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Revision of Holarctic *Illidops* Mason (Hymenoptera, Braconidae): A first step towards resolving a dark taxon and descriptions of three new species

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Abstract. Microgastrinae wasps are an important group of Lepidoptera parasitoids, but also considered a so-called "dark taxon" due to the large amount of undiscovered and unidentifiable diversity. In the Holarctic, this is due to various factors, but lack of up-to-date identification literature and taxonomic revisions is a main contributor. Here, the genus *Illidops* is revised in the Holarctic region for the first time in over 35 years and an updated generic concept is provided. *Illidops albostigmalis* van Achterberg & Fernandez-Triana, 2017 is recorded for the first time from the Palearctic and three new species are formally described: *Illidops oroseira* Höcherl & Fernandez-Triana sp. nov. from the Palearctic, *Illidops doreenae* Höcherl & Fernandez-Triana sp. nov., and *Illidops stefanschmidti* Höcherl & Fernandez-Triana sp. nov. from the Nearctic. A key to all 33 species of *Illidops* occurring in the Holarctic is provided. A first-glance preliminary system is used to evaluate the robustness of species concepts, allowing the inclusion of poorly known species. Many species are associated with new information, including photographs for 29 species, 23 of which are of primary types. Our integrative taxonomy approach including DNA barcoding resulted in nine species now linked to barcodes and the discovery of morphologically cryptic diversity. Shotgun-sequencing was applied for the recovery of barcode sequences of historical specimens. Additionally, annotated translations of original descriptions in Russian for six species and a commented overview of the literature of host species of *Illidops* are provided.

Keywords. Integrative taxonomy, parasitoid wasps, historical specimens, Palearctic fauna, Nearctic fauna.

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Introduction

Microgastrinae wasps are an important group of Lepidoptera parasitoids, but also considered a so-called "dark taxon" due to the large amount of undiscovered and unidentifiable diversity (Fernandez-Triana *et al.* 2020; Beaudin *et al.* 2025). The genus *Illidops* Mason, 1981 currently includes 37 described species found worldwide (Fernandez-Triana *et al.* 2020). With 29 species recorded, the Palearctic represents the most speciose region at present. However, many additional species are known in collections, from both temperate and tropical areas. Although little is known about the ecology of this group, Mason (1981) and other authors (e.g., Wharton 1983) mention that members of *Illidops* seem to occur more frequently in arid environments, such as deserts. Few reared specimens are known and hosts recorded in the literature include species of the families Scythrididae Rebel, 1901 (Wilkinson 1945), Psychidae Boisduval, 1829 (Nixon 1976; Papp 1984), Gelechiidae Stainton, 1854 (Muesebeck 1921), and Crambidae Latreille, 1810 (Fernández-Triana & van Achterberg 2017). The name *Illidops* refers to the characteristic convergence of the lower eye margins, appearing as "squinting eyes" in the type species and some other representatives of the genus (Mason 1981). With its rather long and setose ovipositor sheaths and desclerotized hypopygium, *Illidops* represents one of the genera fitting Mason's (1981) 'microlepidoptera suite of characters'. It is part of the *Apanteles* group of genera, characterized by the females' ovipositor sheaths being mostly setose and relatively long (at least 0.5 × metatibial length), and the ventral margin of the hypopygium being usually flexible and either with one or several pleats (Fernandez-Triana *et al.* 2020).

Many species that are placed in *Illidops* were first grouped together by Nixon (1965) as his *butalidis*-group of *Apanteles* Förster, 1863. He commented that he was "not at all sure that this is a homogenous group" as it contains "a number of widely different species" (Nixon 1965: 182). *Illidops* as a genus was formally introduced by Mason (1981), deriving from Nixon's *butalidis*-group, but only including three of Nixon's nine *butalidis*-group species, leaving out the more aberrant species (Nixon 1976). Papp (1988) later transferred additional species of his *butalidis*- *suevus*- and *vipio*-groups to *Illidops*, leaving the genus altogether with 21 species. The concept of the genus has since been regarded as unsatisfactory and controversial by several authors (e.g., van Achterberg 2002; Yu *et al.* 2016). Some of the species are difficult to place in a genus in an unambiguous manner due to possessing a combination of features typical of the genera *Illidops* Mason, 1981, *Dolichogenidea* Viereck, 1911, *Rhygoplitis* Mason, 1981, and *Napamus* Papp, 1993. Fernandez-Triana *et al.* (2014b, 2020) recognized *Illidops* as a valid genus and provided an updated generic concept with additional morphological features, such as the structure referred to by them as the "scutellar posteriomedian band of rugosity". In addition to the keys provided by Nixon (1965, 1976) and Papp (1984) for the Western Palearctic fauna, Tobias and Kotenko (e.g., Tobias & Kotenko 1986; Kotenko 2007) described species and provided keys for the Eastern Palearctic.

In general, poorly understood taxa in relatively well-studied regions such as the Palearctic present specific challenges apart from species-richness or cryptic morphology alone. Taxonomists are not only confronted with geographically restricted keys (Fernandez-Triana *et al.* 2014a), short or incomplete descriptions resulting in vague species concepts (e.g., Awad *et al.* 2023), scattered and potentially missing types, and lack of host data. Many species have complex histories of synonymizations (e.g., Johansson 2024; Vogel *et al.* 2024), which significantly complicates further progress in revisionary work and species discovery. For such groups, the aim of 'solving it all' in one revision is unachievable or would take decades, potentially still yielding unsatisfying results.

Here, for *Illidops*, we attempt a first step towards resolving some of the problems within the genus in an integrative taxonomy approach: we revise the genus within the entire Holarctic realm as it is currently understood. We provide an updated generic concept, a key to all 33 species known from the Holarctic, photos of many types, gather previously scattered historical information on all the species, and discuss species concepts according to our molecular data and observations of historical literature. In doing so, we aim to provide a basis for further, much needed work in this group and discuss the challenges and gaps that we have encountered while working on this project.

Material and methods

The main sources of specimens for this study are the Canadian National Collection of Insects (CNC), Ottawa, Canada, the Zoologische Staatssammlung München (SNSB-ZSM), Munich, Germany, and the Schmalhausen Institute of Zoology (SIZK), Kyiv, Ukraine. Details of the studied specimens are provided in the Material examined sections, and information on additional, tentatively associated specimens (cf.) is presented in Supp. file 1, which lists all examined material. We downloaded additional sequences and distribution data from the public and private data available to us in the Barcode of Life Data System (BOLD, www.boldsystems.org) (Ratnasingham & Hebert 2007). We used a reverse DNA barcoding and integrative taxonomy approach, in which we first used a molecular workflow for clustering, followed by a morphological workflow and additionally looked at host data to establish our integrative species concepts. Detailed information can be found in Höcherl *et al.* (2024).

Sequencing of COI was done for most specimens at the Canadian Centre for DNA Barcoding (CCDB) using their at-the-time standard protocols and primers, which can be reviewed for each sequence in BOLD. Sequences were managed, analyzed and clustered using the BOLD workbench performing the Barcode Index Numbers (BINs) approach (Ratnasingham & Hebert 2013) to define molecular operational taxonomic units (MOTUs). *Illidops* sequences in BOLD were identified by running a larger Neighbor Joining (NJ) analysis on all available sequences identified as Microgastrinae from Holarctic countries in the BOLD database. This step was included because many sequences of specimens which likely represent members of *Illidops* were expected to be misidentified as *Apanteles*, *Rhygoplitis*, *Dolichogenidea*, *Napamus*, or other genera. Two clusters which most likely included representatives of *Illidops* were identified and further analyses conducted with sequences from these clusters. In addition to the data available in BOLD, DNA from historical specimens (49–84 year old dry material) was extracted following the non-destructive protocol detailed in Patzold *et al.* (2020). Sequence libraries of the historical specimens were constructed using the NEBNext Ultra FS DNA Library Prep Kit at a commercial sequencing facility (StarSEQ GmbH, Mainz, Germany), followed by sequencing on an Illumina NextSeq 500 with a 150-base paired-end approach and an estimated output of 10 million reads per sample. Libraries were assembled de novo using SPAdes ver. 3.15.3 (Prjibelski *et al.* 2020) and decontaminated using Blobtools ver. 1.1.1 (Laetsch & Blaxter 2017). Contigs were checked against the National Center for Biotechnology Information (NCBI) nucleotide database (e-value cutoff of 1e-25) (https://www.ncbi.nlm.nih.gov/nucleotide/).

For the DNA barcode data, NJ topologies were computed using MEGA11 (Tamura *et al.* 2021) applying the Kimura 2-parameter (K2P) model (Kimura 1980) and non-parametric bootstrapping (Felsenstein 1985). In some cases, distance matrices were calculated in BOLD or MEGA11 for intra- or interspecific pairwise distances (p-distances with K2P model). The p-distances between BINs represent pairwise distances given on the respective BIN pages in BOLD. For selected species and BINs, TCS haplotype network analysis implemented in PopART was performed (Clement *et al.* 2002; Leigh & Bryant 2015). In some cases, significantly shorter sequences compared to the remainder of the sample were excluded from the analyses. For haplotype network analysis, the sequence length is indicated in the description of the figures depicting the haplotype networks; sequence alignments are available as Supp. file 7 and Supp. file 8. As BINs and BIN assignments are not static and may change as new data is added to BOLD (Ratnasingham & Hebert 2007, 2013), our BIN assignments refer to the latest download of the dataset DS-ILLIDOPS on 13 Dec 2024. COI sequences are available as Supp. file 3 and Supp. file 6.

Voucher specimens were dried by critical point drying or chemically using a modified Hexamethyldisilazane (HMDS) protocol (Heraty & Hawks 1998). Measurements taken for new taxa described are not diagnostic and often a subset of the type series was measured (always the holotype, to which the first measurement refers, other specimens follow in brackets). All measurements are provided in Supp. file 2. Specimens were photographed using a Keyence VHX-1000 or VHX-6000 digital microscope and panorama stacks were computed using the built-in software of the microscope (Keyence Corporation, Osaka, Japan). Additional photos were taken using an Olympus OMD-EM1 Mk II or a Macropod microphotography system (Macroscopic Solutions, Hartford, USA), both using 5 ×, 10 ×, 20 ×, and 50 × Mitutoyo microscope lenses, with image stacks rendered in Helicon Focus (Helicon Soft, Kharkiv, Ukraine). Photos of types stored at SIZK were taken with a Leica Z16 APO microscope equipped with a Leica FLEXACAM C1 camera and processed by LAS Core software (Leica Microsystems, Wetzlar, Germany) at SIZK. Subsequent processing and construction of image plates and figures was done using Photoshop (Adobe Inc., San José, USA) and Inkscape (Inkscape Community). Images of two holotypes (of previously described species) deposited in the Natural History Museum (Smithsonian Institution, Washington DC, USA) were accessed through the Primary Type Specimens Catalog of the Department of Entomology Collections (https://collections.nmnh.si.edu/search/ento/). The downloaded images were later combined into plates. Those images are available under a CC0 license; in any case, we acknowledge the source of those images here.

Terminology and measurements for morphological comparisons used here are explained in detail in Shaw *et al.* (2024) and Fernandez-Triana *et al.* (2014b). Some characters that are more specific to *Illidops* are detailed in Fig. 1 and discussed in the results section (Figs 2–5).

Abbreviations for morphological characters

F1–F16 = flagellomeres 1–16, respectively
OOL = ocular–ocellar line
POD = posterior ocellus diameter
POL = distance of posterior ocelli
T1 = mediotergite 1
T2 = mediotergite 2
T3–T7 = tergites 3–7, respectively

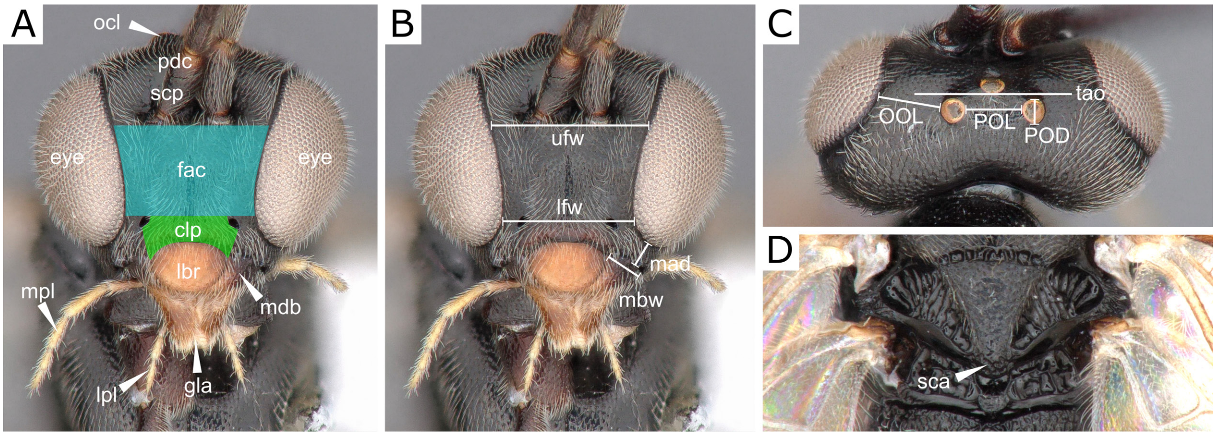

Fig. 1. Morphological characters of the head of *Illidops* Mason, 1981 frequently used for identification. **A–C**. Frontal and dorsal images of the head of *I. splendidus* (Papp, 1974), ♀ (ZSM-HYM-33166-H06). **D**. Scutellum of *I. butalidis* (Marshall, 1889), ♀ (ZSM-HYM-33168-B07). Abbreviations: clp = clypeus; eye = compound eye; fac = face; gla = glossa; lbr = labrum; lfw = lower face width; lpl = labial palp; mad = malar distance; mbw = mandible width; mdb = mandible; mpl = maxillary palp; OOL = ocular-ocellar line = distance between compound eye and a posterior ocellus; pdc = pedicel; POD = posterior ocellar diameter; POL = posterior ocelli distance = distance between posterior ocelli; sca = sculptured area centrally interrupting posterior smooth band of the scutellum; scp = scape; ufw = upper face width. Images altered from Shaw *et al*. (2024).

For morphological species identification, we used various identification keys and compared to type material or authoritatively identified material, if available. We group our species concepts into three categories, depending on how trustworthy we consider them. It has to be noted that, for most species, only morphological data was available and hence the groupings mostly reflect this type of data. The main goal of this is to immediately indicate the robustness of our species concepts for the user of the key and point out the shortcomings of this work at first glance.

The three categories are as follows:
*** Good: we examined the holotype and/or paratypes, and/or photos of types, and/or authoritatively identified specimens, and/or specimens reliably reared from the same host as the holotype.
** Moderate: we did not see any types or reliably identified material but the species is described in sufficient detail and/or detailed drawings are provided, and/or we found images that match the species, and/or the species is unique and less likely to be confused.
* Poor: the species is only known to us from its original description which does not provide enough detail, information is generally scarce.

Details of the concepts are provided for each species and in exceptions a species can be grouped higher or lower based on our subjective judgment. This would be the case, for example, if we saw types of a junior synonym, but are unsure whether the synonymy is justified, or if the photos we had available did not show the relevant structures for the identification of the species. Also, in the case that molecular data contradicts the morphological species concept, this is indicated in the species concept section and if this hampers morphological identification, the category may be lowered due to that. Conditional characters were used in the key (in capital letters) and indicate that in those cases more than one character system has to be considered.

Original descriptions were checked to collect any host information related to type material, which was carefully interpreted (Shaw 2023). Synonyms and current combinations for Lepidoptera hosts were checked in Lepiforum's latest checklist for European Lepidoptera (Rennwald *et al.* 2023). Original descriptions by Tobias (1976) and Kotenko (2004, 2007) that were previously only available in Russian were translated by MK. The terminology of morphological structures was adapted to HAO standards for the sake of uniformity in this manuscript. The unaltered original descriptions are provided in Supp. file 9. Voucher codes that are referred to in the remarks and material examined sections refer to the "SampleID" in BOLD, more information about these specimens can be retrieved from Supp. file 1 or from BOLD. Distribution data of specimens is based on the annotated world checklist, as well as abbreviations and limits for the biogeographical regions used by Fernandez-Triana *et al.* (2020). Abbreviations for biogeographical regions are as follows: NEO = Neotropical; NEA = Nearctic; PAL = Palearctic; OTL = Oriental; AFR = Afrotropical; AUS = Australasian and Oceanian (combined following O'Hara *et al.* 2009). The Holarctic includes the Nearctic and Palearctic regions. For states of the USA and for Canadian provinces and territories, acronyms follow Canada Post (http://www.canadapost.ca/tools/pg/manual/PGaddress-e.asp). Russian subdivisions and acronyms follow Standard ISO 3166 (https://www.iso.org/obp/ui/#iso:code:3166:RU), but see Fernandez-Triana *et al.* (2020) for exceptions.

Acronyms of repositories

CBG = Centre for Biodiversity Genomics
CNC = Canadian National Collection of Insects, Ottawa, Canada
HNHM = Hungarian Natural History Museum, Budapest, Hungary
MNCN = Museo Nacional de Ciencias Naturales, Madrid, Spain
MZH = Finnish Museum of Natural History, Helsinki, Finland
NHMUK = Natural History Museum, London, United Kingdom
PCMAG = Plymouth City Museum and Art Gallery, Plymouth, United Kingdom

RMNH = Naturalis Biodiversity Centre, Leiden, Netherlands
SIZK = Schmalhausen Institute of Zoology, Kyiv, Ukraine
SNSB-ZSM = Zoologische Staatssammlung München, Munich, Germany
USNM = National Museum of Natural History, Washington, USA
ZIN = Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia
ZMHB = Museum für Naturkunde der Humboldt-Universität, Berlin, Germany

Results

Class Insecta Linnaeus, 1758
Order Hymenoptera Linnaeus, 1758
Superfamily Ichneumonoidea Latreille, 1802
Family Braconidae Nees, 1811
Subfamily Microgastrinae Förster, 1862

Genus ***Illidops*** Mason, 1981

Illidops Mason, 1981: 56 (type species: *Illidops butalidis* (Marshall, 1889: 45), by subsequent designation by Mason 1981: 56)

Diagnosis

The genus *Illidops* can be defined at present by its posterior smooth band of the scutellum interrupted centrally by a sculptured area (Fig. 2A–E; although in very few species the sculpture is very weak, mostly limited to a small area on the anterior margin of the mesoscutellar bar or only consists of punctures, Fig. 2F–I); fore wing with vein R1 shorter than pterostigma (~0.3–0.9 × (e.g., Figs 6G, 10F, 12F, 20F), with the exception of *I. kostylevi* (Kotenko, 1986) having R1 as long as the pterostigma (Fig. 25E)), although a few species in the morphologically similar genera *Apanteles*, *Dolichogenidea* and *Rhygoplitis* share this character; propodeum usually strongly sculptured, sculpture mostly reticulate (e.g., Figs 6E, 12D, 31D 48E, 52D; although a few species may have a median, longitudinal carina in addition to the reticulate sculpture (Figs 36A–D, 53C) and some other species may have variously reduced sculpture (e.g., Figs 10E, 25D, 26D, 38C, 56E, 58D, 61D), in extreme cases having an almost entirely smooth propodeum (Figs 19D, 22C)); hind wing with entirely setose vannal lobe (in most species, e.g., Figs 33F, 50H); eyes convergent, at times strongly (Fig. 3A–B; but many species just very slightly convergent (Fig. 3C) or with parallel eyes (Fig. 3D)); T3–T7 medially desclerotized and seemingly pushed forwards (e.g., Figs 6F, 12E, 14E, 28E; although some species do not have this feature and some species in the morphologically similar genera *Apanteles*, *Dolichogenidea* and *Rhygoplitis* share this character).

Remarks

Knowledge on the potential monophyly of *Illidops* or its relationship towards the morphologically similar genera *Rhygoplitis*, *Napamus*, *Apanteles* and *Dolichogenidea* is poor. Phylogenetic relationships among microgastrine genera have so far proved largely intractable both using morphology or molecular methods (or a combination of both), possibly a result of rapid ancient radiation (Banks & Whitfield 2006; Whitfield & Kjer 2008; Whitfield *et al.* 2018). Analyses of phylogenetic relationships of microgastrine wasps either did not include species of *Illidops* (Mardulyn & Whitfield 1999; Whitfield *et al.* 2002; Banks & Whitfield 2006) or had very limited sampling of *Illidops* and closely related genera (Abdoli *et al.* 2024).

All species treated here are part of a taxon that Fernandez-Triana *et al.* (2020) considered the *Apanteles* group, an informal grouping of 26 genera that includes most, but not all of the Apantelini + Microgastrini tribes sensu Mason (1981). This *Apanteles* group is characterized by having mostly setose and relatively long ovipositor sheaths and the hypopygium with the ventral margin flexible and pleated. Within the *Apanteles* group, *Illidops* is part of a larger subgroup defined by the lack of a closed fore wing areolet.

The genus *Illidops* was erected by Mason (1981) with *I. butalidis* (Marshall, 1889) as the type species of the genus. Mason's concept of *Illidops* upon description of the genus included three described species: *A. butalidis* (the type), *A. szaboi* Papp, 1972 (currently a junior synonym of *I. mutabilis* (Telenga, 1955)), and *A. urgo* Nixon, 1965. He based his concept on Nixon's concept of his *butalidis*-group; however, he did not include a large number of the species which Nixon (1965) previously had included: *A. dion* Nixon, 1965 (now a junior synonym of *I. suevus* (Reinhard, 1880)), *A. electilis* (Tobias, 1964), *A. sophrosine* (Nixon, 1976), *A. contortus* Tobias, 1964 (now a junior synonym of *I. naso* (Marshall, 1885)), *A. cloelia* (Nixon, 1965), and *A. evander* Nixon, 1965 (now a junior synonym of *I. naso*). This discrepancy may be explained by the limited access that Mason may have had to types and other specimens from the Palearctic, which is lamented by Tobias & Kotenko (1986), who did not accept his subdivision of *Apanteles* in their key. Papp (1988) later integrated more Palearctic species into *Illidops* by adding species which he and Nixon had previously included in their *butalidis*- (Nixon 1965, 1976; Papp 1981), *suevus*- (Papp 1984) and *vipio* (Papp 1981) groups. Papp himself describes his homologization of European species groups with Mason's genera as a first step "bearing the errors and misunderstandings of a first endeavour" (Papp 1988: 146). Fernandez-Triana *et al.* (2014b) provided an updated diagnosis for the genus, first including the character of the "band of rugosity centrally on the posterior edge of the scutellar disc", which was more or less repeated by Fernandez-Triana *et al.* (2020). Two species were subsequently transferred to other genera, but most of the species remain in *Illidops*. *Apanteles biroicus* Papp, 1973 was transferred back to *Apanteles* by Fernandez-Triana *et al.* (2020), and *Napamus vipio* (Reinhard, 1880) became the type of the genus *Napamus*, described by Papp (1993).

The characters defining the genus were re-examined by Fernandez-Triana *et al.* (2014b) who noted that the lower margin of the eyes converging and metasomal terga 3–7 weakly sclerotized were absent in several species; they proposed a modified definition of *Illidops* that focused on the "band of rugosity centrally on the posterior edge of the scutellar disc", shortened fore wing vein R1 and propodeum fully sculptured but without areola (instead, with a series of short carinae medially on the posterior 0.2–0.3 of the propodeum near the nucha). The previous definitions by Mason (1981) and Fernandez-Triana *et al.* (2014b) were more or less repeated and combined in the world checklist of microgastrine wasps (Fernandez-Triana *et al.* 2020: 39).

For the present study, we had access to many additional specimens and species, including types and photos of types of several species which had neither been studied by Mason nor by Fernandez-Triana. Our study of those specimens suggests that the definition of *Illidops* is more complicated than anticipated, even if only restricted to Holarctic species. The main challenge was that we found more variation in the sculptured area interrupting the posterior smooth band of the scutellum centrally than described by previous authors and some species lacking it completely or almost completely. The degree of convergence of the lower margins of the eyes also varies amongst species of *Illidops* and in some the eyes do not converge. Both characters and their shortcomings are detailed more in a separate section below. Some species of *Illidops* are hence difficult to clearly place as they combine a set of features characteristic of other genera, e.g., *Dolichogenidea* (cosmopolitan), *Rhygoplitis* (NEA, NEO), and *Napamus* (PAL). The separation of these four genera can be challenging for some species. Table 1 provides a comparison between these genera.

Napamus (a genus currently with only two described species) lacks most of the key characters present in *Illidops* and the two genera should almost always be easily distinguished (Ghafouri Moghaddam *et al.* 2021).

Rhygoplitis has some features that resemble some species of *Illidops*, e.g., fore wing R1 short, sculptured area interrupting the posterior smooth band of the scutellum centrally, and propodeum coarsely sculptured and with a median, longitudinal carina (Mason 1981; Whitfield 1997). Additionally, the few DNA barcodes available for *Rhygoplitis* tend to cluster with sequences of *Illidops* in NJ analyses. *Rhygoplitis* has rather strongly defined notauli and the overall body sculpture very coarse; it is also a genus so far only known from the Neotropics and the Nearctic (mostly southern areas).

The vast majority of species of *Dolichogenidea* can easily be distinguished from *Illidops* because all of its species have an entirely smooth band posterior to the scutellum; also the propodeum is very rarely strongly sculptured and, when sculptured, usually not in the common patterns found in *Illidops.* These two genera usually cluster far apart in NJ topologies of Microgastrinae (e.g., Smith *et al.* 2013), although the definition of *Dolichogenidea* is far from resolved (see Mason 1981; Fernandez-Triana *et al.* 2014b; 2020). However, a few species of *Illidops* that we have examined as part of this study have a very weak (sometimes almost absent) sculptured area interrupting the posterior smooth band of the scutellum centrally, and in those species the propodeum is also not strongly sculptured (it is either entirely to mostly smooth or at least smooth on the anterior half of the propodeum). Those few species strongly resemble *Dolichogenidea* – although their sequences still tend to cluster with more ‘typical’ *Illidops* in NJ analyses. Nevertheless, these species with an almost entirely smooth band posterior to the scutellum and smooth propodeum challenge the concept of *Illidops* and it may be found in the future that they are better placed in a different genus. This concerns especially *I. bellicosus* (Papp, 1977) and *I. perseveratus* (Papp, 1977). *Illidops suevu*s also has the posterior band of the scutellum almost entirely smooth but has a strongly sculptured propodeum. For this paper we decided to include them in *Illidops* based on the short vein R1, elongate mouthparts and (in the case of *I. suevus*) the clustering of their sequences.

Shortcomings of some characters used for the identification of *Illidops* Mason, 1981

Area of rugosity posterior to the scutellum

The character “posteriomedian band of rugosity” refers to an area of rugosity posterior to the smooth, at most punctate scutellum and was introduced for *Illidops* by Fernandez-Triana *et al.* (2020). Nixon refers to this as “posterior polished band of scutellum interrupted at middle by small patch of rugosity” (Nixon 1976: 709). After examining many species of *Illidops*, we prefer to refer to this as “posterior smooth band of the scutellum more or less interrupted centrally by sculptured area”. This may range from a clearly visible area of rugosity centrally posterior to the scutellum which also invades the smooth band posterolaterally, such as in *I. scutellaris* (Muesebeck, 1921) and *I.* cf. *naso* (Fig. 2A–B), to a somewhat intermediate state in which the sculpture may be an area of rugosity or punctation which is restricted only to the central part posterior to the scutellum, as in *I.* cf. *mutabilis* (Telenga, 1955), *I. butalidis*, and *I. splendidus* (Papp, 1974) (Fig. 2D–F). In other species, the sculpture does not reach the posterior half of the smooth band entirely, but it seems that the sculpture and punctation of the scutellum invade the smooth posterior band slightly anteriorly, such as in *I. doreenae* Höcherl & Fernandez-Triana sp. nov., *I. oroseira* Höcherl & Fernandez-Triana sp. nov. and *I. suevus* (Fig. 2F–G). This is clearly different from the very smooth area posterior to the scutellum present in many other genera, such as *Apanteles* (Fig. 2H). However, this character can also vary within a single species and barcoding cluster (MOTU), as is the case in *I. oroseira*. It is also difficult to observe in some species, such as *I. suevus*. The character is not always clear-cut and does not separate *Illidops* from other genera alone, although it is not present in other closely related genera which may potentially be confused with *Illidops*, such as *Apanteles*, *Dolichogenidea*, *Napamus* and *Rhygoplitis*. Fernandez-Triana *et al.* (2020) transferred *Apanteles biroicus* from *Illidops* to *Apanteles* based on the lack of the sculptured area centrally interrupting the posterior smooth band of the scutellum and the different propodeum sculpture compared to other members *Illidops*; in light of our findings, this species may need to be reassessed in the future.

Eyes converging towards lower margin of the face

Several authors who published on the *butalidis*-group used the degree of convergence of the eyes towards the lower margin of the face as a character in their keys (Nixon 1976; Papp 1981; Tobias & Kotenko 1986). This character varies among the species of *Illidops*, some clearly show strongly converging inner margins of the eyes, in which case the minimum face width is less than 0.85 × the upper face width. This includes species such as *I. butalidis* (Fig. 3A), *I. splendidus*, *I. terrestris* Wharton, 1983, *I. toreicus* Kotenko, 2007, *I. urgo* (Nixon, 1965), *I. urgens* Kotenko, 2004, *I. naso*, and *I. vitobiasi* Kotenko, 2004 (Fig. 3B). In these cases, the eyes can also appear somewhat bulging, especially on the lower part of the head. In other cases, the eyes are only slightly converging with the minimum face width measuring ~0.85–0.95 × the upper face width (Fig. 3C). This includes species such as *I. buteonis* (Kotenko, 1986), *I. cloelia*, *I. dauricus* Kotenko, 2007, *I. kostjuki* (Kotenko, 1986), and *I. subversor*. Species with almost parallel inner eye margins have a minimum face width of ~0.95–1.05 × the upper face width (Fig. 3D). This includes species such as *I. blandus* (Tobias & Kotenko, 1986), *I. suevus*, and *I. suffectus* (Tobias & Kotenko, 1986). For practical reasons and for measuring the degree of convergence of the eyes, it appears useful to us to compare the upper face width to the minimum face width rather than lower face width, which in many cases can be done as a proxy for lower face width as the result will be the same. In addition to challenges in measuring this character, it is a continuous character with no discrete values, and can hence not really be categorized in a meaningful way. It can only be used for species which are significantly different and such comparisons should always include a measurement of the face width of the species. We are using the character here, with the above reservations, as it has proven useful in the past. For this character in our key, we will use the terminology as detailed above: strongly converging = minimum face width < 0.85 × upper face width; slightly converging = minimum face width ~0.85–0.95 × upper face width; not converging = minimum face width ~0.95–1.05 × upper face width.

Triangle delimited by the ocelli

Another character frequently used to distinguish species of *Illidops* is the shape of the triangle formed by the ocelli. The triangle can be either 'obtuse'/'very low', 'less low' or 'high', which is measured by whether an imaginary tangent posterior to the anterior ocellus crosses the posterior ocelli (illustrated in Fig. 1). If the tangent crosses the posterior ocelli, the triangle is obtuse/very low, such is the case in *I. blandus* and *I. mutabilis* (Fig. 4A), and according to Tobias & Kotenko (1986) also in *I. rostratus* (Tobias, 1976). If the tangent does not touch the posterior ocelli the triangle is high, such as in *I. vitobiasi* (Fig. 4D), *I. buteonis*, *I. cloelia*, *I. suevus*, and more. Some species exhibit an intermediate state which is difficult to interpret and in which the tangent touches the posterior ocelli, such as in *I. toreicus* and *I. subversor* (Tobias & Kotenko, 1986) (Fig. 4B–C), forming a higher triangle. This is also influenced by the size of the ocelli (ocelli diameter = OD), which can vary as well (Fig. 4C–D).

Shape of tergite 2

The shape of T2 has been variously interpreted in historical references. Nixon used it in his 1976 key to distinguish between *I. cloelia* and *A. evander* (now a junior synonym of *I. naso*). Nixon refers to the acuteness of the posterolateral angles in couplet 8 as follows: "almost right-angled" for *I. cloelia* (Fig. 16E) and "acutely drawn out" (Nixon 1976: 709) for *A. evander*/ *I.naso* (Fig. 5A–D). Kotenko uses this character in his 2007 key to distinguish *I. dauricus* and *I. kostjuki* from *I. naso* and *I. assimilis* (Papp, 1976). He uses two characteristics regarding the shape of T2: 1) how much T2 narrows towards the base ("less narrowed" in *I. dauricus* and *I. kostjuki* (Fig. 5E–F) and "more narrowed" in *I. naso* and *I. assimilis* (Fig. 5A–D, 7E)) and 2) the shape of the posterolateral angles ("almost straight" in *I. dauricus* and *I. kostjuki* (Fig. 5E–F) and "distinctly drawn into points" (Kotenko 2007: 179) in *I. naso* and *I. assimilis* (Figs 5A–D, 7E)). We found the posterolateral angles rather difficult to interpret and even observed bilateral variation in some specimens (Fig. 5C–D). The varyingly sinuate posterior margin of T2 also

Table 1. Comparison of relevant characters of *Illidops* Mason, 1981 and morphologically similar genera. An asterisk (*) indicates that very few exceptions are present.

Morphological character	***Illidops* Mason, 1981**	***Dolichogenidea* Viereck, 1911**	***Apanteles* Förster, 1863**	***Rhygoplitis* Mason, 1981**	***Napamus* Papp, 1993**
Posterior smooth band of the scutellum interrupted centrally by sculptured area	most, with varying degree	no	no	yes	no
Fore wing vein R1 shorter than pterostigma	yes	no*	no*	yes	yes
Propodeum sculpture	mostly sculptured (with exceptions)	variable, ranging from entirely smooth propodeum to coarsely sculptured	variable, ranging from entirely smooth propodeum to coarsely sculptured to areolated	mostly coarsely sculptured	variable, ranging from rugose with irregular median carina to smooth and shiny
Lower margins of the eyes converging	most	few	few	no	slightly
Posterior tergites posteriorly desclerotized	most	few	few	no	no
Vannal lobe shape & setosity (*Apanteles*/*Dolichogenidea*)	convex and setose [but rarely straight and bare, e.g., *I. kostylevi*]	convex or slightly straight, and entirely setose*	concave to slightly, without setae or very few, small and scattered setae	convex and setose	convex and setose
Notauli relatively well defined (*Rhygoplitis*)	no	no	no	yes	no
Median carina on propodeum (*Napamus*)	some	no	no	yes	yes/some
Mouth parts elongate (*Napamus*)	some	few	few	no	yes
Inner metatibial spur much longer (1.3 ×) than the outer spur (*Napamus*)	no	no [sometimes inner spur longer but less than 1.3 ×]	no [sometimes inner spur longer but less than 1.3 ×]	no [rarely inner spur longer but less than 1.3 ×]	yes
Wings strongly infumate (*Napamus*)	no	very few	very few	no	yes

adds to this and we are not sure if this character can be reliably used to distinguish species of *Illidops*; it might need to be re-evaluated. The interpretation of the anterior margin in *I. kostjuki* and *I. dauricus* is complicated by anterolateral smooth sclerotized protrusions of the median field with pointed corners which make it difficult to observe the exact limits of the anterior margin of T2.

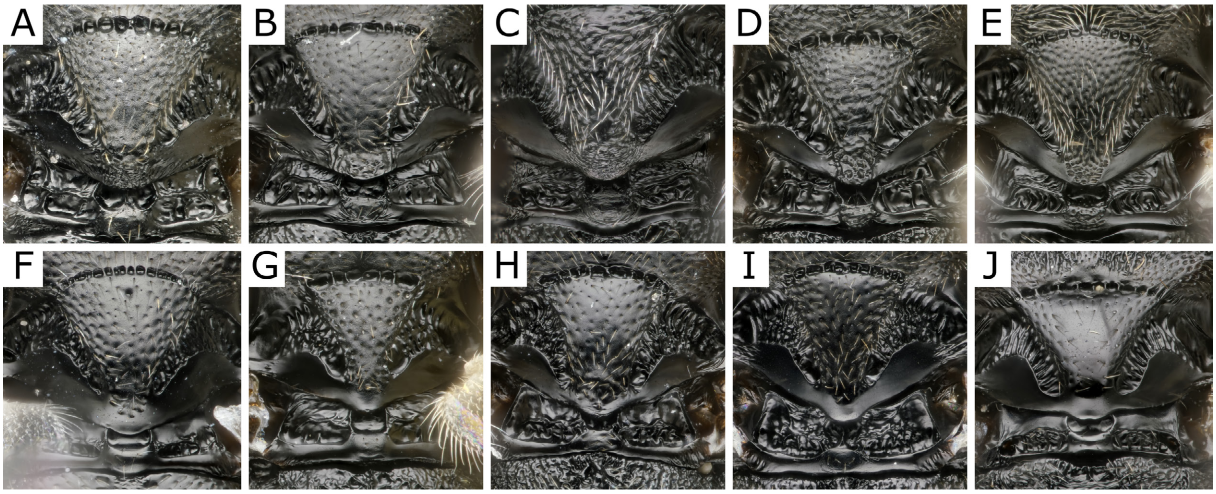

Fig. 2. Dorsal images of the scutellum and surrounding area. **A**. *I. scutellaris* (Muesebeck, 1921), ♀ (HYM00000588). **B**. *I.* cf. *naso* (Marshall, 1885), ♀ (ZSM-HYM-42325-F03). **C**. *I.* cf. *mutabilis* (Telenga, 1955), ♀ (ZSM-HYM-33168-D03). **D**. *I. butalidis* (Marshall, 1889), ♀ (ZSM-HYM-33168-B07). **E**. *I. splendidus* (Papp, 1974), ♀ (ZSM-HYM-33168-H06). **F**. *I. doreenae* Höcherl & Fernandez-Triana sp. nov., holotype, ♀ (HYM00000599). **G**. *I.* cf. *suevus* (Reinhard, 1880), ♀ (ZSM-HYM-33167-H06). **H**. *I. oroseira* Höcherl & Fernandez-Triana sp. nov., holotype, ♀ (ZSM-HYM-42389-G02). **I**. *I. oroseira* Höcherl & Fernandez-Triana sp. nov., paratype, ♀ (ZSM-HYM-42390-A02). **J**. *Apanteles galleriae* Wilkinson, 1932, ♀ (SNSB-ZSM, ZSM-HYM-33154-A11).

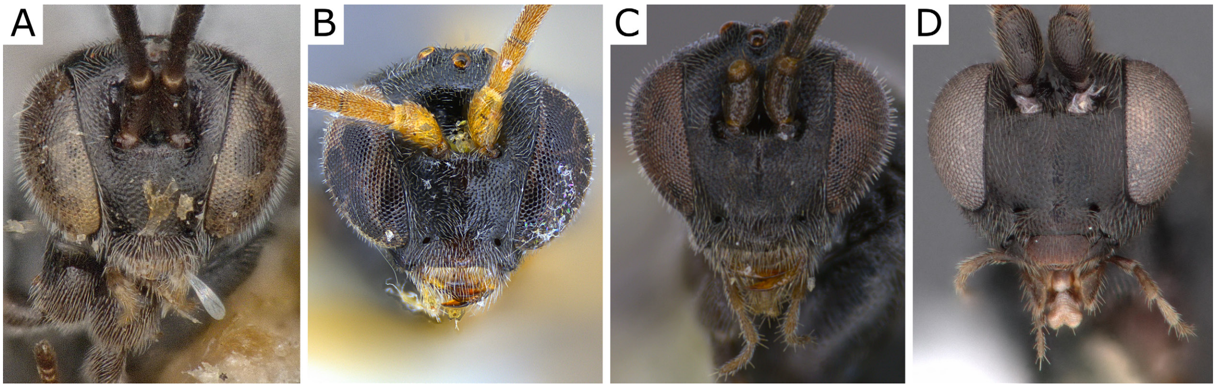

Fig. 3. Frontal images of the heads of different species of *Illidops* Mason, 1981. **A**. *I. butalidis* (Marshall, 1889), ♀ (CNCHYM01525). **B**. *I. vitobiasi* Kotenko, 2004, holotype, ♀ (SIZK). **C**. *I. dauricus* Kotenko, 2007, holotype, ♀ (SIZK). **D**. *I.* cf. *suevus* (Reinhard, 1880), ♀ (ZSM-HYM-42398-E02).

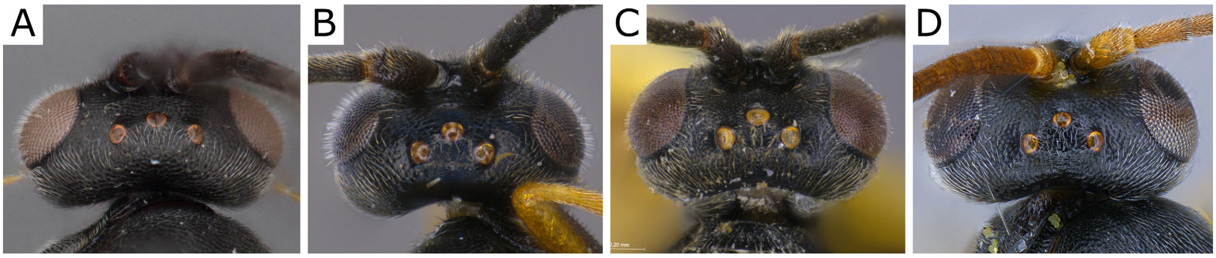

Fig. 4. Dorsal images of the heads of different species of *Illidops* Mason, 1981. **A**. *I.* cf. *mutabilis* (Telenga, 1955), ♀ (ZSM-HYM-33168-D03). **B**. *I. toreicus* Kotenko, 2007, holotype, ♀ (SIZK). **C**. *I. subversor* (Tobias & Kotenko, 1986), holotype, ♀ (SIZK). **D**. *I. vitobiasi* Kotenko, 2004, holotype, ♀ (SIZK).

