to the BIN "BOLD:ACD4002" only. The specimens behind the other two BINs require further taxonomic evaluation.

Leptopilina longipes (Hartig, 1841)

Cothonaspis longipes Hartig, 1841: 356.
Eucoila pusilla Giraud, 1860: 142 syn. nov. (type in MNHN studied by MF).
Rhoptromeris rutilus Belizin, 1966: 12 syn. nov. (type in ZIN studied by GN).

Diagnosis. *Leptopilina longipes* is a size-variable species with relatively slender appearance, medium-long antennae, and the metasoma is notably paler than the head and mesosoma (Fig. 8A).

The species is unique in having the propodeal carina well separated from the mesoscutellum by a part of the metanotum (Fig. 8E). Other species show at most an insignificant gap.

The metapleural ridge 1 and 2 are of similar length, reaching about half the length of the metapleuron (Fig. 8D). In other species, the lengths of ridge 1 and 2 are dissimilar, or they reach the anterior margin of the metapleuron (*L. japonica* and *L. heterotoma*). Whereas other species have a more or less unicoloured body, the metasoma of *L. longipes*, especially of the females, is distinctly paler amber-coloured than the head and mesosoma (Fig. 8A). This colouration pattern is similar

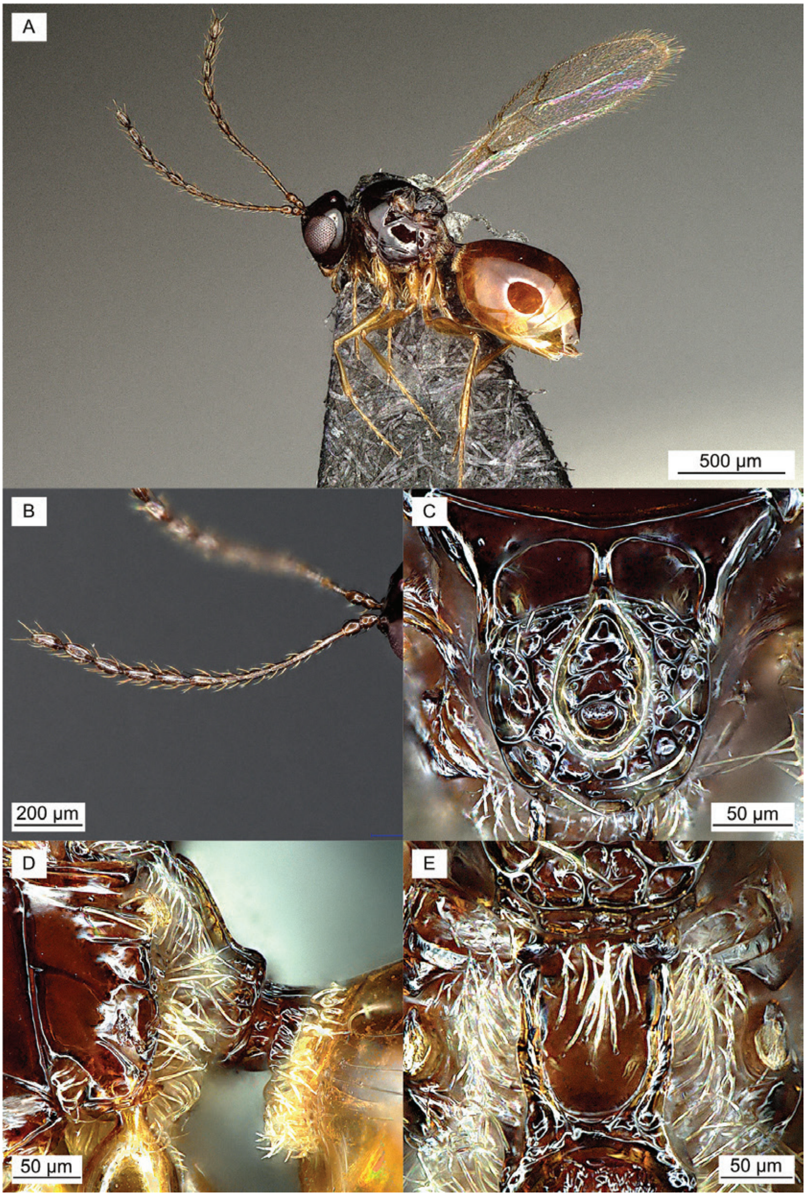

Figure 8. Female specimen of *L. longipes* (ZFMK-TIS-2631095) **A** lateral habitus **B** left antenna **C** dorsal view on mesoscutellum **D** lateral view on metapleuron and base of metacoxa **E** posterior view on mesoscutellum and propodeum.

to that of *L. fimbriata*, where it is usually even more distinct. The surface anterior to the glandular pit of the mesoscutellar plate is concave and areolate (Fig. 8C), as it is in *L. australis* and *L. clavipes*. That area is mostly smooth in all other species. The female antenna is usually more uniformly dark, with all flagellomeres brown to dark brown (Fig. 8B), while all other species have at least a few proximal flagellomeres pale brown or even yellow.

Molecular characterisation.

Maximum intraspecific barcode-distance: 0.5% (2).

Minimum interspecific barcode-distance: 14.3% (*L. clavipes*).

Consensus barcode sequence: 658 bp.

5’-TATAATATATTTTATATTTGGTATTTGATCAAGTATAGTAGGGGCAAGGCTAAGAATAATTATTCGAATAGAGTTAGGGACTGTAACTCAGTTAATTAATAATGATCAGATTTATAATTCTATTGTTACGGCTCATGCATTTGTAATAATTTTTTTTATAGTTATACCTATTATAGTGGGAGGGTTTGGTAATTATTTGGTTCCTTTAATAGTTAGAGTTCCTGACATAGCTTTTCCTCGTCTTAATAATATAAGGTTATGATTATTATTTCCTTCTTTAATTTTAATAATTACAAGAATATTTATTGATCAGGGGGCAGGGACTGGGTGAACGGTGTATCCTCCTTTATCTTTATCTATAAGGCATCCTGGTGTGGCACCTGATTTAGTAATTTTTTTCTTTACATTTGAGGGGGGTATCTTCAATTTTAGGGGCAATTAATTTTATTACTACAATTATAAATATACGACCAAAAATAATATCTATAGATAAAATTTCTTTATTTGTTTGATCTATTTTTTTAACTACAATTTTACTTTTATTATCTTTACCTGTGTTAGCTGGAGGAATTACAATATTATTATTTGATCGTAATTTAAATACTTCTTTTTATGATCCWATTGGAGGGGGGGAWCCTATTTTGTATCARCATTTATTT-3’.

Biology. ***Habitat.*** Occurs in both open and forested localities with mushrooms and decaying plant matter. Found in spruce forests and alder forests, but also in coastal sand dunes. In Japan found mostly in domestic areas. Rarely collected with Malaise traps or by sweep netting.

Flight period. July to September, with a slight peak in August.

Hosts. Reared from *Scaptomyza pallida* and *Drosophila quinaria* species group: *Drosophila kuntzei*, *D. limbata*, *D. phalerata* and emerged together with these hosts in the Netherlands from decaying plant matter (cucumber bait) (Hardy et al. 1992) and *Heracleum mantegazzianum* petioles, as well as from *Agaricus bisporus* (J. E. Lange) Imbach, 1946 (cultivated mushroom) (van Dijken and van Alphen 1998). Also emerged from *Fomitopsis pinicola* (Sw.) P. Karst., 1881 (red-belted conk), where *Leptopilina longipes* probably was parasitoid of *Leucophenga quinquemaculata* Strobl, 1893 (Jonsell et al. 1999). In Japan taken from *Drosophila simulans*, but also *D. immigrans* and the non-Western Palearctic *D. auraria* species complex and *D. nigromaculata* in banana bait (Kimura 2015).

Ex situ reared from *D. subobscura* (Eijs and van Alphen 1999). Not found in fermenting apples (van Dijken and van Alphen 1998).

Population parameters. While there are thelytokous populations in Japan (Wachi et al. 2015), samples from Europe include males and females (Nordlander 1980). Probably univoltine (Hardy et al. 1992). In Japan, *L. longipes* overwinters in prepupal diapause (unpublished data in Kimura 2019). During probing, it holds the antennae remarkably straight and does not touch the substrate; efficient at finding hosts at low densities (van Dijken and van Alphen 1998).

Distribution. Restricted to the Palearctic; mainly northern and central Europe: found in Austria (locus typicus of *Eucoila pusilla*), Bulgaria, Croatia, Czech Republic, Denmark, Finland, Georgia, Germany (locus typicus of *Cothonaspis longipes*), Moldova (locus typicus of *Rhoptromeris rutilus*), the Netherlands, Norway, Sweden, Switzerland, and the United Kingdom. Outside of Europe only known from Japan.

Remarks. We sequenced two specimens of *L. longipes* from two localities. The currently available sequences on BOLD represent a single BIN "BOLD:ACS3295". In DROP, two *CO1* sequences of *L. longipes* are available, both of which match with our sequences (< 2% difference), though one (voucher ID: 330) is listed as unidentified.

Key to the species (both sexes)

1 Metapleural ridge 2 present, reaching or almost reaching the anterior margin (Fig. 9A); mesoscutellar plate elongate drop-shaped or rhombic (Figs 6C, 7C) **2**

– Metapleural ridge 2 absent or present, but reaching at most half the length of the metapleuron (Fig. 9B); mesoscutellar plate less elongate drop-shaped to circular (Figs 2C, 3C, 4C, 5C, 8C). **3**

2 Metacoxa basally with patch of setae (Fig. 9A); mesoscutellar plate rhombic, widest in anterior half (Fig. 10B) and somewhat s-shaped in profile (Fig. 6A); dorsal surface of mesoscutellum mediolaterally areolate, sometimes with intermixing reticulation (Fig. 10B) .... ***L. heterotoma* (Thomson, 1862)**

– Metacoxa basally without patch of setae, at most with a few singular setae (Fig. 9B); mesoscutellar plate usually drop-shaped, widest in posterior half (Figs 7C, 10A) and more evenly convex in lateral view (Fig. 7A); dorsal surface of mesoscutellum usually foveate-reticulate (Fig. 10A), sometimes with additional concentric striae (Fig. 7C) .... ***L. japonica* Novković & Kimura, 2011**

3 Metapleural ridge 3 absent (Fig. 9B); dorsal surface of mesoscutellum striate with radial diverging striae (Fig. 9E). .... ***L. boulardi* (Barbotin, Carton & Kelner-Pillault, 1979)**

– Metapleural ridge 3 well-developed (Fig. 9A); dorsal surface of mesoscutellum foveate-reticulate (Fig. 10A) to areolate-reticulate (Fig. 2C) **4**

4 Mesoscutellar surface continuously foveate-reticulate, not separable into dorsal and posterior surfaces by circumscutellar carina or varying sculpture (Fig. 4C); mesoscutum with rows of setae mediolaterally (Fig. 11A) .... ***L. clavipes* (Hartig, 1841)**

– Mesoscutellar surface separable into dorsal and posterior surface by circumscutellar carina or varying sculpture, usually being foveate-reticulate dorsally and areolate posteriorly (Figs 2E, 3E, 5E, 6E, 7E, 8E); mesoscutum with or without rows of setae mediolaterally **5**

5 Metapleural ridge 2 longer than ridge 1 that is (almost) absent (Fig. 8D); mesoscutum with rows of setae mediolaterally (Fig. 11A) .... ***L. australis* (Belizin, 1966)**

– Metapleural ridge 2 as long as or shorter than ridge 1 that is clearly present; mesoscutum without rows of setae mediolaterally (Fig. 11B). **6**

6 Antennae not very long (♀ 0.7–0.8 times body length, ♂ 1.5–1.6 times body length, Fig. 8B); ♀ antenna claviform (Fig. 8B); surface anterior to the glandular pit of the mesoscutellar plate concave and areolate (Fig. 8C); mesoscutellar plate not notably short (Figs 10A, 8C), weakly sloping posteriorly in lateral view (Fig. 8A); propodeal carinae well separated from the mesoscutellum by a part of the metanotum (Fig. 8E); marginal cell of forewing moderately wide, with vein Rs of almost equal length as 2r (like in an isosceles triangle), accessory veins (M, Rs+M CU_1 and CU_{1a}) usually not very distinct (Fig. 12A) .... ***L. longipes* (Hartig, 1841)**