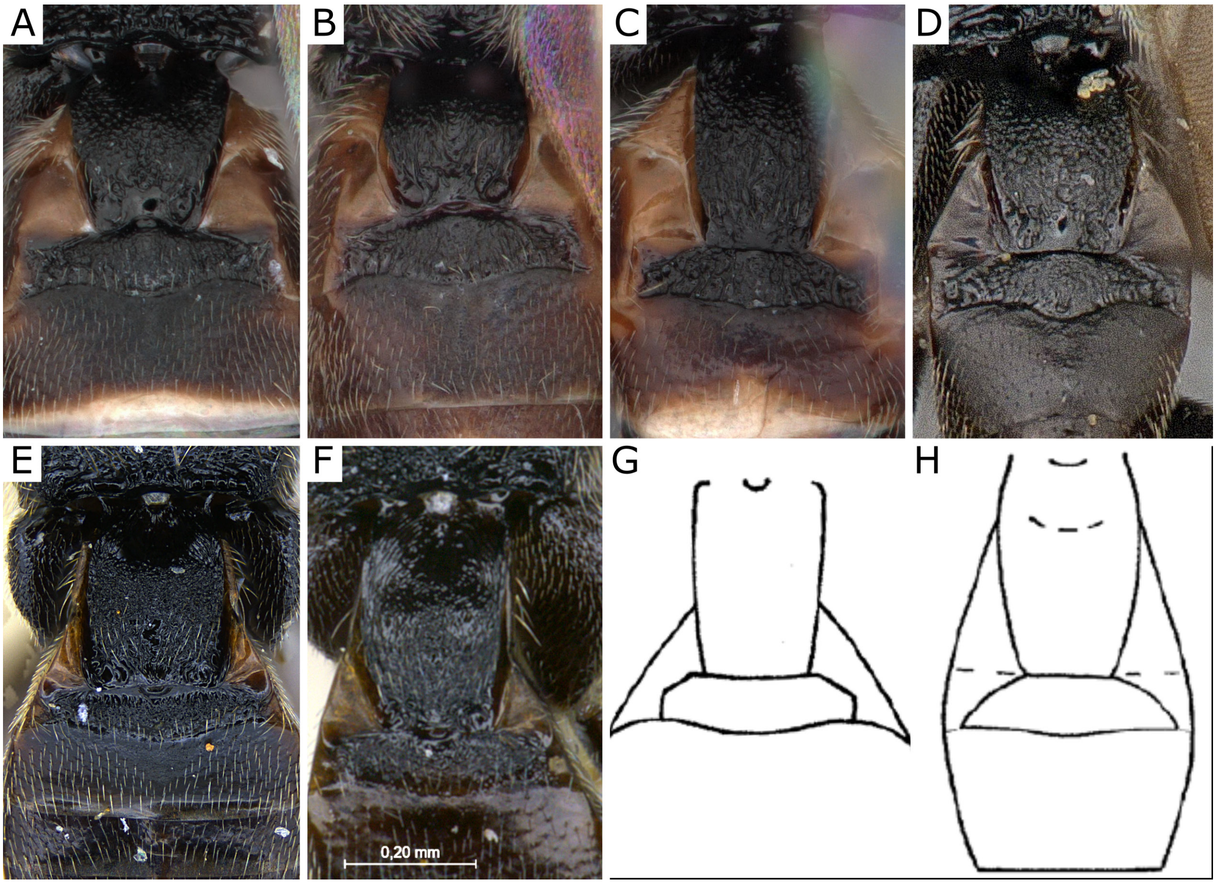

Fig. 5. Dorsal images of the metasoma of different species of *Illidops* Mason, 1981 and drawings. **A–C**. *I.* cf. *naso* (Marshall, 1885), ♀♀ (ZSM-HYM-42325-F03, ZSM-HYM-33168-D11, ZSM-HYM-42391-A10). **D**. *I. naso* (Marshall, 1885), ♂ (CNCHYM00168), paratype of junior synonym *A. contortus* Tobias, 1964. **E**. *I. kostjuki* (Kotenko, 1986), holotype, ♀ (SIZK). **F**. *I. dauricus* Kotenko, 2007, holotype, ♀ (SIZK). **G**. *I. dauricus* Kotenko, 2007, drawing from Kontenko (2007: 180). **H**. *I. naso* (Marshall, 1885), drawing from Kotenko (2007: 181).

Identification key to females

1. Propodeum with complete median carina in addition to reticulate sculpture all over (Figs 36A–D, 53C) 2
– Propodeum without median carina, sculpture variable but very rarely propodeum completely reticulate 3

2. Body color mostly yellow-orange or yellow-brown; T1 strongly widening towards posterior margin (Fig. 53; Kazakhstan) .... ***I. suffectus*** (Tobias & Kotenko, 1986) ***
– Body color black to dark brown; T1 subrectangular to slightly barrel-shaped; BOLD:AEO8226 (Figs 35–36; Germany) .... ***I. oroseira*** Höcherl & Fernandez-Triana sp. nov. ***

3. Body, including head, pale (brownish-red or brownish-yellow) (Fig. 10; Tajikistan) .... ***I. blandus*** (Tobias & Kotenko, 1986)***
– Body mostly, head always, dark (black or dark brown) 4

4. Clypeus either entirely yellow or light brown, contrasting with darker face (Figs 58B, 59B); AND propodeum shiny, smooth or weakly sculptured (but at least with central smooth area; Fig. 58D) 5
– Clypeus dark brown or black, similar in color to face; IF rarely lower half of clypeus yellow-brown (lighter colored than upper half of clypeus and face) THEN propodeum entirely or mostly strongly sculptured 7

5. Glossa elongate; eyes very slightly converging below, lower face width ~0.93 upper face width, eyes not seemingly bulging; clypeus light brown; scape and pedicel dark brown to black; BOLD: AAB5165 (Figs 19–21; Nearctic: Canada) ... ***I. doreenae*** Höcherl & Fernandez-Triana sp. nov. ***
– Glossa of normal proportions; eyes strongly converging below, lower face width < 0.85 upper face width, eyes seemingly bulging; clypeus yellow to bright yellow; scape and pedicel yellow to light brown (Palearctic) 6

6. Posterior smooth band of the scutellum clearly interrupted centrally by sculptured area (Fig. 58D, also compare Fig. 2A–E); darker legs including black or dark brown metacoxa; anteromesoscutum comparatively duller, having a matte appearance (Fig. 58; Kazakhstan, Russia (SAR)) .... ***I. urgens*** Kotenko, 2004 ***
– Posterior smooth band of the scutellum entirely smooth (Fig. 60D, also compare Fig. 2J); legs mostly lightly colored to yellow and metacoxa almost yellow; anteromesoscutum comparatively smoother and shinier (Figs 59–60; Armenia, Azerbaijan, Croatia, Greece, Hungary, Iran, Mongolia, Russia (S), Slovakia, Turkey) .... ***I. urgo*** (Nixon, 1965) ***

7. T2 more or less rectangular, lateral margins more or less parallel-sided; AND posterior margin almost straight; AND T2 width at posterior margin less than 2.5 × its central length; AND T1 more or less parallel-sided with posterior margin sinuate (Fig. 57; Russia (ZAB)) .... ***I. toreicus*** Kotenko, 2007 ***
– T2 either trapezoidal, subtriangular or very narrowly rectangular, lateral margins often not parallel-sided; AND/OR posterior margin usually sinuate; AND/OR T2 width at posterior margin > 3.0 × its central length; AND/OR T1 differently shaped 8

8. Scape flattened; hypopygium short, ending far before apex of metasomal terga (Russia (DA)) .... ***I. planiscapus*** (Tobias, 1976) *
– Scape not flattened; hypopygium variable 9

9. T1 strongly widening towards posterior margin (T1 width at posterior margin > 1.5 × its width at anterior margin); AND hypopygium very short, ending far before apex of metasomal terga 10
– T1 not as strongly widening towards posterior margin; AND/OR hypopygium longer, ending at or beyond apex of metasomal terga 11

10. All coxae pale (yellow to reddish-yellow or yellow-brown), at most infuscate basally; propodeum reticulate; T1 and T2 coarsely rugose; maxillary palps brown to light brown (Figs 48–52; widely distributed across the Palearctic) .... ***I. suevus*** (Reinhard, 1880) **
– At least metacoxa entirely dark (dark brown to black); propodeum uniformly rugose; T1 and T2 punctate to weakly rugose; maxillary palps bright yellow (Fig. 47; Russia (NVS)) .... ***I. subversor*** (Tobias & Kotenko, 1986) ***

11. Scape, pedicel, first few flagellomeres, and most of legs (except for metacoxa) yellow to yellow-brown, rest of body black; AND pterostigma with anterior 0.4 yellow (yellow portion transverse); AND ovipositor sheaths much shorter than metatibia (~0.5) (Fig. 61; Turkmenistan) .... ***I. vitobiasi*** Kotenko, 2004 ***

– Antenna and legs entirely or mostly dark brown to black; AND/OR pterostigma without large pale area; AND/OR ovipositor sheaths longer than half metatibia length 12

12. Ocelli in very low triangle, almost in straight line, posterior tangent to anterior ocellus cutting deeply into posterior ocelli (Fig. 26B, also compare Fig. 4A) 13

– Ocelli always in high triangle, posterior tangent to anterior ocellus at most almost touching posterior ocelli (compare Fig. 4D) 14

13. Eyes at most slightly converging, lower face width ~0.91 upper face width; T2 short, length ~0.25 width; mouthparts elongate (Armenia, Russia (KDA), Uzbekistan) .....***I. rostratus*** (Tobias, 1976) *

– Eyes strongly converging, lower face width ~0.83 upper face width; T2 longer, length ~0.33 width; mouthparts not as elongate (Fig. 26; widely distributed in the Palearctic) ....***I. mutabilis*** (Telenga, 1955) **

14. T1 strongly narrowing towards posterior margin (anterior margin width about 1.5 × posterior margin width); AND T2 subtriangular, very short; AND T2 posterior margin strongly sinuate; AND wings rather strongly infumate (Fig. 56; Tajikistan, Turkmenistan) ....***I. tigris*** (Kotenko, 1986) ***

– T1 not as strongly narrowing towards posterior margin (anterior margin width < 1.5 × posterior margin width); AND/OR T2 either broadly trapezoidal or rectangular; AND/OR T2 margin straight; AND/OR wings hyaline 15

15. Propodeum smooth or almost smooth, shiny at least on upper half (e.g., Figs 22C, 25D) 16

– Propodeum entirely densely sculptured, matte 19

16. Fore wing vein R1 very short, < 0.5 × pterostigma length 17

– Fore wing vein R1 longer, clearly > 0.6 × pterostigma length 18

17. Ovipositor sheaths shorter than metatibia; T1 broad, parallel-sided up to posterior 0.3, only slightly narrowing posteriorly afterwards; T1 posterior width about 2 × T2 length; 1st antennal flagellomere pale, contrasting with remaining darker flagellomeres (Fig. 9; Mongolia) ....***I. bellicosus*** (Papp, 1977) **

– Ovipositor sheaths longer than metatibia; T1 gradually narrowing towards posterior margin; T1 posterior width < 2 × T2 length; antennal flagellomeres not contrasting (Fig. 37; Mongolia) ....***I. perseveratus*** (Papp, 1977) **

18. Pterostigma with comparatively large pale spot at base (brownish-yellow on anterior 0.2), rest of pterostigma brown; clypeus slightly lighter than face; eyes strongly converging, lower face width ~0.8 × upper face width (Figs 22–23; Croatia, Hungary, Kazakhstan, Russia (S), Serbia, Tunisia) ....***I. electilis*** (Tobias, 1964) ***

– Pterostigma entirely to mostly dark brown, at most with small, faint, pale spot at base; clypeus same color as face; eyes are at most slightly drawn close together, lower face width ~0.9 × upper face width (Fig. 25; Russia (ROS), Ukraine) ....***I. kostylevi*** (Kotenko, 1986) ***

19. Eyes drawn very close together downwards, lower face width < 0.85 × upper face width (compare Fig. 3A–B); malar distance very short (Figs 6A, 12B, 14B, 44B, 54B) 20

– Eyes not drawn close together or only slightly drawn downwards, lower face width > 0.86 × upper face width (compare Fig. 3C–D); malar distance usually longer 23

20. T1 strongly narrowing towards posterior margin (anterior margin width 2 × posterior margin width); T2 more or less trapezoidal in shape, T2 width at posterior margin more than 3.0 × its width at anterior margin (Figs 54–55; NEA: USA (CA, FL, GA, TX)) ....***I. terrestris*** Wharton, 1983 ***

– T1 more or less barrel-shaped or parallel-sided, anterior margin about same width as posterior margin width; T2 not trapezoidal in shape, either subquadrate or transverse, T2 width at posterior at most 2.0 × its width at anterior margin (usually much less) 21

21. T1 comparatively narrower and longer, its length more than 1.5 × its maximum width; T2 almost as long as T3; face comparatively narrow, its maximum width approximately equal to its height; BOLD:ACQ9731, BOLD:AEL7562, BOLD:AEI6389 (Figs 12, 14; widely distributed in the Palearctic) ....***I. butalidis*** (Marshall, 1889) ***
– T1 comparatively wider and shorter, its length 1.2–1.3 × its maximum width; T2 much shorter than T3; face comparatively wider, its maximum width much greater than its height 22

22. Pterostigma mostly brown, with pale spot at anterior 0.3; metafemur dark brown, contrasting with mostly light, yellow-brown metatibia (metatibia only with dark spot on posterior 0.2); anteromesoscutum smooth, somewhat shiny, with punctation rather fine; BOLD:AEJ7519 (Fig. 44; Germany, Hungary, Russia (C)) ....***I. splendidus*** (Papp, 1974) ***
– Pterostigma very pale, mostly yellow-white, with thin brown margins; metafemur dark reddish-brown, same color as metatibia; anteromesoscutum matte, with coarse and deep punctures; BOLD:AAD8583 (Fig. 6; Egypt, AFR: United Arab Emirates, Yemen) ....***I. albostigmalis*** van Achterberg & Fernandez-Triana, 2017

23. Metafemur lighter, reddish-yellow; AND all of the following characters: eyes slightly converging; antennae as long as body, preapical segment elongate; mesonotum densely punctate, almost matte; tegulae blackish; pterostigma brown with large pale spot from base to beyond middle; T1 comparatively wide, its length slightly more than its maximum width; ovipositor sheaths slightly shorter than metatibia; rather small, body length 1.9–2.2 mm (Kazakhstan, Russia (S)) ....***I. nigritegula*** (Tobias & Kotenko, 1986) **
– Metafemur darker, black or dark brown; IF rarely (*I. assimilis*) metafemur reddish-yellow, THEN remaining characters not as above 24

24. Head in frontal view elongate, malar distance 1.5 × as long as basal width of mandible; AND most of metasoma dorsally orange-yellow, contrasting with darker T1 (Fig. 8; Spain) ....***I. barcinonensis*** (Marshall, 1898) ***
– Head in frontal view not as elongate, malar distance less than 1.5 × as long as basal width of mandible; metasoma dorsally entirely dark brown to black 25

25. Profemur (except for anterior 0.2 or less) light brown to yellow and all tibiae yellow (Figs 7D, 38B); AND ovipositor sheaths clearly shorter than metatibia 26
– All femora (except for posterior half of profemur) and all tibiae (usually) dark brown to black; ovipositor sheaths of variable length 27

26. Pterostigma with pale basal spot; metafemur mostly brown; maxillary palps mostly pale (yellow-white); BOLD:AAA8769 (Figs 38–40; species very widely distributed in AUS, NEA, NEO, PAL) ....***I. scutellaris*** (Muesebeck, 1921) ***
– Pterostigma entirely dark brown; metafemur mostly pale (yellow); maxillary palps mostly brown (Fig. 7; Mongolia) ....***I. assimilis*** (Papp, 1976) **

27. Ovipositor sheaths clearly shorter than metatibia (~0.8 ×); T1 usually shorter and parallel-sided, barely narrowing posteriorly 28
– Ovipositor sheaths about same length as metatibia (~0.9–1.1 ×); T1 usually more elongate, barrel-shaped 30

28. Metatibia entirely dark; BOLD:AEO8223 (Fig. 16; species widely distributed in the Palearctic) .... ***I. cloelia*** (Nixon, 1965) **
– Metatibia yellow with some infuscation on apical third 29

29. Glossa distinctly elongate; clypeus light/brown, contrasting with entirely black face; T1 narrowing; anteromesoscutum with deep, dense punctation, matte; fore wing vein 1M entirely pale; BOLD:AAC7888 (Figs 45–46; NEA: Canada (YT)) .... ***I. stefanschmidti*** Höcherl & Fernandez-Triana sp. nov. ***
– Glossa not distinctly elongate; clypeus dark, same color as face; T1 barrel-shaped; anteromesoscutum with shallow punctation, shiny; fore wing vein 1M dark in basal 0.5 (Fig. 24; Russia (ALT)) .... ***I. kostjuki*** (Kotenko, 1986) ***

30. Eyes comparatively large, laterally width of eye >2 × as long as width of gena laterally (compare Fig. 41A–H); head in dorsal view distinctly wider than mesoscutum; T1 slightly narrowing posteriorly, 1.4–1.5 × as long as its maximum width; ovipositor sheaths about same length as metatibia; body length 2.8–3.0. mm (Bulgaria, Hungary, Italy, Russia (ZAB, PRI)) .. ***I. sophrosine*** (Nixon, 1976) *
– Eyes comparatively smaller, laterally width of eye no more than 2 × length of gena width laterally (compare Fig. 41I–L) (from here tentative key to the morphologically cryptic species of the *I. naso* complex, based on characters employed by previous authors. We noticed that some of these characters are variable and therefore might be insufficient to differentiate between these four species.) 31

31. T1 and T2 almost smooth, only very lightly rugose; maxillary palps light brown to yellow; fore wing vein C light brown to yellow basally (Fig. 15; Russia (S), Ukraine) .... ***I. buteonis*** (Kotenko, 1986) (***)
– T1 and T2 rugose; maxillary palps brown; fore wing vein C brown basally 32

32. Found in Far East Russia (type series from Transbaikal territory); median field of 2nd abdominal tergite less narrowed towards base, posterolateral angles almost straight (Fig. 17; Russia (ZAB)) ....***I. dauricus*** Kotenko, 2007 (***)
– Widespread in Holarctic, mostly recorded from western Palearctic (holotype from United Kingdom); median field of 2nd abdominal tergite more narrowed towards base, posterolateral angles distinctly drawn into points (Fig. 29; widely distributed in the Palearctic) .... ***I. naso*** (Marshall, 1885) *

Treatment of Holarctic species of Illidops Mason, 1981

Illidops albostigmalis van Achterberg & Fernandez-Triana, 2017
Fig. 6

Illidops albostigmalis van Achterberg & Fernandez-Triana, 2017: 219, pls 42–48.

Type material

Holotype

YEMEN – **Lahj** • ♀; Lahij; Feb. 2001; A. van Harten and A. Sallam leg.; Malaise trap; BOLD Sample ID: WAM 0210; RMNH, RMNH’02.

Other material examined

EGYPT – **Qalyubia** • 1 ♀; El-Obour District; 30.247° N, 31.545° E; 118 m a.s.l.; 1 Oct. 2019; S. Zalat leg.; BOLD Process ID: GMEEO138-21; CBG, BIOUG68113-A11.

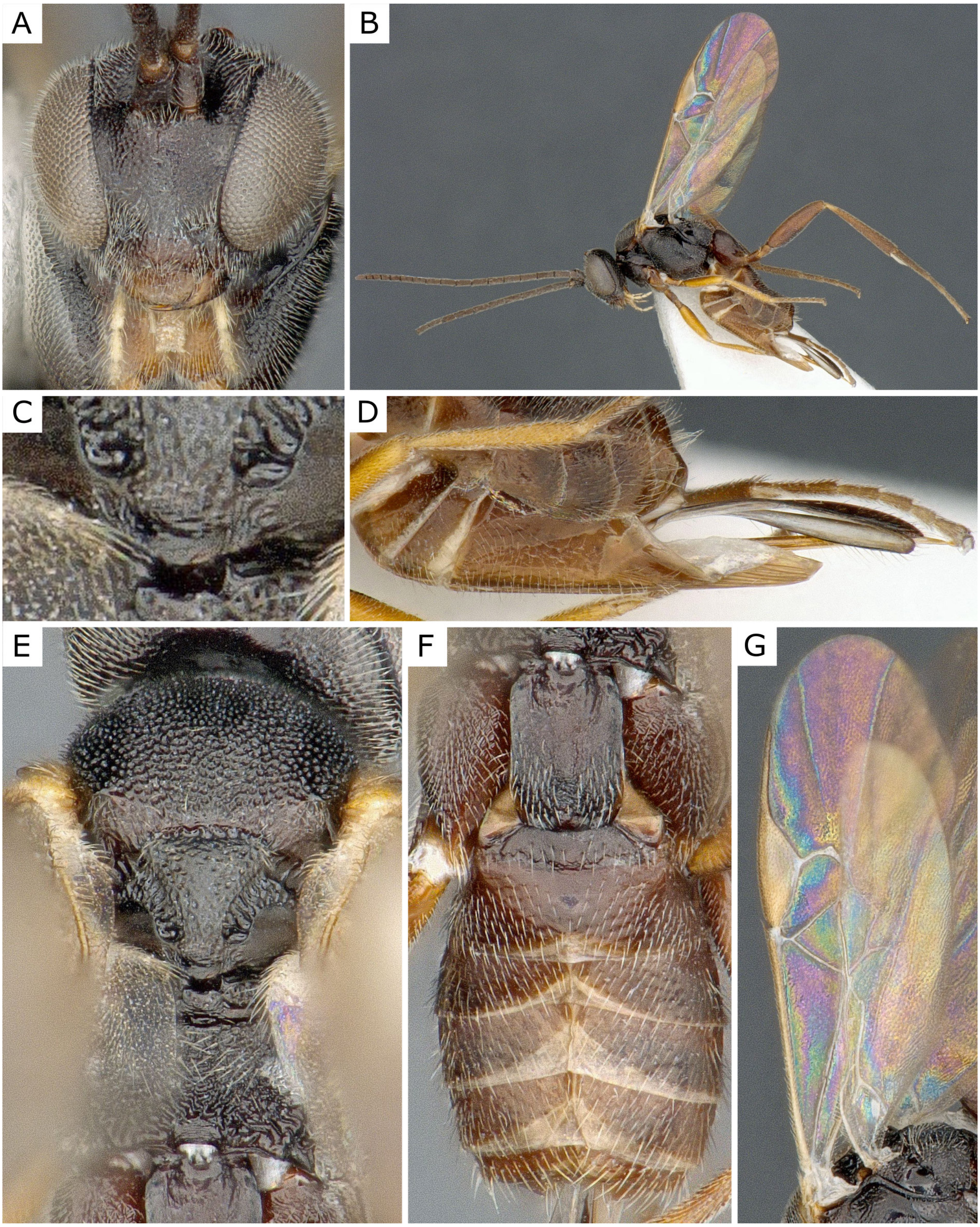

Fig. 6. *Illidops albostigmalis* van Achterberg & Fernandez-Triana, 2017, holotype, ♀ (WAM 0210). **A**. Head, frontal view. **B**. Habitus, lateral view. **C**. Posterior scutellum. **D**. Metasoma, lateral view. **E**. Mesosoma, dorsal view. **F**. Metasoma, dorsal view. **G**. Wings. Images from Fernandez-Triana *et al.* (2020), rearranged.

Species concept

Our species concept is based on our observations of the type material and the information in Fernandez-Triana & Achterberg (2017) → ***.

Ecology / host information

Crambidae: *Prophantis* sp. Two male specimens from Yemen (Hammam 'Ali) were reared ex *Prophantis* sp. (Crambidae), labelled 'coffee berry moth'. These specimens are not included in the type series.

Distribution

AFR: United Arab Emirates, Yemen; PAL: Egypt.

Molecular data

BOLD:AAD8583.

Remarks

Thus far this species was known only from the Afrotropical region, but bordering the Palearctic. With a public record in the BIN associated with *I. albostigmalis* van Achterberg & Fernandez-Triana, 2017 from Egypt (accessible from https://v4.boldsystems.org/index.php/Public_RecordView?processid=GMEEO138-21) and private data from other Palearctic countries, the distribution range clearly reaches into the Palearctic region. BIN BOLD:AAD8583 also includes sequences linked to specimens from Israel, Nigeria, Pakistan, and South Africa, so the species is likely more widely distributed than currently known. However, this includes private data. This species has been reared from *Prophantis* sp. (Crambidae), labeled as 'coffee berry moth' (Fernandez-Triana & van Achterberg 2017).

Illidops assimilis (Papp 1976)

Fig. 7

Apanteles assimilis Papp, 1976: 228, figs 1–5.

Type material

Holotype

MONGOLIA – **Dundgovi Province** • ♀; "Mittelgobi aimak", Delgertsogt District, 20 km S of Delgercogt; [45.9° N, 106.3° E]; 1480 m a.s.l.; 13–14 Jul. 1967; no. 915; HNHM.

Species concept

Our species concept is based on habitus photos of the holotype and available literature, such as Papp (1976, 1986) and Kotenko (2007) → **.

Ecology / host information

Host unknown.

Distribution

PAL: Mongolia.

Molecular data

No molecular data available.

Remarks

The holotype seems to be partially damaged and part of the hypopygium and ovipositor sheaths are missing.

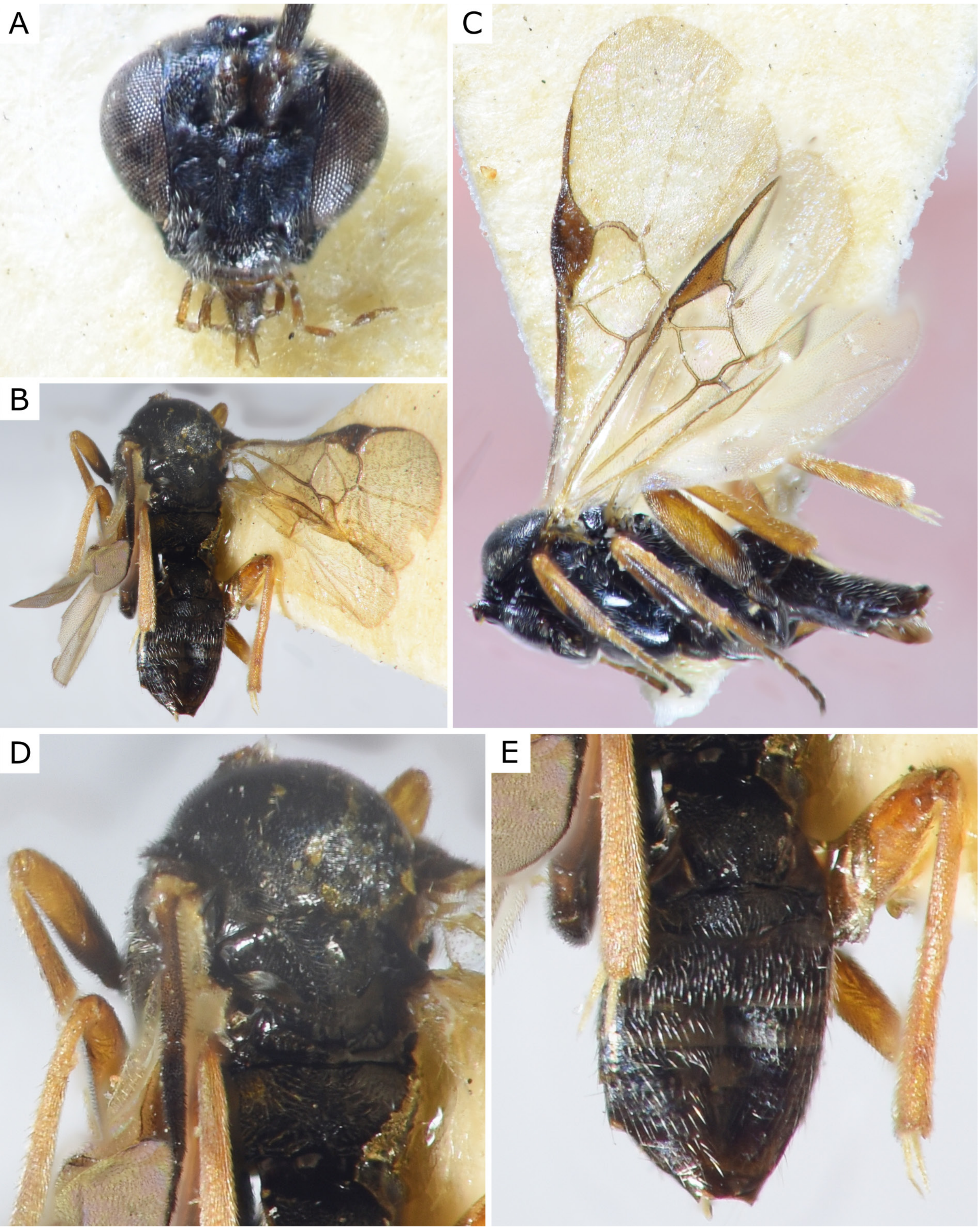

Fig. 7. *Illidops assimilis* (Papp, 1976), holotype, ♀ (HNHM). **A**. Head, frontal view. **B**. Dorsal view. **C**. Lateral and wing, **D**. Mesosoma, dorsal view. **E**. Metasoma, dorsal view.

Illidops barcinonensis (Marshall, 1898)

Fig. 8

Apanteles barcinonensis Marshall, 1898: 179.
Apanteles rhamphus Marshall, 1898: 180.

Type material

Holotype

SPAIN – **Barcelona** • ♀; Barcelona, Vallvidrera “Vallvidriera”; [41.4° N, 2.0° E]; 2 May 1895; A. Cabrera leg.; MNCN.

Species concept

Our species concept is based on our examination of the holotype and the information in Papp (1986, 1988) → ***.

Ecology / host information

Host unknown.

Distribution

PAL: Spain.

Molecular data

No molecular data available.

Remarks

Apanteles rhamphus was synonymized under *Illidops barcinonensis* (Marshall, 1898) by Papp (1986) as part of his redescription of *I. barcinonensis*; the lectotype is deposited at MNCN. However, these species were both only known from a single specimen of the opposite sex, *I. barcinonensis* from a single female and *A. rhamphus* from a single male specimen. We observed that some species and barcoding clusters of *Illidops* show significant sexual dimorphism (more detailed information in the section on *I. suevus*) and have doubts about the synonymy of these names, which we currently cannot investigate further.

Illidops bellicosus (Papp, 1977)

Fig. 9

Apanteles bellicosus Papp, 1977: 222–224, figs 8–10.

Type material

Holotype (photos examined)

MONGOLIA – **Ömnögovi Province** • ♀; “Südgobi aimak”, Bayandalai District, 14 km SE of Somon Bajandalaj; 1450 m a.s.l.; 15 Jun. 1967; no. 803; HNHM; typ. no. 2394.

Species concept

Our species concept is based on our examination of habitus photos of the holotype and the information available in Papp (1977, 1981), and Kotenko (2007) → **.

Ecology / host information

Host unknown.

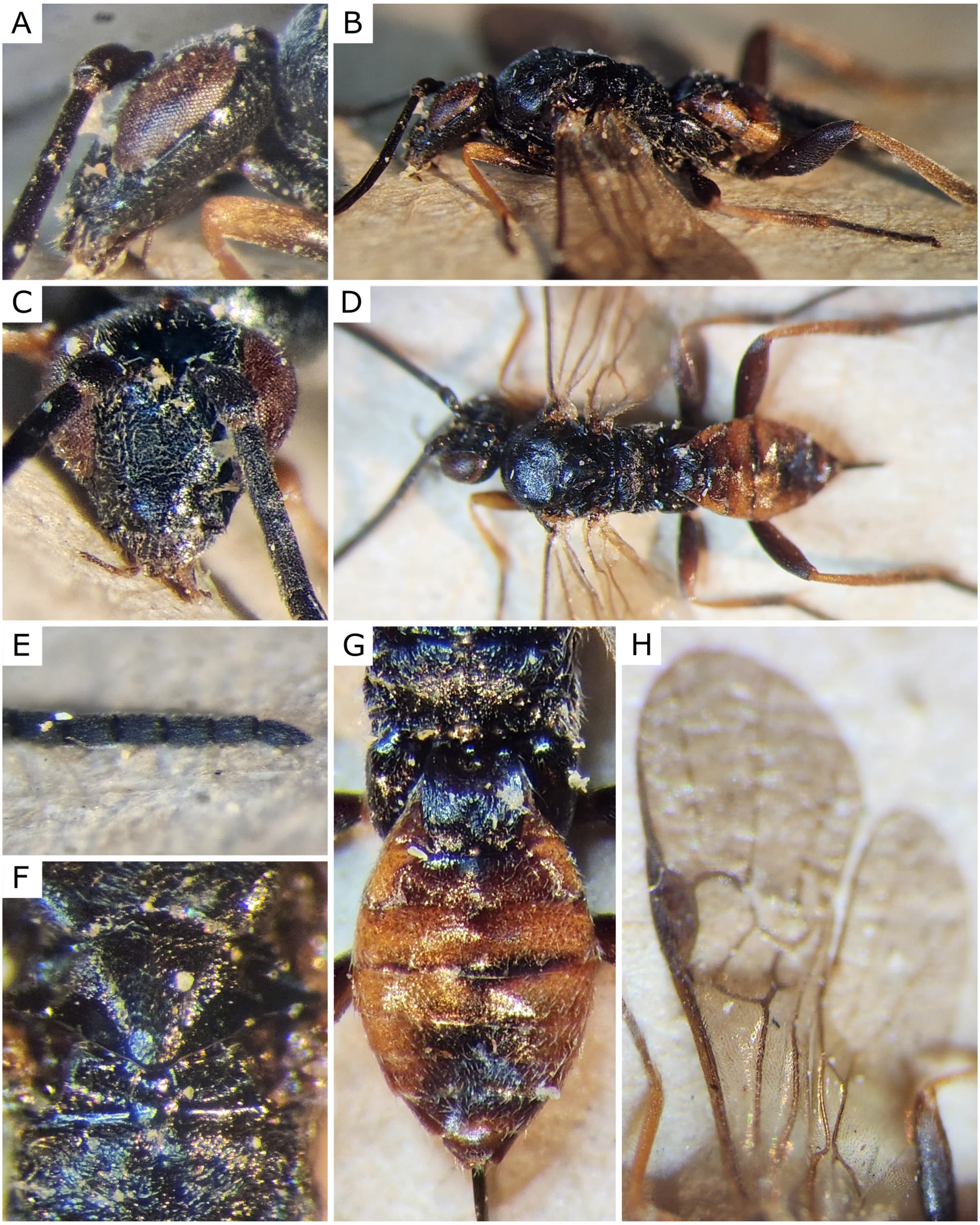

Fig. 8. *Illidops barcinonensis* (Marshall, 1898), holotype, ♀ (MNCN). Photographed with a smartphone handheld through a microscope, stacks computed with Helicon Focus. **A**. Head, lateral view. **B**. Habitus, lateral view. **C**. Head, frontal view. **D**. Habitus, dorsal view. **E**. Apical flagellomeres. **F**. Scutellum and propodeum, dorsal view. **G**. Metasoma, dorsal view. **H**. Wings, dorsal view. Body length of the specimen [from original description]: 4 mm.

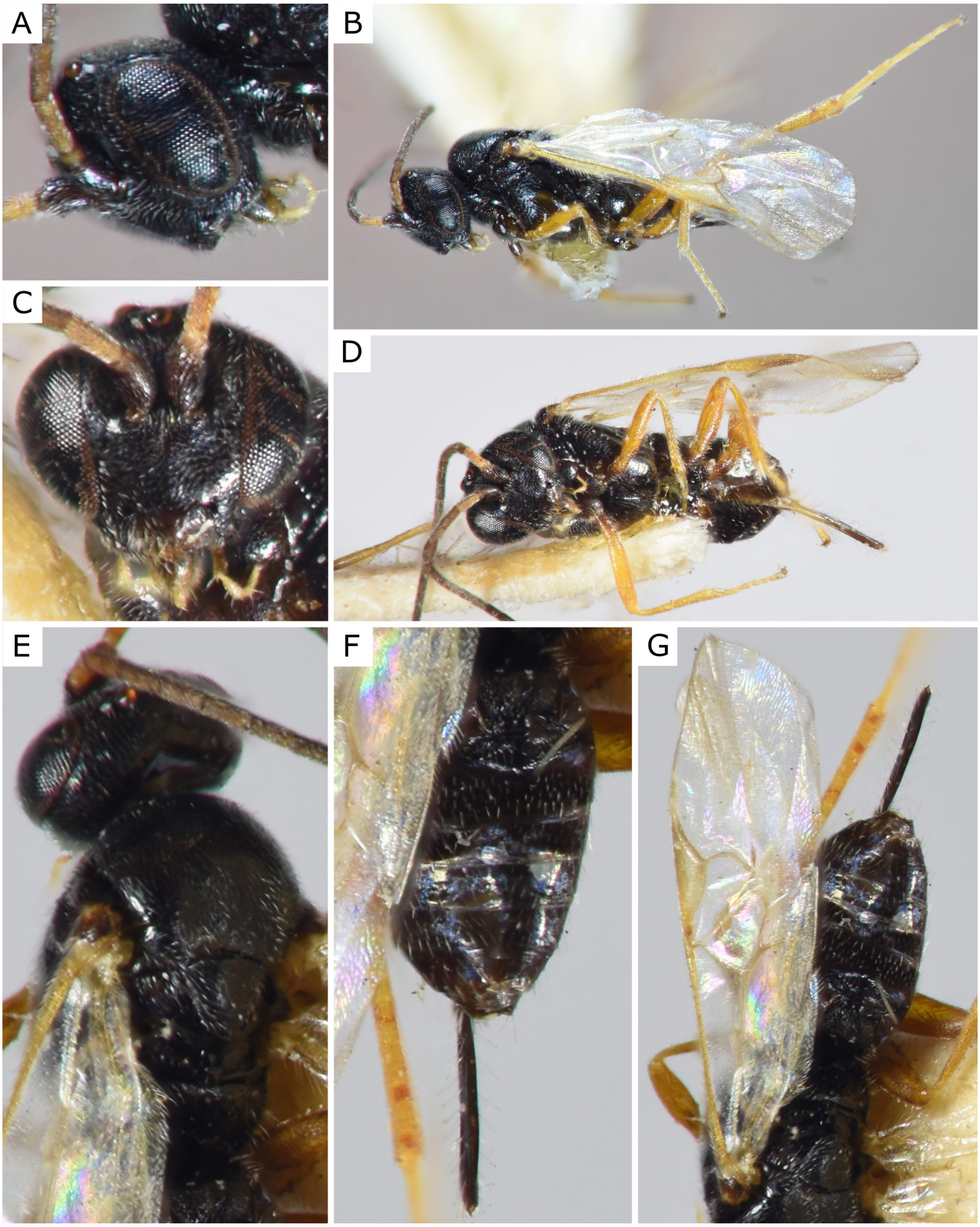

Fig. 9. *Illidops bellicosus* (Papp, 1977), holotype, ♀ (HNHM). **A**. Head, lateral view. **B**. Lateral view and wing. **C**. Head, frontal view. **D**. Ventral view. **E**. Mesosoma, dorsal view. **F**. Metasoma, dorsal view. **G**. Fore wing.

Distribution

PAL: Mongolia.

Molecular data

No molecular data available.

Remarks

The holotype of this species shows a distinct contrast in antenna coloration with the antenna being mostly darker brown to black but the first flagellomere being entirely light brown to yellow ("pale"). However, the starker contrast may potentially be an artifact of long preservation as Papp described the following: "Antenna brown to blackish, first flagellar joint more or less reddish" (Papp 1977: 223). *Illidops bellicosus* (Papp, 1977) is one of the species which challenge our concept of *Illidops* with its entirely smooth propodeum. However, it has a very short fore wing vein R1 and based on the information available to us we could not draw any conclusions.

Illidops blandus (Tobias & Kotenko, 1986)

Fig. 10

Apanteles blandus Tobias & Kotenko, 1986: 753 [423].

Type material

Holotype

TAJIKISTAN – **Khatlon Region** • ♀; vicinity of Külob [Kulyab]; 37.91° N, 69.78° E; 580 m a.s.l.; 18 Jul. 1933; Popov leg.; SIZK.

Species concept

Our species concept is based on our examination of photos of the holotype and the information available in Tobias & Kotenko (1986). In addition to that, the species is morphologically very distinct and unlikely to be confused → ***.

Ecology / host information

Host unknown.

Distribution

PAL: Tajikistan.