– Antennae very long (♀ 1–1.2 times body length, ♂ 1.9–2 times body length, Fig. 5B); ♀ antenna filiform (Fig. 5B); mesoscutellar plate smooth and even anterior of the glandular pit, usually notably short (Fig. 5C), strongly sloping posteriorly in lateral view (Fig. 5A, C); propodeal carinae not separated from the mesoscutellum by a part of the metanotum (Fig. 5E); marginal cell of forewing long and narrow, with vein Rs clearly longer than 2r (like a triangle somewhat tilted outwards), accessory veins (M, Rs+M CU_1 and CU_{1a}) usually distinct (Fig. 12B) .... ***L. fimbriata* (Kieffer, 1901)**

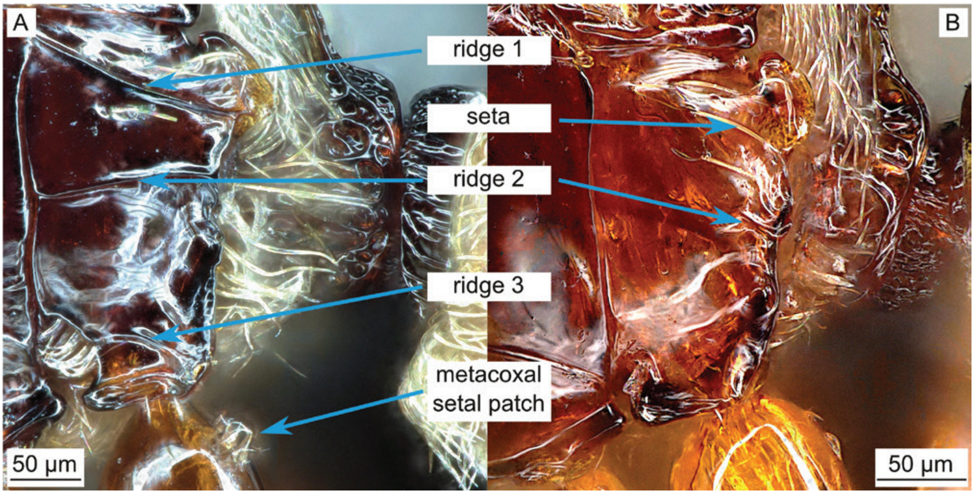

Figure 9. Lateral view on the metapleuron and base of metacoxa, highlighting shape and position of the metapleural ridges (note that their extent is described from posterior to anterior throughout the manuscript) and the metacoxal setae **A** female specimen of *L. heterotoma* (ZFMK-TIS- 2629375, facing left) with highlighted metapleural ridges 1–3 and the setal patch on the metacoxa **B** female specimen of *L. boulardi* (ZFMK-HYM-00039733) with highlighted short ridge 2 and a seta that might be mistaken as a ridge.

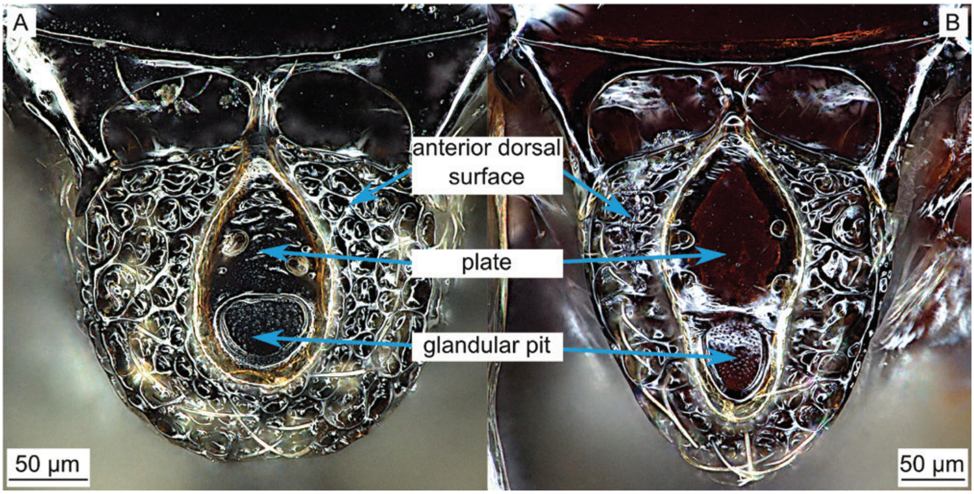

Figure 10. Dorsal view on the mesoscutellum highlighting the anterior dorsal surface, the mesoscutellar plate and its glandular pit **A** female specimen of *L. clavipes* (ZFMK-TIS-2637711) **B** female specimen of *L. heterotoma* (ZFMK-TIS- 2629375).

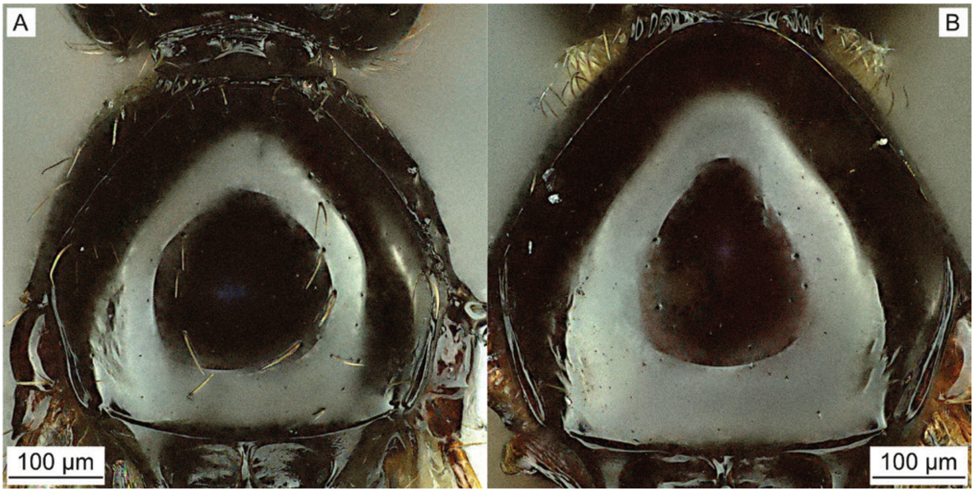

Figure 11. Dorsal view on the mesoscutum showing present or absent rows of setae (the whiteish rings on the mesuscutum are reflections of the ring light used for imaging) **A** female specimen of *L. clavipes* (ZFMK-TIS-2637705) with distinct rows of setae mediolaterally **B** female specimen of *L. heterotoma* (ZFMK-TIS-2629375) without distinct rows of setae mediolaterally.

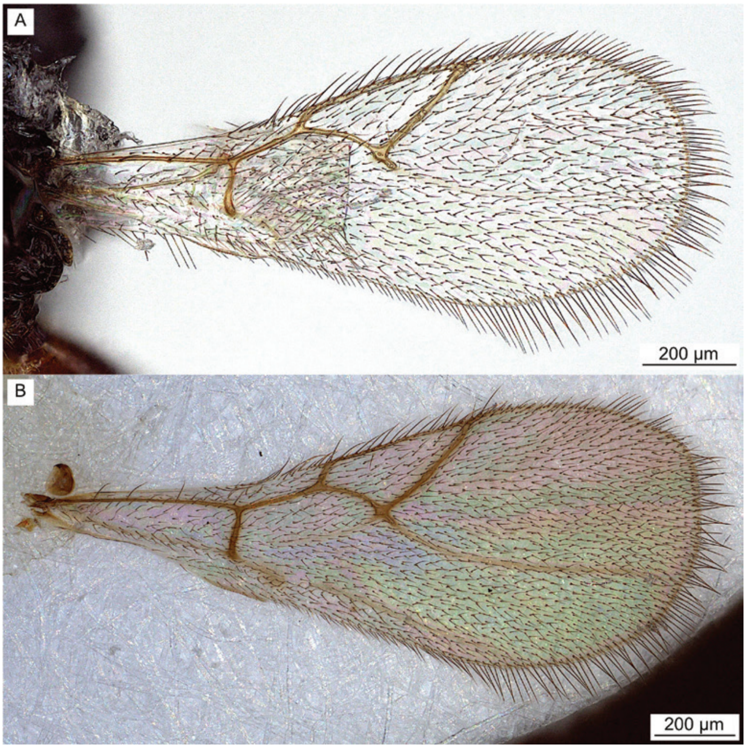

Figure 12. Forewing showing differences in distinctiveness of accessory veins of **A** *L. longipes* (female, ZFMK-TIS- 2631095) with less distinct accessory veins and **B** *L. fimbriata* with more distinct accessory veins (image flipped horizontally, female, ZFMK-TIS-2630887).

World *Leptopilina* species grouped by region

Eastern Palearctic

No regional overview has been published for the Eastern Palearctic, but the Japanese fauna was treated by Novković and Kimura (2011) and Wachi et al. (2015). All of the Western Palearctic species treated in this paper, except *L. australis*, are known to occur in the Eastern Palearctic as well. It can be noted that there is an undescribed species which has been the subject of several scientific studies without having been formally described (referred to in these studies as *Leptopilina myrica*, which is an unavailable nomen nudum) (i.e. Guo et al. 2024; Zhang et al. 2024; Dong et al. 2025).

L. boulardi (Barbotin, Carton & Kelner-Pillault, 1979)
L. clavipes (Hartig, 1841)
L. decemflagella Lue & Buffington, 2016

L. fimbriata (Kieffer, 1901)
L. heterotoma (Thomson, 1862)
L. japonica Novković & Kimura, 2011
L. lasallei Buffington & Guerrieri, 2020
L. longipes (Hartig, 1841)
L. pacifica Novković & Kimura, 2011
L. ryukyuensis Novković & Kimura, 2011
L. tokioensis Wachi & Kimura, 2015
L. tsushimaensis Wachi & Kimura, 2015
L. victoriae Nordlander, 1980

Oriental

There are no regional summaries or studies for this region. Of the Western Palearctic species treated in this study, *L. heterotoma* and *L. japonica* are known to occur, and surely also *L. boulardi* even though we failed to find a published record. Clearly, most of the Oriental *Leptopilina* species remain undescribed.

L. boulardi (Barbotin, Carton & Kelner-Pillault, 1979)
L. cupulifera (Kieffer, 1916) (*Erisphagia*)
L. heterotoma (Thomson, 1862)
L. japonica Novković & Kimura, 2011
L. philippinarum (Kieffer, 1916) comb. nov. (*Eucoila*) Type in MHNH studied by MF
L. rufipes (Cameron, 1908) (*Psilosema*)
L. victoriae Nordlander, 1980

Nearctic

A regional overview was published in Forshage et al. (2013) with additions in Lue et al. (2016) and Bennett et al. (2024). Of the Western Palearctic species treated in this study, several occur in the Nearctic as well: *Leptopilina boulardi*, *L. clavipes*, *L. heterotoma*, and *L. japonica*.

L. boulardi (Barbotin, Carton & Kelner-Pillault, 1979)
L. clavipes (Hartig, 1841)
L. decemflagella Lue & Buffington, 2016
L. heterotoma (Thomson, 1862)
L. japonica Novković & Kimura, 2011
L. leipsi Lue & Buffington, 2016
L. maia Lue & Buffington, 2016
L. nigroclavata (Kieffer, 1907) (*Eucoila*)
L. vitellinipes (Kieffer, 1907) (*Eucoela*)

Afrotropic

A regional overview was published in Quinlan (1988), updated in Allemand et al. (2002) and summarized in van Noort et al. (2015). Species also occurring in the Western Palearctic and treated in this study are *L. boulardi* and *L. heterotoma*, and possibly *L. fimbriata* (yet doubtful record). Despite the relatively large number of described species, knowledge of diversity and distribution of African *Leptopilina* is very scarce and many of these names may be synonyms while other species remain undescribed.