Molecular data

No molecular data available.

Remarks

This is one of the species which challenge the concept of *Illidops*. Transferred to *Illidops* (likely by Kotenko) in Zerova *et al.* (2006).

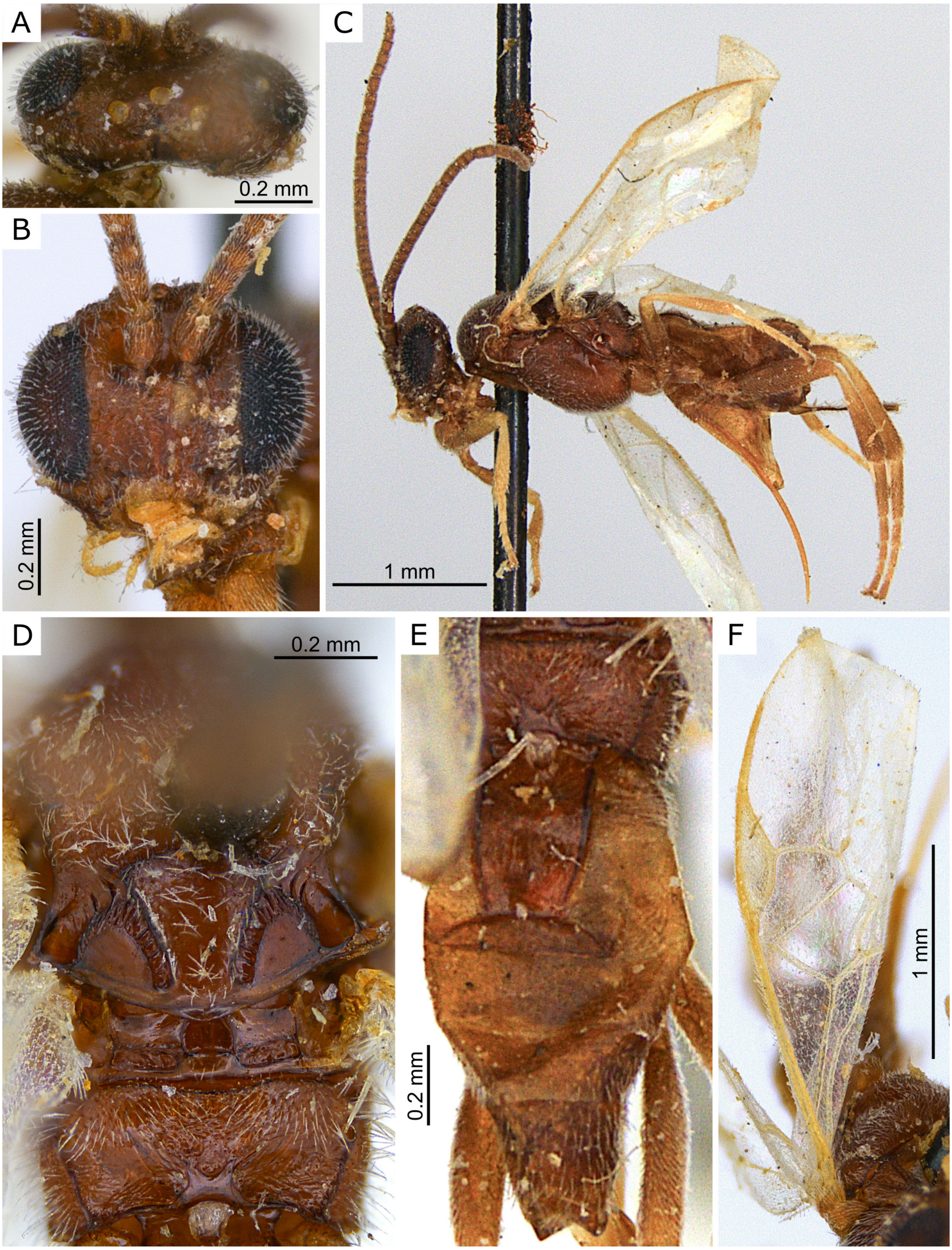

Fig. 10. *Illidops blandus* (Tobias & Kotenko, 1986), holotype, ♀ (SIZK). **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Lateral view. **D**. Mesosoma, dorsal view. **E**. Metasoma, dorsal view. **F**. Fore wing. Body length of the specimen: 2.8 mm.

Illidops butalidis (Marshall, 1889)
Figs 2D, 11–14; Table 2

Apanteles butalidis Marshall, 1889: 450–451.

Other material examined

UNITED KINGDOM – **England** • 1 ♂; Dorset, Portland Bill; 8 May 1939 (coll.), 28 May 1939 (em.); ex. *Scythris senescens*; R.L.E. Ford leg.; D.S. Wilkinson det.; CNC, CNCHYM 01524 • 1 ♀; same data as for preceding; CNC, CNCHYM 01525.

GERMANY – **Bavaria** • 1 ♀; Ruhpolding, Fischbach; 47.709° N, 12.657° E; 720 m a.s.l.; 4–19 Jul. 2016; D. Doczkal and J. Voith leg.; Malaise trap; bulk ID: dv.fiba2.05; SNSB-ZSM, ZSM-HYM-33167-H07 • 1 ♀; same locality as for preceding; 2–16 Aug. 2016; D. Doczkal and J. Voith leg.; Malaise trap; bulk ID: dv.fiba2.07; SNSB-ZSM, ZSM-HYM-33168-B07 • 1 ♀; Eußenheim-Aschfeld, Ammerfeld; 50.007° N, 9.806° E; 280 m a.s.l.; 2–7 Jul. 2014; D. Doczkal leg.; Malaise trap; bulk ID: dd.ammf.08; SNSB-ZSM, ZSM-HYM-33420-G06 • 1 ♀; München, NSG Allacher Lohe, Heide-Mosaik; 48.201° N, 11.483° E; 499 m a.s.l.; 8–23 Jun. 2021; R. Albrecht and GBOL3-Team leg.; Malaise trap; bulk ID: gb.aloh1.01; SNSB-ZSM, ZSM-HYM-42326-G04 • 1 ♀; same locality; 5–21 Jul. 2021; R. Albrecht and GBOL3-Team leg.; Malaise trap; bulk ID: gb.aloh1.03; SNSB-ZSM, ZSM-HYM-42326-H05 • 1 ♂; Moos, Isarmündung, Magerrasen, sumpfig; 48.780° N, 12.966° E; 313 m a.s.l.; 16 Jun. 2021; A. Höcherl leg.; sweep-net; SNSB-ZSM, ZSM-HYM-ZLAB01-A12 • 1 ♀; Willersdorf, Untere Mark, semi-natural forest; 49.733° N, 10.985° E; 292 m a.s.l.; 25 Jun.–12 Jul. 2019; J. Müller leg.; Malaise trap; bulk ID: 6231_4_For; SNSB-ZSM, ZSM-HYM-42379-B03. – **Baden-Württemberg** • 1 ♀; Grenzach-Wyhlen, Hornfelsen, Felswand; 47.559° N, 7.646° E; 350 m a.s.l.; 4–25 Jul. 2011; D. Doczkal and A. Ssymank leg.; Malaise trap; bulk ID: dd.grf42.15; SNSB-ZSM, ZSM-HYM-33420-E09 • 1 ♀; Rötelstein, Steinbruch, Felskante; 47.556° N, 7.679° E; 440 m a.s.l.; 4–25 Jul. 2011; D. Doczkal and A. Ssymank leg.; Malaise trap; bulk ID: dd.grf43.13; SNSB-ZSM, ZSM-HYM-42470-A07 • 1 ♀; Malsch, Hansjakobstr. 7, Garten; 48.884° N, 8.320° E; 120 m a.s.l.; 21 Jun.–5 Jul. 2020; D. Doczkal leg.; Malaise trap; bulk ID: dd.mgart1.09; SNSB-ZSM, ZSM-HYM-33155-C07.

Species concept

Our species concept is based on our examination of authoritatively identified female and male specimens stored in the CNC (identified by Wilkinson, reared ex. *Scythris picaepennis* by Ford) and mainly the information available in Wilkinson (1945), Nixon (1965, 1976), Papp (1981) and Kotenko (2007) → ***.

Ecology / host information

Scythrididae: holotype ex *Scythris fuscoaenea* (Haworth, 1828), *Scythris picaepennis* (Haworth, 1828).

Distribution

PAL: Bulgaria, Croatia, Germany, Hungary, Mongolia, Romania, Russia (ZAB, PRI), Serbia, Slovakia, Spain, Sweden, Tunisia, Turkey, Ukraine, United Kingdom.

Molecular data

BINS: BOLD:ACQ9731, BOLD:AEL7562, BOLD:AEI6389, details in Table 2 and Fig. 11. CNCHYM 01524 was included in the shotgun sequencing of historical DNA and was mapped to the COI sequence of ZSM-HYM-33161-C11.

The three different barcoding clusters we found matching the morphology of this species may or may not represent cryptic diversity. The overall maximum p-distance between all sequences we associate

Table 2. BINs which match the morphological characters of *Illidops butalidis* (Marshall, 1889). Information on the Nearest Neighbor (NN) in the BOLD database is given, including relevant p-distances and distribution.

BIN/ Country	Number of specimens (*n*)	within-BIN max. p-distance	min. NN p-dist.	NN BIN/ Country	Number of specimens (*n*)	NN within-BIN max. p-dist.
BOLD:ACQ9731 Germany	7	0.17%	1.34%	BOLD:AEL7562 Germany	2	0%
BOLD:AEL7562 Germany	2	0%	1.34%	BOLD:ACQ9731 Germany	7	0.17%
BOLD:AEI6389 Germany	5	0.78%	2.73%	BOLD:ACQ9731 Germany	7	0.17%

with the species is 4.17%. We were unable to find consistent morphological differences and consider all three clusters to represent members of *I. butalidis* for now. Minimum interspecific p-distances of Microgastrinae can vary across genera, for more details check Höcherl *et al.* (2024). The sequence from the authoritatively identified male specimen (identified by Wilkinson, reared from *Scythris picaepennis* by Ford) matches our German material from BIN BOLD:ACQ9731 with a barcode similarity of 99.68%.

Remarks

Holotype female, PCMAG. Country of type locality: United Kingdom. *Scythris picaepennis* was recorded as a host of *I. butalidis* by Wilkinson (1945) as the junior synonym *Scythris senescens* (Stainton, 1850), based on a series of specimens reared by Ford.

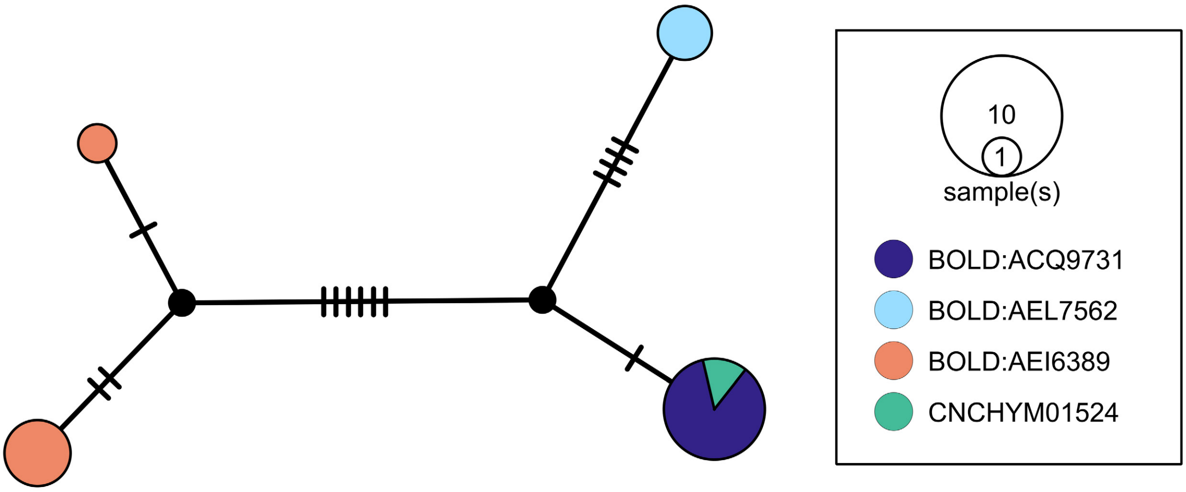

Fig. 11. TCS haplotype network of the three BINs identified as *Illidops butalidis* (Marshall, 1889), including the sequence of historical specimen CNCHYM 01524. Sequence GBDTA1706-21 (BOLD:AEI6389) was removed from the analysis. All sequences were trimmed to 304 bp in order to accommodate CNCHYM 01524. Each hatch mark in the network represents a single mutational change; small black dots at nodes indicate missing haplotypes. The diameter of the circles is proportional to the number of haplotypes sampled and the BINs are color-coded.

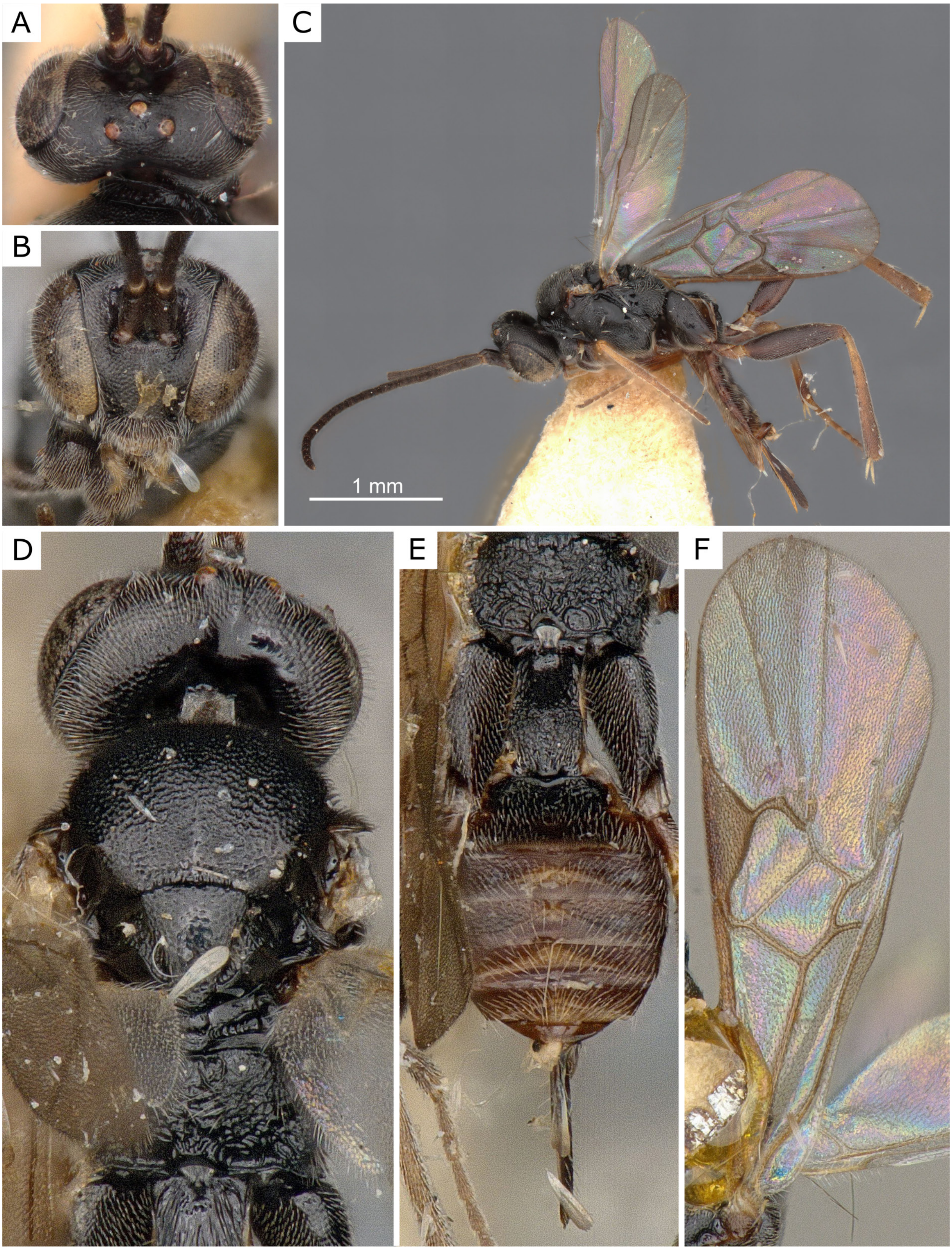

Fig. 12. *Illidops butalidis* (Marshall, 1889), ♀ (CNCHYM 01525). **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Lateral view. **D**. Mesosoma, dorsal view. **E**. Metasoma, dorsal view. **F**. Fore wing. Body length of the specimen: 2.7 mm.

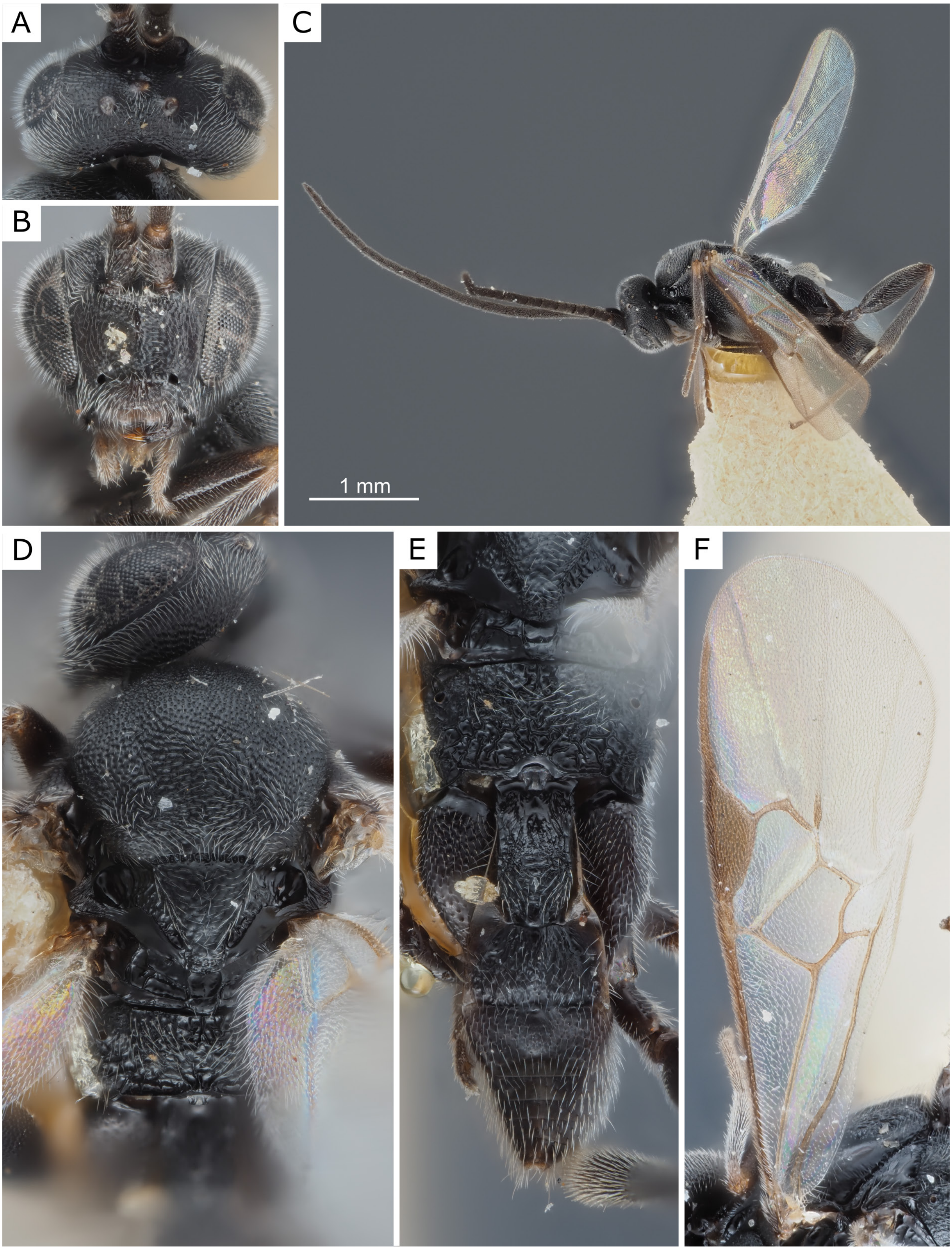

Fig. 13. *Illidops butalidis* (Marshall, 1889), ♂ (CNCHYM 01524). **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Lateral view. **D**. Mesosoma, dorsal view. **E**. Metasoma, dorsal view. **F**. Fore wing. Body length of the specimen: 2.5 mm.

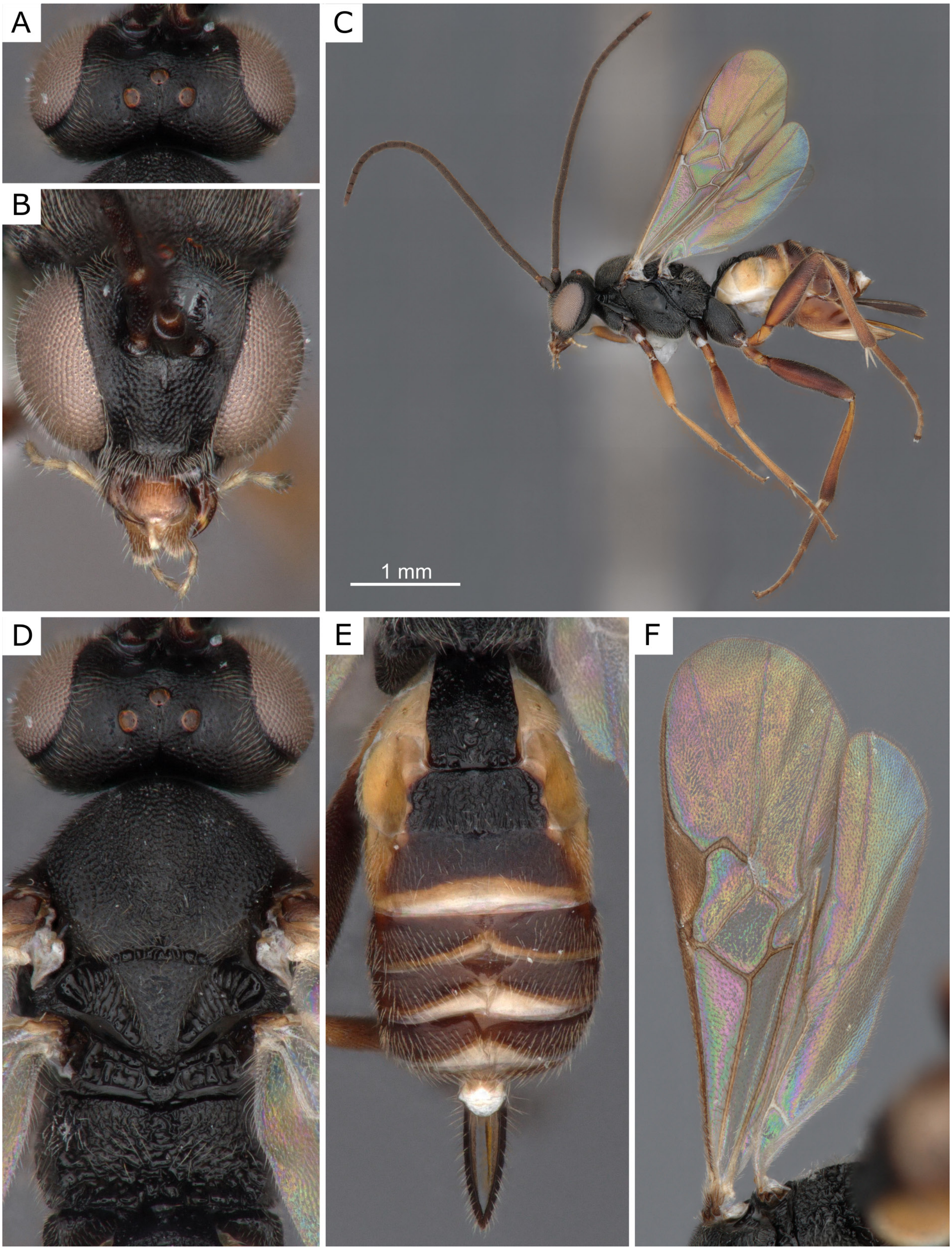

Fig. 14. *Illidops butalidis* (Marshall, 1889), ♀ (ZSM-HYM-33168-B07), BOLD:AEI6389. **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Lateral view. **D**. Mesosoma, dorsal view. **E**. Metasoma, dorsal view. **F**. Fore wing. Body length of the specimen: 3.2 mm.

Illidops buteonis (Kotenko, 1986)

Fig. 15

Apanteles buteonis Kotenko in Tobias & Kotenko, 1986: 756 [424].

Type material

Holotype

UKRAINE – **Donetsk Region** • ♀; Kramatorsk District, Kryva Luka; 48.87° N, 37.90° E; 79 m a.s.l.; 22 Jul. 1982; A. Kotenko leg.; SIZK.

Species concept

Our species concept is based on our examination of photos of the holotype and the information available in Tobias & Kotenko (1986) → ***.

Ecology / host information

Host unknown.

Distribution

PAL: Russia (S), Ukraine.

Molecular data

No molecular data available.

Remarks

This species is part of the *I. naso* complex of morphologically cryptic species (more detailed information in the remarks for *I. naso*). Tobias & Kotenko (1986: 756) used a set of characters to distinguish *I. buteonis* from *I. contortus* (junior synonym of *I. naso*): "Middle field of 2nd abdominal tergite less narrowed toward base, its posterolateral angles almost straight. First abdominal tergite shorter and wide, usually less narrowed toward apex. Wings smoky. Ovipositor valves slightly shorter than hind tibia." We analyzed the T2 shape of various specimens of barcoding clusters morphologically matching these three very similar species, more details can be found above discussing this character. In addition to that, the characterization of T1 shape is not very exact and the wings do not appear more infumate than in the other species, as well as ovipositor sheaths being shorter than the hind tibia (the latter two characters are not repeated in the other side of the couplet).

Illidops cloelia (Nixon, 1965)

Fig. 16

Apanteles cloelia Nixon, 1965: 183–184, fig. 211.

Other material examined

GERMANY – **Bavaria** • 1 ♀; Garmisch-Partenkirchen, Zugspitze, Platt; 47.407° N, 11.008° E; 2005 m a.s.l.; 18 Jul.–2 Aug. 2018; D. Doczkal and J. Voith leg.; Malaise trap; bulk ID: dv.zugsp5.3; obere Grenze Latschengebüsch, kleinräumiges Mosaik mit Zwergstrauchheide und (sub-)alpinen Rasen; SNSB-ZSM, ZSM-HYM-42389-G08.

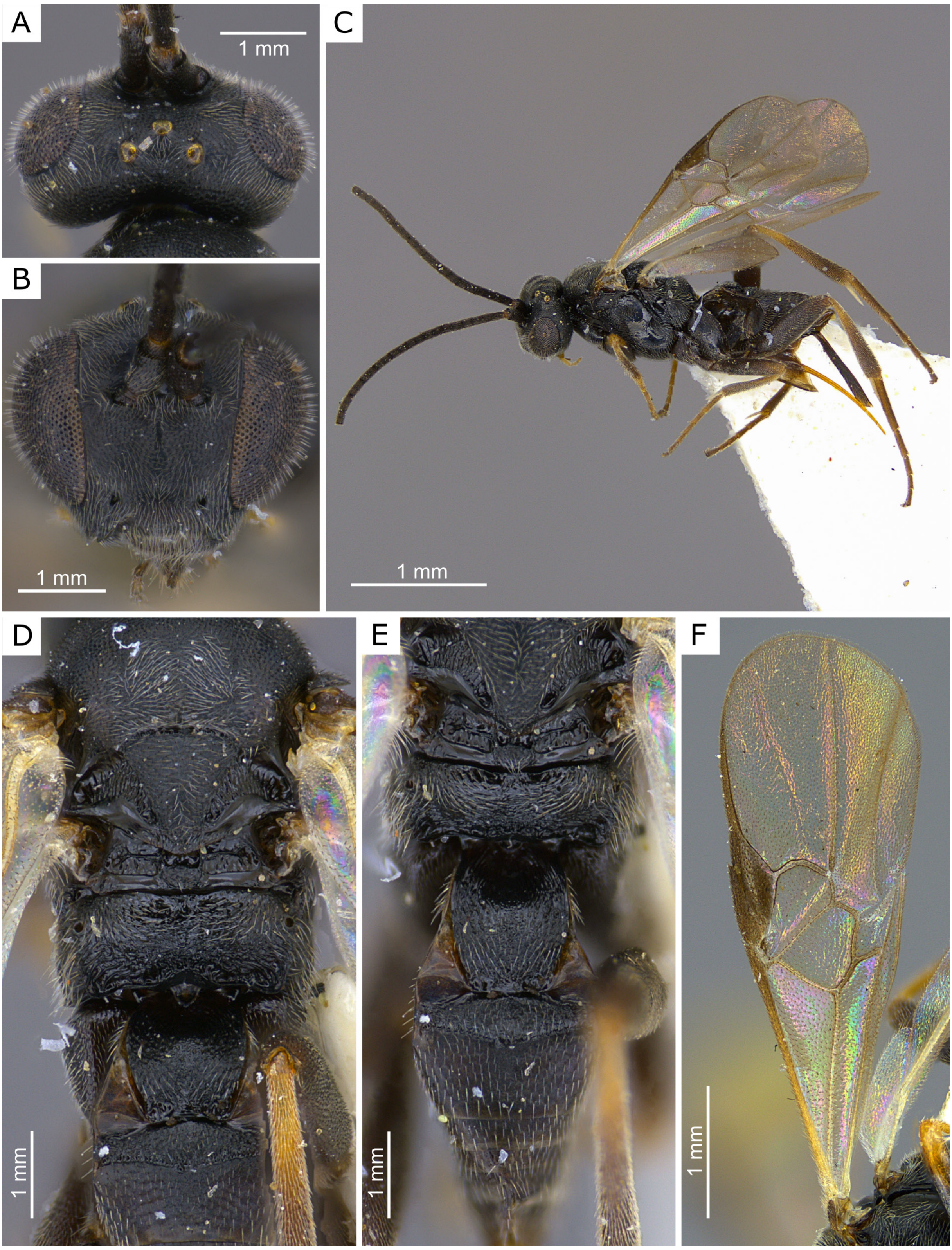

Fig. 15. *Illidops buteonis* (Kotenko, 1986), holotype, ♀ (SIZK). **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Lateral view. **D**. Mesosoma, dorsal view. **E**. Metasoma, dorsal view. **F**. Fore wing. Body length of the specimen: 2.4 mm.

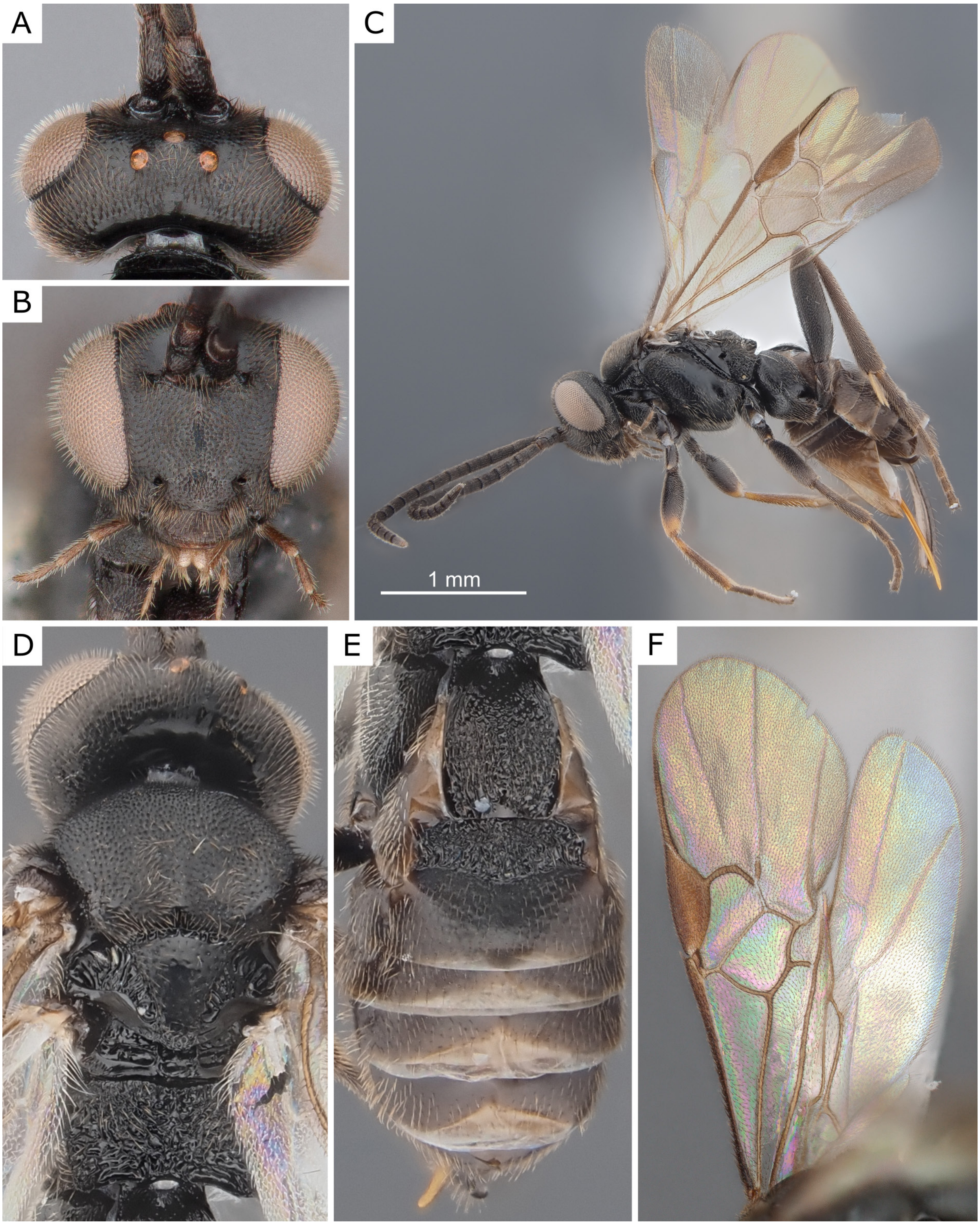

Fig. 16. *Illidops cloelia* (Nixon, 1965), ♀ (ZSM-HYM-42389-G08). **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Lateral view. **D**. Mesosoma, dorsal view. **E**. Metasoma, dorsal view. **F**. Wings. Body length of the specimen: 2.8 mm. Figure from Höcherl *et al*. (2024), minimally altered.

Species concept

The type was examined by Fernandez-Triana *et al.* (2020). Our species concept is based on the information available in Nixon (1965, 1976) and Papp (1981) and the specimens we identified as this species based on morphology, including their associated molecular data. This species is morphologically rather unique → **.

Ecology / host information

Host unknown.

Distribution

PAL: Austria, Germany, Hungary, Korea, Russia (E, NC), Slovakia, Switzerland, Tajikistan, former Yugoslavia.

Molecular data

Molecular data: BOLD:AEO8223.

Remarks

Holotype female, NHMUK. Country of type locality: Switzerland. For more details see Höcherl *et al.* (2024). A male specimen of *I. cloelia* identified by Nixon should be stored at SNSB-ZSM as part of the Haeselbarth collection; however we were unable to locate or examine it as the collection underwent construction during the time of this project.

Illidops dauricus Kotenko, 2007

Fig. 17

Illidops dauricus Kotenko, 2007: 180–181, pl. 79 figs 8–9.

Type material

Holotype

RUSSIA – **Zabaykalsky Krai** • ♀; Borzinsky District, 30 km SW of Borzya, Mt. Odon-Cholon; 50.55° N, 116.19° E; 1100 m a.s.l.; 17 Jul. 1990; A. Kotenko leg.; meadow; SIZK.

Species concept

Our species concept is based on our examination of photos of the holotype and the information available in Kotenko (2007) → ***.

Ecology / host information

Host unknown.

Distribution

PAL: Russia (ZAB).

Molecular data

No molecular data available.

Remarks

This species is part of the *I. naso* complex of morphologically cryptic species (more detailed information in the remarks for *I. naso*). As characters to distinguish this species from *I. naso*, Kotenko (2007: 179) used the T2 shape. We analyzed the T2 shape of various specimens of barcoding clusters morphologically matching these very similar species; more details can be found above discussing this character. In addition to the holotype, there are 2 male paratypes stored at SIZK (Kotenko *et al.* 2014).

Original description sensu Kotenko (2007) (translated from Russian and with updated morphological terminology and comments in brackets when our observations did not match Kotenko's)

[Diagnosis: Similar to *I. kostjuki*, but differs in the following characters:] T1 longer and narrower, 1.6 to 1.7 × as long as than maximum width. Metatibiae dark brown or almost black, in basal third very light, reddish yellow or light brown. Ovipositor sheaths length equal to hind tibia length. 2.4–2.6 [mm, this potentially refers to body length in mm].

Width of head 1.8–1.9 × its length, slightly less than width of mesosoma; head roundly narrowed behind eyes, looking triangular in frontal aspect. Gena 1.4 × as short as eye width (laterally). Ocelli in obtuse triangle [ocelli in high triangle], its base 1.8 × OOL. POL 1.3 × OD [POL 2.7 × OD]. Tangent to anterior edge of the posterior ocelli slightly going behind the posterior edge of anterior ocellus [imaginary tangent posterior to the anterior ocellus does not touch or cross the posterior ocelli]. Eyes slightly converging downwards, their longitudinal diameter 1.7–1.8 × more than their transverse diameter and 1.9 × more than face height. Upper face width 1.1 × lower face width and 1.6 × face height. Anterior margin of clypeus almost straight, 2.7 × less high than face height. Genae height 3.7–3.8 × less than longitudinal eye diameter. Labiomaxillary complex forming a prominent proboscis. Antennae shorter than body, F15 slightly elongated. Mesosoma 1.1 × as short as metasoma. Length of mesosoma 1.6 × its height. Fore wing 1.2–1.3 × as long as hind wing, and approximately equal in length to body. Pterostigma 2.7–2.8 × as long as wide, slightly longer than vein R1; R1 barely longer than the distance from it to the apex of the marginal cell. Vein r shorter than vein 2RS. Vein 1cu-a arising at approximately half of 1st discal cell. Hind wing vein cu-a of the hind wing slightly curved. Length of metafemur almost 4.0 × more than its width and 1.2 × less than the length of the metatibia. Metatarsus 1.2 × as long as metatibia. Ratio of holotype metatarsomere lengths as follows 4.2 : 2.5 : 1.8 : 1.0 : 1.1. T1 almost parallel-sided from base, noticeably narrowed in the apical third of its length. T2 about 2.0 × as short as T3. Hypopygium protruding far beyond the apex of the metasoma. Ovipositor sheaths slightly widened posteriorly and slightly curved downwards.

Sculpture. Head softly punctated dorsally, with a satin sheen. Gena on a narrow strip along the posterior margin of the eye with sparser punctation, more or less shiny, rest of gena densely punctated, almost matte. Face and clypeus finely punctate, with weak satin sheen. Face in median part with a noticeable tuberous longitudinal keel. Mesoscutum anteriorly more densely punctated with weak satin sheen, its horizontal part more sparsely punctated, shining. Scuto-scutellar sulcus narrow, crenulated. Scutellum in the anterior and median parts with sparser punctation, shiny. Entire propodeum densely wrinkly-punctated, matte, in the posterior half the sculpture is rougher than in anterior. Outer side of the metacoxal with sparse punctures, shiny. Posterior half of T1 and T2 lightly sculptured, matte. Subsequent abdominal tergites almost smooth, shiny.

Coloration. Body black. Antennae and tegulae black. Palps darkened. Wings smoky. Pterostigma, vein R1 and most other veins dark brown. Legs darkly colored, mostly black or dark brown.

"Holotype – ♀, Chit.[Chitinsky District, Zabaykalsky Krai, Russia]: 30 km SW Borzi, Mt. [Mountain range] Odon-Cholon, 1100 m, meadow, 17.VII, 1990 (A.K[otenko]) [SIZK]. Paratypes. 1♂, with label like holotype; Chit.[Chitinsky District, Zabaykalsky Krai, Russia]: 1♂, Daursky Researve, N shore of the lake Zun-Torey , tract Irel'zhin, beam, 7.VII.1990 (A.K[otenko])."