L. africana (Kieffer, 1911) (*Eucoila*)
L. apella Quinlan, 1988
L. atraticeps (Kieffer, 1911) (*Ectolyta*)
L. boulardi (Barbotin, Carton & Kelner-Pillault, 1979)
L. cavernicola (Kieffer, 1913) (*Eucoila*)
L. drosophilae (Kieffer, 1913) (*Eucoila*)
L. dulcis (Quinlan, 1986) (*Cothonaspis*)
L. fannius Quinlan, 1988
L. faunus Quinlan, 1988
L. fenerivae (Kieffer, 1910) (*Psilosema*)
L. fimbriata (Kieffer, 1901), doubtful record
L. freyae Allemand & Nordlander, 2002
L. guineaensis Allemand & Nordlander, 2002
L. heterotoma (Thomson, 1862)
L. itys Quinlan, 1988
L. mahensis (Kieffer, 1911) (*Erisphagia*)
L. misensus Quinlan, 1988
L. orientalis Allemand & Nordlander, 2002
L. pisonis Quinlan, 1988
L. syphax Quinlan, 1988
L. thetus Quinlan, 1988
L. vesta Quinlan, 1988
L. victoriae Nordlander, 1980

Oceanic/australasian

No regional overview has been published but the Australian fauna is listed in Paretas-Martinez et al. (2013) and the Hawaiian fauna was treated by Beardsley (1989). Species also occurring in the Western Palearctic and treated in this study are *L. boulardi* and *L. heterotoma*. Despite the relatively large number of described species, knowledge of diversity and distribution of *Leptopilina* in this region is very scarce and several of these names may be synonyms while others remain undescribed.

Here we synonymise the genus *Ditanyomeria* Yoshimoto, 1963 (1963b) under *Leptopilina* syn. nov. Alfred Kinsey had received some figitids from the Marquesas islands, and due to his documented interest in variation described them as four different species of the same species group even if they were quite similar (Kinsey 1939). The holotypes were intended to be deposited at the Hawaii BPBM, but apparently, they never arrived there (as noted by Yoshimoto 1963a). In Kinsey's collection at AMNH there are specimens of all species, but explicitly paratypes, which perhaps indicates that the holotypes have indeed been lost rather than never sent. Weld (1952) considered Kinsey's species tentatively to belong to a separate, undescribed genus and referred to it as "new genus F". Yoshimoto (1963a), however, was of the impression that Kinsey had used the phrase *Eucoila* (*Marquesiana*) to indicate a new subgenus rather than just a species group. Thus, erroneously believing that *Marquesiana* was an available name of genus-group level rank, he raised it to full genus rank. He did so without having seen Kinsey's specimens, but adding and describing specimens of his own which he considered to belong to one of Kinsey's species. Later the same year, Yoshimoto (1963b) had realised that *Marquesiana* was an unavailable name and instead described the new genus as *Ditanyomeria* (still without having seen the type material). Looking at Kinsey's paratypes at AMNH, it is obvious that they are *Leptopilina* and at least close to *L. boulardi*, but species-level synonymy for exotic groups has not been considered here.

Furthermore, Yoshimoto had plenty of other *Leptopilina* specimens available, but he described those as new species under the genus name *Pseudeucoila* Ashmead, 1903. At the time, the name *Leptopilina* was not in use, and the name *Pseudeucoila* was being used by many authors for various relatively small representantives of Eucoilini and Ganaspini (though the name *Pseudeucoila* is actually a junior synonym of *Trybliographa*, synonymy proposed by Hellén, 1960).

Also, *Hexarhoptra* Hedicke, 1922 from the Bismarck archipelago is a new generic synonym (syn. nov.).

L. aequorea (Yoshimoto, 1962) comb. nov. (*Pseudeucoila*) Type in USNM studied by GN and MF

L. boulardi (Barbotin, Carton & Kelner-Pillault, 1979)

L. cerina (Hedicke, 1922) comb. nov. (Type species of *Hexarhoptra* syn. nov.) Type in ZMHB studied by MF

L. grandissima (Yoshimoto, 1962) comb. nov. (*Pseudeucoila*) Type in BPBM studied by MF

L. heterotoma (Thomson, 1862)

L. lateralis (Yoshimoto, 1963) comb. nov. (*Pseudeucoila*) Type in BPBM not studied, placement based on original description

L. lonchaeae (Cameron, 1912) (*Heptamerocera*)

L. maria (Girault, 1930) (*Hexaplasta*)

L. marquesiana (Kinsey, 1939) comb. nov. (*Eucoila*) (Type species of *Ditanyomeria* syn. nov.) Holotype absent in BPBM (where original description states deposition), but paratype in AMNH studied by MF

L. mellosa (Kinsey, 1939) comb. nov. (*Eucoila*) Holotype absent in BPBM (where original description states deposition), but paratype in AMNH studied by MF

L. negatrix (Kinsey, 1939) comb. nov. (*Eucoila*) Holotype absent in BPBM (where original description states deposition), but paratype in AMNH studied by MF

L. orta (Kinsey, 1939) comb. nov. (*Eucoila*) Holotype absent in BPBM (where original description states deposition), but paratype in AMNH studied by MF

L. rugipunctata (Yoshimoto, 1962) (*Pseudeucoila*)

Neotropic

There are no regional summaries or studies for this region. Of the Western Palearctic species treated in this study, *L. boulardi* and *L. heterotoma* are known to occur. Knowledge of diversity and distribution of *Leptopilina* in this region is very scarce and several of these names may be synonyms while many others remain undescribed. An additional Carribean species is about to be formally described, indicated by a preprint (Lindsey et al. 2025).

L. areolata (Kieffer, 1901) comb. nov. (*Eucoila*) (replacement name for *Aglaotoma longicornis* Ashmead, 1894 nec *Cothonaspis longicornis* Hartig, 1840, junior secondary homonym in *Eucoila* replaced before 1961) Type in USNM studied by GN and MF

L. atriclavata (Ashmead, 1896) comb. nov. (*Rhoptromeris*) Type in USNM studied by GN and MF

L. boliviensis (Kieffer, 1908) comb. nov. (*Ganaspis*) Type in ZMHB studied by MF

L. punctata (Kieffer, 1901) comb. nov. (*Eucoela*) (replacement name for *Heptamerocera gracilicornis* Ashmead, 1896 nec *Eucoila gracilicornis* Cameron, 1888, junior secondary homonym in *Eucoila* replaced before 1961) Type in USNM studied by GN and MF

Discussion

The seven species of *Leptopilina* occurring in the Western Palearctic can be identified comparatively easily morphologically and by their *CO1* barcode (but see details below). Additionally, they can be divided in accordance with a few simple parameters of life history and distribution. *Leptopilina boulardi*, *L. heterotoma* and *L. japonica* are primarily associated with fruit (though the environmental distribution of *L. heterotoma* is very broad and it is also associated with plant detritus and fungi), whereas *L. australis* and *L. fimbriata* are primarily in plant detritus, and *L. clavipes* and *L. longipes* seem to be primarily in fungi (but also found in plant detritus).

L. australis and *L. boulardi* have a southernly distribution, occur more in open habitats, and seem restricted by temperature. On the opposite, *L. clavipes* and *L. longipes* are somewhat more northernly and boreal. They seem to prefer moist, cool habitats, and occur in Southern Europe probably only inside forests or at higher elevations. *Leptopilina fimbriata* and *L. heterotoma* are both widespread and ecologically broad and seem to occur anywhere. *Leptopilina japonica* probably has not reached its full geographic potential in the Western Palearctic and will keep spreading in the coming years, though a lack of humidity may limit establishment in the Mediterranean region (Murata et al. 2013; Rossi-Stacconi et al. 2025).

All species except *L. australis* have barcode information available. On BOLD, there are additional BINs to those that we associated with the species presented here, that contain specimens identified as *L. clavipes* and *L. japonica*. These BINs require a taxonomic review. The remaining four species have unique BINs and are unambiguously identifiable via the *CO1* barcode.

We purposely designed the key to not rely on the presence or absence of the dorsomedial rows of setae on the mesoscutum to differentiate between *L. clavipes* and *L. australis*. This was the case in some earlier identification resources (Nordlander 1980; Van Alphen et al. 1991). However, these setae are susceptible to damage and can therefore be difficult or near impossible to detect (even as cuticular punctures) when fallen off. Instead, we focused on the metapleural ridges which are remarkably constant and easy to see (in sufficient magnification and lighting). Of the traditional diagnostic characters, those of the mesoscutellum (e.g. the shape of the mesoscutellar plate) are reliable, though with some variation and overlap as outlined in detail above.

The data in our synopsis highlight multiple areas where more research is required:

First, there is a comparably small number of distribution records from Eastern Europe and we are not aware of any field study focusing on *Leptopilina* from this region, which results in an underrepresentation of this region in the data.

Second, there is little information on the rarely collected *L. australis*. Considering the fact that it is sharing habitat and flight period with other *Leptopilina* (van Alphen et al. 1991), the low number of records might reflect true low abundance, at least in the sampled locations.

Third, due to a lack of field data, it is unclear to what extent *L. japonica* attacks frugivorous Drosophilidae other than *D. suzukii* outside of anthropogenic habitats (i.e. orchards) and thereby possibly competes with *L. boulardi* and *L. heterotoma* in Europe and North America. The more specialized *L. boulardi* might face higher levels of competition, if *L. japonica* starts to attack native *Drosophila* species to a relevant extent. On the other hand, *L. boulardi* and *L. heterotoma* readily attack *D. suzukii*, which is a dead-end host to both (Chabert et al. 2012), and therefore, a *L. japonica*-induced reduction of *D. suzukii* populations could benefit the native parasitoids. Due to their respective host ranges (Suppl. material 3) and habitat preferences, it is unlikely that the *Leptopilina* that are specialized on non-frugivorous hosts are directly affected by the alien species to a notable extent.

Fourth, the degree of intra-specific mating or hybridization with non-native species of is unknown. Hybrids from cross-breeding experiments of *L. japonica* with *L. ryukyuensis* and *L. victoriae* did not create progeny at latest after F2 (Novković et al. 2011). No similar experiments have been conducted with *L. japonica* and *Leptopilina* species native to the Western Palearctic.

Despite the aforementioned required research, compared to the global Figitidae, the Western Palearctic *Leptopilina* are well studied taxonomically, and regarding their life history and distribution, making them an exception in the widely dark parasitoid wasp taxa (Hausmann et al. 2020). They might indicate a direction and goal for the minimum level of knowledge that is necessary for all species in order to make them accessible and applicable in applied entomology, conservation, ecology and beyond.

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References

Abram PK, Franklin MT, Hueppelsheuser T, Carrillo J, Grove E, Eraso P, Acheampong S, Keery L, Girod P, Tsuruda M, Clausen M, Buffington ML, Moffat CE (2022) Adventive Larval Parasitoids Reconstruct Their Close Association with Spotted-Wing Drosophila in the Invaded North American Range. Environmental Entomology 51(4): 670–678. https://doi.org/10.1093/ee/nvac019

Abram PK, McPherson AE, Kula R, Hueppelsheuser T, Thiessen J, Perlman SJ, Curtis CI, Fraser JL, Tam J, Carrillo J, Gates M, Scheffer S, Lewis M, Buffington M (2020) New records of *Leptopilina*, *Ganaspis*, and *Asobara* species associated with *Drosophila suzukii* in North America, including detections of *L. japonica* and *G. brasiliensis*. Journal of Hymenoptera Research 78: 1–17. https://doi.org/10.3897/jhr.78.55026

Allemand R, Lemaître C, Boulétreau M, Vavre F, Nordlander G, van Alphen JJM, Carton Y (2002) Phylogeny of six African *Leptopilina* species (Hymenoptera: Cynipoidea, Figitidae), parasitoids of *Drosophila*, with description of three new species. Annales de La Société Entomologique de France (N.S.) 38(4): 319–332. https://doi.org/10.1080/00379271.2002.10697346

Astrin JJ, Stüben PE (2008) Phylogeny in cryptic weevils: molecules, morphology and new genera of western Palaearctic Cryptorhynchinae (Coleoptera: Curculionidae). Invertebrate Systematics 22(5): 503–522. https://doi.org/10.1071/IS07057

Bächli G (2021) Insecta Diptera Drosophilidae. In: Bologna MA, Zapparoli M, Oliverio M, Minelli A, Bonato L, Cianferoni F, Stoch F (Eds) Checklist of the Italian Fauna. Version 1.0. https://www.lifewatchitaly.eu/checklist/detail.php?id=23197 [May 31, 2021]

Bächli G (2023) Checkliste der Taufliegen Deutschlands (Diptera: Drosophilidae). Kehlmaier C, Stuke J-H (Eds). Catalogus dipterorum Germaniae 6: 1–28. https://doi.org/10.20363/CdG.Drosophilidae.2023.ix.25

Bächli G (2024) Drosophilidae. In: Haenni J-P, Bächli G, Bernasconi M, Dufour C, Fisler L, Gonseth Y, Lods-Crozet B, Monnerat C, Pollini Paltrinieri L (Eds) 2024. Diptera – Checklist. Fauna Helvetica 35: 488–492.