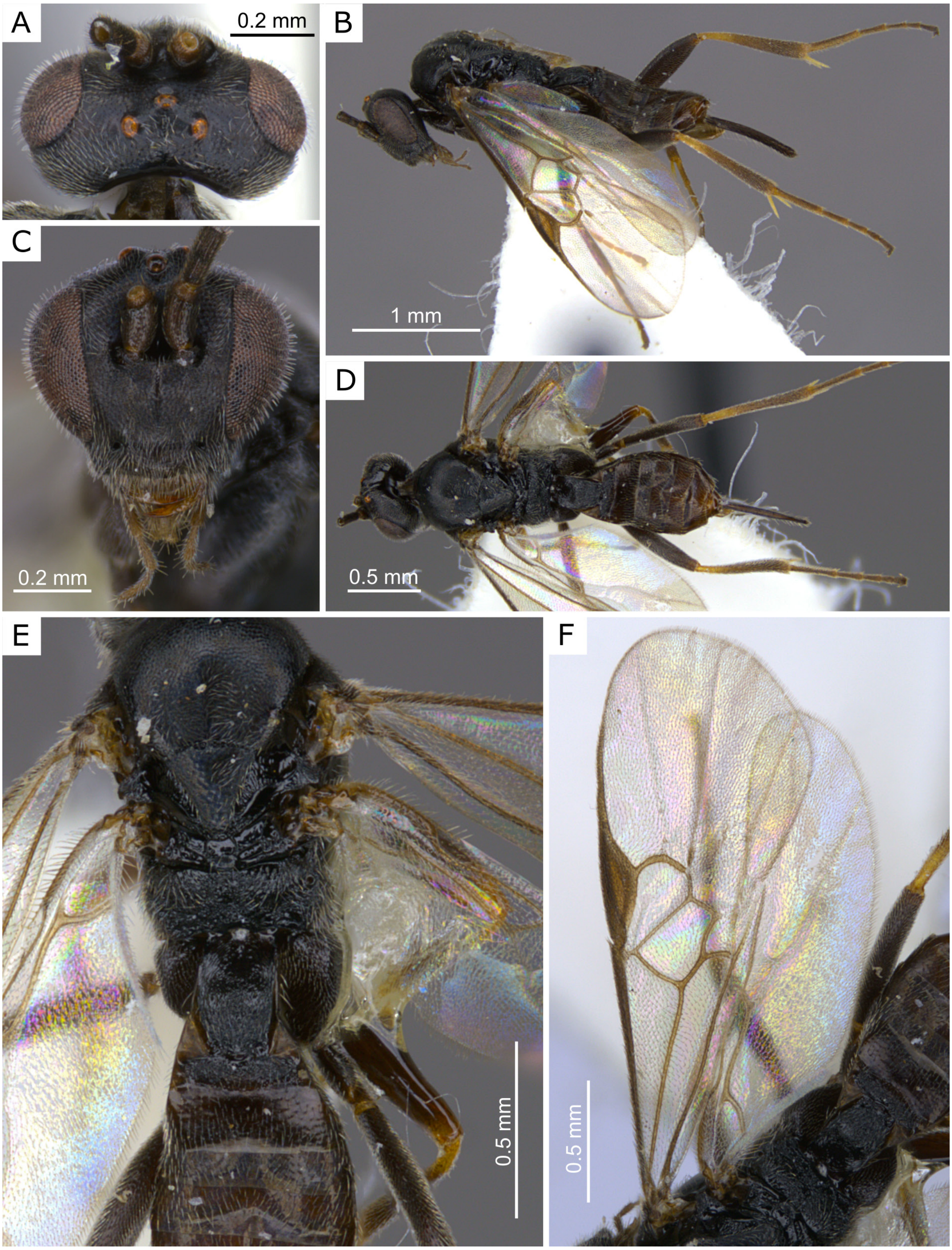

Fig. 17. *Illidops dauricus* Kotenko, 2007, holotype, ♀ (SIZK). **A**. Head, dorsal view. **B**. Lateral view. **C**. Head, frontal view. **D**. Mesosoma, dorsal view. **E**. Metasoma, dorsal view. **F**. Fore wing. Body length of the specimen: 2.6 mm.

Illidops doreenae Höcherl & Fernandez-Triana sp. nov.

urn:lsid:zoobank.org:act:3A46EE66-F7E9-46B2-A124-930CD72C1DB0

Figs 2F, 18–21; Table 3

Diagnosis

This species resembles *I. urgo* and *I. urgens* in the lighter coloration of the clypeus and smooth propodeum. It differs in its elongate glossa, the eyes barely converging towards the lower margin of the face, clypeus light brown, and scape and pedicel dark brown to black. It also resembles *I. kostylevi* based on the smooth propodeum and r1 longer than 0.5 of the pterostigma length. The new species differs in the following characters: clypeus coloration light and contrasting with the remaining face, glossa rather elongate, T2 shiny and with straight margin (compared to slightly sculptured with a sinuate margin in *I. kostylevi*), and smooth band posterior to the mesoscutellar disc invaded anteriorly by punctures (compared to much stronger sculpture in *I. kostylevi*). The species can readily be distinguished from the other Nearctic species (*I. scutellaris* and *I. terrestris*) by its entirely smooth propodeum.

Etymology

This species is named to honour Doreen Watler, who has supported not only AH, but also countless other visiting students and researchers over the past > 20 years during research stays at the CNC. By this, she has contributed significantly to advancements in entomology, and specifically in microgastrine taxonomy. We are very grateful to her.

Type material

Holotype

CANADA – **Yukon Territory** • ♀; Champagne; 60.790° N, 136.437° W; 733 m a.s.l.; 8 Jul. 2006; H. Goulet and C. Boudreault leg.; sweeping; plants along road; CNC, HYM00000599.

Paratypes

CANADA – **Yukon Territory** • 6 ♀♀; same data as for holotype; CNC, HYM00000583, HYM00000584, HYM00000587, HYM00000599, HYM00000628, HYM00000629 • 1 ♀; same data as for holotype; SNSB-ZSM, HYM00000579 • 3 ♀♀; same data as for holotype; 10 Jul. 2006; CNC, HYM00001685, HYM00001693, HYM00001696.

Other material examined

CANADA – **Alberta** • 1 ♀; Saskatoon Mountains, Beaverlodge vicinity, natural meadow; 55.22005° N, 119.282° W; 962 m a.s.l.; 27 Jul. 2007; J. Otani leg.; sweeping; natural meadow; CNC, MIC 000696. – **Ontario** • 1 ♀; Leeds and Grenville, Elizabethtown-Kitley, 4452 Rowsome Rd., Elizabethtown; 44.621° N, 75.773° E; 112 m a.s.l.; 7 Sep. 2010; James Sones leg.; Malaise Trap; CNC, BIOUG01284-D11 • 2 ♀♀; Toronto, Rouge National Urban Park, Sector 10; 43.8157° N , 79.207° E; 151 m a.s.l.; 15 Sep. 2013; BIO Team leg.; Pan traps; CNC, BIOUG08036-D11, BIOUG08036-F09. – **Yukon Territory** • 5 ♀♀; same data as for holotype; 10 Jul. 2006; CNC, HYM00001722, HYM00001688, HYM00001691, HYM00001692, HYM00001724.

Description

Female

MEASUREMENTS. Body length: 2.8 (2.95) mm. Fore wing length: 2.5 (2.45) mm. Antenna shorter than body.

HEAD. Face: eyes very slightly converging below, inner margin of eyes almost straight. Minimum face width/maximum face width: 0.94 (0.93). Malar distance/mandible width: 0.85 (0.73). Face densely punctate, punctures on lower half of the face elongate through fusion with adjacent ones, appearing to form striae on lower half of face. Ocelli in high triangle, posterior tangent to anterior ocellus not touching posterior pair. OOL/POD: 2.64 (2.50). POL/POD: 2.50 (2.13). F2 length/width: 2.78 (2.78). F15 length/width: 1.16 (1.22). F2 length/F15 length: 2.27 (2.27).

MESOSOMA. Anteromesoscutum with: dense shallow punctures. Mesoscutellar disc punctate. Posterior bar of mesoscutellum polished, median area with some punctures anteriorly. Propodeum entirely polished with some small rugosities radiating posterior centrally from nucha.

METASOMA. T1 shape: anterior 0.6 almost parallel-sided, narrowing in posterior 0.4. T1 sculpture: anterior 0.6 and posterior tip polished, band of weak sculpture and setosity at posterior 0.1–0.3. T1 width (anterior, maximum, posterior): 0.22, 0.24, 0.17 (0.19, 0.21, 0.17) mm. T1 central length/ posterior width: 2.00 (1.75). T2 trapezoideal, very short, posterior margin sinuate. T2 polished or very lightly sculptured, shiny. T2 width at posterior margin/central length: 3.0 (3.40). Posterior margin of T3–T7 slightly desclerotized but mediotergites not appearing to be pushed forward. Hypopygium not enlarged, its posterior end about in line with end of apical tergites. Ventral margin of hypopygium with desclerotized area showing several pleats. Ovipositor sheaths broad and setose over most of their length. Ovipositor distinctly downcurved at apical 0.3. Ovipositor sheaths length/metatibial length: 0.81 (0.95). Metafemur length/width: 0.33 (0.30). Tarsal claws: simple.

WINGS. Length of fore wing veins r/2RS: 1.86 (1.28). Pterostigma length/width: 2.05 (2.38). Point of insertion of vein r in pterostigma: clearly beyond half length of pterostigma. Angle of vein r with fore wing anterior margin: slightly outwards, inclined towards fore wing apex. Length of vein R1/distance of distal end of R1 to distal end of vein 3RS: 1.64 (1.80).

COLORATION. Body color: mostly dark brown to black, some specimens (including some males and a female paratype) show a broad stripe of lighter coloration lateroventrally on mesosoma (see Fig. 21G). Head color: head including face dark brown to black, clypeus and labrum contrasting lighter brown, palpi pale except for slightly darker base. Antenna completely dark brown to black. Legs: all coxae brown to black. Femora: pro- and mesofemur with paler coloration apically, metafemur entirely dark brown. Tibiae varying between specimens: protibia from yellow to light brown (holotype); mesotibia lighter basally, darker brown apically; metatibia completely brown (holotype, paratype: metatibia yellow on basal 0.7, darker apically). Tarsi brown. Tegula and humeral complex dark brown to black. Fore wing: pterostigma brown, some specimens with slightly lighter area at basal 0.1, wing veins in basal third brown (YT, type series), transparent (variation A), or a combination of brown and transparent (variation B).

Male

Unknown.

Biology / ecology

Host unknown.

Distribution

NEA: Canada (AB, BC, NB, ON, YT), USA (AK).

Molecular data

Molecular data: BOLD:AAB5165 and BOLD:ACL9543, details in Table 3 and Fig. 18.

Remarks

We found molecular and morphological variation within this species; however, we interpret the differences in DNA barcodes and morphology as rather minor and inconsistent with distribution. The species is represented in two BINs, BOLD:AAB5165 and BOLD:ACL9543. The maximum pairwise distance within the species (including both BINs) is 3.27%. Variation A is represented by two specimens from the same BIN as the holotype (BOLD:AAB5165) but the specimens were collected farther south in Canada (AB, ON). They differ from the Yukon specimens by having the veins in the basal third of the fore wing transparent except for the anterior margin of the wing (C+SC+R). Variation B clusters in BIN BOLD:ACL9543 and mainly differs by the specimens being much smaller than the type series and

Table 3. BINs which match the morphological characters of *Illidops doreenae* Höcherl & Fernandez-Triana sp. nov. Information on the Nearest Neighbor in the BOLD database is given, including relevant p-distances and distribution.

BIN/ Country	Number of specimens (n)	within-BIN max. p-distance	min. NN p-dist.	NN BIN/ Country	Number of specimens (n)	NN within-BIN max. p-dist.
BOLD:AAB5165 Canada	26	2.14%	1.18%	BOLD:ACL9543 Canada	13	1.02%
BOLD:ACL9543	13	1.02%	1.18%	BOLD:AAB5165 Canada	26	2.14%

variation A. For now, we consider all three to be part of the same species. However, we excluded the two variations from the type series as they may in the future prove to represent separate species. This species challenges our concept of *Illidops*, because it also partially fits the concept of *Dolichogenidea*. Based on the sculptured area interrupting the posterior smooth band of the scutellum centrally (which in this case consists of punctures), the short R1, and the COI sequences which match most closely other sequences associated with *Illidops*, we place it in *Illidops* for now. There are no morphologically similar species of *Dolichogenidea* found in the Nearctic.

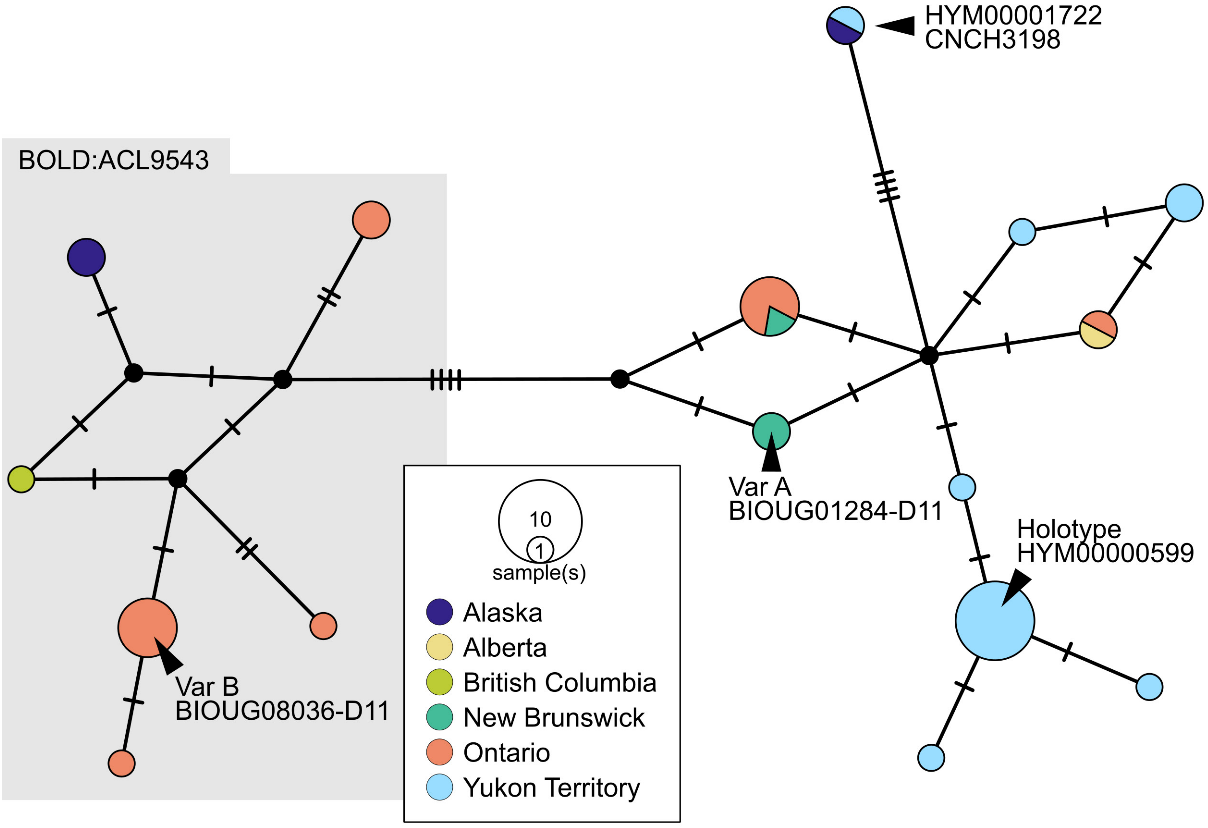

Fig. 18. TCS haplotype network of BINs BOLD:AAB5165 and BOLD:ACL9543, sequence length for analysis: 523 bp. BOLD:ACL9543 is marked by a gray background, all other haplotypes are part of BOLD:AAB5165. The states of the sampling localities can be differentiated based on coloration. Each hatch mark in the network represents a single mutational change; small black dots at nodes indicate missing haplotypes. The diameter of the circle is proportional to the number of haplotypes sampled

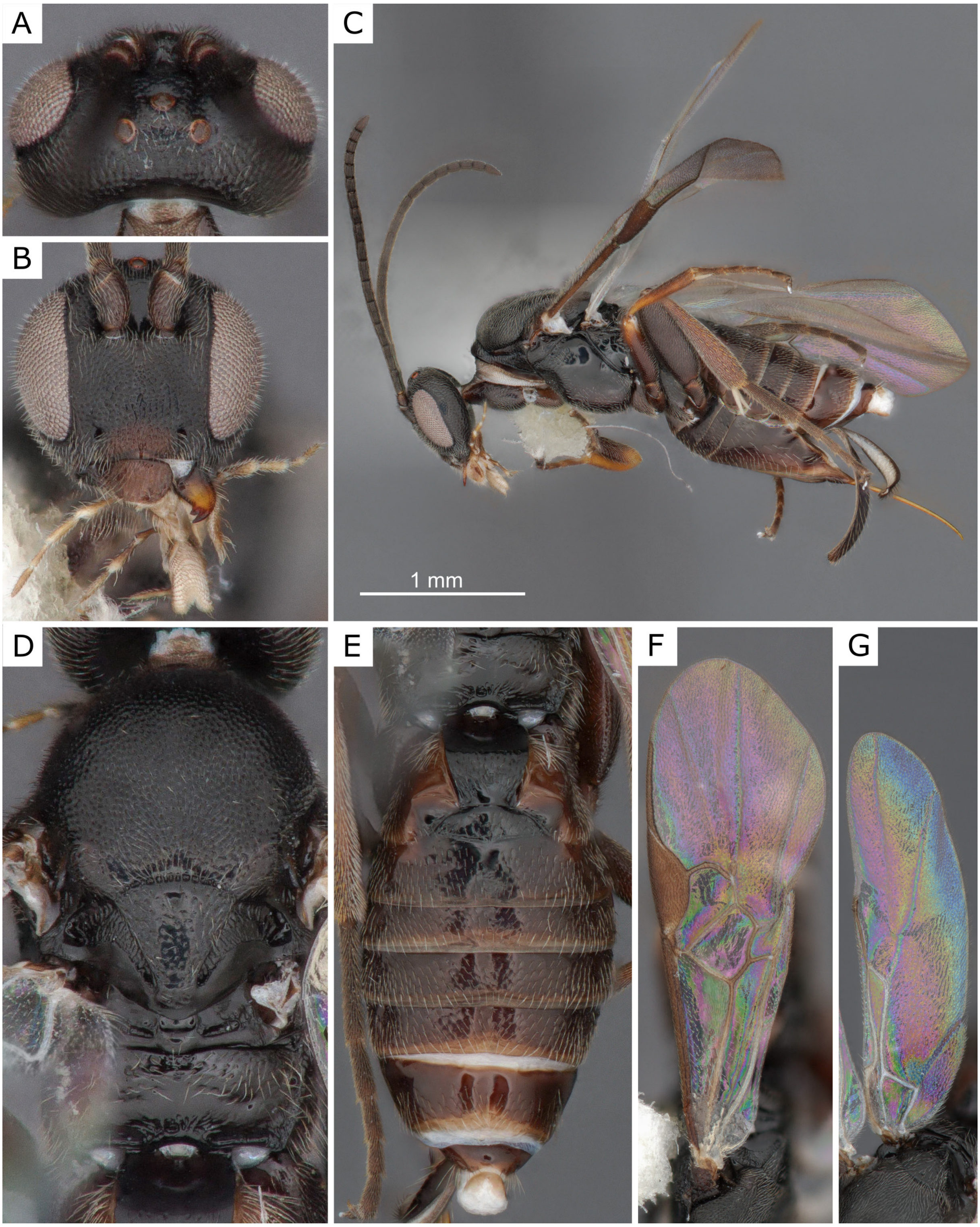

Fig. 19. *Illidops doreenae* Höcherl & Fernandez-Triana sp. nov., holotype, ♀ (HYM00000599), BOLD:AAB5165. **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Habitus, lateral view. **D**. Mesosoma, dorsal view. **E**. Metasoma, dorsal view. **F**. Fore wing. **G**. Hind wing. Body length of the specimen: 2.8 mm.

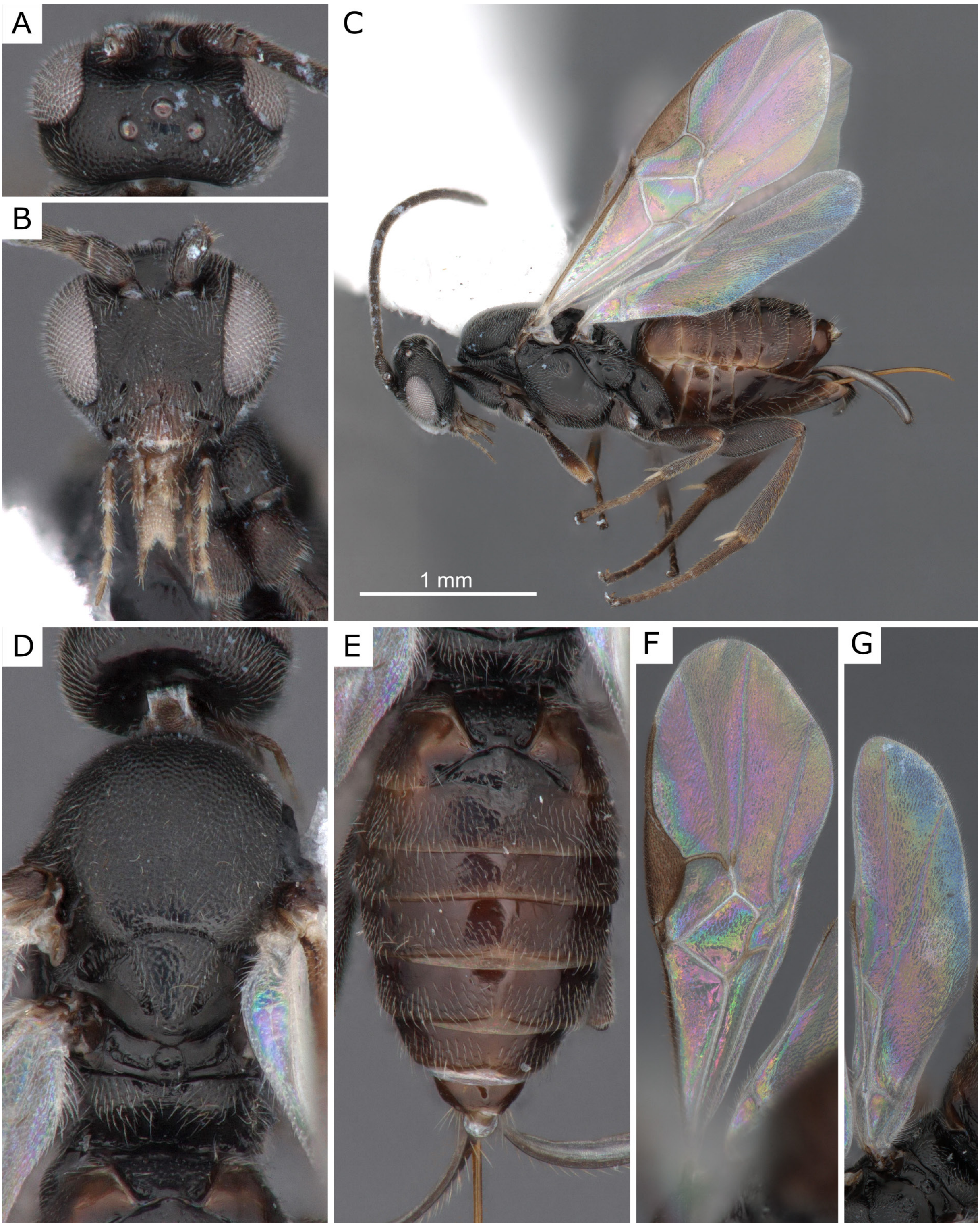

Fig. 20. *Illidops doreenae* Höcherl & Fernandez-Triana sp. nov., ♀ (BIOUG01284-D11), var A, BOLD:ACL9543. **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Habitus, lateral view. **D**. Mesosoma, dorsal view. **E**. Metasoma, dorsal view. **F**. Fore wing. **G**. Hind wing. Body length of the specimen: 2.6 mm.

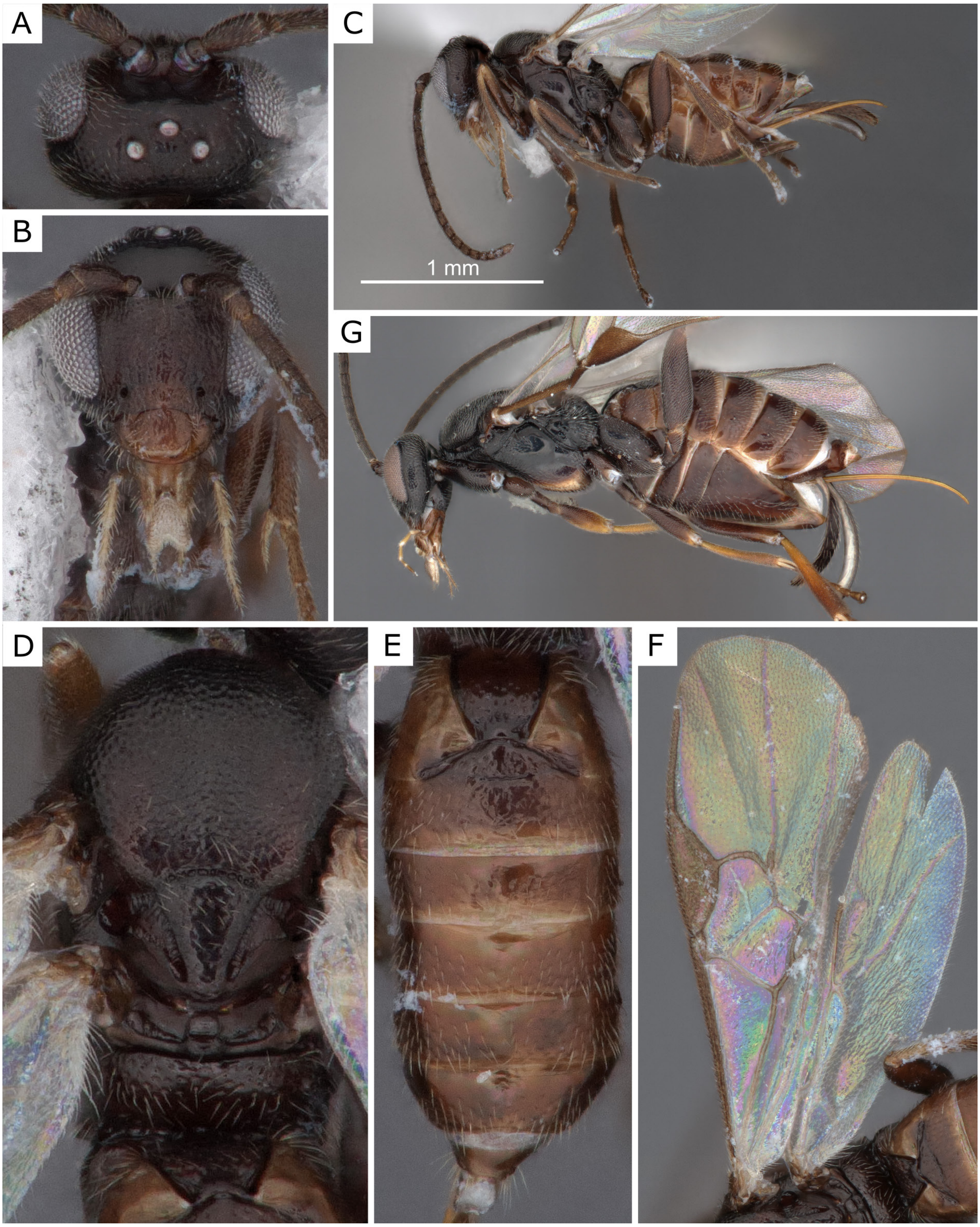

Fig. 21. A–F. *Illidops doreenae* Höcherl & Fernandez-Triana sp. nov., ♀ (BIOUG8036-D11), var B, BOLD:ACL9543. **G**. *Illidops doreenae* Höcherl & Fernandez-Triana sp. nov., ♀ (HYM00000579), BOLD:AAB5165. **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Habitus, lateral view. **D**. Mesosoma, dorsal view. **E**. Metasoma, dorsal view. **F**. Wings. **G**. Lateral view with light coloration on mesosoma. Body length of the specimen: 2.1 mm.

Illidops electilis (Tobias, 1964)
Figs 22–23

Apanteles electilis Tobias, 1964: 226–227, fig. 46.

Type material

Paratype
KAZAKHSTAN – **[Akmola Region]** • 1 ♀; Kokshetau, "Tersakkan W Akmol."; 15 Jun. 1957; V.I. Tobias leg.; [on *Ferula songorica*]; CNC, CNCHYM 00104.

Species concept

Our species concept is based on our examination of a female paratype stored at the CNC, photos of a female paratype stored at HMNM, and the information available in Tobias (1964), Tobias & Kotenko (1986), Nixon (1976), and Papp (1981). → ***.

Ecology / host information

Host unknown.

Distribution

PAL: Croatia, Hungary, Kazakhstan, Russia (S), Serbia, Tunisia.

Molecular data

No molecular data available.

Remarks

Holotype female, ZIN. Country of type locality: Kazakhstan.

Illidops kostjuki (Kotenko, 1986)
Fig. 24

Apanteles kostjuki Kotenko, 1986: 756 [424].

Type material

Holotype
RUSSIA – **Altay** • ♀; Kurayskiy Range, nearby Aktash, middle course of the river Yarly-Yary; [50.32° N, 87.60° E]; 2400 m a.s.l.; 25 Jul. 1976; Kostyuk leg.; southern slope with forbs; SIZK.

Species concept

Our species concept is based on our examination of photos of a paratype located at SIZK and the information available in Tobias & Kotenko (1986) and Kotenko (2007) → ***.

Ecology / host information

Tortricidae: *Aphelia stigmatana* (Eversmann, 1844).

Distribution

PAL: Russia (ALT).

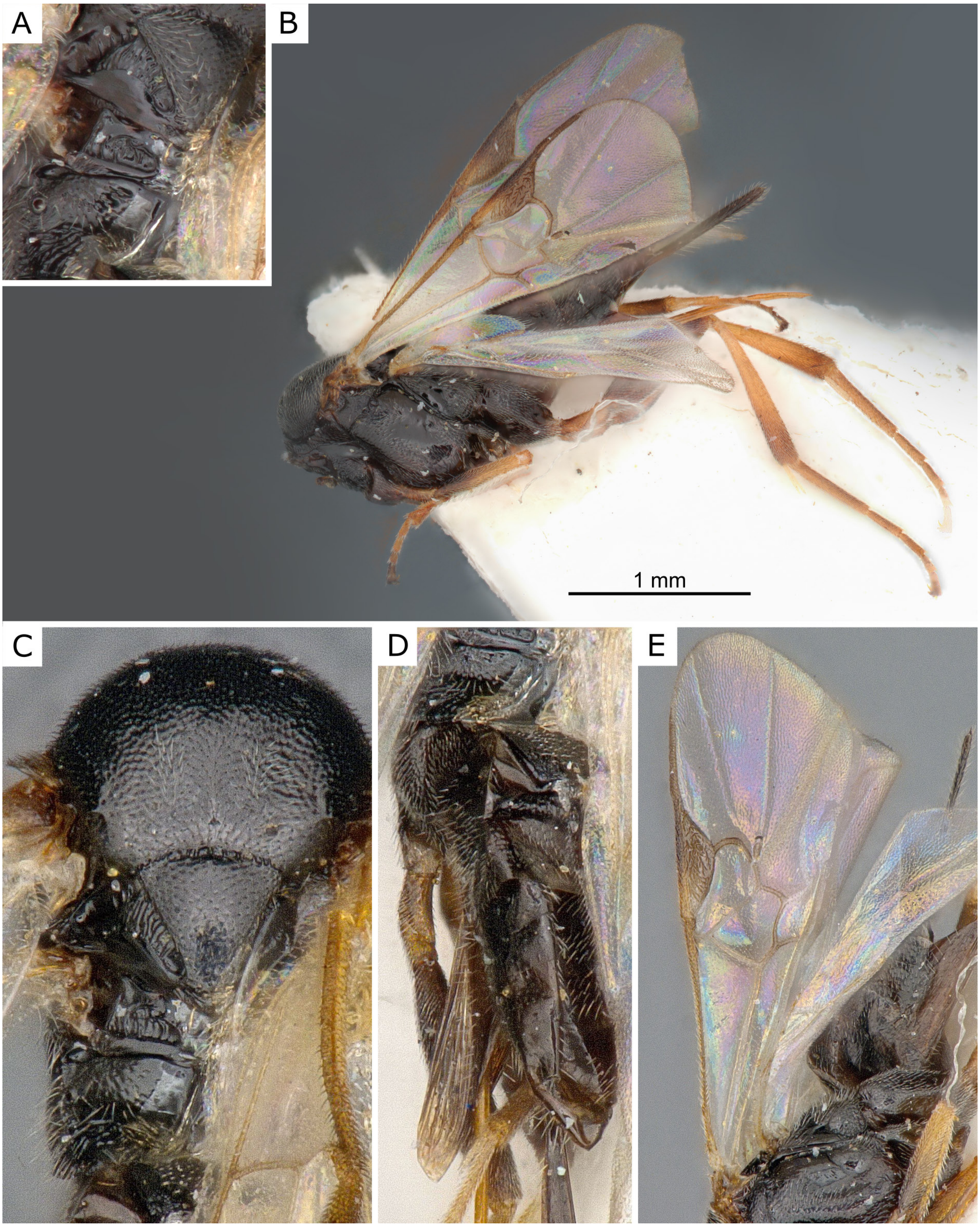

Fig. 22. *Illidops electilis* (Tobias, 1964), paratype, ♀ (CNCHYM 00104). **A**. Detail of the scutellum and propodeum. **B**. Habitus, lateral view. **C**. Mesosoma, dorsal view. **D**. Metasoma, dorsolateral view. **E**. Wings. Body length of the specimen [without head]: 2.2 mm.

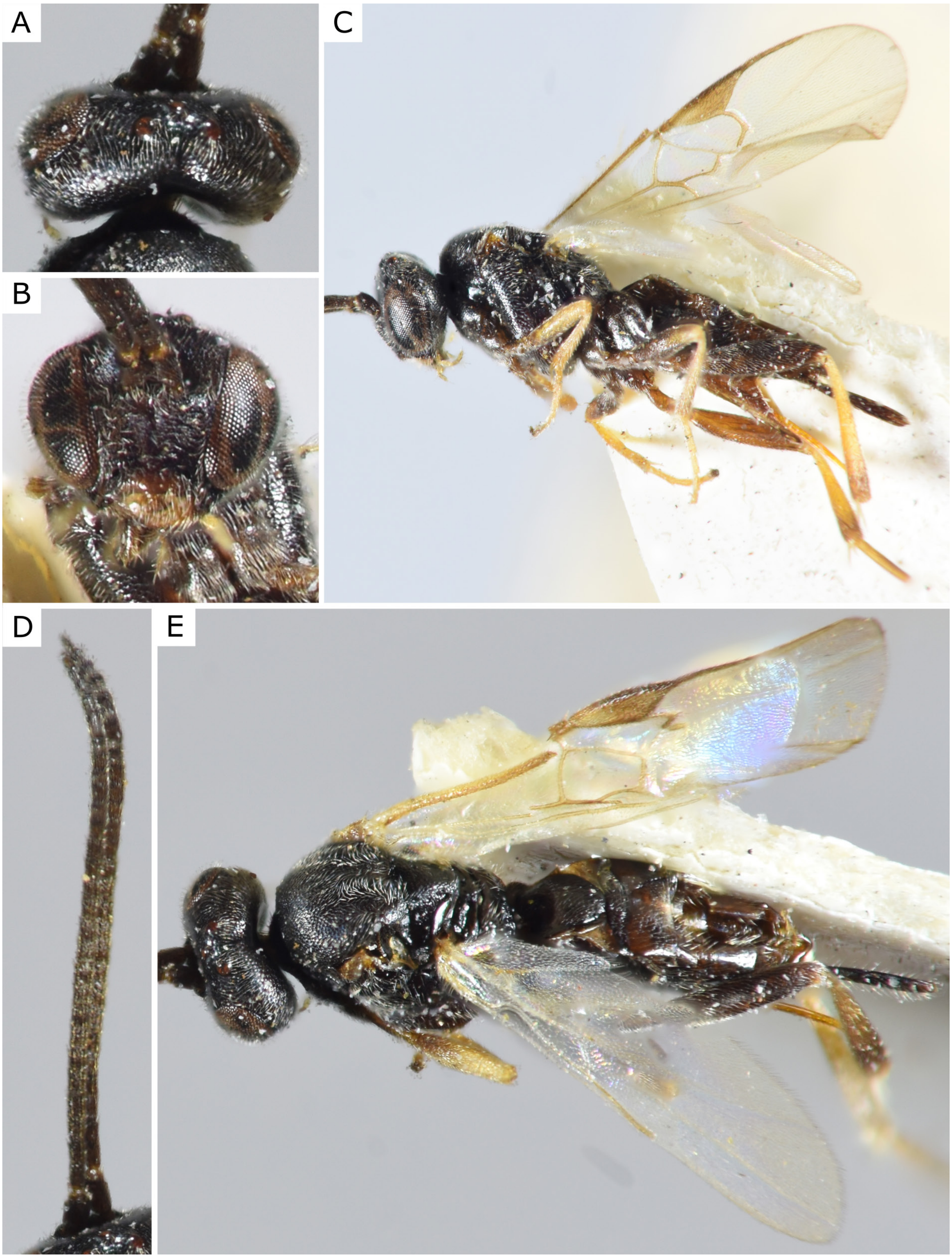

Fig. 23. *Illidops electilis* (Tobias, 1964), paratype, ♀ (HNHM). **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Lateral view. **D**. Antennae. **E**. Habitus dorsolateral view.

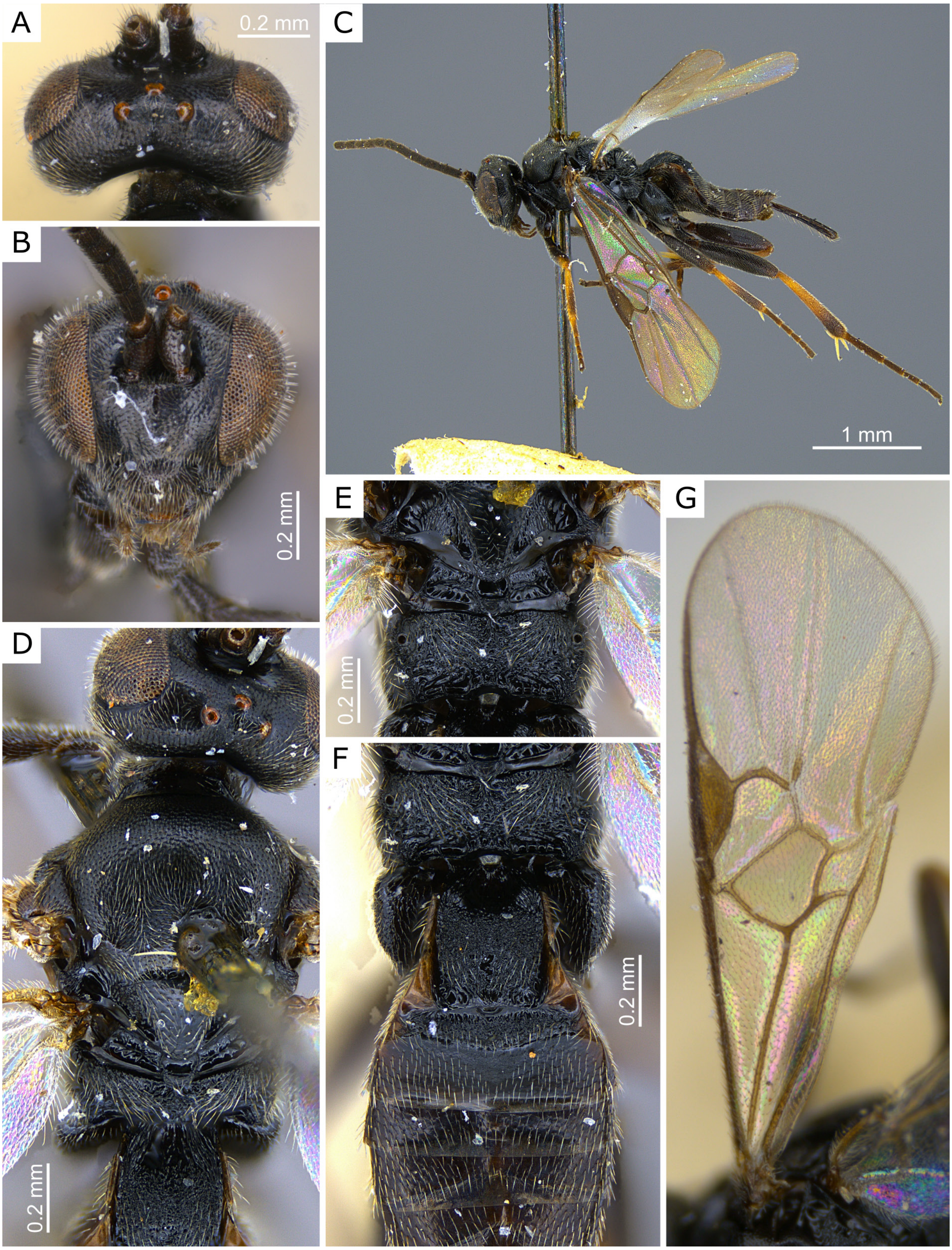

Fig. 24. *Illidops kostjuki* (Kotenko, 1986), paratype, ♀ (SIZK). **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Lateral view. **D**. Mesosoma, dorsal view. **E**. Partial mesosoma, dorsal view. **F**. Metasoma, dorsal view. **G**. Fore wing. Body length of the specimen: 2.9 mm.

Molecular data

No molecular data available.

Remarks

Host information from the original description: “Parasite of *Aphelia stigniatana* Ev. (Tortricidae). Cocoons isolated, white” (Tobias & Kotenko 1986: 756). The host information is from the holotype and indicated on the holotype labels, the paratype labels do not include any host information. Two female and 3 male paratypes are stored at SIZK, 1 female and 2 males with the same label as the holotype (Zerova *et al.* 2006).

Illidops kostylevi (Kotenko, 1986)

Fig. 25

Apanteles kostylevi Kotenko, 1986: 754 [424], pl. 243 fig. 4.

Type material

Holotype

UKRAINE – **Zaporizhzhia** • ♀; [Melitopol District (Yakymivka settlement hromada)], [Bohatyr] Altagyr; [46.63° N, 35.28° E]; [13 m]; 13 Jun. 1983; A. Kotenko leg.; SIZK.

Species concept

Our species concept is based on our examination of photos of the holotype and the information available in Tobias & Kotenko (1986) → ***.

Ecology / host information

Host unknown.

Distribution

PAL: Russia (ROS), Ukraine.

Molecular data

No molecular data available.

Illidops mutabilis (Telenga, 1955)

Figs 26–27

Apanteles mutabilis Telenga, 1955: 84–85 [97–98].
Apanteles szaboi Papp, 1972: 341–343, figs 14–17.

Other material examined

HUNGARY – **Pest County** • 1 ♂; Apajpuszta; [47.22527° N, 19.39620° E]; 18 Sep. 1952; M. Móczár leg.; J. Papp det.; paratype of *Apanteles szaboi* Papp, 1972; CNC, CNCHYM 01527. – **Budapest** • 1 ♀; Budapest; 31 Dec. 1931; Biró leg.; J. Papp det.; paratype of *Apanteles szaboi* Papp, 1972; CNC, CNCHYM 01528.

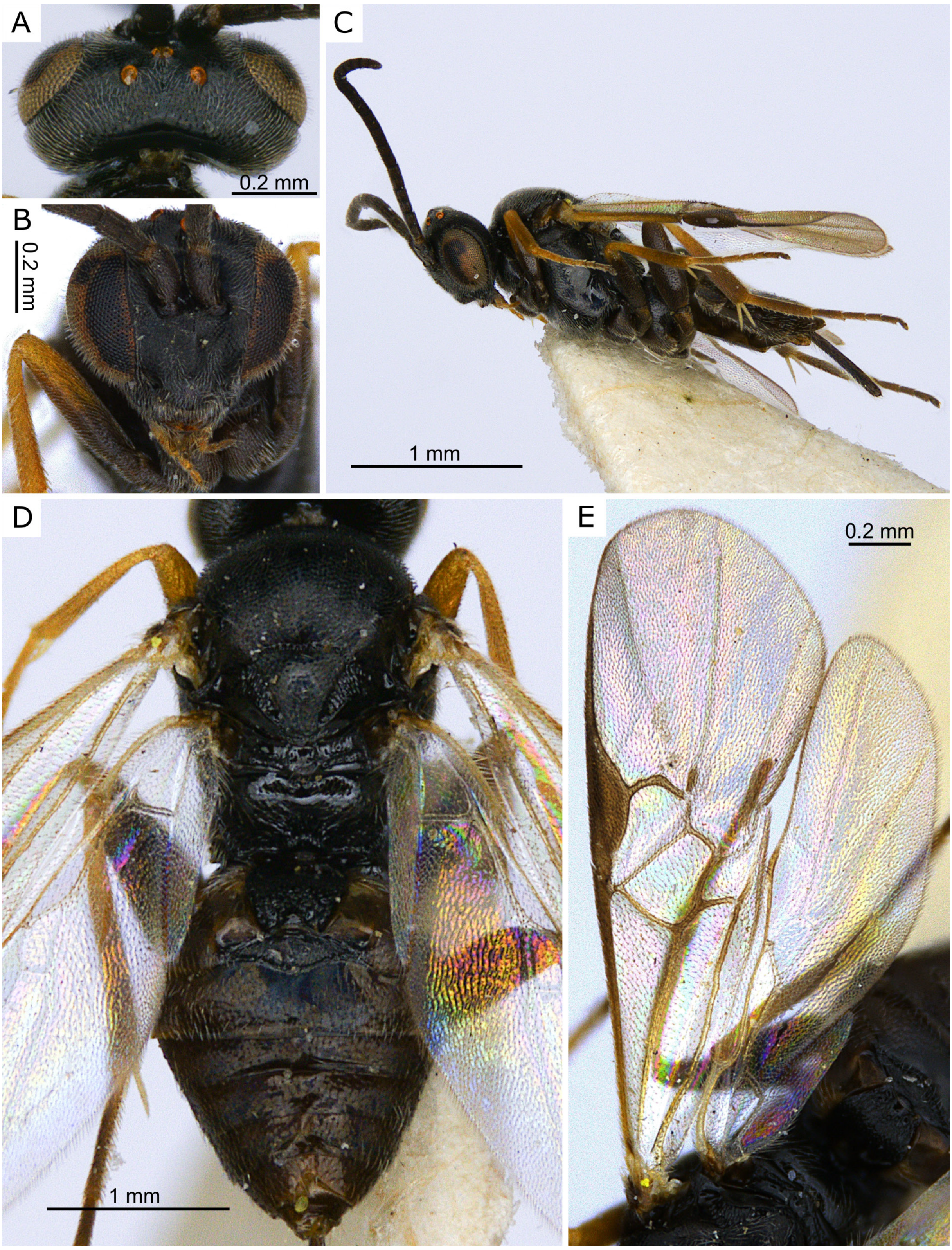

Fig. 25. *Illidops kostylevi* (Kotenko, 1986), holotype, ♀ (SIZK). **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Lateral view. **D**. Meso- and metasoma, dorsal view. **E**. Wings. Body length of the specimen: 2.4 mm.

Species concept

Our species concept is based on our observations of a female and male paratype of the junior synonym *A. szaboi* deposited at the CNC, the COI sequence of the male paratype, and information from Papp (1972, 1981), Tobias & Kotenko (1986) and Kotenko (2007). The molecular information is conflicting and there are several unsolved questions, including the synonymy of *A. szaboi* → **.

Ecology / host information

?Pyralidae: *?Etiella zinckenella*.

Distribution

PAL: Austria, Bulgaria, Georgia, Hungary, Kazakhstan, Mongolia, Romania, Russia (KDA), Serbia, Slovakia, Spain, Tunisia, Turkey, Ukraine.

Molecular data

A female and male paratype of the junior synonym *A. szaboi* are stored at the CNC and both had a leg picked for sequencing in 2016. However, the male specimen did not yield any sequence and the resulting sequence of the female specimen is rather short (164 bp), but of medium to high quality. The male paratype (CNCHYM 01527) was later included in our test of attempting to sequence historical DNA via shotgun sequencing and yielded a COI sequence of 600 bp. It aligns for 532 bp with the sequences of our fresh German material in BIN BOLD:AEI2559 (Fig. 28) and they match 100%. However, with 13 mutations over a length of 164 bp (7.93% difference) the sequence of the female paratype does not match the sequences in BIN BOLD:AEI2559, the voucher specimens of the cluster which we tentatively associate with this species. Unfortunately, we were unable to sequence the female specimen again. The reasons for this mismatch could be due to an error in the sequences, or it might be that the female and male paratypes do not belong to the same species. Both specimens were collected almost 20 years apart from different locations in Hungary, so we cannot currently draw any conclusions about the association of the sexes.

Remarks

Syntypes female and male, depository unknown. Country of type locality: Ukraine. Female holotype of *A. szaboi* at HNHM, country of type locality: Hungary.

Apanteles szaboi was synonymized by Kotenko (Tobias & Kotenko 1986), which was disputed by Papp (1988) in a subsequent paper. Then, in 2007, Kotenko listed it again as a synonym of *I. mutabilis* (Kotenko 2007). With the type depository of *I. mutabilis* unknown, we cannot currently make an unambiguous conclusion on these two names; rather, we accept the most recent treatment by Kotenko (2007) as a provisional solution, but caution that there is no solid basis at present to support Kotenko's view over Papp's. The characters differentiating *A. szaboi* from *I. urgo*, *I. mutabilis* and *I. electilis* according to Papp (1981: 272) are: "Head in frontal view, in comparison to next three species, appearing rather elongated i.e. as broad between eyes as high medially. Glossa long, about half as long as basitarsus of the fore leg. Ocelli small, forming a very low triangle: hind imaginary tangent to anterior ocellus transecting posterior pair of ocelli". Particularly the rather elongate glossa indicates that this species should be reexamined and compared to *I. rostratus*; see more details in the remarks of that species. Papp's description of *A. szaboi* matches the female deposited at the CNC (CNCHYM 01528), although we would not consider the ocelli particularly small. As the type depository of *I. mutabilis* is unknown and we had no paratypes available, our current concept of *I. mutabilis* is mostly based on the paratypes of *A. szaboi*; however, as mentioned before, we were unable to investigate this synonymy. In addition to that, the male and female paratypes available at the CNC might not represent the same species. Both specimens were collected almost 20 years apart from different locations in Hungary, so we cannot currently draw any conclusions

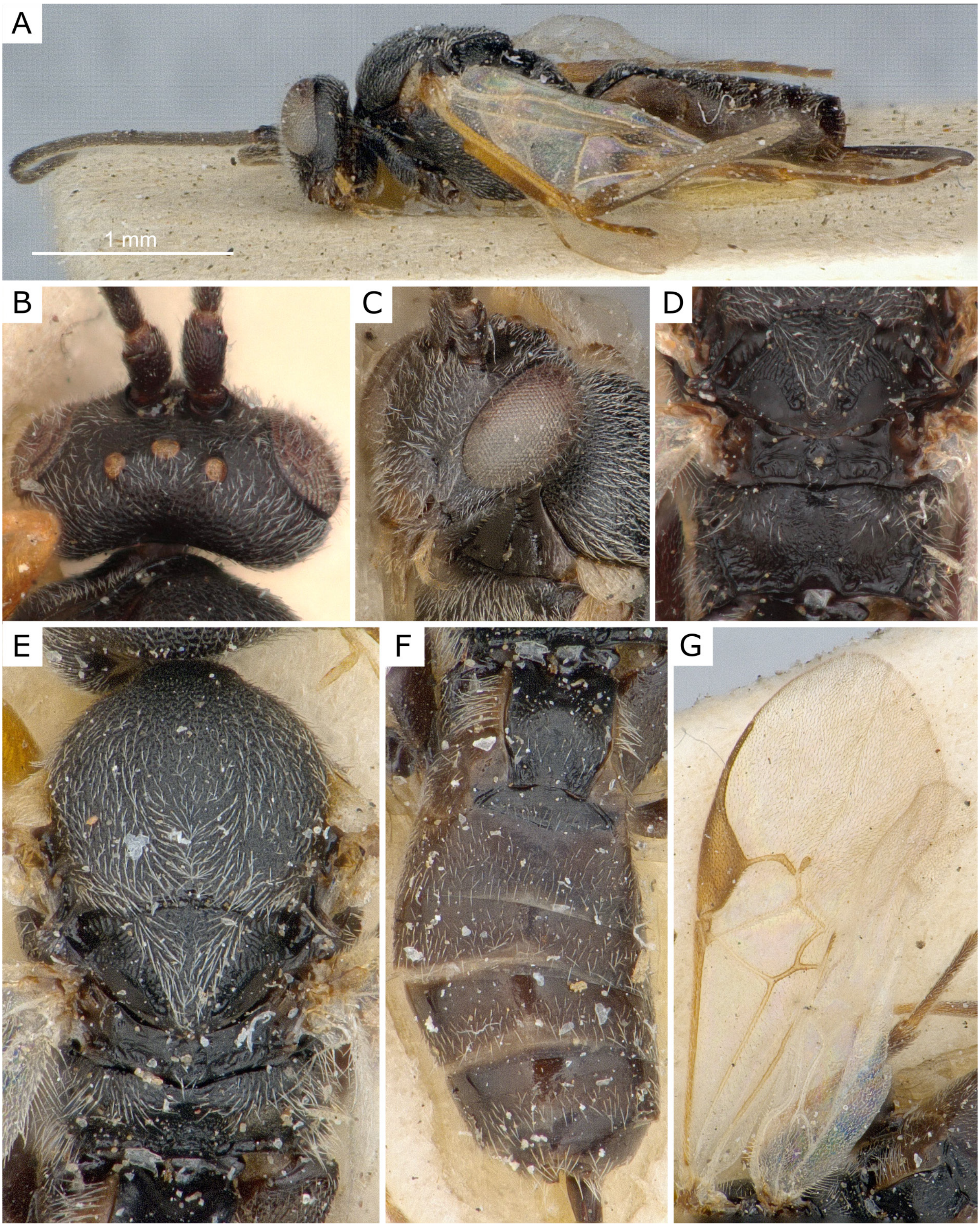

Fig. 26. *Illidops mutabilis* (Telenga, 1955), ♀ (CNCHYM 01528), paratype of junior synonym *Apanteles szaboi* Papp, 1972. **A**. Lateral view. **B**. Head, dorsal view. **C**. Head latero-frontal. **D**. Scutellum and propodeum. **E**. Mesosoma, dorsal view. **F**. Metasoma, dorsal view. **G**. Wing. Body length of the specimen: 3.0 mm.

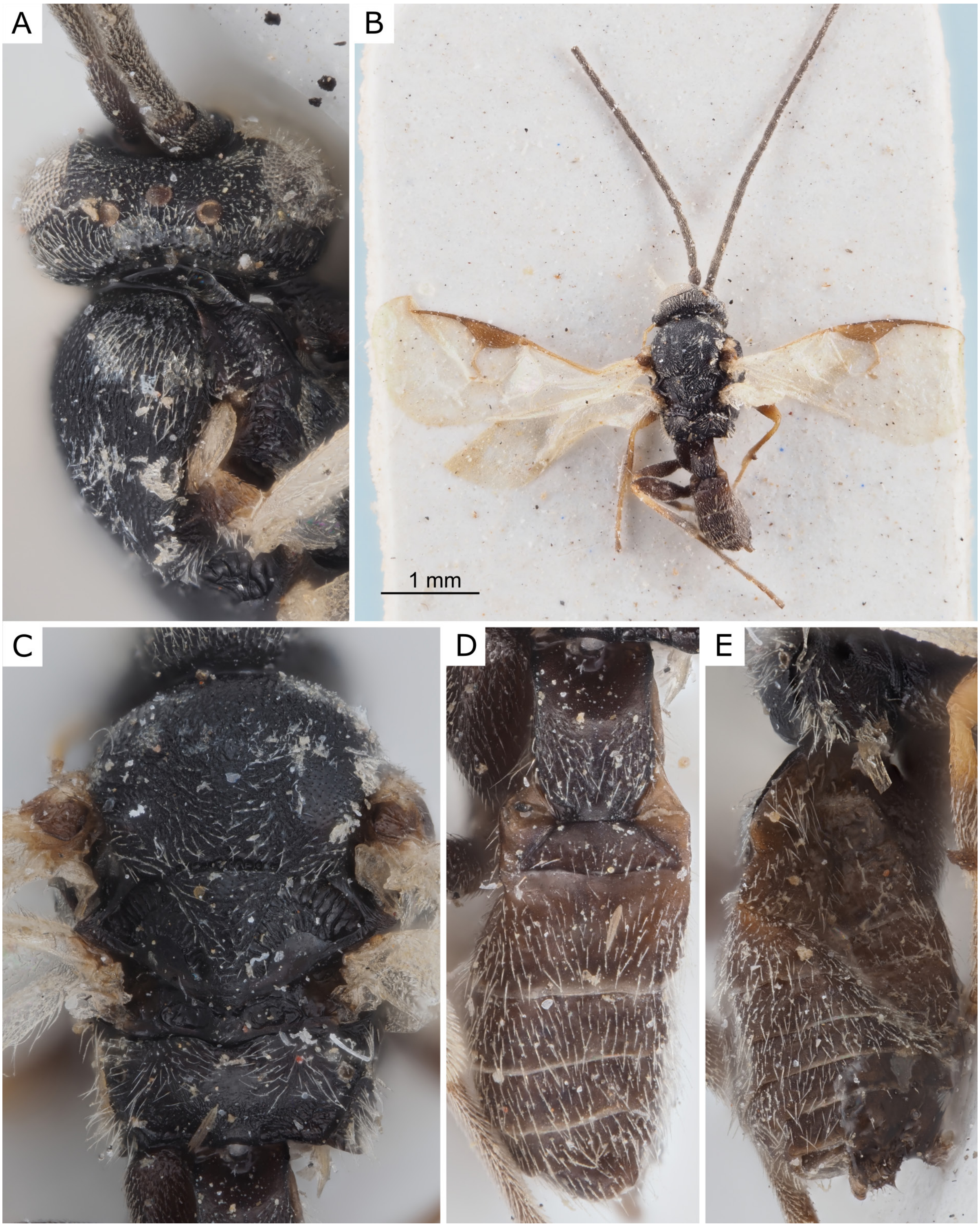

Fig. 27. *Illidops mutabilis* (Telenga, 1955), ♂ (CNCHYM 01527), paratype of junior synonym *Apanteles szaboi* Papp, 1972. **A**. Head dorsal and mesoscutum, dorsolateral view. **B**. Dorsal view. **C**. Mesosoma, dorsal view. **D**. Metasoma, dorsal view. **E**. Metasoma, lateral view. Body length of the specimen: 2.8 mm.

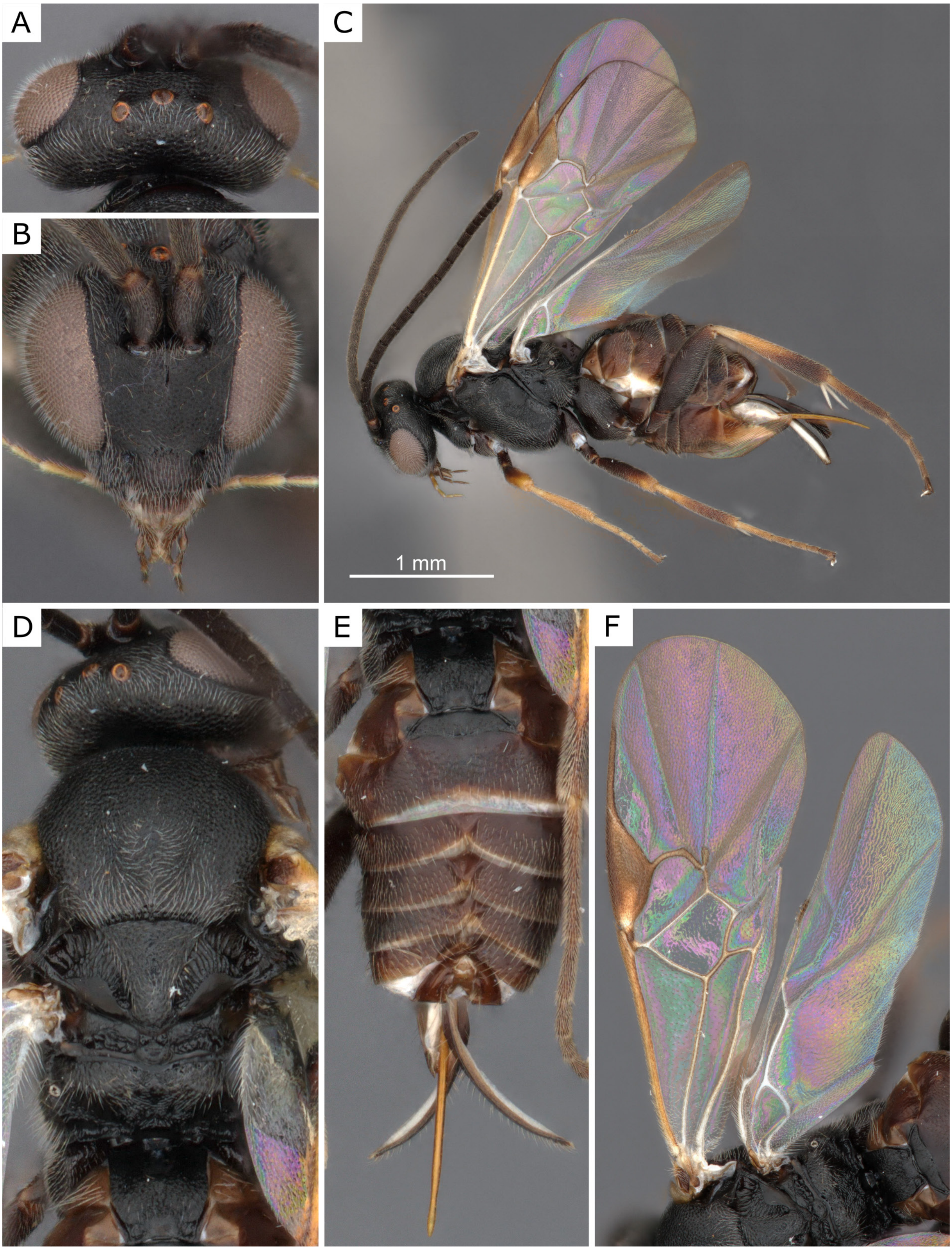

Fig. 28. *Illidops* cf. *mutabilis* (Telenga, 1955), ♀ (ZSM-HYM-33168-D03). **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Lateral view. **D**. Mesosoma, dorsal view. **E**. Metasoma, dorsal view. **F**. Wing. Note: additional, detailed photo of the scutellar area in Fig. 2C. Body length of the specimen: 3.0 mm.

about the association of the sexes. For further information on male and female specimen associations by Papp based mostly on sampling locality, see the remarks under *I. barcinonensis*. Voucher specimens of BOLD:AEI2559 (Fig. 28) morphologically match the current concept of *I. mutabilis*. However, with the holotype depository unknown, progress in this taxon is impeded. The host is not recorded from any type material and the association first appears in Tobias & Kotenko (1986), and not many details about the rearing event are provided: "Parasite of *Etiella zinckenella* Tr. (Phycitidae); cocoons rosy, isolated" (Tobias & Kotenko 1986: 753).

Illidops naso (Marshall, 1885)
Figs 29–30; Tables 4–5

Apanteles naso Marshall, 1885: 203.
Apanteles contortus Tobias, 1964: 224–225, fig. 45.
Apanteles crantor Nixon, 1965: 183, figs 205, 209.
Apanteles evander Nixon, 1965: 183, fig. 207.
Apanteles coresia Nixon, 1973: 198.

Other material examined

KAZAKHSTAN – **[Karaganda Region]** • 1 ♂; Kyzylzhar, Monadyr [Street]; [49.98° N, 72.61° E]; [460 m]; 22 Jun. 1958; V.I. Tobias leg.; [V.I. Tobias det.]; paratype of *Apanteles contortus* Tobias, 1964; CNC, CNCHYM 00168. – **[Akmola Region]** • 1 ♀; Kokshetau, "Tersakkan W Akmol."; 15 Jun. 1957; V.I. Tobias leg.; [V.I. Tobias det.]; paratype of *Apanteles contortus* Tobias, 1964; CNC, CNCHYM 00169.

Species concept

Our species concept is based on our examination of the female and male paratypes of the junior synonym *A. contortus* stored in the CNC and the information available in Marshall (1885), Tobias (1964), Tobias & Kotenko (1986), Nixon (1965, 1973, 1976), and Papp (1981, 1988) → *.

Ecology / host information

Host unknown.

Distribution

PAL: Afghanistan, Armenia, Azerbaijan, Bulgaria, Croatia, Finland, Georgia, Greece, Hungary, Iran, Kazakhstan, Korea, Kyrgyzstan, Macedonia, Moldova, Mongolia, Romania, Russia (KC, VOR), Serbia, Slovakia, Switzerland, Turkey, Turkmenistan, United Kingdom, Uzbekistan.

Molecular data

We observed specimens of six barcoding clusters which morphologically rather resemble *Illidops naso*: BOLDAEI3308 (Figs 2B, 31), BOLD:AEI9858 (Fig. 32), BOLD:AEK1062 (Fig. 33) BOLD:AEO8212 (Fig. 34), BOLD:AAD3865, and a single disparate sequence of a male *A. contortus* paratype. However, these clusters are far apart from each other with minimum p-distances ranging between 6.03% and 11.35%. The clusters are clearly separated, even though only few specimens are available for some. The Nearest Neighbors (NN) in the BOLD database are different clusters, not identified to species level (compare Table 4). Only BOLD:AAD3865 is quite close to its NN which is BOLD:AEA1257 with a minimum p-distance of 2.37%. However, we were unable to observe any specimens of the NN and the morphology observed by us so far is cryptic in any case, so we cannot draw any conclusions. Most NNs have no species-level identification associated and we do not currently have access to specimens associated with most of these clusters. Only BOLD:AAK4166, which includes representatives from Canada that are stored at the CNC, allowed for some morphological analysis and we found the characters of representatives of this cluster similar to *I. cloelia*, not the *I. naso* complex. In addition, the NN BIN of BOLD:AEI9858 includes representatives that we associated with *I. cloelia*. What we can conclude based on the molecular data available to us is that these clusters likely form a complex of morphologically cryptic species associated with the names *I. naso* (and its four junior synonyms), *I. buteonis* and *I. dauricus*.

We attempted matching one of our clusters to a pre-existing name via DNA barcoding by sequencing a male paratype of *A. contortus* stored at the CNC and collected in Kazakhstan in Kyzylzhar, Karaganda. CNCHYM 00168 was included in the shotgun sequencing of historical DNA and was mapped to the COI sequence of ZSM-HYM-33161-C11. Karaganda is the neighboring province to Akmola, in which the holotype locality "6km NE from Ylektykol Lake" is located. However, the sequence of this specimen did not match any of our clusters. We did a BLAST search in BOLD and the sequence matched the publicly available sequence of specimen CGTURK-1496, part of BIN BOLD:AAH1044 from northeastern Turkey with 99.05% similarity. The specimen appears to be a male and we cannot draw any conclusions based on the photo available in the database.

Remarks

Holotype male, NHMUK. Country of type locality: United Kingdom. The type was examined by Fernandez-Triana *et al.* (2020).

This species is morphologically very similar to *I. buteonis* and *I. dauricus*. We do not think that it is currently possible to reliably differentiate these species based on morphological characters. Firstly, because we observed that some characters used by previous authors are quite variable, even in specimens within a single barcoding cluster we associate morphologically with these species. Secondly, we found additional cryptic diversity via DNA barcoding with at least six different barcoding clusters matching the morphology of these three species, which appear in several places in a NJ analysis of *Illidops* (Fig. 62). We did not find sufficient characters to differentiate these molecular clusters morphologically (see notes on T2 shape and Fig. 5) or unambiguously match any of them to one of the previously described species. These species are likely part of a complex of morphologically cryptic species, hence, in this paper, we refer to them as part of the *I. naso* complex.

In addition to that, the name *Illidops naso* currently has 4 junior synonyms associated with it (see Table 5). The holotype of *I. naso* is male, was not reared and no female paratypes are assigned or other female specimens from the same locality mentioned in the original description. The type locality according to the description is: "On the sand-hills at the mouth of the Exe, opposite Star-Cross, Devon." (Marshall 1885: 203). The holotype of *A. contortus* is female and a rather long series of female and male specimens is mentioned in the original description, not reared, but partially collected from the same localities. The holotype of *A. crantor* Nixon, 1965 is female and in the original description only female specimens as material examined are indicated. The holotype of *A. evander* is female and a single female paratype is mentioned in the original description. The holotype of *A. coresia* Nixon, 1973 is female and the only specimen associated with this species in the original description. *Apanteles coresia* was described as part of the *metacarpalis*-group of *Apanteles*, not the *butalidis*-group. Nixon mentions that it is aberrant within this group due to its rather uniformly rugose propodeum. Nixon (1976) synonymized *A. crantor* under *A. contortus*, Papp (1981) synonymized *A. evander* and *A. contortus* under *A. naso* without providing details on his reasoning, and *A. coresia* was synonymized between 1981 and 1986, but we could not find by which author. The association between male and female specimens of *I. naso* were likely made based on the type series of *A. contortus*; however, matching female and male specimens of *Illidops* based on morphology is rather difficult due to the sexual dimorphism within this group observed by previous authors and ourselves. Tobias' male and female specimens were partially collected from the same single localities, but that is by no means a guarantee that they belong to the same species. We have found 2–3 different BINs associated with the *I. naso* complex in a single Malaise trap collecting event

Table 4. BINs which match the morphological characters of *Illidops naso* (Marshall, 1885) the most. Information on the Nearest Neighbor in the BOLD database is given, including relevant minimum p-distances and distribution.

BIN/ Country	Number of specimens (n)	Within-BIN max. p-distance	Min. NN p-dist.	NN/ Country	Number of specimens (n)	NN within-BIN max. p-dist.
BOLD:AEO8212 Germany	2	0%	6.9%	BOLD:AFN9174	n/a	n/a
BOLD:AEI3308 Germany	2	0%	3.77%	BOLD:AAK4166 Canada, Russia, USA	25	0.72%
BOLD:AEK1062 Germany	2	0%	7.06%	BOLD:AAK4166 Canada, Russia, USA	25	0.72%
BOLD:AEI9858 Germany, Finland	34	0.96%	6.74%	BOLD:AEO8223 Germany *I. cloelia*	2	0%
BOLD:AAD3865 United Arab Emirates	5	1.44%	2.37%	BOLD:AEA1257 Pakistan, Iran	4	0%
Apanteles contortus paratype 99.05% matching **BOLD:AAH1044** Turkey	5	0%	5.78%	BOLD:AAF9897 Turkey	11	0.78%

Table 5. *Illidops naso* and junior synonyms and their type information.

Species name	Holotype	Country of type locality	Type repository
Apanteles naso Marshall, 1885	Male	United Kingdom	NHMUK
Apanteles contortus Tobias, 1964	Female	Kazakhstan	Type repository unknown, potentially ZIN, female paratype available at HNHM, male at CNC
Apanteles crantor Nixon, 1965	Female	Greece, Crete	HNHM
Apanteles evander Nixon, 1965	Female	Finland	MZH
Apanteles coresia Nixon, 1973	Female	Finland	MZH

in several independent cases. We conclude that there is no good way to associate male and females of a species of *Illidops* unless both specimens were reared from the same host individual (or, less ideal, at least the same host species), or via DNA barcoding. With this strong sexual dimorphism combined with morphological crypsis, we cannot judge whether all of these current synonyms were rightly synonymized, and they will need to be dealt with when attempting to resolve this complex.

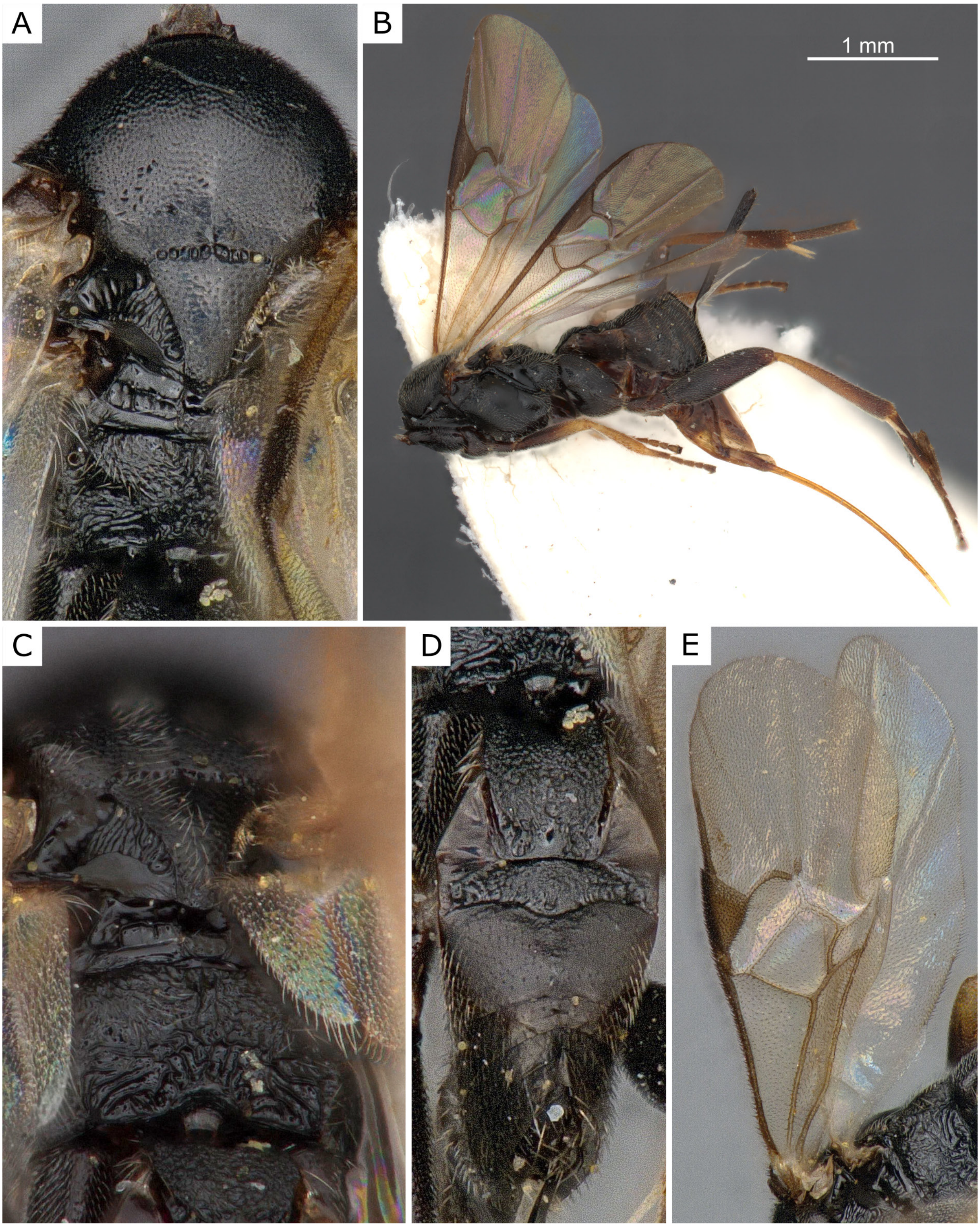

Fig. 29. *Illidops naso* (Marshall, 1885), ♀ (CNCHYM 00169), paratype of junior synonym *Apanteles contortus* Tobias, 1964. **A**. Mesosoma, dorsal view. **B**. Lateral view. **C**. Scutellum and propodeum, dorsal view. **D**. Metasoma, dorsal view. **E**. Wings. Body length of the specimen: 2.9 mm.

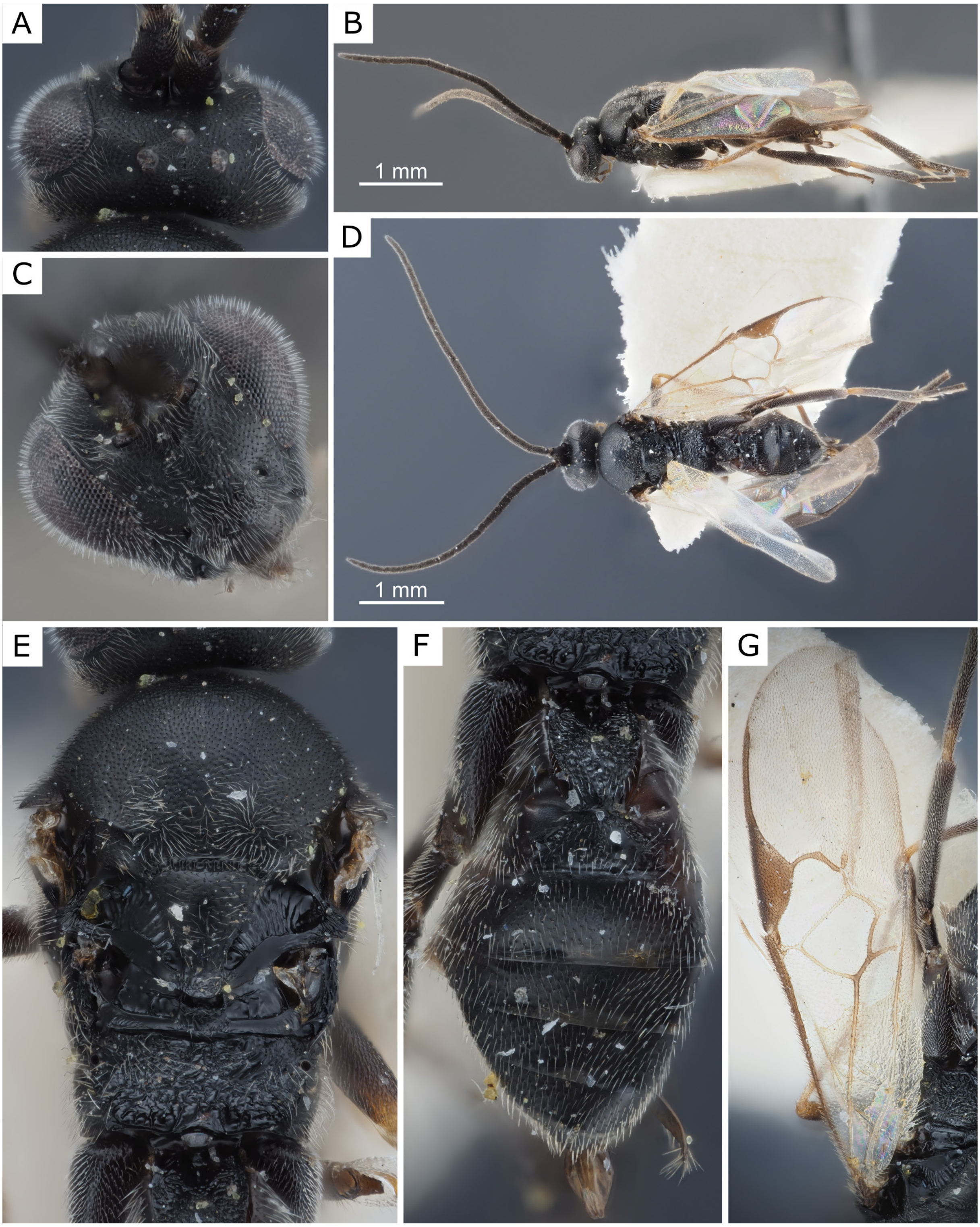

Fig. 30. *Illidops naso* (Marshall, 1885), ♂ (CNCHYM 00168), paratype of junior synonym *Apanteles contortus* Tobias, 1964. **A**. Head, dorsal view. **B**. Lateral view. **C**. Head, frontal view. **D**. Dorsal view. **E**. Mesosoma, dorsal view. **F**. Metasoma, dorsal view. **G**. Fore wing. Body length of the specimen: 3.2 mm.

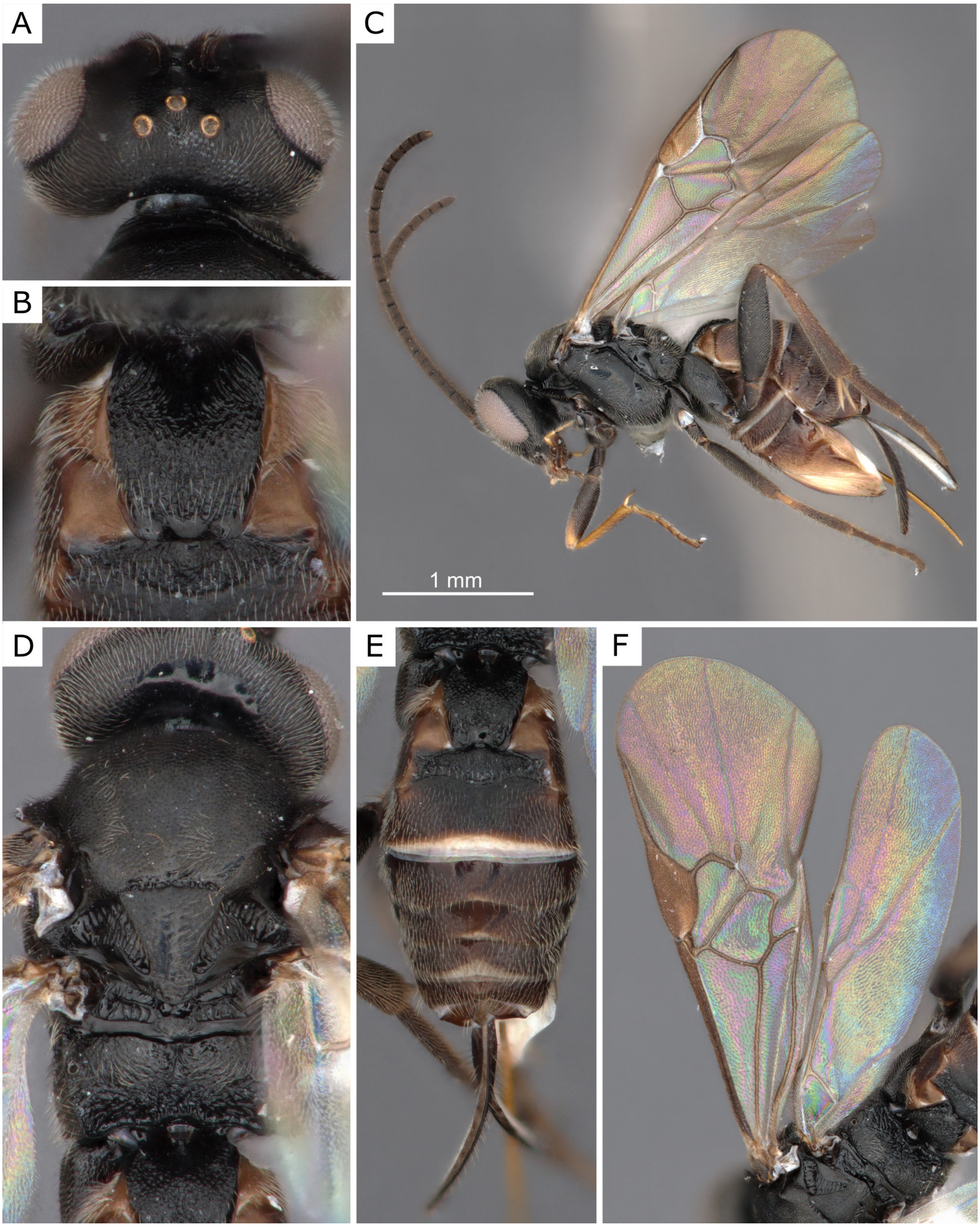

Fig. 31. *Illidops* cf. *naso* (Marshall, 1885), ♀ (ZSM-HYM-42325-F03), BOLD:AEI3308. **A**. Head, dorsal view. **B**. T1. **C**. Lateral view. **D**. Mesosoma, dorsal view. **E**. Metasoma, dorsal view. **F**. Wings. Note: additional, detailed photo of the scutellar area in Fig. 2B. Body length of the specimen: 2.8 mm.