Bächli G, Vilela CR, Andersson Escher S, Saura A (2004) The Drosophilidae (Diptera) of Fennoscandia and Denmark. Fauna Entomologica Scandinavica 39: 362. https://doi.org/10.1163/9789047414681

Beardsley JW (1989) Hawaiian Eucoilidae (Hymenoptera: Cynipoidea), Key to Genera and Taxonomic Notes on Apparently Non-Endemic Species. Proceedings of the Hawaiian Entomological Society 29: 165–193.

Beers EH, Beal D, Smytheman P, Abram PK, Schmidt-Jeffris R, Moretti E, Daane KM, Looney C, Lue C-H, Buffington M (2022) First records of adventive populations of the parasitoids *Ganaspis brasiliensis* and *Leptopilina japonica* in the United States. Journal of Hymenoptera Research 91: 11–25. https://doi.org/10.3897/jhr.91.82812

Bennett AMR, Buffington ML, Deans AR, Forshage M, Melika G, Mikó I, Smith DR (2024) Checklists of the Ceraphronoidea, Cynipoidea, Evanioidea, Stephanoidea and Trigonalyoidea (Hymenoptera) of Canada, Alaska and Greenland. Journal of Hymenoptera Research 97: 1163–1220. https://doi.org/10.3897/jhr.97.130428

Blaimer BB, Gotzek D, Brady SG, Buffington ML (2020) Comprehensive phylogenomic analyses re-write the evolution of parasitism within cynipoid wasps. BMC Evolutionary Biology 20(1): 155. https://doi.org/10.1186/s12862-020-01716-2

Buffington ML, Nylander JAA, Heraty JM (2007) The phylogeny and evolution of Figitidae (Hymenoptera: Cynipoidea). Cladistics 23: 403–431. https://doi.org/10.1111/j.1096-0031.2007.00153.x

Buffington ML, Forshage M, Liljeblad J, Tang C-T, van Noort S (2020) World Cynipoidea (Hymenoptera): A Key to Higher-Level Groups. Hines H (Ed.). Insect Systematics and Diversity 4(4): 1. https://doi.org/10.1093/isd/ixaa003

Carton Y, Nappi A (1991) The *Drosophila* immune reaction and the parasitoid capacity to evade it: genetic and coevolutionary aspects. Acta oecologica (Montrouge, France) 12(1): 89–104.

Carton Y, Boulétreau M, van Alphen JJM, van Lenteren JC (1986) The *Drosophila* parasitic wasps. In: Ashburner M, Carson HL, Thompson JN (Eds) The Genetics and Biology of Drosophila. Academic Press, London, 347–394.

Chabert S, Allemand R, Poyet M, Eslin P, Gilbert P (2012) Ability of European parasitoids (Hymenoptera) to control a new invasive Asiatic pest, *Drosophila suzukii*. Biological Control 63: 40–47. https://doi.org/10.1016/j.biocontrol.2012.05.005

Daane KM, Wang X, Hogg BN, Biondi A (2021) Potential host ranges of three Asian larval parasitoids of *Drosophila suzukii*. Journal of Pest Science 94: 1171–1182. https://doi.org/10.1007/s10340-021-01368-1

Daane KM, Wang X-G, Biondi A, Miller B, Miller JC, Riedl H, Shearer PW, Guerrieri E, Giorgini M, Buffington ML, van Achterberg K, Song Y, Kang T, Yi H, Jung C, Lee DW, Chung B-K, Hoelmer KA, Walton VM (2016) First exploration of parasitoids of *Drosophila suzukii* in South Korea as potential classical biological agents. Journal of Pest Science 89: 823–835. https://doi.org/10.1007/s10340-016-0740-0

Dong Z, Xu Z, Zhang J, Gyo Y, Zhang Q, Pang L, Feng T, Shi W, Sheng Y, Huang J, Chen J (2025) Chromosome-level genome sequencing and assembly of the parasitoid wasp *Leptopilina myrica*. Scientific Data 12: 235. https://doi.org./10.1038/s41597-025-04577-w

Driessen G, Hemerik L, van Alphen JJM (1990) *Drosophila* species, breeding in the stinkhorn (*Phallus impudicus* Pers.) and their larval parasitoids. Netherlands Journal of Zoology 40(3): 409–427. https://doi.org/10.1163/156854290X00019

Edgar RC (2004) MUSCLE: A Multiple Sequence Alignment Method with Reduced Time and Space Complexity. BMC Bioinformatics 5(1): 113. https://doi.org/10.1186/1471-2105-5-113

Eijs IEM, van Alphen JJM (1999) Life history correlations: Why are hymenopteran parasitoids an exception? Ecology Letters 2: 24–35. https://doi.org/10.1046/j.1461-0248.1999.21045.x

Evenhuis NL (2025) The insect and spider collections of the world website. http://hbs.bishopmuseum.org/codens/ [Last accessed: 11th April 2025]

Fleury F, Ris N, Allemand R, Fouillet P, Carton Y, Boulétreau M (2004) Ecological and genetic interactions in *Drosophila*–parasitoids communities: A case study with *D. melanogaster*, *D. simulans* and their common *Leptopilina* parasitoids in south-eastern France. Genetica 120: 181–194. https://doi.org/10.1023/B:GENE.0000017640.78087.9e

Fleury F, Gilbert P, Ris N, Allemand R (2009) Ecology and life history evolution of frugivorous *Drosophila* parasitoids. In: Prevost G (Ed.) Advances in Parasitology. Parasitoids of *Drosophila*. Academic Press, Burlington, 3–44. https://doi.org/10.1016/S0065-308X(09)70001-6

Fontal-Cazalla FM, Buffington ML, Nordlander G, Liljeblad J, Ros-Farre P, Nieves-Aldrey JL, Pujade-Villar J, Ronquist F (2002) Phylogeny of the Eucoilinae (Hymenoptera: Cynipoidea: Figitidae). Cladistics 18(2): 154–199. https://doi.org/10.1111/j.1096-0031.2002.tb00147.x

Forshage M, Nordlander G (2008) Identification Key to European Genera of Eucoilinae (Hymenoptera, Cynipoidea, Figitidae). Insect Systematics & Evolution 39(3): 341–359. https://doi.org/10.1163/187631208794760885

Forshage M, Nordlander G, Buffington ML (2013) Eucoilinae of North America: A revised catalog of genera and described species. Proceedings of the Entomological Society of Washington 115(3): 225–255. https://doi.org/10.4289/0013-8797.115.3.225

Forshage M, Bowdrey J, Broad G, Spooner B, van Veen F (2017) Checklist of British and Irish Hymenoptera - Cynipoidea. Biodiversity Data Journal 5: e8049. https://doi.org/10.3897/BDJ.5.e8049

Förster A (1869) Ueber die Gallwespen. Verhandlungen Der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien (19): 328–370.

Gariepy TD, Abram PK, Adams C, Beal D, Beers E, Beetle J, Biddinger D, Brind'Amour G, Bruin A, Buffington M, Burrack H, Daane KM, Demchak K, Fanning P, Gillett A, Hamby K, Hoelmer K, Hogg B, Isaacs R, Johnson B, Lee JC, Levensen HK, Loeb G, Lovero A, Milnes JM, Park KR, Prade P, Regan K, Renkema JM, Rodriguez-Saona C, Neupane S, Jones C, Sial A, Smythman P, Stout A, Van Timmeren S, Walton VM, Wilson JK, Wang X (2024) Widespread establishment of adventive populations of *Leptopilina japonica* (Hymenoptera, Figitidae) in North America and development of a multiplex PCR assay to identify key parasitoids of *Drosophila suzukii* (Diptera, Drosophilidae). NeoBiota 93: 63–90. https://doi.org/10.3897/neobiota.93.121219

German Barcode of Life Consortium (Wägele W, Haszprunar G, Eder J, Xylander W, Borsch T, Quandt D, Grobe P, Pietsch S, Geiger M, Astrin J, Rulik B, Hausmann A, Moriniere J, Holstein J, Krogmann L, Monje C, Traunspurger W, Hohberg K, Lehmitz R, Müller K, Nebel M, Hand R) (2011) GBOL Webportal. https://www.bolgermany.de

Giorgini M, Wang X-G, Wang Y, Chen F-S, Hougardy E, Zhang H-M, Chen Z-Q, Chen H-Y, Liu C-X, Cascone P, Formisano G, Carvalho GA, Bernardi D, Buffington ML, Daane KM, Hoelmer KA, Guerrieri E (2019) Exploration for native parasitoids of *Drosophila suzukii* in China reveals a diversity of parasitoid species and narrow host range of the dominant parasitoid. Journal of Pest Science 92: 509–522. https://doi.org/10.1007/s10340-018-01068-3

Girod P, Lierhmann O, Urvois T, Turlings TCJ, Kenis M, Haye T (2018a) Host specificity of Asian parasitoids for potential classical biological control of *Drosophila suzukii*. Journal of Pest Science 91: 1241–1250. https://doi.org/10.1007/s10340-018-1003-z

Girod P, Borowiec N, Buffington ML, Chen G, Fang Y, Kimura MT, Peris-Felipo FJ, Ris N, Wu H, Xiao C, Zhang J, Aebi A, Haye T, Kenis M (2018b) The parasitoid complex of *D. suzukii* and other fruit feeding *Drosophila* species in Asia. Scientific Reports 8(1): 11839. https://doi.org/10.1038/s41598-018-29555-8

Gonzalez-Cabrera J, Moreno-Carrillo G, Sanchez-Gonzalez JA, Mendoza-Ceballos MY, Arredondo-Berna HC (2019) Single and Combined Release of *Trichopria drosophilae* (Hymenoptera: Diapriidae) to Control *Drosophila suzukii* (Diptera: Drosophilidae). Neotropical Entomology 48: 949–956. https://doi.org/10.1007/s13744-019-00707-3

Gornostaev NG, Ruchin AB, Esin MN, Lazebny OE, Kulikov AM (2023) Vertical Distribution of Fruit Flies (Diptera: Drosophilidae) in Deciduous Forests in the Center of European Russia. Insects 14(10): 822. https://doi.org/10.3390/insects14100822

Gornostaev NG, Lyupina YV, Lazebny OE, Kulikov AM (2024) Seasonal Dynamics of Fruit Flies (Diptera: Drosophilidae) in Natural Parks of Moscow City, Russia. Insects 15(6): 398. https://doi.org/10.3390/insects15060398

Guindon S, Dufayard J-F, Lefort V, Anisimova M, Hordijk W, Gascuel O (2010) New Algorithms and Methods to Estimate Maximum-Likelihood Phylogenies: Assessing the Performance of PhyML 3.0. Systematic Biology 59(3): 307–321. https://doi.org/10.1093/sysbio/syq010

Guinet B, Vogel J, Kacem Haddj El Mrabet N, Peters RS, Hrcek J, Buffington ML, Varaldi J (2025) Dating the origin of a viral domestication event in parasitoid wasps attacking Diptera. Proceedings of the Royal Society B: Biological Sciences 292(2039): 20242135. https://doi.org/10.1098/rspb.2024.2135

Guo Y, Zhang J, Sheng Y, Pang L, Wang Y, Huang J, Chen J (2024) Biological characteristics of *Leptopilina myrica* and the effects of its parasitism on host immunity. Chinese Journal of Biological Control 40(4): 793–803.

Hardy ICW, van Alphen JJM, van Dijken MJ (1992) First record of *Leptopilina longipes* (Hymenoptera: Eucoilidae) in The Netherlands, and its host identified. Entomologische Berichten Amsterdam 52(9): 128–130.

Hausmann A, Krogmann L, Peters RS, Rduch V, Schmidt S (2020) GBOL III: DARK TAXA. iBOL Barcode Bulletin 10 (1). https://doi.org/10.21083/ibol.v10i1.6242

Hebert PDN, Penton EH, Burns JM, Janzen DH, Hallwachs W (2004) Ten species in one: DNA barcoding reveals cryptic species in the neotropical skipper butterfly *Astraptes fulgerator*. Proceedings of the National Academy of Sciences 101(41): 14812–14817. https://doi.org/10.1073/pnas.0406166101

Hellén W (1960) Die Eucoilinen Finnlands (Hym. Cyn.). Fauna Fennica 9: 3–31.

Hoang DT, Chernomor O, Von Haeseler A, Minh BQ, Vinh LS (2018) UFBoot2: Improving the Ultrafast Bootstrap Approximation. Molecular Biology and Evolution 35(2): 518–522. https://doi.org/10.1093/molbev/msx281

Jafari S, Müller B, Rulik B, Rduch V, Peters RS (2023) Another crack in the Dark Taxa wall: A custom DNA barcoding protocol for the species-rich and common Eurytomidae (Hymenoptera, Chalcidoidea). Biodiversity Data Journal 11: e101998. https://doi.org/10.3897/BDJ.11.e101998

Janssen A, Driessen G, Haan M, Roodbol N (1988) The impact of parasitoids on natular populations of temperate woodland *Drosophila*. Netherlands Journal of Zoology 38(1): 61–73. https://doi.org/10.1163/156854288X00049

Jonsell M, Nordlander G, Jonsson M (1999) Colonization patterns of insects breeding in wood-decaying fungi. Journal of Insect Conservation 3: 145–161. https://doi.org/10.1023/A:1009665513184

Kahanpää J (2014) Checklist of the Braulidae, Camillidae, Diastatidae and Drosophilidae of Finland (Diptera, ephydroidea). ZooKeys 441: 333–338. https://doi.org/10.3897/zookeys.441.7057

Kapli P, Lutteropp S, Zhang J, Kobert K, Pavlidis P, Stamatakis A, Flouri T (2017) Multi-rate Poisson tree processes for single-locus species delimitation under maximum likelihood and

Markov chain Monte Carlo. Valencia A (Ed.). Bioinformatics 33(11): 1630–1638. https://doi.org/10.1093/bioinformatics/btx025

Karlsson D, Hartop E, Forshage M, Jaschhof M, Ronquist F (2020) The Swedish Malaise Trap Project: A 15 Year Retrospective on a Countrywide Insect Inventory. Biodiversity Data Journal 8: e47255. https://doi.org/10.3897/BDJ.8.e47255

Kettani K, Ebejer MJ, Ackland DM, Bächli G, Barraclough D, Barták M, Carles-Tolrá M, Černý M, Cerretti P, Chandler P, Dakki M, Daugeron C, De Jong H, Dils J, Disney H, Droz B, Evenhuis N, Gatt P, Graciolli G, Grichanov IY, Haenni J-P, Hauser M, Himmi O, Macgowan I, Mathieu B, Mouna M, Munari L, Nartshuk EP, Negrobov OP, Oosterbroek P, Pape T, Pont AC, Popov GV, Rognes K, Skuhravá M, Skuhravý V, Speight M, Tomasovic G, Trari B, Tschorsnig H-P, Vala J-C, von Tschirnhaus M, Wagner R, Whitmore D, Woźnica AJ, Zatwarnicki T, Zwick P (2022) Catalogue of the Diptera (Insecta) of Morocco—an annotated checklist, with distributions and a bibliography. ZooKeys 1094: 1–466. https://doi.org/10.3897/zookeys.1094.62644

Kimura MT (2015) Prevalence of exotic frugivorous *Drosophila* species, *D. simulans* and *D. immigrans* (Diptera: Drosophilidae), and its effects on local parasitoids in Sapporo, northern Japan. Applied Entomology and Zoology 50(4): 509–515. https://doi.org/10.1007/s13355-015-0361-8

Kimura MT (2019) Overwintering of reproductively mature females of a pro-ovigenic parasitic wasp, *Leptopilina heterotoma* (Hymenoptera: Figitidae). Entomological Science 22(3): 264–269. https://doi.org/10.1111/ens.12365

Kimura MT, Novković B (2015) Local adaptation and ecological fitting in host use of the *Drosophila* parasitoid *Leptopilina japonica*. Ecological Research 30(3): 499–505. https://doi.org/10.1007/s11284-015-1244-8

Kinsey AC (1939) New Figitidae from the Marquesas Islands. Bernice P Bishop Museum Bulletin no 142: 193–197.

Lindsey AR, Lue C-H, Davis JS, Borjon LJ, Mauthner SE, Fricke LC, Eads L, Murphy M, Drown MK, Faulk C, Buffington ML, Tracey WD (2025) Genomics and reproductive biology of *Leptopilina* n. sp. Buffington, Lue, Davis & Tracey sp. nov. (Hymenoptera: Figitidae): An asexual parasitoid of Caribbean *Drosophila*. 45 pp. https://doi.org/10.1101/2025.03.28.645512

Lue C-H, Driskell AC, Leips J, Buffington ML (2016) Review of the genus *Leptopilina* (Hymenoptera, Cynipoidea, Figitidae, Eucoilinae) from the Eastern United States, including three newly described species. Journal of Hymenoptera Research 53: 35–76. https://doi.org/10.3897/jhr.53.10369

Lue C-H, Buffington ML, Scheffer S, Lewis M, Elliott TA, Lindsey ARI, Driskell A, Jandova A, Kimura MT, Carton Y, Kula RR, Schlenke TA, Mateos M, Govind S, Varaldi J, Guerrieri E, Giorgini M, Wang X, Hoelmer K, Daane KM, Abram PK, Pardikes NA, Brown JJ, Thierry M, Poirié M, Goldstein P, Miller SE, Tracey WD, Davis JS, Jiggins FM, Wertheim B, Lewis OT, Leips J, Staniczenko PPA, Hrcek J (2021) DROP: Molecular voucher database for identification of *Drosophila* parasitoids. Molecular Ecology Resources 21(7): 2437–2454. https://doi.org/10.1111/1755-0998.13435

Martin J, Vogel J, Peters RS, Herz A (2023) First record of *Leptopilina japonica* Novković & Kimura, 2011 (Hymenoptera: Figitidae) in Germany, a parasitoid of the spotted wing Drosophila *Drosophila suzukii* (Matsumura, 1931) (Diptera: Drosophilidae). Journal of Applied Entomology 147(10): 1067–1073. https://doi.org/10.1111/jen.13182

Matsuura A, Mitsui H, Kimura MT (2018) A preliminary study on distributions and oviposition sites of *Drosophila suzukii* (Diptera: Drosophilidae) and its parasitoids on wild cherry tree in Tokyo, central Japan. Applied Entomology and Zoology 53: 47–53. https://doi.org/10.1007/s13355-017-0527-7

Mazzetto F, Marchetti E, Amiresmaeili N, Sacco D, Francati S, Jucker C, Dindo ML, Lupi D, Tavella L (2016) *Drosophila* parasitoids in northern Italy and their potential to attack the exotic pest *Drosophila suzukii*. Journal of Pest Science 89: 837–850. https://doi.org/10.1007/s10340-016-0746-7

Meier R, Shiyang K, Vaidya G, Ng PKL (2006) DNA barcoding and taxonomy in Diptera: A tale of high intraspecific variability and low identification success. Systematic Biology 55(5): 715–728. https://doi.org/10.1080/10635150600969864

Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, Von Haeseler A, Lanfear R (2020) IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. Molecular Biology and Evolution 37(5): 1530–1534. https://doi.org/10.1093/molbev/msaa015

Moiroux J, Delava E, Fleury F, van Baaren J (2013) Local adaptation of a *Drosophila* parasitoid: Habitat-specific differences in thermal reaction norms. Journal of Evolutionary Biology 26(5): 1108–1116. https://doi.org/10.1111/jeb.12122

Müller B, Thormann J, Von Der Mark L, Astrin J, Rulik B (2024) Supplemental lab-protocol for barcoding primers: dEURYT-BRBM2, LCO1490-JJ, LCO1490-JJ2 & LCO1490-JJ3 v1. https://doi.org/10.17504/protocols.io.6qpvr96kbvmk/v1

Murata Y, Novković B, Suwito A, Kimura MT (2013) Diapause and cold tolerance in Asian species of the parasitoid *Leptopilina* (Hymenoptera: Figitidae). Physiological Entomology 38: 211–218. https://doi.org/10.1111/phen.12024

van Noort S, Buffington ML, Forshage M (2015) Afrotropical Cynipoidea (Hymenoptera). ZooKeys 494: 1–176. https://doi.org/10.3897/zookeys.493.6353

Nordlander G (1980) Revision of the genus *Leptopilina* Förster, 1869 with notes on the status of some other genera (Hymenoptera, Cynipoidea: Eucoilidae). Entomologica Scandinavica 11: 428–453. https://doi.org/10.1163/187631280794710024

Nordlander G, Grijpma P (1991) Systematics and biology of *Rhoptromeris strobigena* sp. n., a parasitoid of chloropids inhabiting conifer cones (Hymenoptera: Cynipoidea: Eucoilidae). Entomologica Scandinavica 22(2): 209–218. https://doi.org/10.1163/187631291X00084

Novković B, Mitsui H, Suwito A, Kimura MT (2011) Taxonomy and phylogeny of *Leptopilina* species (Hymenoptera: Cynipoidea: Figitidae) attacking frugivorous drosophilid flies in Japan, with description of three new species. Entomological Science 14(3): 333–346. https://doi.org/10.1111/j.1479-8298.2011.00459.x

Özbek Çatal B, Çalişkan Keçe AF, Ulusoy MR (2021) Distribution and host plants of Drosophilidae (Diptera) species detected in fruit orchards of the Eastern Mediterranean Region of Turkey. Mustafa Kemal University Journal of Agricultural Sciences 26(2): 431–442. https://doi.org/10.37908/mkutbd.873838

Pannebakker BA, Zwaan BJ, Beukeboom LW, van Alphen JJM (2004) Genetic diversity and *Wolbachia* infection of the *Drosophila* parasitoid *Leptopilina clavipes* in Western Europe. Molecular ecology 13(5): 1119–1128. https://doi.org/10.1111/j.1365-294X.2004.02147.x

Pannebakker BA, Garrido NRT, Zwaan BJ, van Alphen JJM (2008) Geographic variation in host-selection behaviour in the *Drosophila* parasitoid *Leptopilina clavipes*. Entomologia Experimentalis et Applicata 127(1): 48–54. https://doi.org/10.1111/j.1570-7458.2008.00666.x

Paretas-Martínez J, Forshage M, Buffington ML, Fisher N, La Salle J, Pujade-Villar J (2013) Overview of Australian Cynipoidea (Hymenoptera): Australian Cynipoidea. Australian Journal of Entomology 52(1): 73–86. https://doi.org/10.1111/j.1440-6055.2012.00877.x

Poolman Simons MTT, Suverkopp BP, Vet LEM, Moed G (1992) Comparison of learning in related generalist and specialist eucoilid parasitoids. Entomologia Experimentalis et Applicata 64: 117–124. https://doi.org/10.1111/j.1570-7458.1992.tb01601.x

Powell G, Vogel J, Martin J (2025) First British record of *Leptopilina japonica* (Hymenoptera: Figitidae), an Asian larval parasitoid of spotted wing drosophila. British Journal of Entomology and Natural History 38: 65–70.

Poyet M, Havard S, Prevost G, Chabrerie O, Doury G, Gibert P, Eslin P (2013) Resistance of *Drosophila suzukii* to the larval parasitoids *Leptopilina heterotoma* and *Asobara japonica* is related to haemocyte load. Physiological Entomology 38(1): 45–53. https://doi.org/10.1111/phen.12002

Puillandre N, Brouillet S, Achaz G (2021) ASAP: assemble species by automatic partitioning. Molecular Ecology Resources 21(2): 609–620. https://doi.org/10.1111/1755-0998.13281

Puppato S, Grassi A, Pedrazzoli F, De Cristofaro A, Ioriatti C (2020) First Report of *Leptopilina japonica* in Europe. Insects 11(9): 611. https://doi.org/10.3390/insects11090611

Quicray M, Wilhelm L, Enriquez T, He S, Scheifler M, Visser B (2023) The *Drosophila*-parasitizing wasp *Leptopilina heterotoma*: A comprehensive model system in ecology and evolution. Ecology and Evolution 13(1): e9625. https://doi.org/10.1002/ece3.9625

Quinlan J (1988) A revision of some Afrotropical genera of Eucoilidae (Hymenoptera). Bulletin of the British Museum (Natural History) 56(4): 171–229.