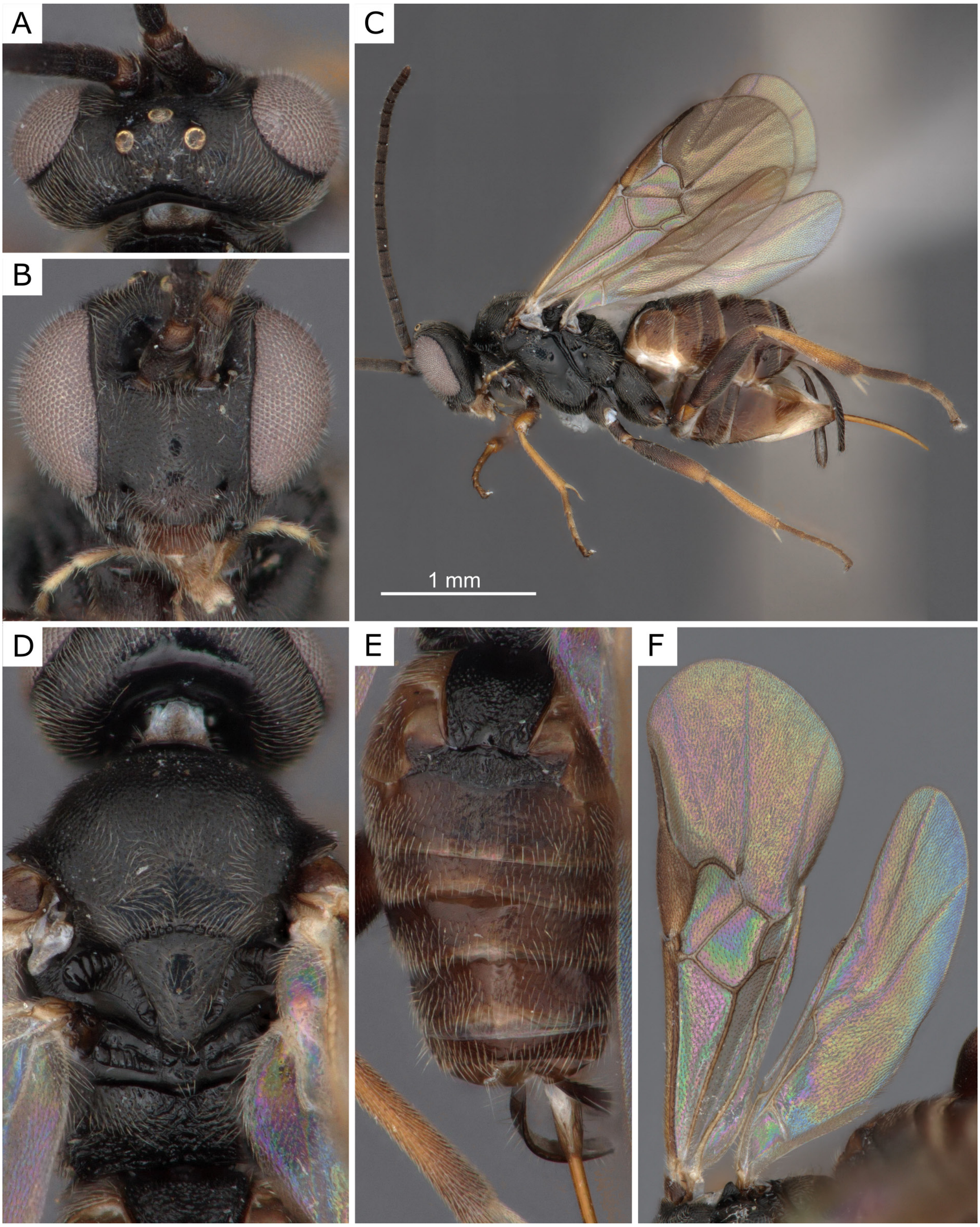

Fig. 32. *Illidops* cf. *naso* (Marshall, 1885), ♀ (ZSM-HYM-42388-H05), BOLD:AEI9858. **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Lateral view. **D**. Mesosoma, dorsal view. **E**. Metasoma, dorsal view. **F**. Wings. Body length of the specimen: 2.8 mm.

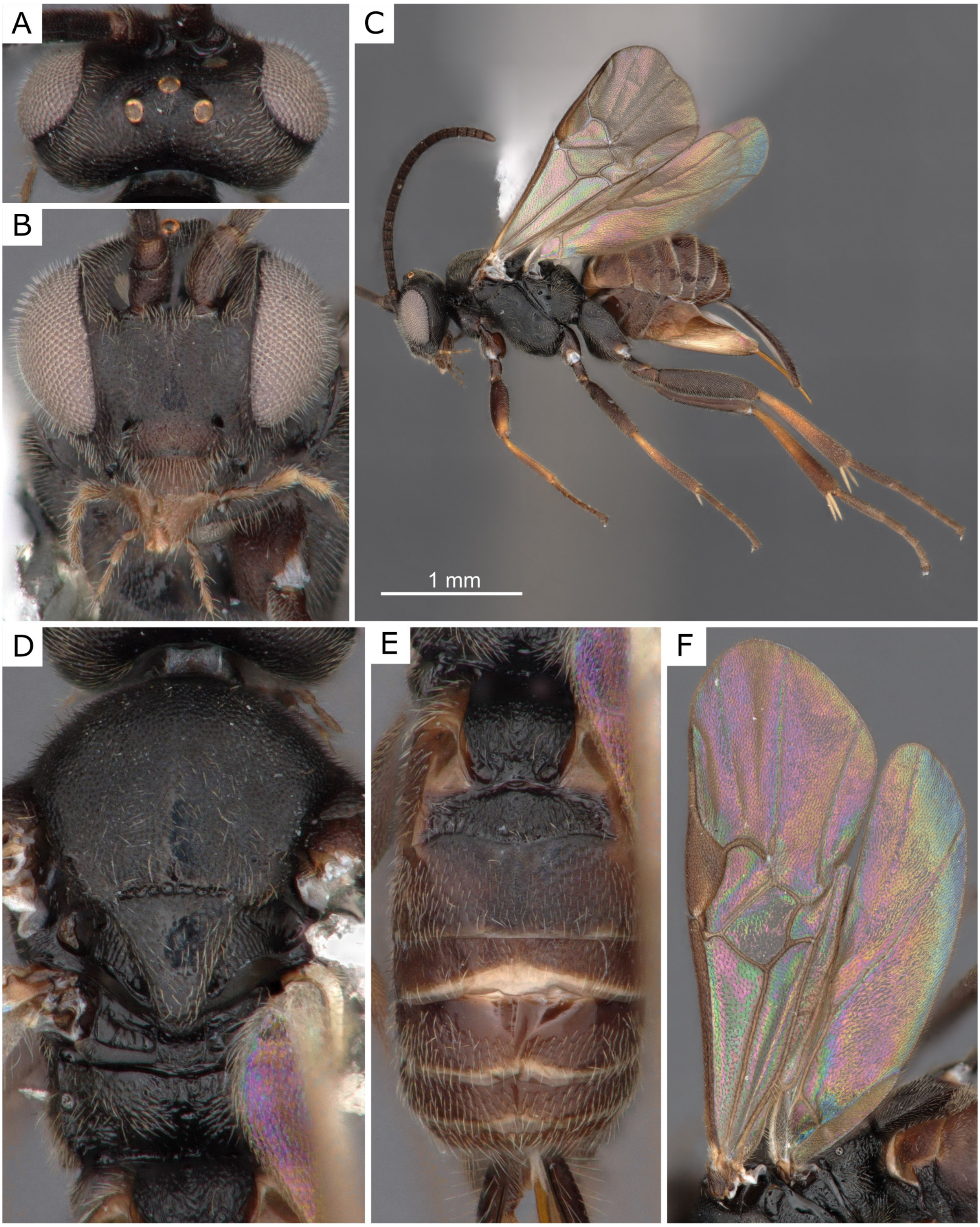

Fig. 33. *Illidops* cf. *naso* (Marshall, 1885), ♀ (ZSM-HYM-33168-D11), BOLD:AEK1062. **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Lateral view. **D**. Mesosoma, dorsal view. **E**. Metasoma, dorsal view. **F**. Wings. Body length of the specimen: 2.6 mm.

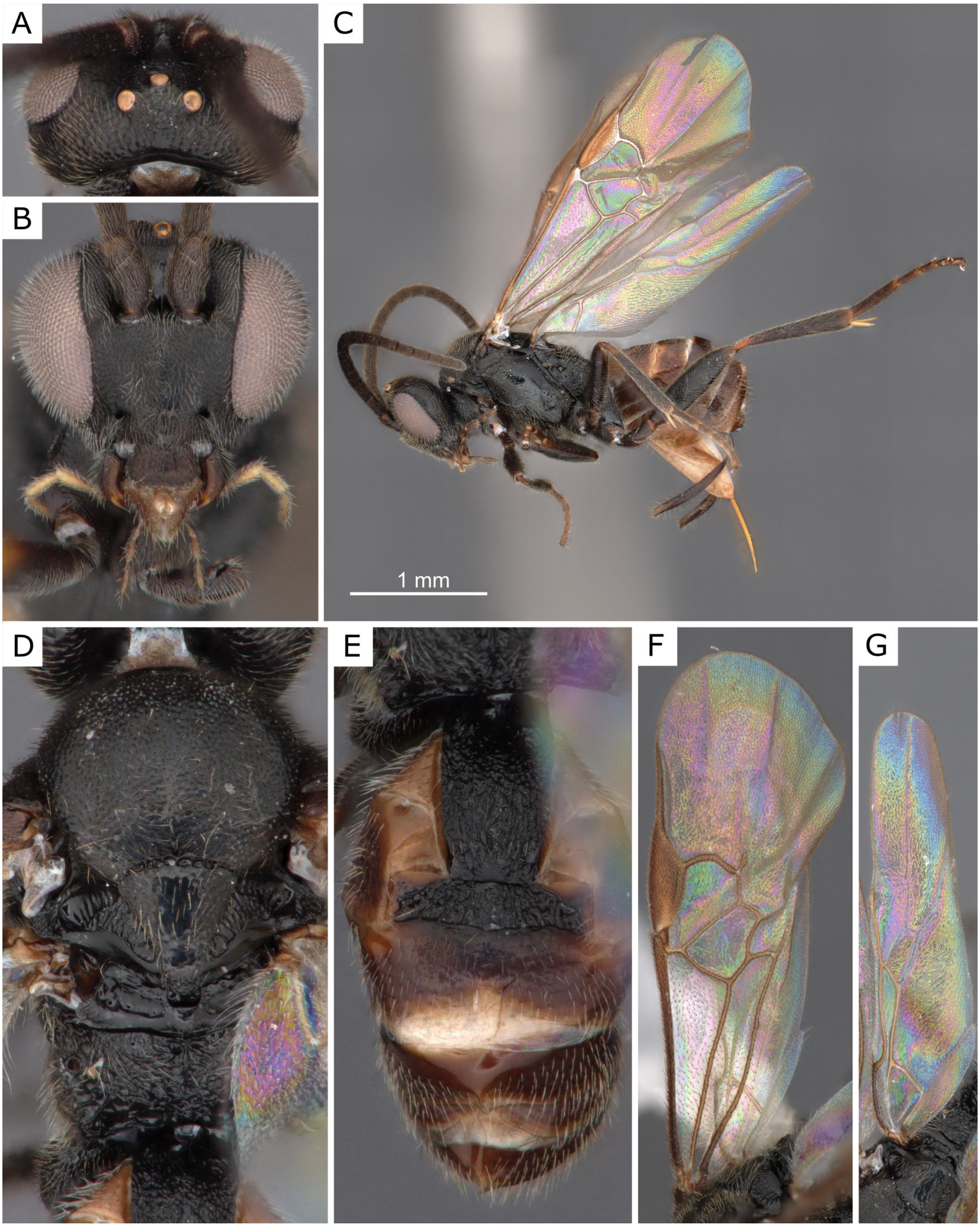

Fig. 34. *Illidops* cf. *naso* (Marshall, 1885), ♀ (ZSM-HYM-42391-A10), BOLD:AEO8212. **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Lateral view. **D**. Mesosoma, dorsal view. **E**. Metasoma, dorsal view. **F–G**. Wings. Body length of the specimen: 2.8 mm.

One of the sequenced specimens (ZSM-HYM-42448-E05, a member of BOLD:AEI9858) was reared by Tina Schulz from *Aroga velocella* (Zeller, 1839), a species of Gelechiidae.

Illidops nigritegula (Tobias & Kotenko, 1986)

Apanteles nigritegula Tobias & Kotenko, 1986: 755 [425].

Species concept

Our species concept is based on the information available in Tobias (1964) and Tobias & Kotenko (1986). In addition to that, the species is quite morphologically distinct and unlikely to be confused. → **.

Ecology / host information

Host unknown.

Distribution

PAL: Kazakhstan, Russia (S).

Molecular data

No molecular data available.

Remarks

Type and depository unknown. Country of type locality: Kazakhstan. This species was formally described by Tobias & Kotenko (1986). Prior to that, Tobias (1964) regarded it as a variety of *A. electilis*, describing it as *A. electilis* var. *nigritegula* nov. (Tobias, 1964), providing more detailed information on the potential type locality that did not make it into the 1986 key. We translated this information, the locality indicated by Tobias (1964: 227) is: "Tselinograd Region: Kokshetau Mountains, on flowers of *Ferula songorica*, 15 VI 1957, 2 females (V. Tobias)". This is one of the very few species of *Illidops* with a large pale spot from the base to beyond the middle of the pterostigma, in addition it is rather small, measuring only 1.9–2.2 mm (Tobias & Kotenko 1986: 755).

Illidops oroseira Höcherl & Fernandez-Triana sp. nov.

urn:lsid:zoobank.org:act:939111F6-3BAA-4E01-A71F-933FE8C716F1

Figs 2H–I, 35–36

Diagnosis

This species resembles *I. suffectus* in the coarsely rugose to reticulate propodeum with a median carina. However, it differs in its overall coloration: entirely black to dark brown (compared to mostly yellow in *suffectus*), and T1 shape: subrectangular to slightly barrel-shaped T1 (compared to widening in *suffectus*).

Etymology

This species was collected from elevations above 1800 m in the Alps. The coarse propodeum sculpture including the median carina reminds the authors of an aerial view of a mountain range. Considering this, the species epithet is derived from Greek and translates to "mountain range".

Type material

Holotype

GERMANY – **Bavaria** • ♀; Garmisch-Partenkirchen, Zugspitze, Platt; 47.407° N, 11.008° E; 2005 m a.s.l.; 18 Jul.–2 Aug. 2018; D. Doczkal and J. Voith leg.; Malaise trap; bulk ID: dv.zugsp5.3; SNSB-ZSM, ZSM-HYM-42389-G02.

Paratypes

GERMANY – **Bavaria** • 1 ♀; same data as for holotype; 2–13 Aug. 2018; bulk ID: dv.zugsp5.4; SNSB-ZSM, ZSM-HYM-42390-A02 • 1 ♀; same data as for holotype; 47.405° N, 11.009° E; 1980 m a.s.l.; 18 Jul.–2 Aug. 2018; bulk ID: dv.zugsp7.3; SNSB-ZSM, ZSM-HYM-42390-G06 • 1 ♀; Oberstdorf, Koblat; 47.423° N, 10.357° E; 2005 m a.s.l.; 4–25 Jul. 2014; D. Doczkal, S. Schmidt and J. Voith leg.; Malaise trap; bulk ID: ds.kobl3.3; SNSB-ZSM, ZSM-HYM-42470-C08.

Description

Female

MEASUREMENTS. Body length: 2.90 (2.90–3.35) mm. Fore wing length: 2.95 (2.55–2.95) mm. Antenna shorter than body.

HEAD. Face: eyes very slightly converging below, inner margin of eyes almost straight. Minimum face width/maximum face width: 0.95 (0.92–0.95). Malar distance/mandible width: 1.43 (1.06–1.67). Face softly punctate. Ocelli in high triangle, posterior tangent to anterior ocellus not touching posterior pair. OOL/POD: 2.44 (2.00–2.55). POL/POD: 2.05 (1.90–2.22). F2 length/width: 2.54 (2.37–2.54). F15 length/width: 1.33 (1.17–1.3). F2 length/F15 length: 2.36 (2.21–2.36).

MESOSOMA. Anteromesoscutum mostly with shallow punctures. Mesoscutellar disc punctate. Posterior smooth band of mesoscutellum in some specimens, including holotype, appearing somewhat interrupted centrally by punctures of scutellar disc, giving impression of a very slightly sculptured area interrupting posterior smooth band of scutellum centrally. Propodeum sculpture coarse, with strongly elevated longitudinal median carina (which has some small rugosities or small carinae radiating perpendicularly).

METASOMA. T1 shape: slightly barrel-shaped with sinuous posterior margin. T1 sculpture: mostly sculptured. T1 width (anterior, maximum, posterior): 0.27, 0.41, 0.37 (0.20–0.27, 0.37–0.41, 0.24–0.39) mm. T1 central length: 0.38 (0.35–0.40) mm. T1 length/width at posterior margin: 1.03 (0.97–1.08). T2 shape: more or less rectangular, posterior margin slightly sinuate, lateral margins concave. Mediotergite 2 sculpture: mostly coarsely sculptured. T2 width at posterior margin/length: 3.06 (2.90–3.24). Posterior margin of T3–T7 slightly desclerotized, but mediotergites not appearing to be pushed forward. Hypopygium not enlarged, its posterior end about in line with end of apical tergites. Ventral margin of hypopygium with desclerotized area showing few pleats. Ovipositor sheaths broad and setose over most of their length. Ovipositor sheaths length/metatibial length: 0.55 (0.53–0.57). Metafemur length/width: 0.27 (0.25–0.32). Tarsal claws: simple.

WINGS. Length of fore wing veins r/2RS: 1.19 (1.06–1.20). Pterostigma length/width: 2.79 (2.58–2.79). Point of insertion of vein r in pterostigma: clearly beyond half length of pterostigma. Angle of vein r with fore wing anterior margin: clearly outwards, inclined towards fore wing apex. Length of vein R1/length of pterostigma: 0.94 (0.94–1.00). Length of vein R1/distance of distal end of R1 to distal end of vein 3RS: 1.25 (1.25–1.5).

COLORATION. Body color: mostly dark brown to black, except for tibiae and tarsi. Head color: head including face, clypeus and labrum completely dark brown to black, palpi pale except for slightly darker base. Antenna completely dark brown to black. All coxae and femora dark brown to black, pro- and mesofemora with slightly paler apical tip. All tibiae orange-brownish. Tegula and humeral complex dark brown. Fore wing: pterostigma brown, wing veins in basal third dark brown, becoming slightly lighter towards apex.

Male

Unknown.

Ecology / host information

Host unknown.

Distribution

PAL: Germany.

Molecular data

4 Sequences in BOLD, BIN BOLD:AEO8226.

Remarks

We place this species in *Illidops* because it fits our current concept of the genus and due to its similarity to another species in the genus, *I. suffectus*. Both *I. oroseira* sp. nov. and *I. suffectus* have characters that fit within the current concept of *Illidops*: the posterior smooth band of the scutellum is interrupted centrally by a sculptured area (although it varies slightly between specimens in *I. oroseira* and the sculpture is very weak, similar to *I. suevus*, and limited to a small area on the anterior margin of the mesoscutellar bar); the fore wing vein R1 is shorter than the pterostigma; the propodeum is strongly sculptured, with the sculpture reticulate. *Illidops oroseira* does not have some of the other characters typical of *Illidops* (but neither do some other species within the genus): the eyes are only very slightly convergent towards the lower inner margin (not at all in *I. suffectus*); T3–T7 are only slightly medially desclerotized and do not appear pushed forwards (similar in *I. suffectus*). Both *I. suffectus* and *I. oroseira* have a similar propodeum sculpture which is quite unique in *Illidops* (coarsely reticulate rugose, with strongly elevated longitudinal median carina which has some small rugosities or small carinae radiating perpendicularly).

The Nearest Neighbor (NN) of BIN BOLD:AEO8226 has a minimum p-distance of 6.56% (BOLD:ACP4312). The NN-BIN includes a single specimen from Bulgaria, BIOUG15445-A06, which is linked to a private sequence, but upon examination of a lateral habitus image could represent a species of *Illidops* (short R1). We also performed a BLAST search in the BOLD database and found that the closest public match is BIOUG85322-C11 (BOLD:AET9368) which was collected in California, USA, and has 92.99% COI sequence similarity. Apart from the Bulgarian and Californian specimens, which are the closest matches, the sequences mostly match specimens mostly identified morphologically by us as *Illidops*. But there are some similarly close matches which represent different genera: for one, there is a 92.69% similarity in the COI sequence with a specimen identified as *Dolichogenidea murinanae* (CNCHYM 00190). Upon examination of a lateral photo, the specimen does not seem to be a misidentified representative of *Illidops*. The same is true for *Parapanteles hyposidrae*, which has several specimens at 92.08% COI sequence similarity, but is clearly not a member of *Illidops* (at least upon photo observation and identification by a Microgastrinae expert). Another record of *Pholetesor* sp. with 91.95% COI similarity also seemingly does not represent a misidentified specimen of *Illidops*.

Since all of these molecular analyses are only based on sequences of the COI gene, microgastrine genera in general are in urgent need of revision, and no reliable phylogeny is available at the moment, we cannot draw any conclusions from this. More details are discussed below in the section on DNA barcoding. Summarizing this, it is difficult to clearly state whether this species is part of *Illidops* or not. Morphologically, it seems very similar to *I. suffectus* and most of the molecular data also places it in *Illidops* rather than any other genus. For now, we place this species within *Illidops*, but this status may need to be revised in the future.

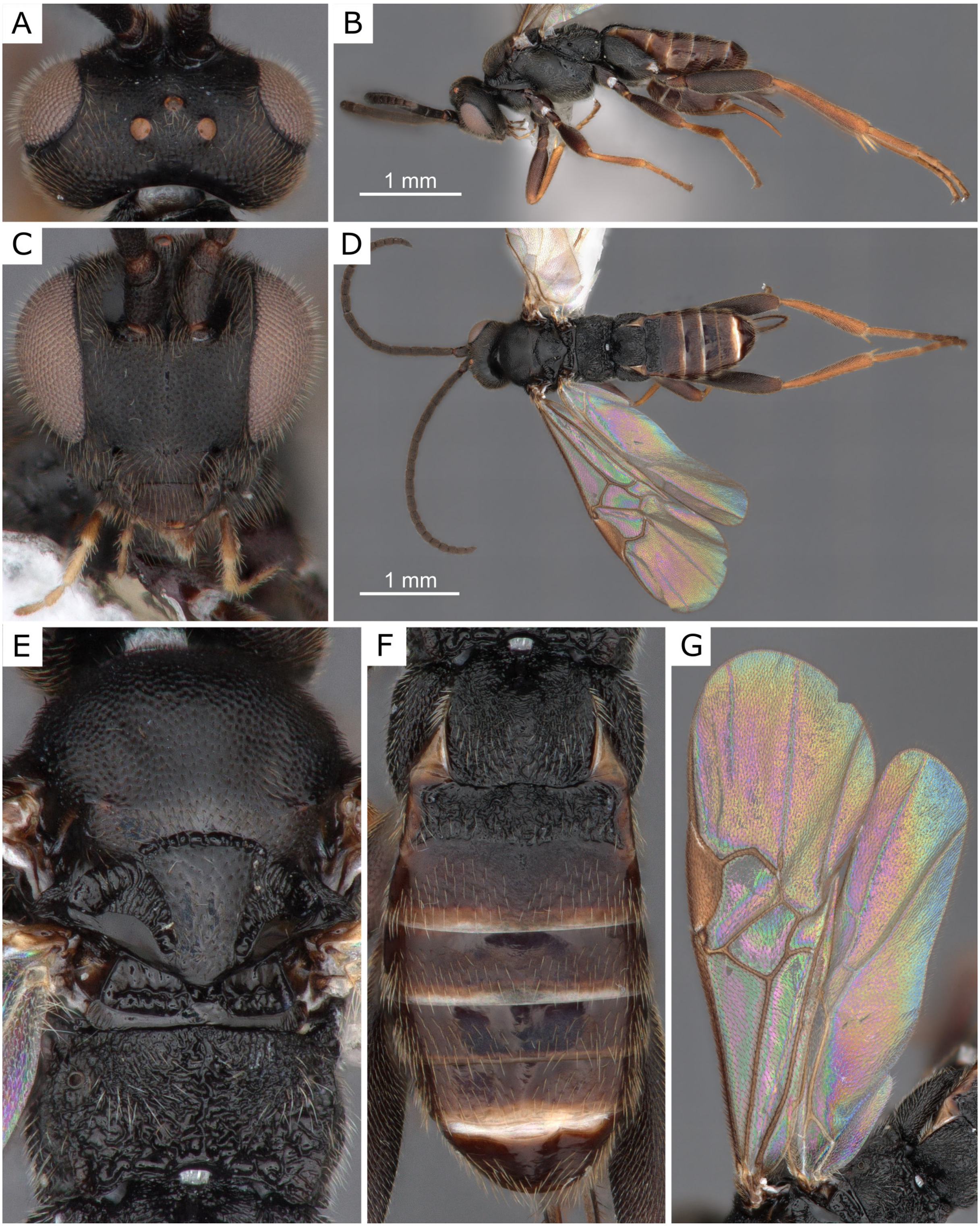

Fig. 35. *Illidops oroseira* Höcherl & Fernandez-Triana sp. nov., holotype, ♀ (ZSM-HYM-42389-G02). **A**. Head, dorsal view. **B**. Habitus, lateral view. **C**. Head, frontal view. **D**. Habitus, dorsal view. **E**. Mesosoma, dorsal view. **F**. Metasoma, dorsal view. **G**. Wings. Body length of the specimen: 2.9 mm.

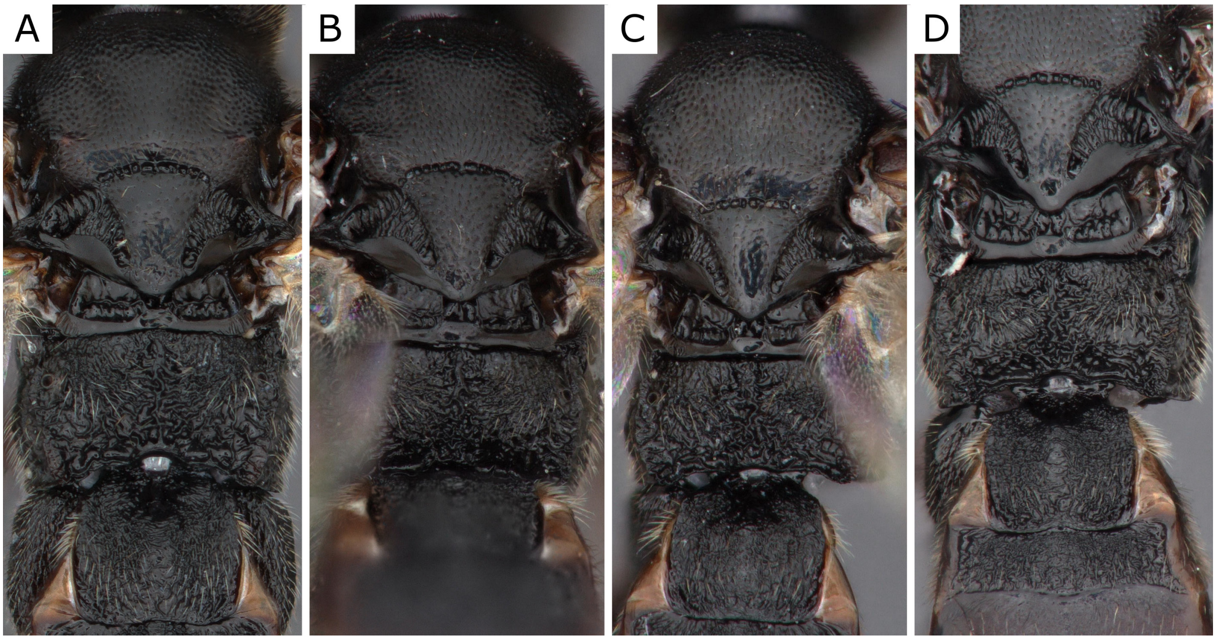

Fig. 36. *Illidops oroseira* Höcherl & Fernandez-Triana sp. nov., partial dorsal meso- and metasoma. **A**. Holotype, ♀ (ZSM-HYM-42389-G02). **B**. Paratype, ♀ (ZSM-HYM-42390-G06). **C**. Paratype, ♀ (ZSM-HYM-42470-C08). **D**. Paratype, ♀ (ZSM-HYM-42390-A02).

Illidops perseveratus (Papp, 1977)
Fig. 37

Apanteles perseveratus Papp, 1977: 234–236, figs 38–41.

Type material

Holotype

MONGOLIA – **Bayankhongor Province** • ♀; "Bajanchongor aimak", 47 km E of checkpoint Caganbulag, spring Talyn Bilgech bulag; 1200 m a.s.l.; 23 Jun. 1967; Z. Kaszab leg.; no. 838; HNHM, typ. no. 2405.

Species concept

Our species concept is based on our examination of habitus photos of the holotype and the information available in Papp (1977, 1981) and Kotenko (2007) → **.

Ecology / host information

Host unknown.

Distribution

PAL: Mongolia.

Molecular data

No molecular data available.

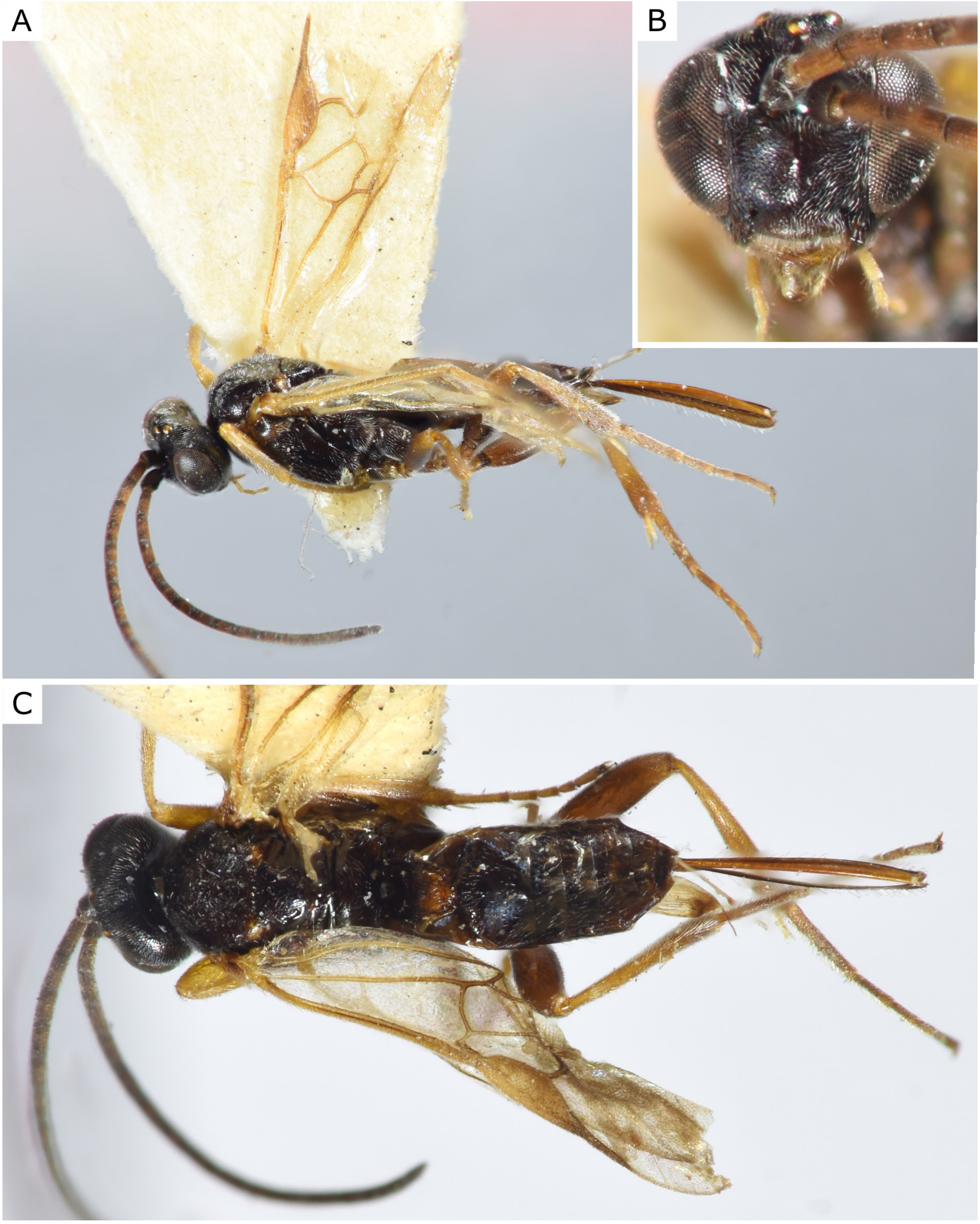

Fig. 37. *Illidops perseveratus* (Papp, 1977), holotype, ♀ (HNHM). **A**. Habitus, lateral view. **B**. Head, frontal view. **C**. Habitus, dorsal view. Body length of the specimen [from original description]: 3.0 mm.

Remarks

Illidops perseveratus is one of the species which challenge our concept of *Illidops* with its smooth propodeum and entirely polished posterior smooth band of the scutellum: "Hind polished part of axilla reaching up to middle of scutellum." (Papp 1977: 253). However, it has a very short fore wing vein R1 and based on the information available to us we could not place it unambiguously within any other genus.

Illidops planiscapus (Tobias, 1976)

Apanteles planiscapus Tobias, 1976: 248–249.

Species concept

Our species concept is based on the information available in Tobias (1976), Tobias & Kotenko (1986) and Papp (1988). → *.

Ecology / host information

Tentative information provided in the original description, check remarks for more details.

Distribution

PAL: Russia (DA).

Molecular data

No molecular data available.

Remarks

Holotype female, ZIN. Country of type locality: Russia. Type depository inferred from Tobias & Kotenko (1986) by Fernandez-Triana *et al.* (2020). Tobias provided a tentative host identification for the holotype of *I. planiscapus* (Tobias, 1976), although he placed a question mark in front of it, so it is rather uncertain. Tobias' (1976) putative host of this species is *Talis quercella* ([Denis & Schiffermüller], 1775), a Crambidae, collected from a Poaceae grass in the Caucasus region. This species was transferred to *Illidops* by Papp (1988), but he already stated that his placement of this species is rather provisional, as he only knew it from its original description. Tobias & Kotenko (1986) did not consider it part of the *butalidis* group, but rather proposed a new *planiscapus* group. We consider that the morphology potentially does not match the set of characters diagnostic of the *butalidis* and *suevus* groups in the past, and our more current concept of *Illidops*. The species has a much less angled radial vein (r) and it is not "slanting outwards" (Mason 1981) as it does in most species of *Illidops* (illustrated in Fig. 242; Tobias & Kotenko 1986: 751, drawing 2). We cannot verify this and we do not have specimens available resembling this species, or access to the holotype. We are not satisfied with the placement of this species in *Illidops*. However, similar to Papp (1988), we cannot transfer this species to any genus as we have not seen any material and the original description is not sufficient to place it with certainty in any other genus. The species is partially illustrated in Tobias & Kotenko (1986: 751).

Original description sensu Tobias (1976) (translated from Russian and with updated morphological terminology)

Female. 3.5 mm. Malar distance equal to basal width of mandible; face in upper part with shining tubercle, face height 1.5 × its width; distance between tentorial pits 3 × distance between tentorial pit to eye margin. Scape strongly compressed from sides so that its length is about same as its width frontally but looking 3 × as long when seen laterally; length of F14 and F15 1.3 × their width. Fore wing veins C+SC+R thickened; fore wing vein 1cu-a arising from around basal third of 1st discal cell. Length of metafemur 4.5 × its width. T1 more or less barrel-shaped, with its anterior (strongly) and posterior (slightly) narrowed, T1 length equal to T1 greatest width (centrally); T1 and T2 with central impression on its posterior half; ovipositor sheaths slightly longer than half of metatibia.

Sculpture. Head mildly punctured, slightly shining, antennal sockets smooth; mesoscutum roughly punctured, without granular microsculpture, shining between punctures, especially on sides; scutellum slightly punctured, shining; mesopleura anteriorly punctured, posteriorly smooth; mesonotum punctured; propodeum roughly wrinkly-punctured, T1 and T2 densely wrinkly-punctured, T3 with soft granular punctures, shining, other tergites slightly rough, shining. Anteromesoscutum with sparse setae, thickened before scutellum and on anterolateral corners of scutellum.

Coloration. Femora, except for base and apex of profemur, apex of mesofemur, metafemur medially, tibiae and tarsi of all legs, except brown apex of metatibia, yellowish-brown; veins C+SC+R and pterostigma, except for its brown margins, yellow. The male is unknown.

Holotype: female, Dagestan, Makhachkala, steppe grass moth (? *Talis quercella* Schiff.) on wild grasses, 4 VIII 1972 (Krasova).

Illidops rostratus (Tobias, 1976)

Apanteles rostratus Tobias, 1976: 248, pl. 67 fig. 4.

Species concept

Our species concept is based on the information available in Tobias (1976), Tobias & Kotenko (1986), and Papp (1988). → *.

Ecology / host information

Host unknown.

Distribution

PAL: Armenia, Russia (KDA), Uzbekistan.

Molecular data

No molecular data available.

Remarks

Holotype female, ZIN. Country of type locality: Russia. Type depository inferred from Tobias & Kotenko (1986) by Fernandez-Triana *et al.* (2020). We were unable to observe any identified or unidentified material matching this species, or the type. According to its original description, this species may resemble *Napamus* due to the enlarged mouthparts ("proboscis, the protruding part of which is approximately equal to the height of face with clypeus" (Tobias 1976: 248)), however it lacks other diagnostic characters for the genus, such as the infumate wings, dark metatibial spurs, and more (Ghafouri Moghaddam *et al.* 2021). We are not entirely sure about the difference between this species and *I. mutabilis* as we found that the specimens of BIN BOLD:AEI2559 which we consider to match *I. mutabilis* morphologically and also the paratype of *A. szaboi* have a rather enlarged glossa. Both species as well as *A. szaboi* should be reexamined and compared; additional differences that should be taken into account can be found in Tobias & Kotenko (1986).

Original description sensu Tobias (1976) (translated from Russian and with updated morphological terminology)

Female. 2.5 mm. Head elongated, with long malar distance and long proboscis, the protruding part of the proboscis approximately equal to the height of the face including the clypeus (fig. 67, 4); gena roundly narrowed, in lateral view half the width than the transverse width of eye; ocelli in strongly obtuse triangle; tangent to posterior margin of front ocellus crossing anterior margin of posterior ocelli; POL 4 × OD, and 1.5 × OOL; longitudinal diameter of eye 2.0 × that of transversal, and 3.5 × that of malar distance, shape of eye oval; face slightly wider than high; clypeus slightly separated from face, straight along front margin, distance between tentorial pits 2.0 × distance between tentorial pit and eye margin; malar distance 1,5 × basal width of mandible; maxillary palps equal to height of face with clypeus, their two apical segments together slightly longer than 3rd, and equal to length of 2nd. Antennae bristly, shorter than body; scape slightly shorter than F1; segments in basal half of flagellum twice as long as their width, shortened towards apex of flagellum, so that F14 and F15 are more or less quadrate. Mesosoma length 1.25 × its height; notauli not developed; scutoscutellar suture narrow, weakly crenulated. Wings equal to length of meso- and metasoma taken together; fore wing vein R1 length equal to pterostigma length, slightly longer than distance from it to apex of wing; vein r slightly longer than vein 2RS, forming angle with it; fore wing vein 1cu-a arising before middle of 1st discal cell. Length of metafemur 4.0 × its width; larger spur of metatibia noticeably shorter than half of basitarsus; fifth segment of metatarsus slightly shorter than third, and 0.67 × second tarsomere; T1 slightly longer than its width at the middle, roundly narrowed at apical third; T2 length 0.3 × T3 length, with broadly spaced oblique grooves. Ovipositor with comparatively narrow sheaths, equal in length to metatibia.

Sculpture. Body with short setae, rather dense on mesonotum, concealing sculpture when viewed at an angle. Head, mesosoma and T1 with dense, uniform grained punctation, matt, other tergites of metasoma mildly scabrous, shining.

Coloration. Black; maxillary palps brown; tegulae yellow; apices of profemur, protibiae and tarsi, bases of meso- and metatibiae brownish-yellow; tibial spurs whitish; wings translucent, with light brown veins, pterostigma pale medially and brown at margins, veins C+SC+R yellowish, vein R1 dark brown.

Male. It differs from female by slightly longer R1 (1.5 × distance from it to apex of wing), smoother sculpture posterolaterally on mesosoma, propodeum, and on basal half of T1. Glassy-transparent wings with mostly unpigmented veins (only few veins on posterior half of wing are pigmented, such as r, 2RS, and 2M).

Holotype: female, Krasnodar Territory, Gelendzhik, 8 V 1973 (Tobias). Paratype: male, Yerevan, Kanaker Garden, 16 V 1971 (Tobias).

Illidops scutellaris (Muesebeck, 1921)

Figs 2A, 38–40

Apanteles scutellaris Muesebeck, 1921: 533–534.

Type material

Paratypes

UNITED STATES – **California** • 1 ♂; Pasadena; J.E. Graf leg.; Muesebeck det.; ex. *Phthorimaea operculella*; CNC, CNCHYM 00212. – **Florida** • 1 ♀; Palm Beach County, Belle Glade; 30 May 1944; N. Hayslip leg.; “reared from potatoes”; CNC, CNCHYM 00213.

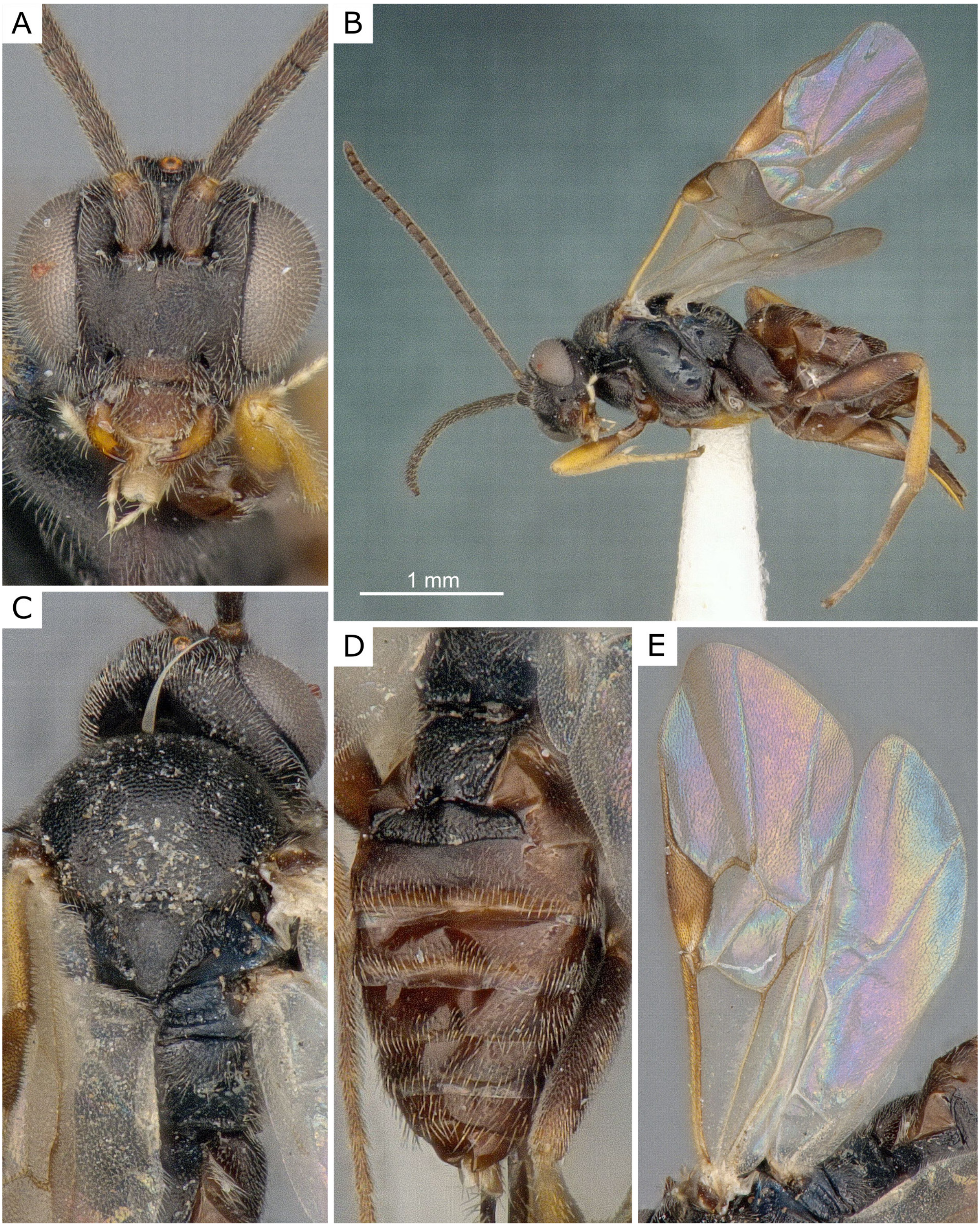

Fig. 38. *Illidops scutellaris* (Muesebeck, 1921), paratype, ♀ (CNCHYM 00213), reared "from Potatoes". **A**. Head, frontal view. **B**. Lateral view. **C**. Mesosoma, dorsal view. **D**. Metasoma, dorsal view. **E**. Wings. Body length of the specimen: 2.8 mm.

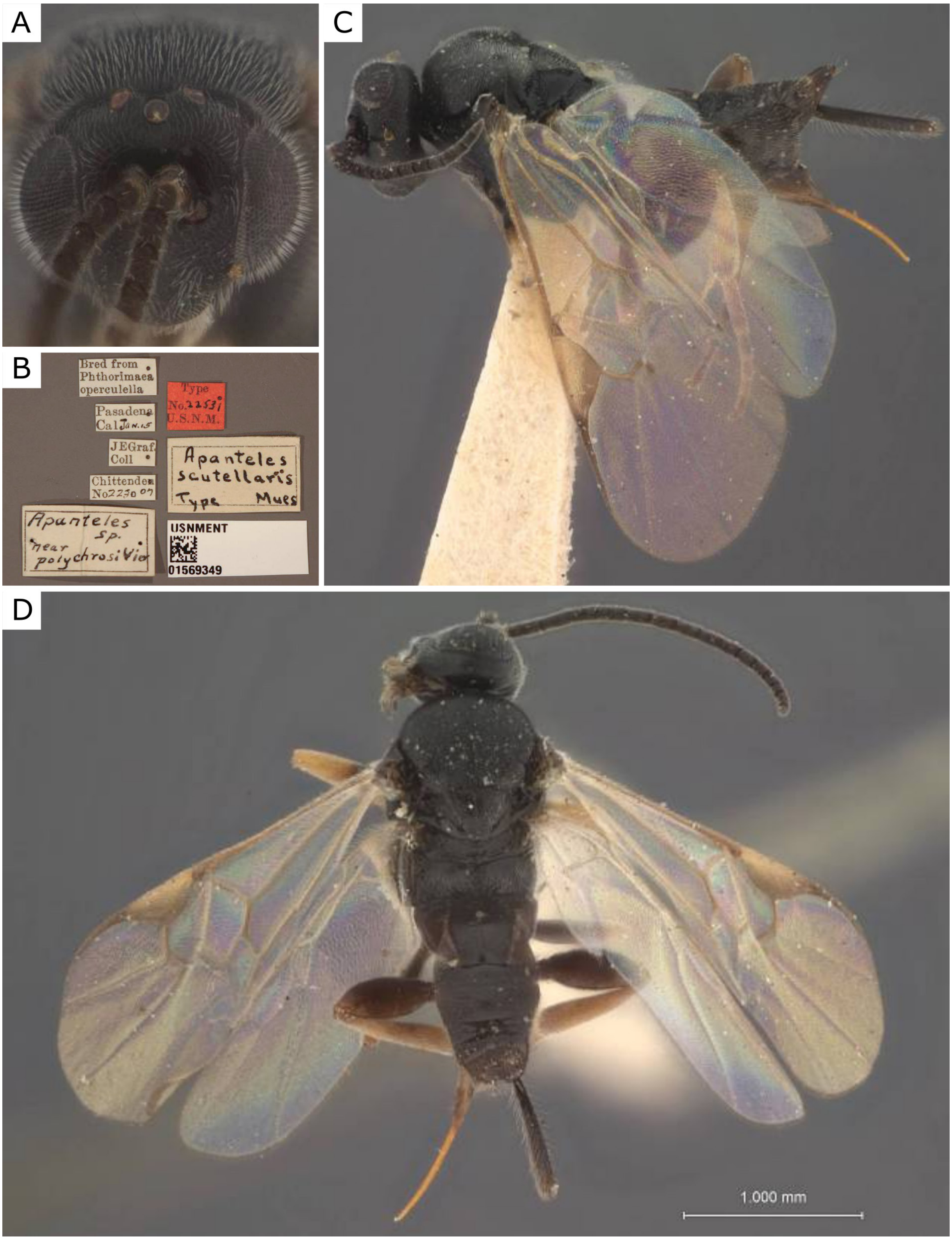

Fig. 39. *Illidops scutellaris* (Muesebeck, 1921), holotype, ♀ (USNMENT01569349), USNM. **A**. Head, frontal view. **B**. Labels. **C**. Wing and habitus, lateral view. **D**. Dorsal view. Body length of the specimen [from original description]: 2.6 mm. Photos downloaded from the USNM online type catalogue (http://n2t.net/ark:/65665/3ef38d4f1-c0ae-4dfd-a9fd-a3f4a1837738) available under CC0 license.

Other material examined

CANADA – **Yukon Territory** • 2 ♀♀; Champagne; 60.790° N, 136.437° W; 733 m a.s.l.; 8 Jul. 2006; H. Goulet and C. Boudreault leg.; CNC, HYM00000588, HYM00000627 • 1 ♀; Tahkini River road; 60.875° N, 135.386° W; 693 m a.s.l.; 6 Jul. 2006; H. Goulet and C. Boudreault leg.; CNC, HYM00000560.

Species concept

Our species concept is based on our examination of habitus photos of the holotype (available via the Smithsonian Website), our examination of authoritatively identified and reared specimens stored in the CNC, and the information available in Muesebeck (1921) and Tobias & Kotenko (1986) → ***.

Ecology / host information

Type series (including holotype) reared ex Gelechiidae: *Phthorimaea operculella* (Zeller, 1873).

Distribution

AUS: Hawaiian Islands; NEA: United States (AZ, CA, FL, TX); NEO: Mexico; PAL: Bulgaria, Cyprus, Greece, Hungary, Iran.

Molecular data

BOLD:AAA8769.

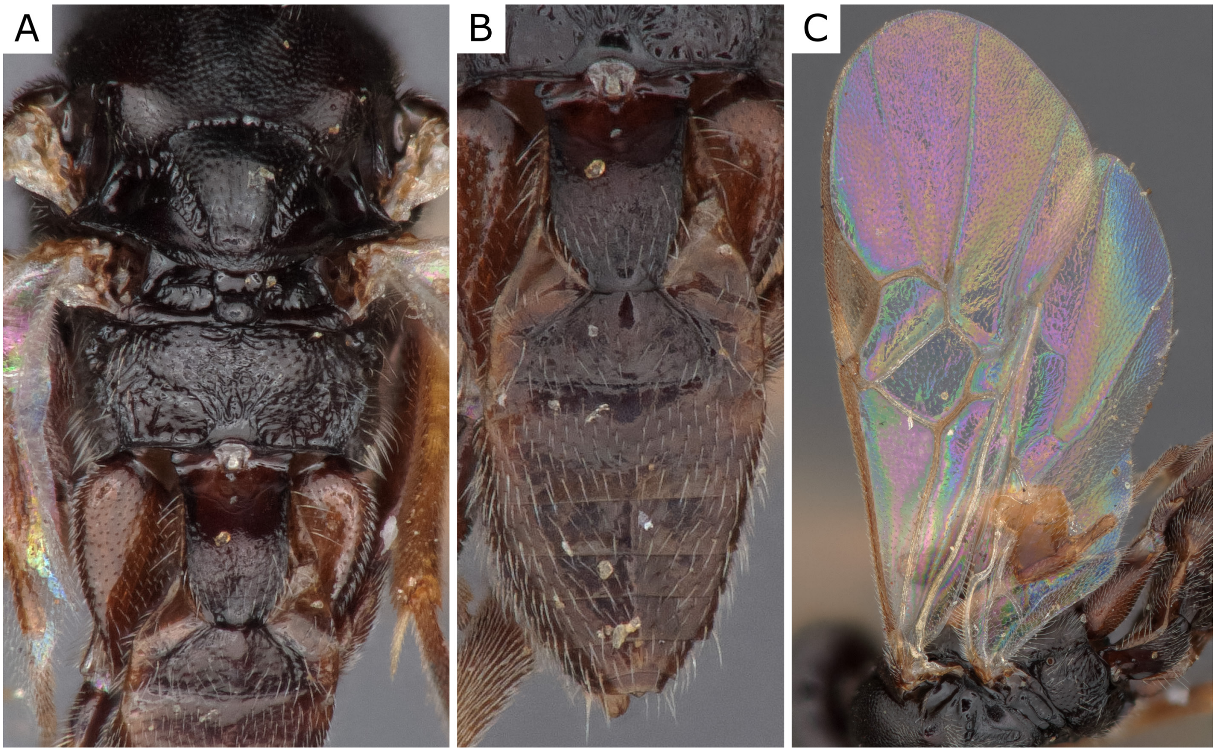

Fig. 40. *Illidops scutellaris* (Muesebeck, 1921), ♂ (CNCHYM 00212), identified by Muesebeck and reared ex *Phthorimaea operculella*. **A**. Partial meso- and metasoma (no diffusion). **B**. Metasoma (with diffusion). **C**. Wings.

Remarks

Holotype female, USNM. Country of type locality: United States. The type was examined. In the original description, the type is reported to have been reared from *Phthorimaea operculella* by J.E. Graf in California, together with four females and three males (Muesebeck 1921). Mason had this species available in his collection and considered it to be part of *Apanteles*, rather than *Illidops* (Mason 1981). Papp (1981) and Tobias & Kotenko (1986) listed it in the *butalidis* group and Papp (1988) transferred it to *Illidops*. This species fits well in our concept of *Illidops*.

Illidops sophrosine (Nixon, 1976)

Table 6

Apanteles sophrosine Nixon, 1976: 713, fig. 9.

Species concept

Our species concept is based mostly on the information available in Nixon (1976), which was reiterated in following publications by Papp (1981), Tobias & Kotenko (1986), and Kotenko (2007). → *.

Ecology / host information

Host unknown.

Distribution

PAL: Bulgaria, Hungary, Italy, Russia (ZAB, PRI).

Molecular data

We observed specimens of two barcoding clusters which morphologically resemble *I. sophrosine* (also see Table 6 and Figs 41–43): BOLD:ADU8837 and BOLD:AEO8202. However, these clusters are far apart from each other with minimum p-distances of 6.0%. The clusters are clearly separated, also taking into account the within-BIN maximum p-distances of 0.8% (BOLD:ADU8837) and 0.16% (BOLD:AEO8202). The Nearest Neighbors (NN) in the BOLD database are different clusters, found in different biogeographic regions and not identified to species level. Only BOLD:ADU8837 is quite close to its NN BOLD:AEI2994 with a minimum p-distance of 1.77%; however we were unable to observe any specimens of the NN BIN – and the morphology is quite cryptic in any case, so we cannot draw any conclusions based on morphology at this point. It is currently impossible to match any of these BINs unambiguously to the name *I. sophrosine* and there may be more barcoding clusters and cryptic morphology in the future, which is why we prefer to keep the clusters as *I.* cf. *sophrosine* for now.

Remarks

Holotype female, NHMUK. Country of type locality: Italy. The type was examined by Fernandez-Triana *et al.* (2020).

This species is morphologically similar to the *I. naso* complex. According to Nixon (1976), *I. sophrosine* can be distinguished from *A. contortus* (jun. syn. of *I. naso*), *A. evander* (jun.syn. of *I. naso*) and *I. cloelia* based on the following characters: "Eyes large; in lateral view of head fully twice as wide as width of head behind them; head from above markedly wider than mesoscutum" (Nixon 1976: 709). We found the character regarding the width of the eyes rather difficult to observe depending on specimen orientation, but it seems to be relatively consistent among our barcoding clusters (compare Fig. 41). The two barcoding clusters we consider to be associated with *I. sophrosine* can currently not be clearly distinguished by morphology.

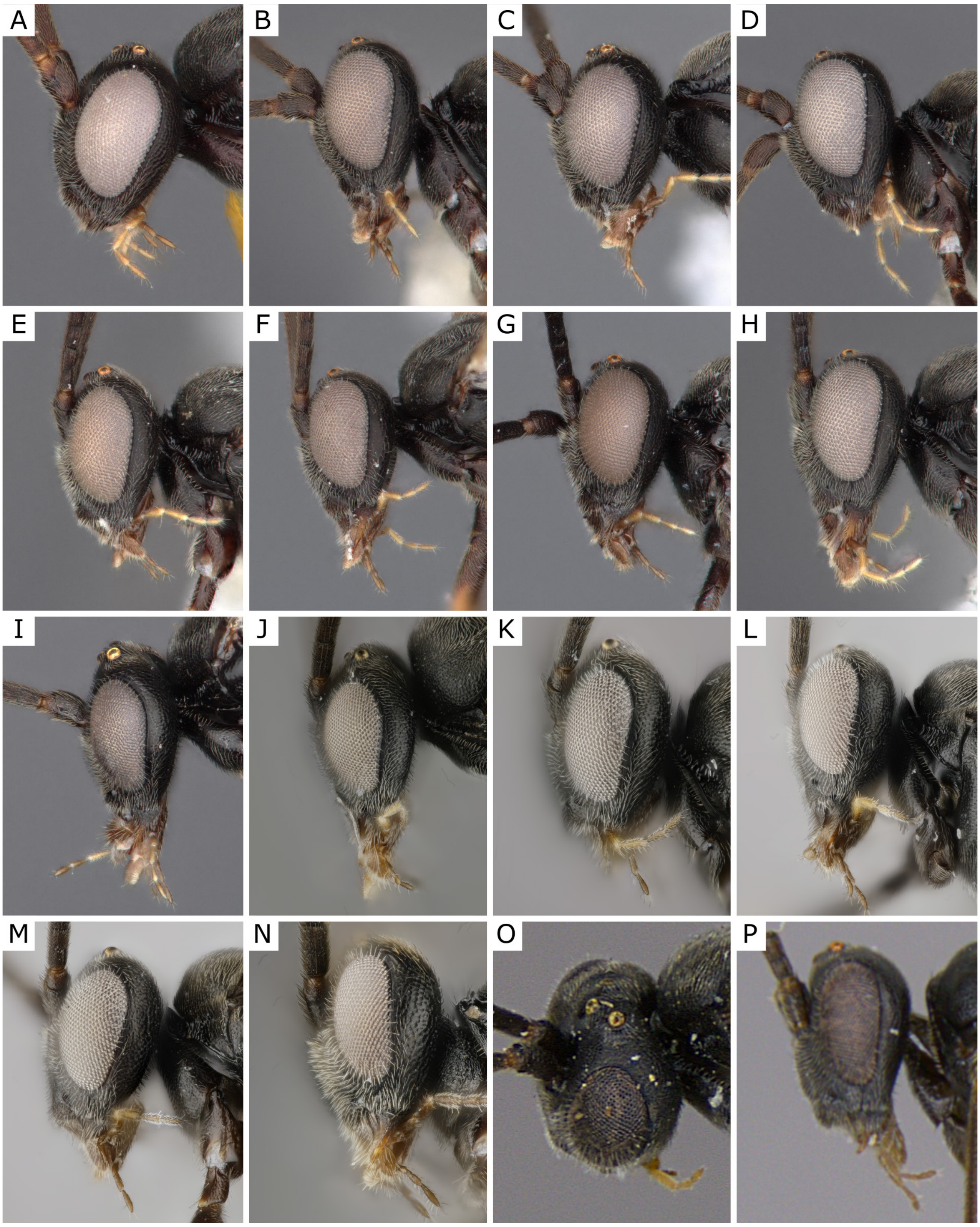

Fig. 41. Heads in lateral view of members of clusters tentatively associated with *I. sophrosine* (Nixon, 1976), or other species of the *I. naso* complex, all ♀♀. **A**–**H**. *I.* cf. *sophrosine* (Nixon, 1976). **A**–**D**. BOLD:ADU8837 (specimens IDs: **A**. ZSM-HYM-33162-D12. **B**. ZSM-HYM-33169-A06. **C**. ZSM-HYM-33169-A08. **D**. ZSM-HYM-33169-H02). **E**–**H**. BOLD:AEO8202 (specimens IDs: **E**. ZSM-HYM-42325-A05. **F**. ZSM-HYM-42325-A04. **G**. ZSM-HYM-42325-C07. **H**. ZSM-HYM-42380-C11). **I**–**N**. *I.* cf. *naso* (Marshall, 1885). **I**–**K**. BOLD:AEI9858. **L**. BOLD:AEI3308. **M**. BOLDAEK1062. **N**. BOLDAEO8212 (specimens IDs: **I**. ZSM-HYM-42388-H06. **J**. ZSM-HYM-33164-B01. **K**. ZSM-HYM-42388-H04. **L**. ZSM-HYM-42325-F03. **M**. ZSM-HYM-33168-D11. **N**. ZSM-HYM-42391-A10). **O**. *I. buteonis* (Kotenko, 1986), holotype (SIZK). **P**. *I. dauricus* Kotenko, 2007, holotype (SIZK).

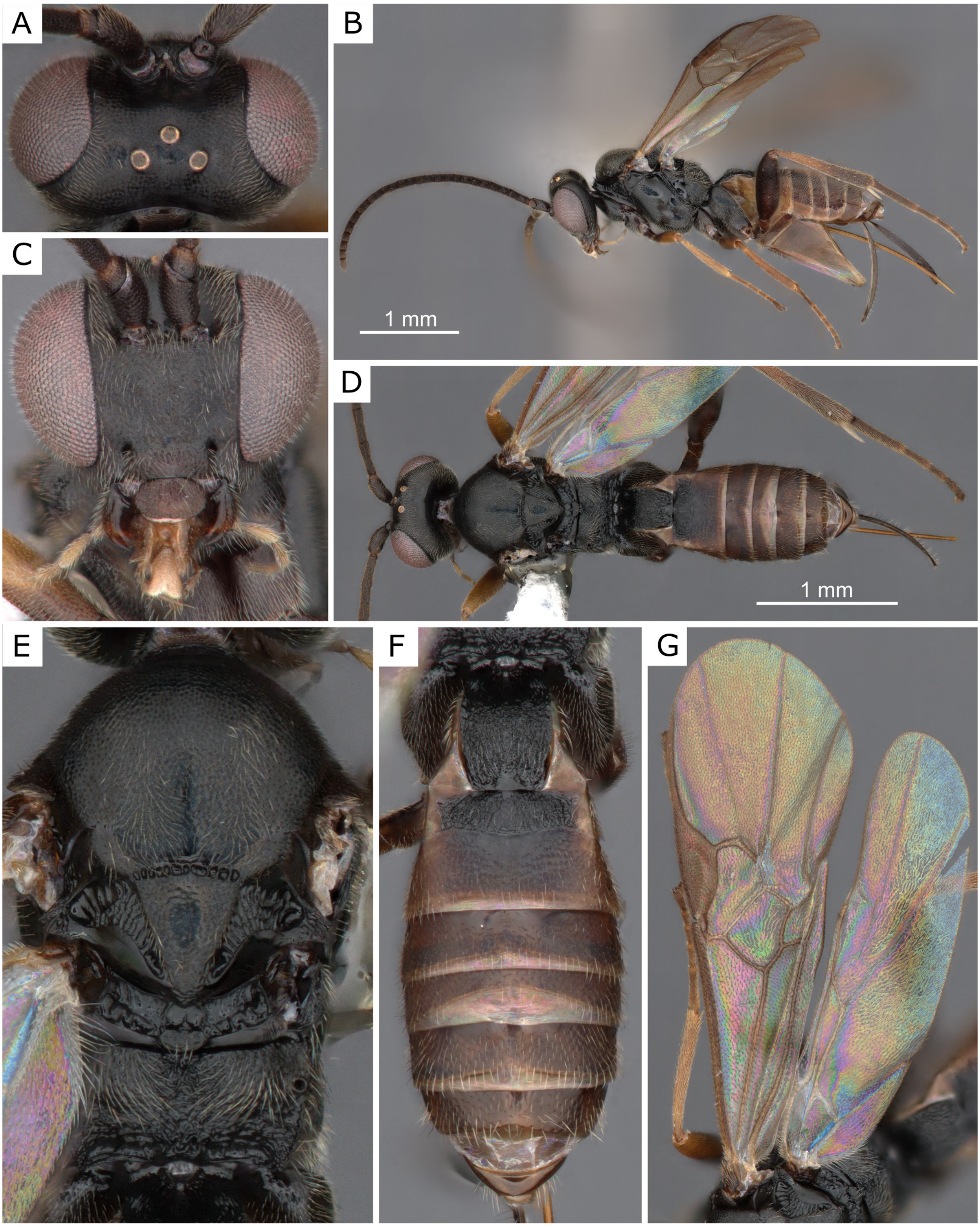

Fig. 42. *Illidops* cf. *sophrosine* (Nixon, 1976), ♀ (ZSM-HYM-33169-A05), BOLD:ADU8837. **A**. Head, dorsal view. **B**. Lateral view. **C**. Head, frontal view. **D**. Dorsal view. **E**. Mesosoma, dorsal view. **F**. Metasoma, dorsal view. **G**. Wings. Body length of the specimen: 3.3 mm.

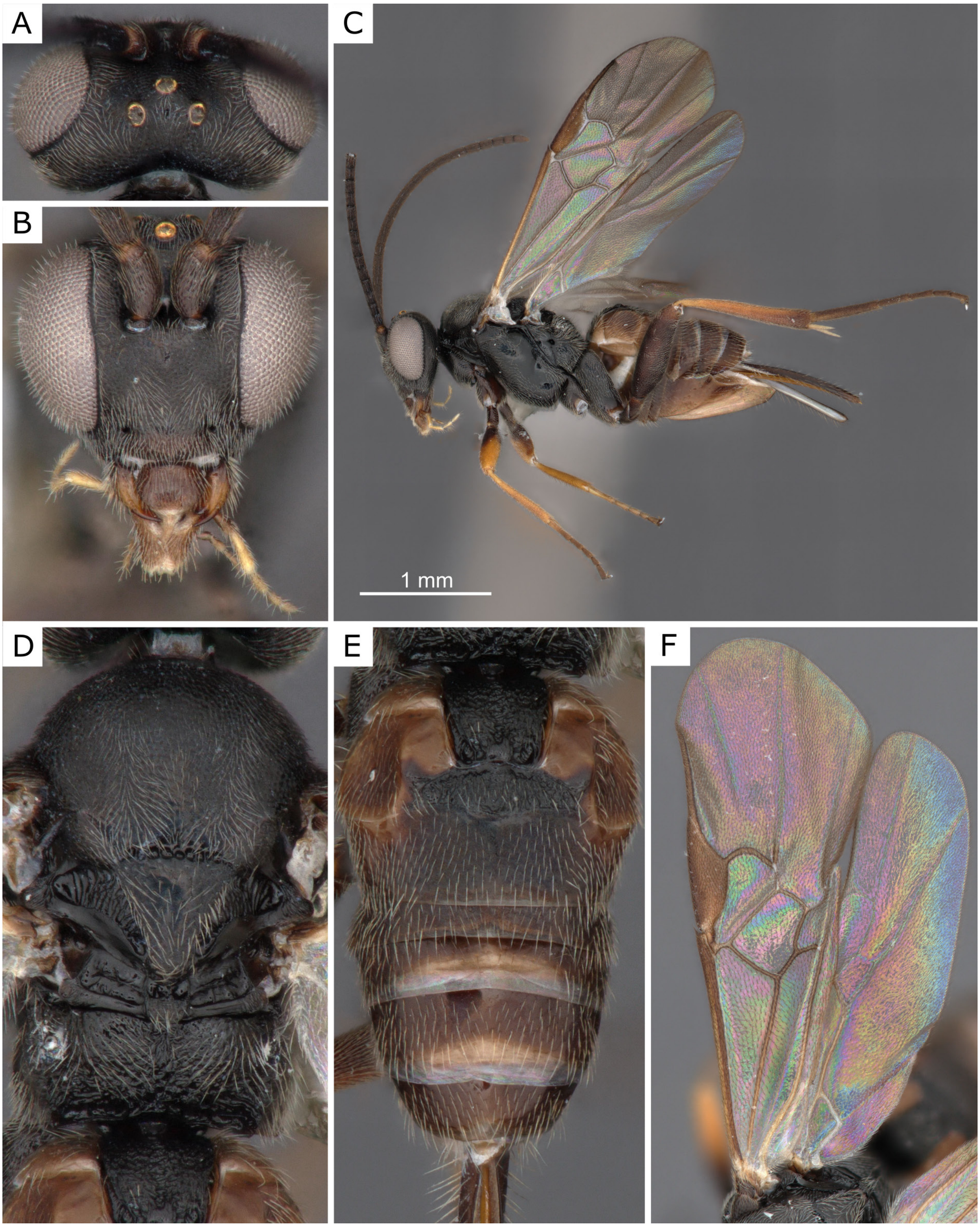

Fig. 43. *Illidops* cf. *sophrosine* (Nixon, 1976), ♀ (ZSM-HYM-42380-C11), BOLD:AEO8202. **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Lateral view. **D**. Mesosoma, dorsal view. **E**. Mesosoma, dorsal view. **F**. Wings. Body length of the specimen: 3.0 mm.

Table 6. BINs which most match the morphological characters of *I. sophrosine* (Nixon, 1976). Information on the Nearest Neighbor in the BOLD database is given, including relevant minimum p-distances and distribution.

BIN/ Country	Number of specimens (n)	Within-BIN max. p-distance	Min. NN p-dist.	NN BIN/ Country	Number of specimens (n)	NN within-BIN max. p-dist.
BOLD:ADU8837 China, Germany, Georgia	20	0.8%	1.77%	BOLD:AEI2994 China	2	0%
BOLD:AEO8202 Germany, Finland	12	0.16%	4.31%	BOLD:AAK4166 Canada, USA, Russia	24	0.72%

Illidops splendidus (Papp, 1974)
Figs 2E, 44

Apanteles splendidus Papp, 1974: 333–335, figs 19–23.

Material examined

GERMANY – **Bavaria** • 1 ♀; Lkr. Kelheim, Siegenburg, ‘Bombodrom’; 48.755° N, 11.791° E; 411 m a.s.l.; 8–26 May 2017; D. Doczkal and J. Voith leg.; Malaise trap; bulk ID: dv.sieg3.02; Silbergrasrasen, Besenginster; SNSB-ZSM, ZSM-HYM-33168-H06.

Species concept

Our species concept is based on Papp (1974, 1981) and Tobias & Kotenko (1986), habitus photos of the holotype, and the specimens we identified as this species based on morphology and their associated molecular data. In addition to that, the species is quite morphologically distinct and unlikely to be confused. → ***.

Ecology / host information

Host unknown.

Distribution

PAL: Germany, Hungary, Russia (C).

Molecular data

BOLD:AEJ7519.

Remarks

Holotype female, HNHM. Country of type locality: Hungary. For more details see Höcherl *et al.* (2024).

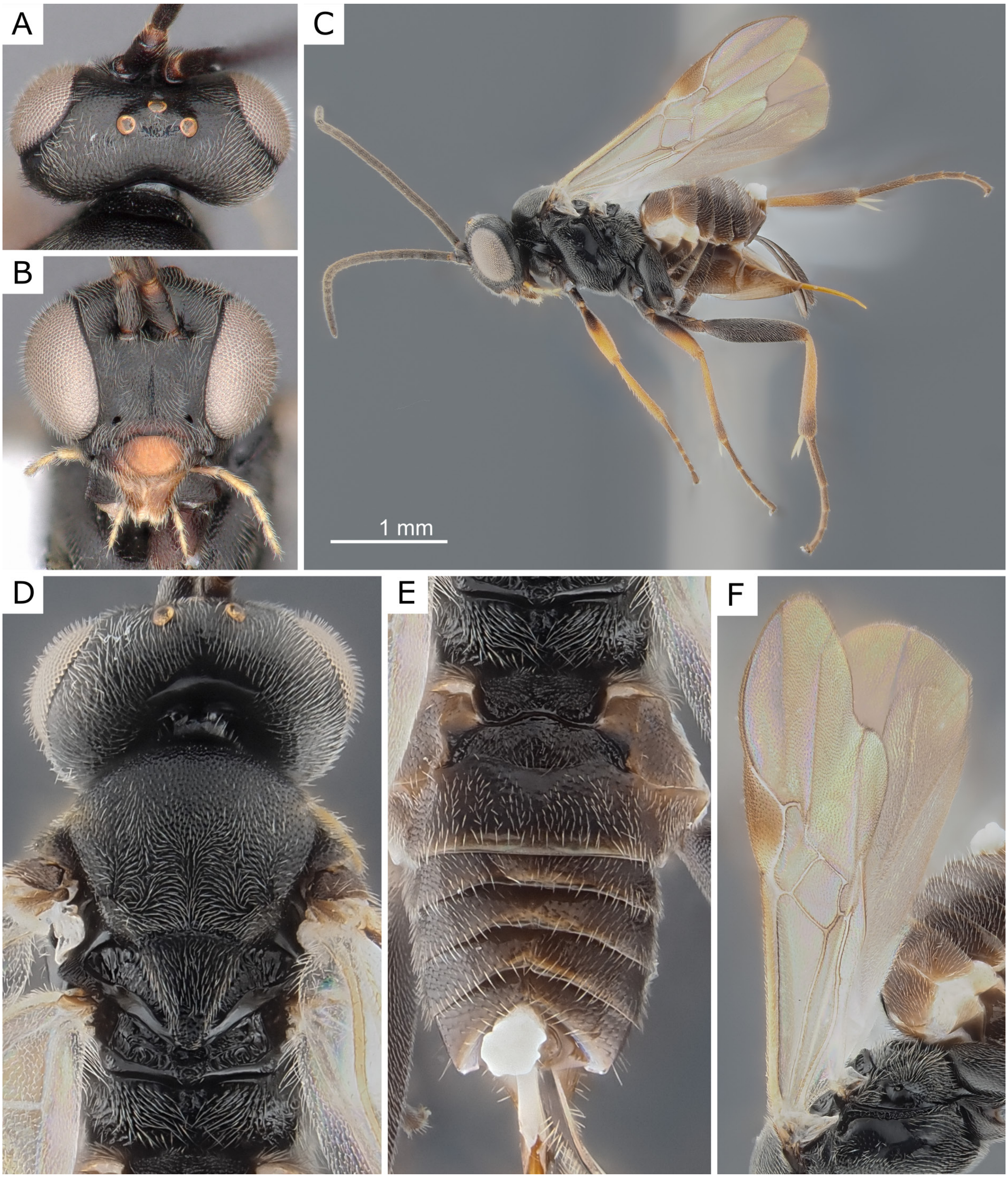

Fig. 44. *Illidops splendidus* (Papp, 1974), ♀ (ZSM-HYM-33166-H06). **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Habitus, lateral view. **D**. Mesosoma, dorsal view. **E**. Metasoma, dorsal view. **F**. Wings. Body length of the specimen: 2.9 mm. Figure from Höcherl *et al*. (2024), minimally altered.

Illidops stefanschmidti Höcherl & Fernandez-Triana sp. nov.

urn:lsid:zoobank.org:act:2ED8B14C-32E6-4B73-9583-A9AF3A8C232F

Figs 45–46

Diagnosis

This species resembles *I. kostjuki*, but differs in its distinctly elongate glossa, its light/brown clypeus which distinctly contrasts with the entirely black face, its narrowing T1, anteromesoscutum with deep, dense punctures, and fore wing vein 1M entirely pale. The species can be distinguished from *I. scutellaris* by its dark brown profemur except for the apical 0.2 or less (compared to the entirely pale profemur in *I. scutellaris*), entirely dark metafemur (compared to the metafemur with lighter coloration in *I. scutellaris*), metatibia light with apical 0.3 dark/brown (compared to apical 0.1 dark in *I. scutellaris*), C+SC-R entirely dark (compared to light in *I. scutellaris*), maxillary palps dark (compared to light in *I. scutellaris*), and the labrum rather elongate with a width/length ratio of < 1.40 (compared to > 1.45 in *I. scutellaris*).

Etymology

This species is named to honor Dr Stefan Schmidt (1962–2024), who brought the authors together for this project by selecting Microgastrinae as a taxon to be treated as part of the GBOLIII: Dark Taxa project. Stefan was our teacher and friend and he is being missed profusely.

Type material

Holotype

CANADA – **Yukon Territory** • ♀; Kluane National Park; 60.683° N, 138.005° W; 625 m a.s.l.; 13 Jul. 2006; H. Goulet and C. Boudreault leg.; CNC, HYM00001781.

Paratype

CANADA – **Yukon Territory** • 1 ♀; same data as for holotype; CNC, HYM00001782.

Description

Female

MEASUREMENTS. Body length: 2.63 (2.33) mm. Fore wing length: 2.15 (2.30) mm. Antenna shorter than body (head to apex of metasoma).

HEAD. Face: eyes not converging below, inner margins of eyes almost straight. Minimum face width/maximum face width: 0.97 (0.97). Malar distance/mandible width: 1.00 (0.94). Glossa and labrum elongated. Face softly punctate. Ocelli in high triangle, posterior tangent to anterior ocellus not touching posterior pair. OOD/POD: 2.85 (2.57). POL/POD: 2.92 (2.5). F2 length/width: 2.27 (2.42). F15 length/width: 1.10 (1.05). F2 length/F15 length: 2.27 (2.30).

MESOSOMA. Anteromesoscutum: densely punctate. Mesoscutellar disc: punctate. Posterior smooth band of the scutellum interrupted centrally by a sculptured area (rugose) and also with a thin, rugose area on the entire posterior margin (of the posterior smooth band of the mesoscutellum) (Fig. 45D). Propodeum sculpture completely irregularly rugose.