Rambaut A (2018) FigTree. https://github.com/rambaut/figtree/releases/tag/v1.4.4

Ratnasingham S, Hebert PDN (2007) BOLD: The barcode of life data system (http://www.barcodinglife.org). Molecular Ecology Notes 7(3): 355–364. https://doi.org/10.1111/j.1471-8286.2007.01678.x

Ratnasingham S, Hebert PDN (2013) A DNA-Based Registry for All Animal Species: The Barcode Index Number (BIN) System. PLoS ONE 8(7): e66213. https://doi.org/10.1371/journal.pone.0066213

Ronquist F, Forshage M (2004) Fauna Europaea: Hymenoptera - Cynipoidea, Figitidae. In: de Jong YSDM (Ed.) (2023) Fauna Europaea: version 2023.03. https://fauna-eu.org [currently offline; last accessed before 2024]

Rossi-Stacconi MV, Abram PK, Anfora G, Beers E, Biondi A, Borowiec N, Carrillo J, Collatz J, Colmagro A, Johnson BC, Daane K, Dal Zotto G, Döbeli H, Fanning P, Fellin L, Gariepy T, Giorgini M, Grassi A, Guerrieri E, Herz A, Isaacs R, Lee J, Lisi F, Loeb GM, Lupi D, Martin J, Masetti A, Moffat C, Mori N, Park KR, Prade P, Puppato S, Rodriguez-Saona C, Schmidt S, Seehausen L, Sial AA, Tavella L, Tortorici F, Urbaneja-Bernat P, Van Timmeren S, Walton VM, Wang G, Wang X (2025) Adventively established *Leptopilina japonica*: a new opportunity for augmentative biocontrol of *Drosophila suzukii*. Journal of Pest Science, 1–17. https://doi.org/10.1007/s10340-025-01907-0

Rousse P, Borowiec N, Reynaud P (2023) Un nouvel auxiliaire potentiel pour freiner *Drosophila suzukii*. Phytoma (761): 45–47.

Schlenke TA, Morales J, Govind S, Clark AG (2007) Contrasting infection strategies in generalist and specialist wasp parasitoids of *Drosophila melanogaster*. PLoS pathogens 3(10): 1486–1501. https://doi.org/10.1371/journal.ppat.0030158

Truett GE, Heeger P, Mynatt RL, Truett AA, Walker JA, Warman ML (2000) Preparation of PCR-quality mouse genomic DNA with hot sodium hydroxide and Tris (HotSHOT). BioTechniques 29: 52–54. https://doi.org/10.2144/00291bm09

van Alphen JJM, Vet LEM (1986) An evolutionary approach to host finding and selection. In: Waage J, Greathead D (Eds) Insect parasitoids: 13th symposium of the Royal Entomological Society of London, London (UK), September 1985. Academic Press (London), 51–78.

van Alphen JJM, Nordlander G, Eijs I (1991) Host habitat finding and host selection of the *Drosophila* parasitoid *Leptopilina australis* (Hymenoptera, Eucoilidae), with a comparison of the niches of European *Leptopilina* species. Oecologia 87(3): 324–329. https://doi.org/10.1007/BF00634586

von Dalla-Torre KW, Kieffer J-J (1910) Cynipidae. Das Tierreich 24. R. Friedländer und Sohn, Berlin, 891 pp. https://doi.org/10.5962/bhl.title.1077

van Dijken MJ, van Alphen JJM (1998) The ecological significance of differences in host detection behaviour in coexisting parasitoid species. Ecological Entomology 23: 265–270. https://doi.org/10.1046/j.1365-2311.1998.00130.x

Vasilita C, Feng V, Hansen AK, Hartop E, Srivathsan A, Struijk R, Meier R (2024) Express barcoding with NextGenPCR and MinION for species-level sorting of ecological samples. Molecular Ecology Resources, e13922. https://doi.org/10.1111/1755-0998.13922

Vavre F, Mouton L, Pannebakker BA (2009) *Drosophila*-parasitoid communities as model systems for host-*Wolbachia* interactions. In: Prevost G (Ed.) Advances in Parasitology. Parasitoids of Drosophila. Academic Press, Burlington, 299–331. https://doi.org/10.1016/S0065-308X(09)70012-0

Vet LEM (1983) Host-habitat location through olfactory cues by *Leptopilina clavipes* (Hartig) (Hym.: Eucoilidae), a parasitoid of fungivorous *Drosophila*: the influence of conditioning. Netherlands Journal of Zoology 33(3): 225–248. https://doi.org/10.1163/002829683X00101

Vet LEM, Hoeven R (1984) Comparison of the behavioural response of two *Leptopilina* species (Hymenoptera: Eucoilidae), living in different microhabitats, to kairomone of their host (Drosophilidae). Netherlands Journal of Zoology 34(2): 220–227. https://doi.org/10.1163/002829684X00173

Vet LEM, van Alphen JJM (1985) A comparative functional approach to the host detection behaviour of parasitic wasps. 1. A qualitative study on Eucoilidae and Alysiinae. OIKOS 44: 478–486. https://doi.org/10.2307/3565789

Vuarin P, Allemand R, Moiroux J, van Baaren J, Gibert P (2012) Geographic variations of life history traits and potential trade-offs in different populations of the parasitoid *Leptopilina heterotoma*. Die Naturwissenschaften 99(11): 903–912. https://doi.org/10.1007/s00114-012-0972-7

Wachi N, Nomano FY, Mitsui H, Kasuya N, Kimura MT (2015) Taxonomy and evolution of putative thelytokous species of *Leptopilina* (Hymenoptera: Figitidae) from Japan, with description of two new species. Entomological Science 18: 41–54. https://doi.org/10.1111/ens.12089

Wang X-G, Nance AH, Jones JML, Hoelmer KA, Daane KM (2018) Aspects of the biology and reproductive strategy of two Asian larval parasitoids evaluated for classical biological control of *Drosophila suzukii*. Biological control: theory and applications in pest management 121: 58–65. https://doi.org/10.1016/j.biocontrol.2018.02.010

Weld LH (1952) Cynipoidea (Hym.) 1905–1950, being a supplement to the Dalla Torre and Kieffer monograph – the Cynipidae in Das Tierreich, Lieferung 24, 1910 and bringing the systematic literature of the world up to date, including keys to families and subfamilies and lists of new generic, specific and variety names. Privately printed, Ann Arbor, 351 pp.

Xie J, Vilchez I, Mateos M (2010) Spiroplasma Bacteria Enhance Survival of *Drosophila hydei* attacked by the parasitic wasp *Leptopilina heterotoma*. PLoS ONE 5(8): e12149. https://doi.org/10.1371/journal.pone.0012149

Yoshimoto C (1963a) Synopsis of Polynesian Cynipoidea. Pacific Insects 5(2): 433–443.

Yoshimoto C (1963b) Corrections to Yoshimoto, 1963. Pacific Insects 5(4): 898.

Zhang J, Lu Z, Dong Z, Wang H, Shan J, Xu Z, Huang J, Chen J (2024) The complete mitochondrial genome of *Leptopilina myrica* (Hymenoptera: Figitidae). Mitochondrial DNA Part B 10(1): 11–14. https://doi.org/10.1080/23802359.2024.2444643

Appendix 1

Leptopilina australis

Belgium • 1 ♀; West Flanders, Ypres, De Triangel; 50.84180°N, 2.88380°E; ca 20 m a.s.l.; 2–23 Jul. 2022; Fons Verheyde leg.; Malaise trap, urban park (bushes); specimen ID: ZFMK-TIS-2637706 (ZFMK).

Leptopilina clavipes

Belgium • 1 ♀; Limburg, Peer, Siberië; 51.06400°N, 5.45300°E; ca 70 m a.s.l.; 18 Jun. 2022; L. Crevecoeur leg.; car net; specimen ID: ZFMK-TIS-2637711 (ZFMK). • 1 ♀; West Flanders, Ypres, De Triangel; 50.84180°N, 2.88380°E; ca 20 m a.s.l.; 2–23 Jul. 2022; Fons Verheyde leg.; Malaise trap, urban park (bushes); specimen ID: ZFMK-TIS-2637705 (ZFMK).

Leptopilina fimbriata

Austria • 1 ♀; Carinthia, Steiner Alpen, Vellach; 46.41600°N, 14.55550°E; ca 910 m a.s.l.; 21 Aug. 2021; Haseke & Remschak leg.; specimen ID: ZFMK-TIS-2635157 (ZFMK). • 1 ♂; Styria, Oststeir, Huegelland, Limbach/Lendvia; 46.89270°N, 15.94890°E; ca 330 m a.s.l.; 4 Jun. 2021; Haseke & Remschak leg.; specimen ID: ZFMK-TIS-2635155 (ZFMK).

Belgium • 1 ♂; West Flanders, Ypres, De Triangel; 50.84180°N, 2.88380°E; ca 20 m a.s.l.; 2–23 Jul. 2022; Fons Verheyde leg.; Malaise trap, urban park (bushes); specimen ID: ZFMK-TIS-2637707 (ZFMK). • 1 ♀; West Flanders, Ypres, De Triangel; 50.84270°N, 2.88400°E; ca 20 m a.s.l.; 2–23 Jul. 2022; Fons Verheyde leg.; Malaise trap, urban park (pool vegetation); specimen IDs: ZFMK-TIS-2637708 (ZFMK). • 1 ♀; same collection data as for preceding; 23 Jul.-6 Aug. 2022; specimen IDs: ZFMK-TIS-2637710 (ZFMK).

Germany • 2 ♂♂; Baden-Württemberg, Karlsruhe, Malsch, Hansjakobstraße; 48.88350°N, 8.31970°E; ca 120 m a.s.l.; 26 Apr.-10 May 2020; Dieter Doczkal leg.; Malaise trap, garden; specimen IDs: ZFMK-TIS-2634694 (ZFMK), ZFMK-TIS-2634697 (ZFMK). • 1 ♂; Baden-Württemberg, Tübingen, Steinenberg; 48.53060°N, 9.03120°E; ca 470 m a.s.l.; 25 Apr.-13 May 2014; T. Kothe, M. Engelhardt, Christian König leg.; Malaise trap; specimen ID: ZFMK-TIS-2629383 (ZFMK). • 1 ♂; Hesse, Waldeck-Frankenberg, NP Kellerwald-Edersee, „Maierwiesen“; 51.15470°N, 9.00150°E; ca 360 m a.s.l.; 19 Aug.-2 Sep. 2021; GBOL III leg.; Malaise trap; specimen ID: ZFMK-TIS-2634815 (ZFMK). • 1 ♀, 1 ♂; Hesse, Waldeck-Frankenberg, National Park Kellerwald-Edersee, Banfehaus; 51.16700°N, 8.97490°E; ca 270 m a.s.l.; 22 Jul.-5 Aug. 2021; GBOL III leg.; Malaise trap (Krefeld), old floodplain of the Banfe; female specimen ID: ZFMK-TIS-2632871 (ZFMK); male specimen ID: ZFMK-TIS-2632869 (ZFMK). • 1 ♂; Hesse, Waldeck-Frankenberg, National park Kellerwald-Edersee, „Maierwiesen“; 51.15550°N, 9.00150°E; ca 360 m a.s.l.; 22 Jun.-8 Jul. 2021; GBOL III leg.; Malaise trap (Krefeld); specimen ID: ZFMK-TIS-2632547 (ZFMK). • 1 ♂; Hesse, Werra-Meißner-Kreis, Großalmerode, Jonasbach, Privatgarten (Loc. 3); 51.26250°N, 9.77680°E; ca 470 m a.s.l.; 14–27 Oct. 2020; GBOL III leg.; Malaise trap, Unattended garden with *Rubus* sp and *Urtica dioica*; specimen ID: ZFMK-TIS-2631068 (ZFMK). • 2 ♀♀, 1 ♂; North Rhine-Westphalia, Bonn, Garden of Museum Koenig; 50.72150°N, 7.11370°E; ca 70 m a.s.l.; 4 Jul. 2022; Josefine Schwingeler, Jonathan Vogel leg.; sweep net, Various habitats; female specimen IDs: HM141-05-DD (ZFMK), HM148-12-DD (ZFMK); male specimen ID: HM149-01-EE (ZFMK). • 2 ♀♀, 2 ♂♂; North Rhine-Westphalia, Bonn, Mehlem, Deichmanns Aue 62; 50.67090°N, 7.18460°E; ca 60 m a.s.l.; 25 Aug.-4 Sep. 2021; GBOL III leg.; Malaise trap; female specimen IDs: ZFMK-TIS-2632668 (ZFMK), ZFMK-TIS-2632671 (ZFMK); male specimen IDs: ZFMK-TIS-2632667 (ZFMK), ZFMK-TIS-2632670 (ZFMK). • 1 ♂; North Rhine-Westphalia, Windeck, Siegaue, Schladern; 50.80000°N, 7.58500°E; ca 120 m a.s.l.; 2–9 May 2017; ZFMK et al. leg.; Malaise trap; specimen ID: ZFMK-TIS-2630899 (ZFMK). • 1 ♀; same collection data as for preceding; 9–16 May 2017; specimen ID: ZFMK-TIS-2630928 (ZFMK).• 2 ♂♂; same collection data as for preceding; 16–23 May 2017; specimen IDs: ZFMK-TIS-2630882 (ZFMK), ZFMK-TIS-2630883 (ZFMK). • 1 ♀; same collection data as for preceding; 23–30 May 2017; specimen ID: ZFMK-TIS-2627856 (ZFMK). • 1 ♀; same collection data as for preceding; 30 May-6 Jun. 2017; specimen ID: ZFMK-TIS-2630887 (ZFMK). • 4 ♂♂; same collection data as for preceding; 6–13 Jun. 2017; specimen IDs: ZFMK-TIS-2631077 (ZFMK), ZFMK-TIS-2631078 (ZFMK), ZFMK-TIS-2631079 (ZFMK), ZFMK-TIS-2631080 (ZFMK). • 2 ♀♀, 1 ♂; same collection data as for preceding; 13–20 Jun. 2017; female specimen IDs:

ZFMK-TIS-2630021 (ZFMK), ZFMK-TIS-2630022 (ZFMK); male specimen ID: ZFMK-TIS-2630020 (ZFMK). • 1 ♀; same collection data as for preceding; 20–27 Jun. 2017; specimen ID: ZFMK-TIS-2631084 (ZFMK). • 1 ♂; same collection data as for preceding; 27 Jun.-4 Jul. 2017; specimen ID: ZFMK-TIS-2631050 (ZFMK). • 1 ♂; same collection data as for preceding; 4–11 Jul. 2017; specimen ID: ZFMK-TIS-2631094 (ZFMK). • 2 ♂♂; same collection data as for preceding; 18–25 Jul. 2017; specimen IDs: ZFMK-TIS-2630946 (ZFMK), ZFMK-TIS-2632724 (ZFMK). • 1 ♂; same collection data as for preceding; 1–8 Aug. 2017; ZFMK et al. leg.; specimen ID: ZFMK-TIS-2630886 (ZFMK). • 1 ♂; same collection data as for preceding; 30 Aug.-5 Sep. 2017; specimen ID: ZFMK-TIS-2632715 (ZFMK). • 2 ♀♀; same collection data as for preceding; 26 Sep.-3 Oct. 2017; specimen IDs: ZFMK-TIS-2631056 (ZFMK), ZFMK-TIS-2631057 (ZFMK). • 3 ♀♀, 4 ♂♂; Rhineland-Palatinate, Vulkaneifel, Juenkerath, private garden; 50.33460°N, 6.59450°E; ca 450 m a.s.l.; 7 Aug. 2021; Jonathan Vogel leg.; sweep net, garden and wet meadow with chicken coop; female specimen IDs: ZFMK-TIS-2632337 (ZFMK), ZFMK-TIS-2632618 (ZFMK), ZFMK-TIS-2632619 (ZFMK); male specimen IDs: ZFMK-TIS-2632335 (ZFMK), ZFMK-TIS-2632336 (ZFMK), ZFMK-TIS-2632338 (ZFMK), ZFMK-TIS-2632339 (ZFMK). • 1 ♀, 8 ♂♂; same collection data as for preceding; 50.33420°N, 6.59520°E; wet meadow with higher vegetation; female specimen ID: ZFMK-TIS-2632572 (ZFMK); male specimen IDs: ZFMK-TIS-2632568 (ZFMK), ZFMK-TIS-2632569 (ZFMK), ZFMK-TIS-2632570 (ZFMK), ZFMK-TIS-2632571 (ZFMK), ZFMK-TIS-2632573 (ZFMK), ZFMK-TIS-2632574 (ZFMK), ZFMK-TIS-2632575 (ZFMK), ZFMK-TIS-2632576 (ZFMK). • 3 ♂♂; Rhineland-Palatinate, Vulkaneifel, Juenkerath, private garden; 50.33430°N, 6.59500°E; ca 450 m a.s.l.; 6–8 Aug. 2021; Jonathan Vogel leg.; Malaise trap, wet meadow, right next to ditch; specimen IDs: ZFMK-TIS-2632549 (ZFMK), ZFMK-TIS-2632550 (ZFMK), ZFMK-TIS-2632551 (ZFMK). • 1 ♂; Saxony, Mittelsachsen, Nat. res. Kirstenmuehle-Schanzenbachtal; 51.14920°N, 12.89690°E; ca 180 m a.s.l.; 16 Jul. 2021; Jonathan Vogel leg.; sweep net; specimen ID: ZFMK-TIS-2634853 (ZFMK).

LITHUANIA • 1 ♂; Alytus, Alytus, Žuvintas; 54.43950°N, 23.58870°E; ca 80 m a.s.l.; 23 Jun.-5 Jul. 2022; Andrius Petrasiunas leg.; Malaise trap; specimen ID: ZFMK-TIS-2637733 (ZFMK).

NORWAY • 2 ♀♀; Vestfold, Borrevann, Horten natursenter; 59.41720°N, 10.43860°E; ca 30 m a.s.l.; 1 Jul-2 Aug. 2015; Arnstein Staverløkk leg.; Malaise trap; specimen IDs: NOFIG544 (NINA), NOFIG747 (NINA).

Leptopilina heterotoma

BELGIUM • 1 ♀; Antwerpen, Mechelen; 51.03200°N, 4.48800°E; ca 10 m a.s.l.; 7 Jul. 2017; Jan Soors leg.; light trap, private garden; specimen ID: ZFMK-TIS-2635113 (ZFMK).

GERMANY • 2 ♀♀; Baden-Württemberg, Karlsruhe, Malsch, Hansjakobstraße; 48.88350°N, 8.31970°E; ca 120 m a.s.l.; 26 Apr.-10 May 2020; Dieter Doczkal leg.; Malaise trap, garden; specimen IDs: ZFMK-TIS-2634695 (ZFMK), ZFMK-

TIS-2634696 (ZFMK). • 1 ♀; Baden-Württemberg, Rems-Murr-Kreis, Aspach bei Backnang; 48.96600°N, 9.39900°E; ca 280 m a.s.l.; 15–30 Apr. 2013; Lars Krogmann, J. Holstein, T. Kothe leg.; Malaise trap; specimen ID: ZFMK-TIS-2632783 (ZFMK). • 1 ♀; Baden-Württemberg, Stuttgart, Espan; 49.61670°N, 9.26670°E; ca 280 m a.s.l.; 28 Jul.-28 Aug. 2014; F. Woog leg.; Malaise trap; specimen ID: ZFMK-TIS-2632780 (ZFMK). • 1 ♀, 2 ♂♂; Baden-Württemberg, Stuttgart, Espan; 49.61670°N, 9.26670°E; ca 280 m a.s.l.; 20 Sep.-20 Oct. 2014; F. Woog leg.; Malaise trap; female specimen ID: ZFMK-TIS-2629375 (ZFMK); male specimen IDs: ZFMK-TIS-2629370 (ZFMK), ZFMK-TIS-2629371 (ZFMK). • 1 ♀; Baden-Württemberg, Tübingen, Steinenberg; 48.53060°N, 9.03120°E; ca 470 m a.s.l.; 31 Jul.-14 Aug. 2014; T. Kothe, M. Engelhardt, Christian König leg.; Malaise trap; specimen ID: ZFMK-TIS-2632740 (ZFMK). • 1 ♀; Bavaria, Landshut, Landwirtschaft Siegl/Pfarrkofen; 48.65810°N, 12.10210°E; ca 470 m a.s.l.; 4 Mar.-1 Apr. 2022; NaPa leg.; vane trap, control, conventional farm; specimen ID: ZFMK-TIS-2635283 (ZFMK). • 1 ♀; Hesse, Gießen, Nat. res. Holzwäldchen bei Gleiberg; 50.60420°N, 8.63170°E; ca 200 m a.s.l.; 14 Jun. 2021; GBOL III leg.; sweep net; specimen ID: ZFMK-TIS-2632592 (ZFMK). • 1 ♂; Hesse, Waldeck-Frankenberg, NP Kellerwald-Edersee, „Große Küche“; 51.15640°N, 8.98790°E; ca 320 m a.s.l.; 19 Aug.-2 Sep. 2021; GBOL III leg.; Malaise trap; specimen ID: ZFMK-TIS-2634812 (ZFMK). • 4 ♀♀, 4 ♂♂; Hesse, Werra-Meißner-Kreis, Witzenhausen, Dohrenbach, „Gut Fahrenbach“ (Loc. 9); 51.31110°N, 9.85130°E; ca 210 m a.s.l.; 16 Oct. 2020; GBOL III leg.; sweep net, cow meadow next to beech forest with rich vegetation; female specimen IDs: ZFMK-TIS-2631040 (ZFMK), ZFMK-TIS-2631042 (ZFMK), ZFMK-TIS-2631043 (ZFMK), ZFMK-TIS-2631047 (ZFMK); male specimen IDs: ZFMK-TIS-2631041 (ZFMK), ZFMK-TIS-2631044 (ZFMK), ZFMK-TIS-2631045 (ZFMK), ZFMK-TIS-2631046 (ZFMK). • 2 ♀♀, 2 ♂♂; North Rhine-Westphalia, Bonn, Garden of Museum Koenig; 50.72150°N, 7.11370°E; ca 70 m a.s.l.; 4 Jul. 2022; Josefine Schwingeler, Jonathan Vogel leg.; sweep net, Various habitats; female specimen IDs: HM118-06-BB (ZFMK), HM126-02-CC (ZFMK); male specimen IDs: HM105-05-AA (ZFMK), HM123-11-BB (ZFMK). • 1 ♀; North Rhine-Westphalia, Bonn, Mehlem, Deichmanns Aue 62; 50.67090°N, 7.18460°E; ca 60 m a.s.l.; 25 Aug.-4 Sep. 2021; GBOL III leg.; Malaise trap; specimen ID: ZFMK-TIS-2632669 (ZFMK). • 1 ♀; North Rhine-Westphalia, Bonn, ZFMK garden; 50.72130°N, 7.11370°E; ca 70 m a.s.l.; 27 Jun.-4 Jul. 2017; Jonathan Vogel leg.; vinegar bait trap, bushes near cherry tree; specimen ID: ZFMK-HYM-00039732 (ZFMK). • 1 ♂; North Rhine-Westphalia, Bonn, ZFMK garden; 50.72180°N, 7.11320°E; ca 70 m a.s.l.; 16 Aug. 2021; OEP Arthropod course leg.; sweep net; specimen ID: ZFMK-TIS-2632470 (ZFMK). • 1 ♂; North Rhine-Westphalia, Bonn, ZFMK garden; 50.72180°N, 7.11320°E; ca 70 m a.s.l.; 23 Jun. 2022; Tobias Salden leg.; yellow pan trap; specimen ID: ZFMK-TIS-2637731 (ZFMK). • 1 ♂; North Rhine-Westphalia, Bonn, ZFMK garden; 50.72180°N, 7.11320°E; ca 70 m a.s.l.; 15 Jul 2024; OEP Arthropod course leg.; sweep net; specimen ID: ZFMK-HYM-00039731 (ZFMK). • 1 ♀; North

Rhine-Westphalia, Rhein-Sieg-Kreis, Altendorf; 50.58220°N, 7.02000°E; ca 240 m a.s.l.; 28 Jun.-12 Jul. 2021; Isabel Kilian et al. leg.; barber trap, summer wheat with cow dung; specimen ID: ZFMK-TIS-2635290 (ZFMK). • 2 ♀♀; North Rhine-Westphalia, Rhein-Sieg-Kreis, Altendorf; 50.58220°N, 7.02000°E; ca 240 m a.s.l.; 28 Jun.-12 Jul. 2021; Isabel Kilian et al. leg.; barber trap, summer wheat with digestate substrate; specimen IDs: ZFMK-TIS-2635287 (ZFMK), ZFMK-TIS-2635289 (ZFMK). • 5 ♀♀; North Rhine-Westphalia, Windeck, Siegaue, Schladern; 50.80000°N, 7.58500°E; ca 120 m a.s.l.; 2–9 May 2017; ZFMK et al. leg.; Malaise trap; specimen IDs: ZFMK-TIS-2630898 (ZFMK), ZFMK-TIS-2630900 (ZFMK), ZFMK-TIS-2630901 (ZFMK), ZFMK-TIS-2630902 (ZFMK), ZFMK-TIS-2630903 (ZFMK). • 1 ♀; same collection data as for preceding; 6–13 Jun. 2017; specimen ID: ZFMK-TIS-2631076 (ZFMK). • 1 ♀; Rhineland-Palatinate, Alzey-Worms, Wine fields north of Monsheim; 49.64060°N, 8.21370°E; ca 140 m a.s.l.; 10–18 Jul. 2021; Carolin Gilgenbach leg.; Malaise trap; specimen ID: ZFMK-TIS-2632630 (ZFMK). • 1 ♀; Saxony, Leipzig, Rötha, Haeckelstrasse; 51.19520°N, 12.42330°E; ca 140 m a.s.l.; 16 Jul. 2021; Jonathan Vogel leg.; sweep net; specimen ID: ZFMK-TIS-2632456 (ZFMK). • 2 ♂♂; Saxony, Mittelsachsen, Nat. res. Kirstenmuehle-Schanzenbachtal; 51.14920°N, 12.89690°E; ca 180 m a.s.l.; 16 Jul. 2021; Jonathan Vogel leg.; sweep net; specimen IDs: ZFMK-TIS-2634854 (ZFMK), ZFMK-TIS-2634855 (ZFMK).

NORWAY • 5 ♀♀; Hedmark, Kongsvinger, Gropa; 60.14400°N, 12.07600°E; ca 200 m a.s.l.; 3 Aug. 2011; Frode Ødegaard leg.; specimen IDs: NOFIG73 (NINA), NOFIG1317 (NINA), NOFIG1222 (NINA), NOFIG1318 (NINA), NOFIG1224 (NINA).

THE NETHERLANDS • 1 ♀, 1 ♂; Gelderland, Beusichem; 51.95720°N, 5.28130°E; ca 0 m a.s.l.; 14–15 Aug. 2021; P. Hoekstra leg.; yellow pan trap; female specimen ID: ZFMK-TIS-2641453 (ZFMK); male specimen ID: ZFMK-TIS-2641454 (ZFMK). • 1 ♂; Limburg, Maastricht, Sint-Pietersberg Zuid; 50.81640°N, 5.68380°E; ca 60 m a.s.l.; 15 Sep. 2019; P. Hoekstra leg.; hand picked; specimen ID: ZFMK-TIS-2637709 (ZFMK).

Leptopilina japonica

BELGIUM • 1 ♀; West Flanders, Ypres, De Triangel; 50.84180°N, 2.88380°E; ca 20 m a.s.l.; 29 Oct.-12 Nov. 2022; Fons Verheyde leg.; Malaise trap, urban park (bushes); specimen ID: ZFMK-TIS-2637792 (ZFMK).

GERMANY • 1 ♀; Baden-Württemberg, Rhein-Neckar-Kreis, Dossenheim, JKI, Schwabenheimer Str. 101; 49.44670°N, 8.64230°E; ca 110 m a.s.l.; 17–22 Sep. 2021; Jakob Martin leg.; rearing (raspberry), pesticide-free raspberry cultivars on experimental field; specimen ID: 21_07040102 (JKI). • 1 ♂; same collection data as for preceding; 22 Sep. 2021; Jakob Martin, Annette Herz leg; specimen ID: SMNS_Hym_Hym_014630 (SMNS). • 1 ♀; same collection data as for preceding; 6 Oct. 2021; specimen ID: SMNS_Hym_Hym_014629 (SMNS). • 6 ♀♀; Bavaria, Würzburg, LWG Veithöchstheim; 49.84010°N, 9.87760°E; ca 220 m a.s.l.; 30 May 2023; Sophie Reiher leg.; rearing (*Rubus fruticosus* Asterina), area of research center; specimen IDs: ZFMK-Hym-00039555 (ZFMK), ZFMK-Hym-00039556 (ZFMK), ZFMK-Hym-00039557 (ZFMK), ZFMK-Hym-00039558 (ZFMK), ZFMK-Hym-00039559 (ZFMK), ZFMK-Hym-00039560 (ZFMK). • 1 ♀; Brandenburg, Frankfurt (Oder), Pesticide-free experimental field; 52.34700°N, 14.50700°E; ca 70 m a.s.l.; 21 Sep. 2023; Anja Kreuz leg.; rearing (blackberry). • 1 ♀; same collection data as for preceding; Sep. 2024; rearing (strawberry); specimen ID: ZFMK-HYM-00039740 (ZFMK). • 1 ♀; Hesse, Darmstadt-Dieburg, Reinheim; 49.82580°N, 8.82490°E; ca 170 m a.s.l.; Oct. 2021; R. Weber leg.; rearing (raspberry), residential garden; specimen ID: ZFMK-TIS-2641360 (ZFMK). • 1 ♀; Hesse, Waldeck-Frankenberg, National park Kellerwald-Edersee, Maierwiesen; 51.15550°N, 9.00150°E; ca 360 m a.s.l.; 22 Jun.-8 Jul. 2021; GBOL III leg.; Malaise trap (Krefeld); specimen ID: ZFMK-TIS-2632548 (ZFMK). • 3 ♀♀, 1 ♂; North Rhine-Westphalia, Bonn, Garden of Museum Koenig; 50.72150°N, 7.11370°E; ca 70 m a.s.l.; 4 Jul. 2022; Josefine Schwingeler, Jonathan Vogel leg.; sweep net, Various habitats; female specimen IDs: HM108-08-AA (ZFMK), HM120-08-BB (ZFMK), HM133-09-CC (ZFMK); male specimen ID: HM135-11-CC (ZFMK). • 1 ♀; same collection data as for preceding; 16 Jun. 2023; Inci Baez, Tobias Salden leg.; specimen ID: ZFMK-Hym-00039549 (ZFMK). • 1 ♀, 2 ♂♂; same collection data as for preceding; 16 Aug. 2021; OEP Arthropod course leg.; female specimen ID: ZFMK-TIS-2632471 (ZFMK); male specimen IDs: ZFMK-TIS-2632469 (ZFMK), ZFMK-TIS-2632472 (ZFMK). • 1 ♂; North Rhine-Westphalia, Bonn, ZFMK garden; 50.72180°N, 7.11320°E; ca 70 m a.s.l.; 23 Jun. 2022; Tobias Salden leg.; yellow pan trap; specimen ID: ZFMK-TIS-2637732 (ZFMK). • 1 ♀; same collection data as for preceding; 4 Oct. 2022; sweep net; specimen ID: ZFMK-TIS-2635306 (ZFMK). • 1 ♀; Rhineland-Palatinate, Bad Dürkheim, Neustadt an der Weinstraße; 49.37330°N, 8.19960°E; ca 130 m a.s.l.; 14 Oct. 2022; Camilla Englert leg.; hand picked, raspberry cultivars on experimental field; specimen ID: ZFMK-TIS-2641361 (ZFMK). • 1 ♀; same collection data as for preceding; 15 Oct 2022; rearing (raspberry); specimen ID: 22_N_Lj1 (JKI). • 5 ♀♀, 3 ♂♂; Rhineland-Palatinate, Südliche Weinstraße, Böbingen; 49.28280°N, 8.23640°E; ca 120 m a.s.l.; 29 Jun. 2023; Clara Boeninger leg.; hand picked. • 35 ♀♀; same collection data as for preceding; 29 Jun. 2023; sweep net. • 1 ♂; same collection data as for preceding; 19 Jul. 2023; hand picked.

Switzerland • 5 ♀♀, 5 ♂♂; Basel-Landschaft, Liestal, Liestal; 47.48900°N, 7.73530°E; ca 320 m a.s.l.; 31 Jul. 2022; Heinz Döbeli leg.; rearing (elderberry). • 1 ♀, 1 ♂; Basel-Landschaft, Liestal, Ziefen; 47.43270°N, 7.70490°E; ca 420 m a.s.l.; 31 Jul.-3 Oct. 2021; Heinz Döbeli leg.; rearing (elder); female specimen ID: ZFMK-HYM-00039708 (ZFMK); male specimen ID: ZFMK-HYM-00039707 (ZFMK). • 1 ♀, 1 ♂; Basel-Landschaft, Liestal, Ziefen; 47.44070°N, 7.70850°E; ca 480 m a.s.l.; 26 Jun.-1 Aug. 2022; Heinz Döbeli leg.; rearing (cherry); female specimen ID: ZFMK-HYM-00039709 (ZFMK); male specimen ID: ZFMK-HYM-00039713 (ZFMK). • 1 ♀; Basel-Landschaft, Liestal, Ziefen; 47.41700°N, 7.69110°E; ca 460 m a.s.l.; 15 Aug.-8 Oct. 2022; Heinz Döbeli leg.; rearing (elder); specimen ID: ZFMK-HYM-00039710 (ZFMK). • 1 ♀, 1 ♂; Basel-Landschaft, Liestal, Ziefen; 47.43270°N, 7.70460°E; ca 420 m a.s.l.; 28 Jul. 2023; Heinz Döbeli leg.; rearing (blackberry); female specimen ID: ZFMK-HYM-00039706 (ZFMK); male specimen ID: ZFMK-HYM-00039715 (ZFMK). • 2 ♂♂; Basel-Landschaft, Liestal, Ziefen; 47.43260°N, 7.70430°E; ca 420 m a.s.l.; 16 Aug.-3 Sep. 2023; Heinz Döbeli leg.; rearing (elder); specimen IDs: ZFMK-HYM-00039712 (ZFMK), ZFMK-HYM-00039714 (ZFMK). • 1 ♀; Basel-Landschaft, Liestal, Ziefen; 47.43270°N, 7.70480°E; ca 420 m a.s.l.; 25–29 May 2024; Heinz Döbeli leg.; vinegar bait trap; specimen ID: ZFMK-HYM-00039711 (ZFMK).

United Kingdom • 1 ♀; Ashford, Kent; 51.18940°N, 0.89420°E; ca 70 m a.s.l.; 27 Oct.-5 Nov. 2024; Glen Powell leg.; residential garden near orchards; specimen ID: ZFMK-HYM-00039729 (ZFMK).

Leptopilina longipes

Germany • 1 ♀; North Rhine-Westphalia, Windeck, Siegaue, Schladern; 50.80000°N, 7.58500°E; ca 120 m a.s.l.; 4–11 Jul. 2017; ZFMK et al. leg.; Malaise trap; specimen ID: ZFMK-TIS-2631095 (ZFMK).

Norway • 1 ♂; Hedmark, Kongsvinger, Gropa; 60.14400°N, 12.07600°E; ca 200 m a.s.l.; 3 Aug. 2011; Frode Ødegaard leg.; specimen ID: NOFIG576 (NINA).

Supplementary material 1

Leptopilina material from GBOLI-III and partners examined for this study

Authors: Jonathan Vogel

Data type: xlsx

Link: https://doi.org/10.3897/jhr.98.165583.suppl1

Supplementary material 2

Leptopilina CO1 sequence IDs (specimen, BOLD and DROP)

Authors: Jonathan Vogel, Arnstein Staverløkk

Data type: xlsx

Link: https://doi.org/10.3897/jhr.98.165583.suppl2

Supplementary material 3

Host records of Western Palearctic *Leptopilina* species

Authors: Jakob Martin

Data type: pdf

Link: https://doi.org/10.3897/jhr.98.165583.suppl3

Supplementary material 4

Parasitoid wasp community of the Western Palearctic *Leptopilina* species

Authors: Jakob Martin

Data type: pdf

Link: https://doi.org/10.3897/jhr.98.165583.suppl4

Supplementary material 5

Distribution records with sources of the Western Palearctic *Leptopilina* species

Authors: Mattias Forshage

Data type: xlsx

Link: https://doi.org/10.3897/jhr.98.165583.suppl5