METASOMA. T1 shape: posterior half parallel-sided then slightly narrowing posteriorly with straight posterior margin. T1 sculpture: mostly sculptured. T1 width (anterior, maximum, posterior): 0.21, 0.27, 0.23 (0.19, 0.28, 0.23) mm. T1 central length: 0.31 (0.27) mm. T1 length/width at posterior margin: 1.36 (1.16). T2 shape: more or less rectangular, very short, posterior margin sinuate. Mediotergite 2 sculpture: mostly sculptured. T2 width at posterior margin/length: 3.78 (3.88). Posterior margins of T3–T7 slightly desclerotized but mediotergites not appearing to be pushed forward. Hypopygium not enlarged, its

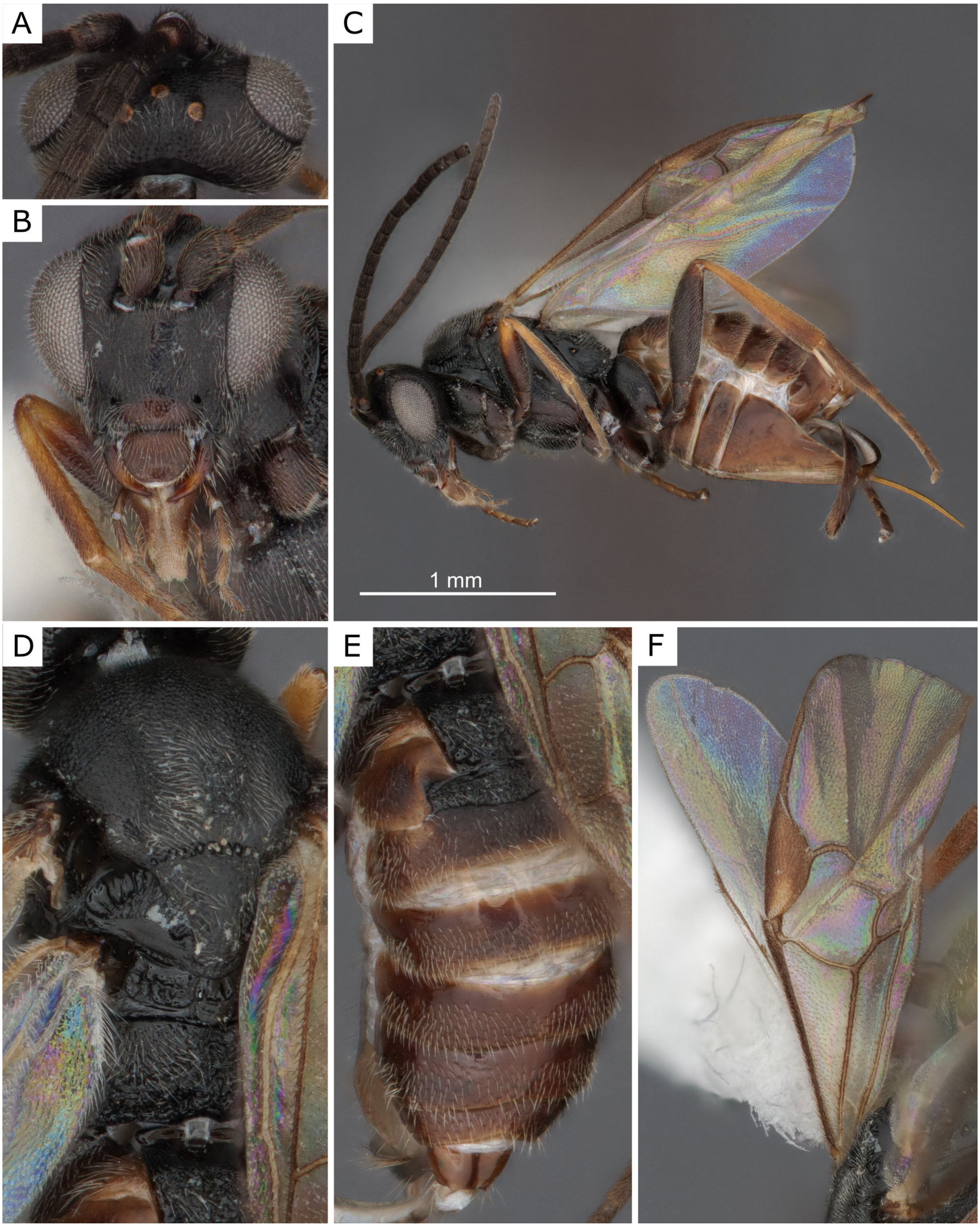

Fig. 45. *Illidops stefanschmidti* Höcherl & Fernandez-Triana sp. nov., holotype, ♀ (HYM00001781). **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Habitus, lateral view. **D**. Mesosoma, dorsal view. **E**. Metasoma, dorsolateral view. **F**. Wings. Body length of the specimen: 2.6 mm.

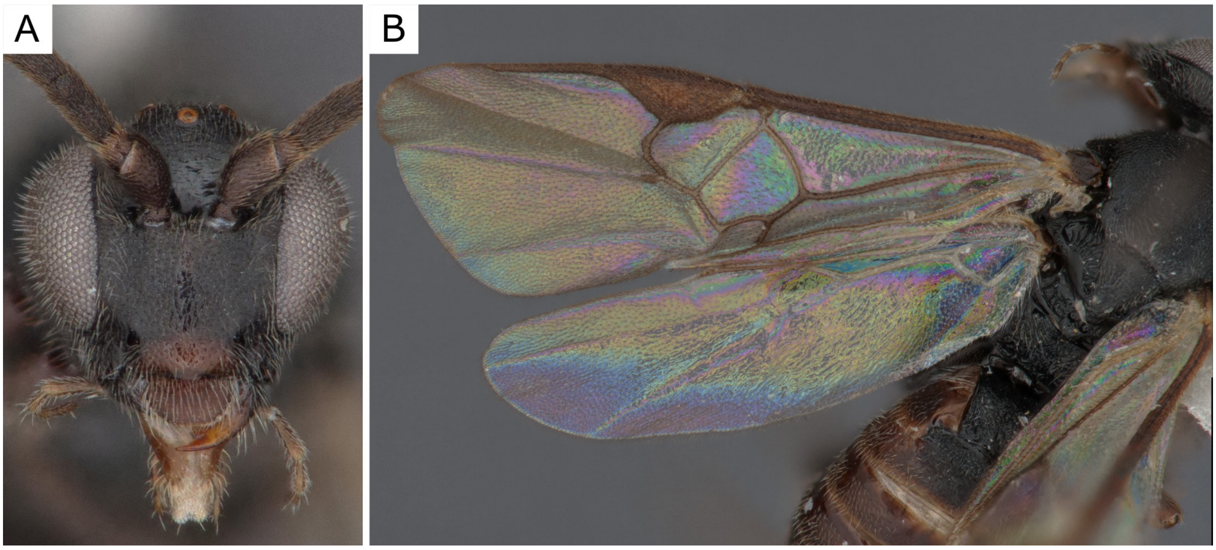

Fig. 46. *Illidops stefanschmidti* Höcherl & Fernandez-Triana sp. nov., paratype, ♀ (HYM00001782). **A**. Head, frontal view. **B**. Wings.

posterior end about in line with end of apical tergites. Ventral margin of hypopygium with desclerotized area showing several pleats. Ovipositor sheaths broad and setose over most of their length. Ovipositor sheaths length/metatibial length: 0.76 (0.74). Metafemur length/width: 0.28 (0.27). Tarsal claws: simple.

Wings. Length of fore wing veins r/2RS: 1.22 (1.17). Pterostigma length/width: 2.55 (2.41). Point of insertion of vein r in pterostigma: clearly beyond half length of pterostigma. Angle of vein r with fore wing anterior margin: clearly outwards, inclined towards fore wing apex. Length of vein R1/length of pterostigma: 0.82 (1.00). Length of vein R1/distance of distal end of R1 to distal end of vein 3RS: 1.33 (1.37).

Coloration. Body color: mostly dark brown to black. Head color: head dark brown to black, clypeus and labrum lighter brown contrasting with almost black face, palpi brown. Antenna completely dark brown to black. All coxae and femora dark brown to black, pro- and mesofemora with slightly paler apical tips. All tibiae and tarsi orange-brownish. Tegula and humeral complex dark brown. Fore wing: pterostigma brown, holotype with lighter area on basal third of pterostigma, barely visible in paratype. Wing veins in basal third dark brown (C+SC+R), brown (M+CU) to light brown (1A).

Male

Unknown.

Biology/ecology

Host unknown.

Distribution

NEA: Canada (YT).

Molecular data

This species clusters in BIN BOLD:AAC7888, the Nearest Neighbor (NN) is BOLD:AET9368, with one publicly available sequence, BIOUG85322-C11. The minimum p-distance between both BINs is 1.45%. In our NJ-analyses, the species clusters close to *I. scutellaris*, which clusters in BIN BOLD:AAA8769. The NN of this BIN is BOLD:AFQ9589 and the distance between both BINs is 1.44%. *Illidops stefanschmidti* sp. nov. and *I. scutellaris* sequences differ by a minimum p-distance of 3.01%. Both species can be distinguished morphologically by the combination of several characters (see diagnosis).

Illidops subversor (Tobias & Kotenko, 1986)

Fig. 47

Apanteles subversor Tobias & Kotenko, 1986: 748–750 [420–423].

Species concept

Our species concept is based on our examination of photos of the holotype and the information available in Tobias & Kotenko (1986) and Kotenko (2007). In addition, the species is morphologically very distinct and unlikely to be confused. → ***.

Ecology / host information

Host unknown.

Distribution

PAL: Russia (NVS).

Type material

Holotype

RUSSIA – **Novosibirsk Region** • ♀; Karasuksky District, Troitskoe; [53.72° N, 77.82° E]; [100 m]; Aug. 1974; Kulikov leg.; steppe; SIZK.

Molecular data

No molecular data available.

Remarks

This is one of the very few species of *Illidops* with T1 widening. Transferred to *Illidops* (likely by Kotenko) in Zerova *et al.* (2006).

Illidops suevus (Reinhard, 1880)

Fig. 48; Tables 7–8

Apanteles suevus Reinhard, 1880: 364.
Apanteles minutus Szépligeti, 1896: 305.
Apanteles brevisternis Tobias, 1964: 229–230, fig. 49.
Apanteles suspicax Tobias, 1964: 230–231, fig. 50.
Apanteles dion Nixon, 1965: 183, fig. 206.
Apanteles sesostris Nixon, 1976: 714–715, fig. 16.

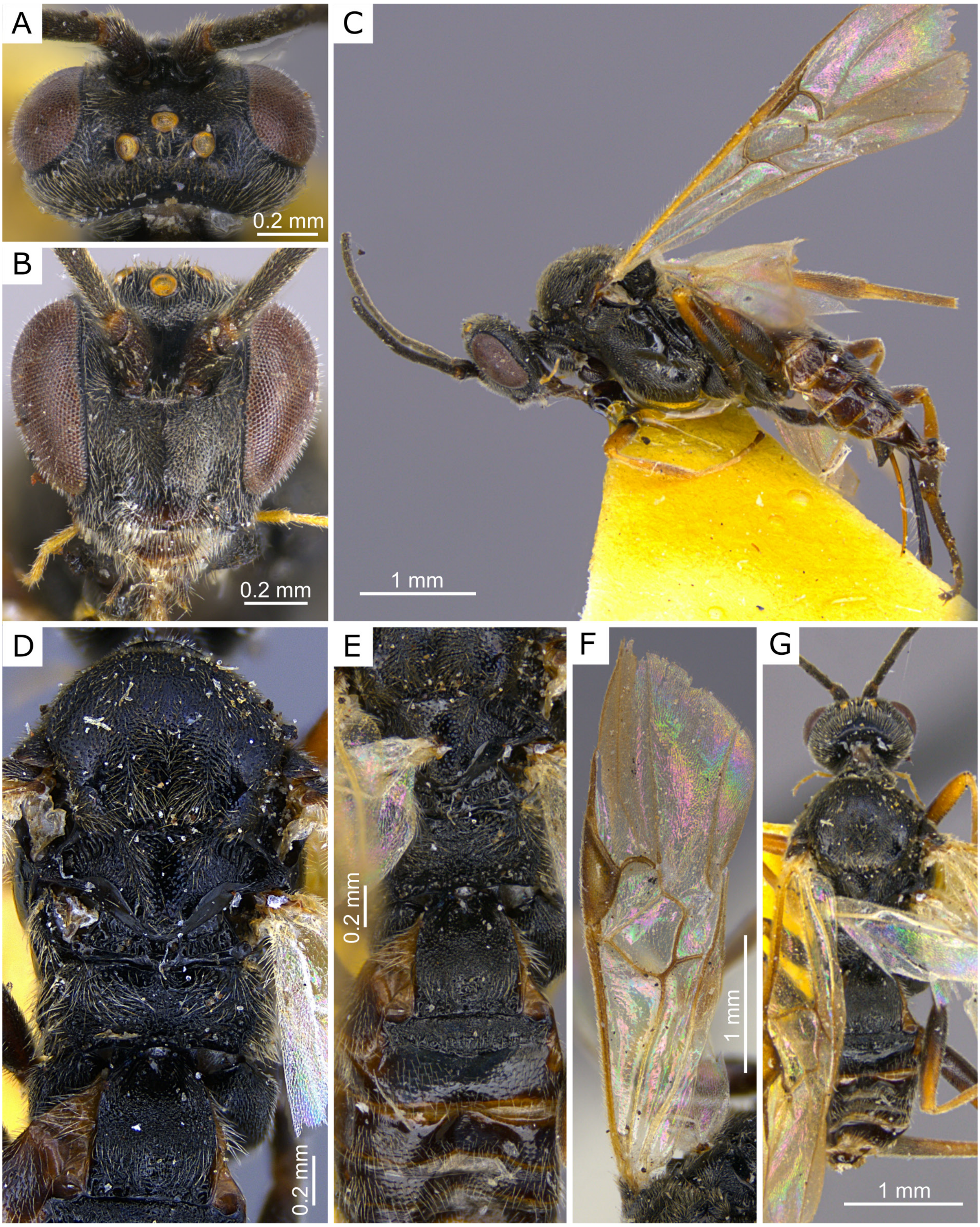

Fig. 47. *Illidops subversor* (Tobias & Kotenko, 1986), holotype, ♀ (SIZK). **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Lateral view. **D**. Mesosoma, dorsal view. **E**. Meso-/metasoma, dorsal view. **F**. Fore wing. **G**. Dorsal view. Body length of the specimen: 4.5 mm.

Other material examined

UKRAINE – **Kherson Region** • 1 ♀; Chornomorsk [Chornomorskyi Nature Reserve], Ivano-Rybalchansky area; [46.457° N, 32.149° E]; [4 m]; 14 Aug. 1978; A. Kotenko leg.; A. Kotenko det.; mixed grass; CNC, CNCHYM 01526.

Species concept

Our species concept is based on our examination of an authoritatively identified female specimen stored in the CNC (CNCHYM 01526, identified by Kotenko) and the information available in Tobias (1964), Nixon (1965, 1976), Papp (1981), and Tobias & Kotenko (1986). In addition, the species is morphologically very distinct and unlikely to be confused. However, molecular data showed high cryptic diversity in this species, so we consider our overall current concept moderate rather than good → **

Ecology / host information

Psychidae: *Rebelia* sp. (Papp 1984), *Epichnopterix* sp. according to Nixon's (1976) treatment of junior synonym *A. dion*.

Distribution

PAL: Armenia, Austria, Bulgaria, Croatia, Czech Republic, France, Germany, Greece, Hungary, Iran, Kazakhstan, Korea, Macedonia, Malta, Moldova, Mongolia, Montenegro, Poland, Romania, Russia (IRK), Serbia, Slovakia, Switzerland, Ukraine, United Kingdom.

Molecular data

We observed specimens of three barcoding clusters which morphologically match the concept of *I. suevus*: BOLD:ACT9426 (Fig. 49), BOLD:AEI1345 (Figs 50–51) and BOLD:AEJ7522 (Fig. 52). However, these clusters are far apart from each other with minimum p-distances of 9.63% (BOLD:AEJ7522–BOLD:ACT9426), 13.57% (BOLD:AEI1345–BOLD:ACT9426), and 13.63% (BOLD:AEI1345–AEJ7522). The clusters are clearly separated, also taking into account the much lower within-BIN maximum p-distances ranging between 0.32% and 2.03% (see Table 7). The Nearest Neighbors (NN) in the BOLD database are different clusters, not identified to species level, and, in two cases, only male specimens are available. All three BINs match the morphology of *I. suevus*, and we cannot find consistent morphological differences other than some difference in size between the specimens of BOLD:ACT9426 and the other two clusters. We consider it likely that *I. suevus* represents a complex of morphologically cryptic species but we cannot match any of our clusters to the name *I. suevus* or other junior synonyms based on morphology. In addition to that, the NN BINs (and their NN's) would also need to be considered and identified.

Remarks

The posterior smooth band of the scutellum of the material available to us is barely invaded by punctures from the scutellar disc and shows little to no sculpture, and the propodeum is very coarsely reticulate, much more sculptured than in most *Illidops*. The hypopygium of voucher specimens of the BINs we tentatively associate with this species is also much less flexible and pleated than in other species of *Illidops*. This species represents one of the more aberrant species of *Illidops* and the former *butalidis*-group (e.g., Nixon 1965, 1976; Papp 1984) but has been considered to fit the concept of the genus by many authors (e.g., Papp 1988; Fernandez-Triana *et al.* 2020). Nixon (1965, 1976) did not include *Apanteles suevus* in his *butalidis*-group. However, he described a junior synonym of the species, *Apanteles dion*, as part of the group and commented that *A. dion* is a "is a highly aberrant species and I am not satisfied that I am correct in placing it in the *butalidis-group*" (Nixon 1965: 183), and later comments that the species is "occupying a marginal position within the group" (Nixon 1976: 713). He had also included *A. sesostris* Nixon, 1976 in the *butalidis*-group, only known from the male holotype

Table 7. BINs which match the morphological characters of *I. suevus* (Reinhard, 1880). Information on the Nearest Neighbor (NN) in the BOLD database is given, including relevant p-distances and distribution.

BIN/ Country	Number of specimens (n)	Within-BIN max. p-distance	Min. NN p-dist.	NN/ Country	Number of specimens (n)	NN within-BIN max. p-dist.
BOLD:AEI1345 Turkey, Germany, Finland	9	1.12%	3.1%	BOLD:AAZ8761 Turkey	1	N.A.
BOLD:AEJ7522 Germany	3	0.32%	7.54%	BOLD:AFN8552 Lebanon	9	1.61%
BOLD:ACT9426 Germany, Iran	2	2.03%	4.8%	BOLD:ADZ9328 Israel, Lebanon	3	0.64%

Table 8. *Illidops suevus* (Reinhard, 1880) and junior synonyms as well as their type information.

Species name	Holotype	Country of type locality	Type repository
Apanteles suevus Reinhard, 1880	Female	Germany	ZMHB
Apanteles minutus Szépligeti, 1896	Female	Hungary	HNHM
Apanteles brevisternis Tobias, 1964	Female	Kazakhstan	ZIN
Apanteles suspicax Tobias, 1964	Female	Kazakhstan	ZIN
Apanteles dion Nixon, 1965	Female	Czech Republic	Národni Múzeum, Entomologické oddeleni, Praha
Apanteles sesostris Nixon, 1976	Male	United Kingdom	NHMUK

and another future synonym of *I. suevus*. Papp (1984), in his own words, "developed" Nixon's species groups and described the *suevus*-group as a new species group which comprised this single species. In that process, he studied many types and synonymized several species under the concept of *A. suevus*. Papp (1988) later integrated the Palearctic species into Mason's genera and in that process considered *A. suevus* as part of *Illidops*.

The species is represented by three barcoding clusters (BINs) in our dataset. There are no significant morphological differences between these clusters (compare Figs 49–52), except for one specimen being noticeably larger than representatives of the other two clusters. Additional specimens matching this species morphologically have been located by JFT in MNCN and there is another specimen stored at the CNC from Iran. This 'species' may potentially represent a complex of morphologically cryptic species. The genus of the potential Psychidae host, *Rebelia* sp., was identified through rearing experiments by Dr L. Gozmány in Montenegro and includes some very widespread species. Locality details of the junior synonym types and additional information can be reviewed in Papp (1984).

Illidops suevus has five junior synonyms (see Table 8). *Apanteles polonicus* Fahringer, 1936 is listed as a junior synonym of *I. suevus* in Taxapad (Yu *et al.* 2016), the world checklist (Fernandez-Triana *et al.* 2020), and potentially more literature. However, Fahringer (1936) did not describe this as a new

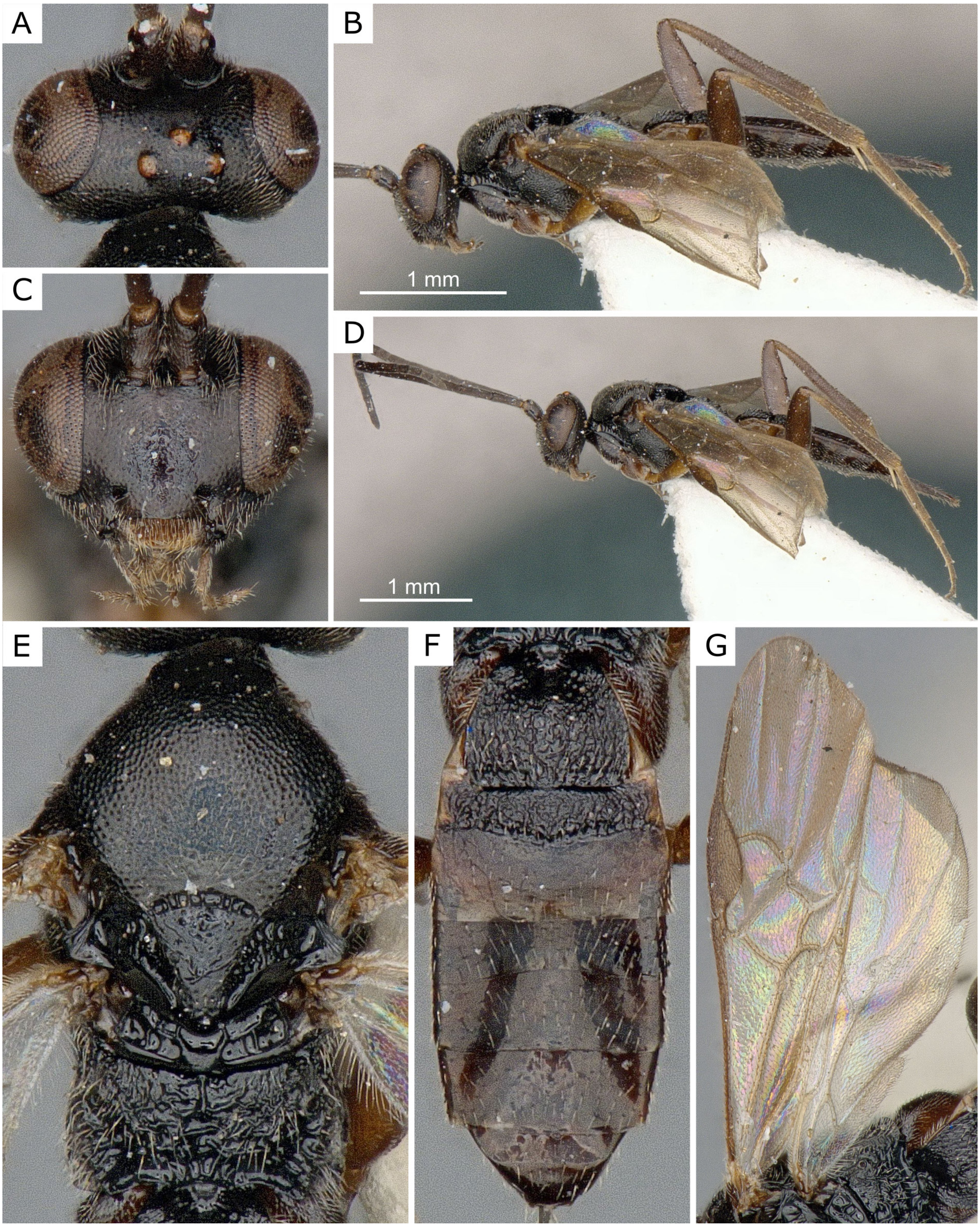

Fig. 48. *Illidops suevus* (Reinhard, 1880), ♀ (CNCHYM 01526). **A**. Head, dorsal view. **B, D**. Lateral views. **C**. Head, frontal view. **E**. Mesosoma, dorsal view. **F**. Metasoma, dorsal view. **G**. Dorsal view. Body length of the specimen: 3.2 mm. Images from Fernandez-Triana *et al*. (2020), rearranged.

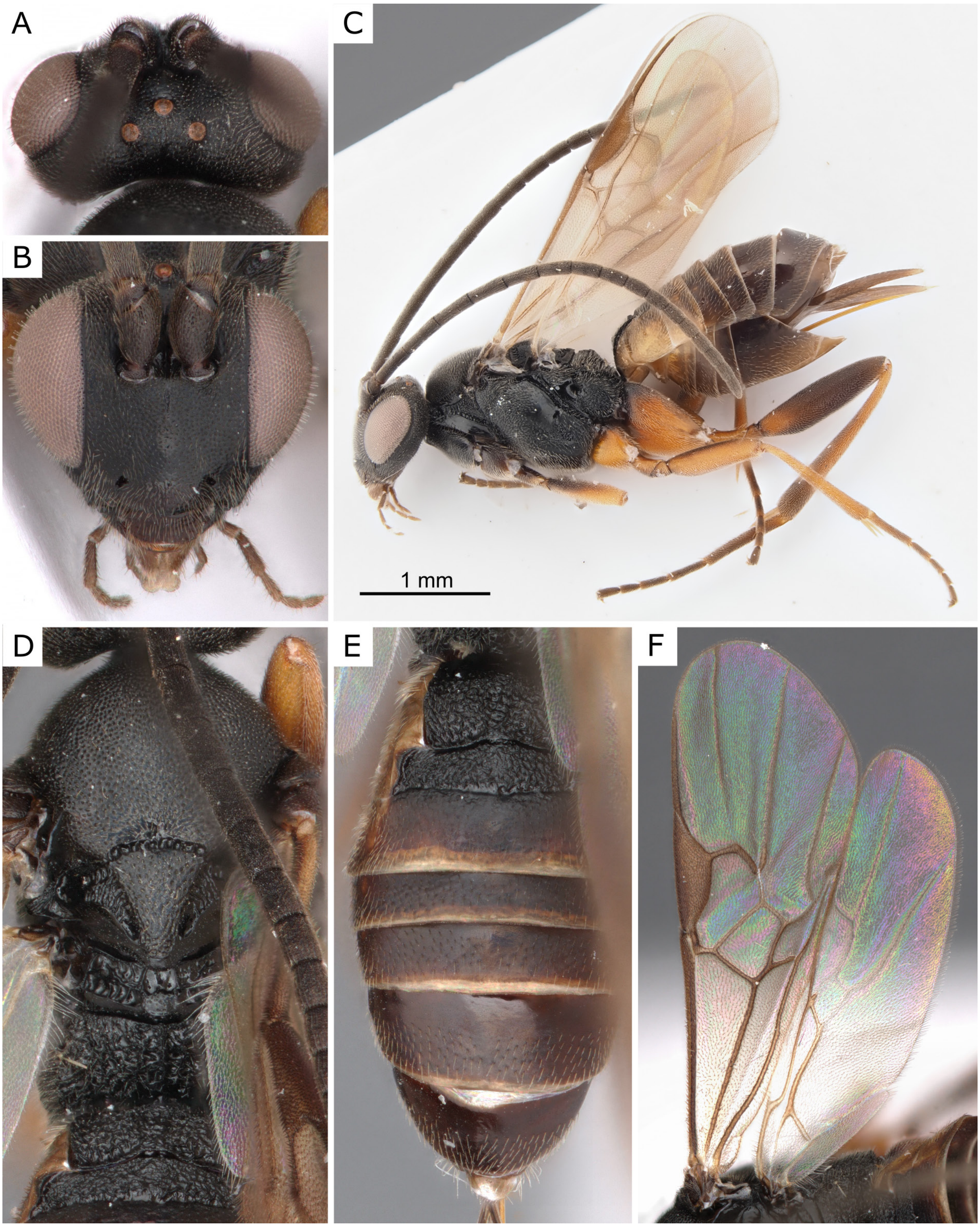

Fig. 49. *Illidops* cf. *suevus* (Reinhard, 1880), ♀ (BC-ZSM-HYM-24067-C12), BOLD:ACT9426. **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Lateral view. **D**. Mesosoma, dorsal view. **E**. Metasoma, dorsal view. **F**. Wings. Body length of the specimen: 3.9 mm.

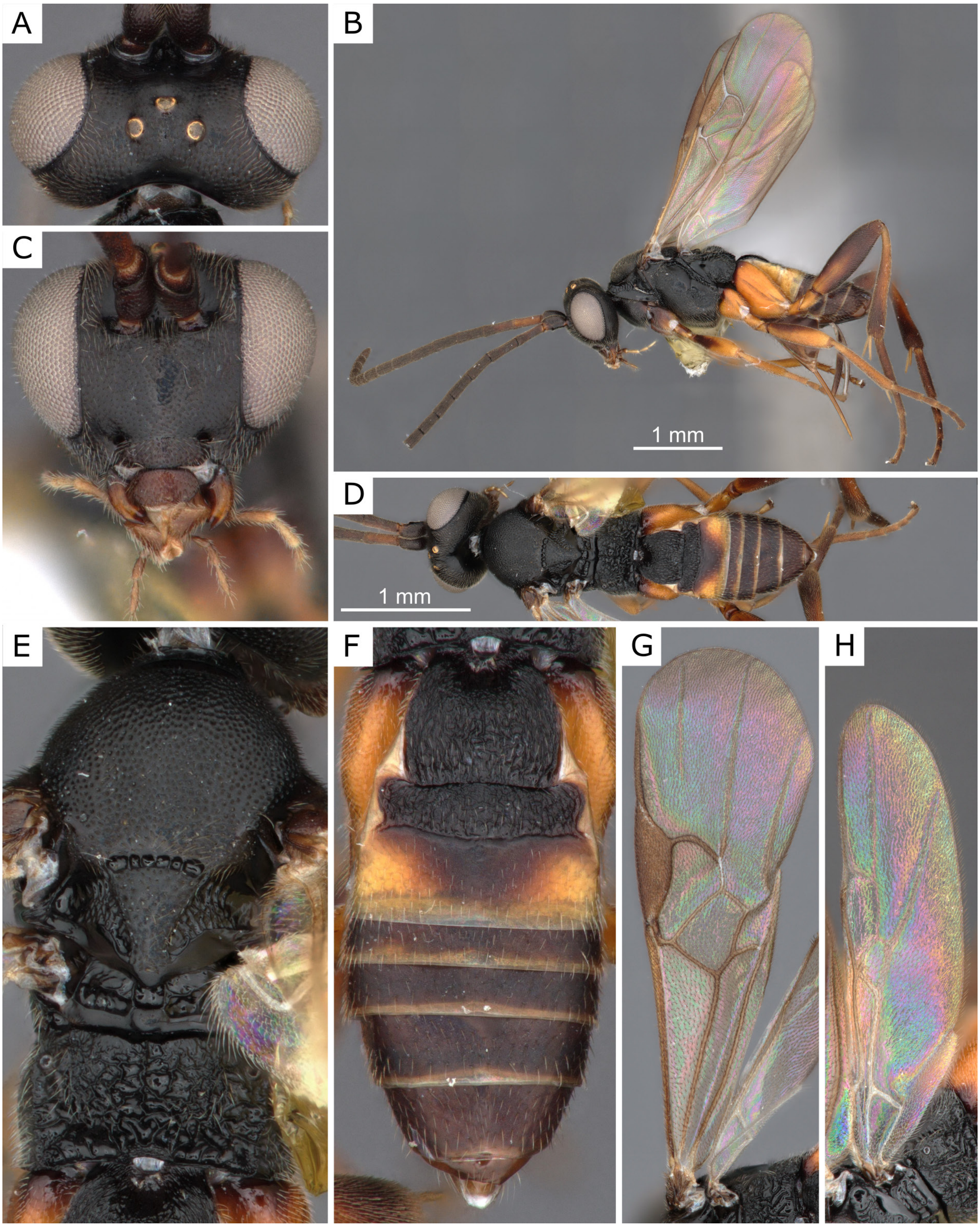

Fig. 50. *Illidops* cf. *suevus* (Reinhard, 1880), ♀ (ZSM-HYM-33167-H06), BOLD:AEI1345. **A**. Head, dorsal view. **B**. Lateral view. **C**. Head, frontal view. **D**. Dorsal view. **E**. Mesosoma, dorsal view. **F**. Metasoma, dorsal view. **G**. Fore wing. **H**. Hind wing. Note: Additional, detailed photo of the scutellar area in Fig. 2G. Body length of the specimen: 3.0 mm.

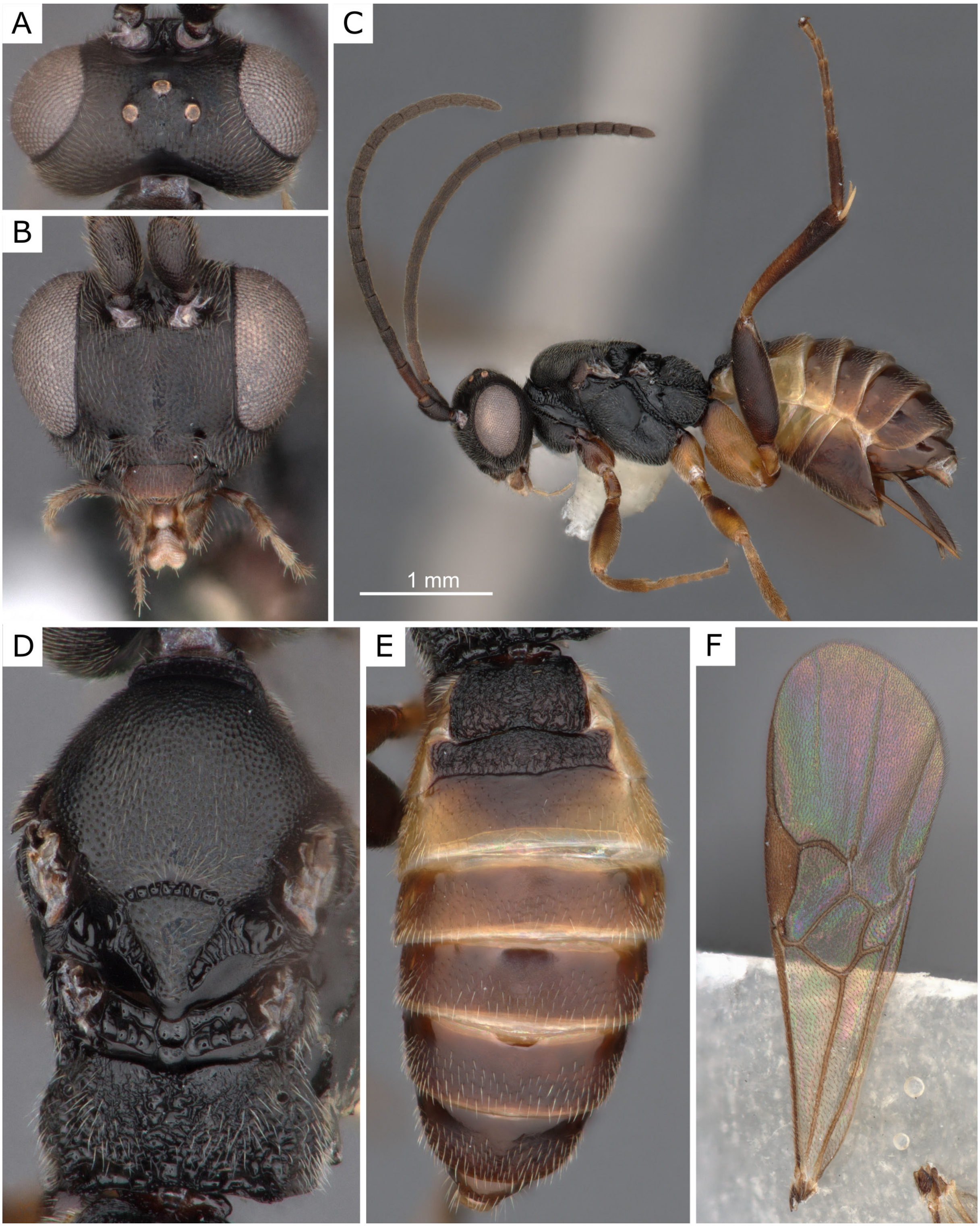

Fig. 51. *Illidops* cf. *suevus* (Reinhard, 1880), ♀ (ZSM-HYM-42398-E02), BOLD:AEI1345. **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Lateral view. **D**. Mesosoma, dorsal view. **E**. Metasoma, dorsal view. **F**. Fore wing. Body length of the specimen: 3.4 mm.

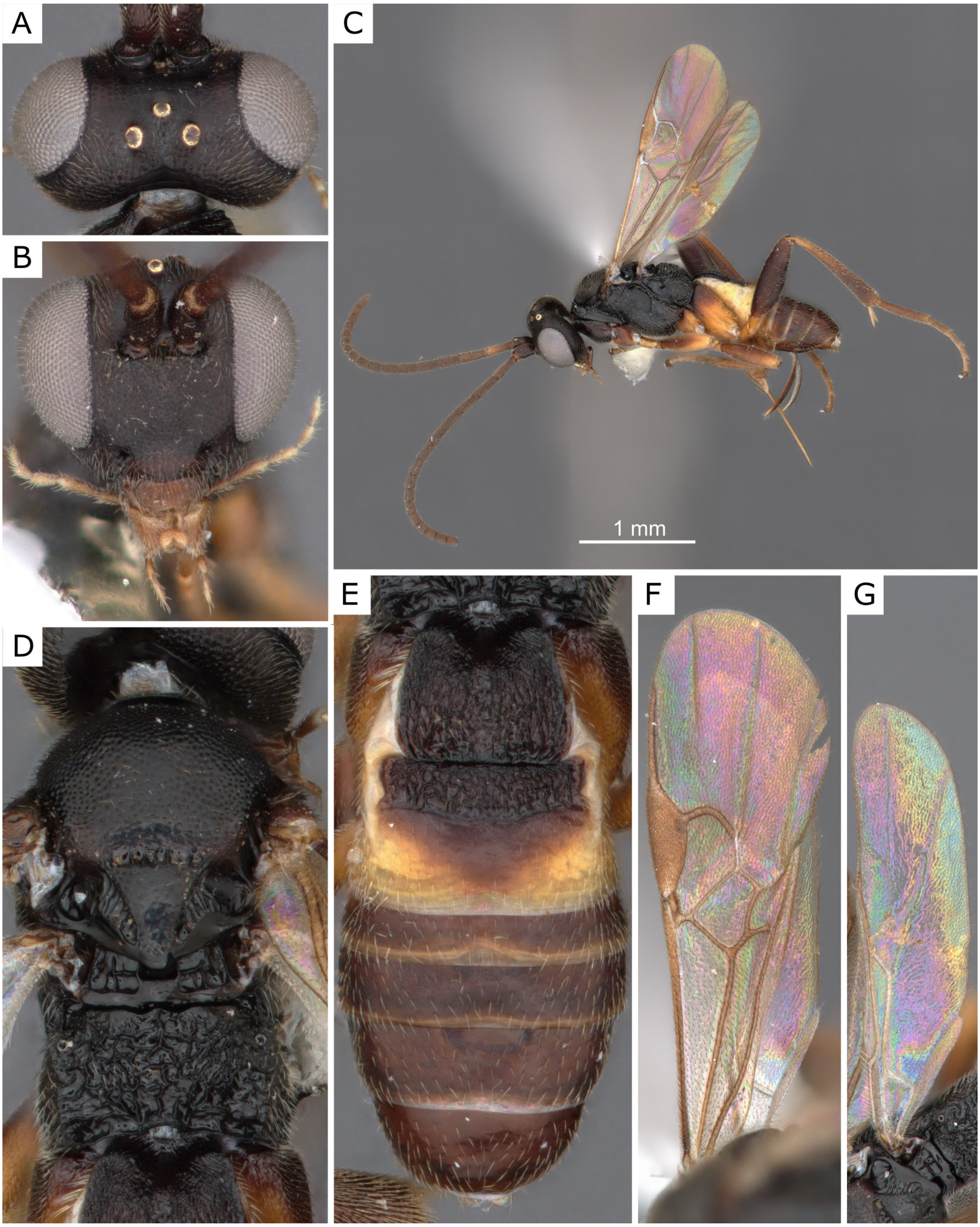

Fig. 52. *Illidops* cf. *suevus* (Reinhard, 1880), ♀ (ZSM-HYM-33164-B03), BOLD:AEJ7522. **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Lateral view. **D**. Mesosoma, dorsal view. **E**. Metasoma, dorsal view. **F**. Fore wing, **G**. Hind wing. Body length of the specimen: 2.7 mm.

species, he merely mentioned a variant of *A. suevus* described by Niezabitowski (1909). His wording is: "Niezabitowsky describes an ab. [aberration] (*polonicus* m.) as follows" (Fahringer 1936: 205) and then repeats Niezabitowsky's (1909) morphological description of a specimen collected in Poland, Bieńkowice. We conclude that this name was never formally assigned and can hence be disregarded as a junior synonym of *I. suevus* for potential efforts to match the different barcoding clusters to existing names. The specimen described by Niezabitowsky is most likely stored in Krakow, Museum of Natural History and Institute of Systematics and Evolution of Animals, Polish Academy of Sciences collection (Haris 2016).

Illidops suffectus (Tobias & Kotenko, 1986)

Fig. 53

Apanteles suffectus Tobias & Kotenko, 1986: 750 [420], pl. 241 figs 4–7.

Type material

Holotype

KAZAKHSTAN – **Almaty Region** • ♀; near Almaty, Kargalinka River; [43.31° N, 76.82° E]; 8 Jun. 1964; Savicheva leg.; SIZK.

Species concept

Our species concept is based on our examination of photos of the holotype and the information available in Tobias & Kotenko (1986). In addition, the species is morphologically very distinct and unlikely to be confused → ***.

Ecology / host information

Host unknown.

Distribution

PAL: Kazakhstan.

Molecular data

No molecular data available.

Remarks

Fernandez-Triana *et al.* (2020) list ZIN as the depository of the holotype, but it is currently located at SIZK on loan, where a female paratype with the same label as the holotype is also stored (Zerova *et al.* 2006).

Illidops terrestris Wharton, 1983

Figs 54–55

Illidops terrestris Wharton, 1983: 667–670, figs 1–4.

Type material

Paratypes

UNITED STATES – **California** • 1 ♀; Thousand Palms; 21 Mar. 1955; W.R.M. Mason leg.; CNC, CNCHYM 01520. – **Florida** • 1 ♀; Oneco; 4 Jun. 1953; J.C. Martin leg.; CNC, CNCHYM 01521. – **Texas** • 1 ♀; Kerrville; 19 Jun. 1959; W.R.M. Mason leg.; CNC, CNCHYM 01522 • 1 ♀; same data as for preceding; 17 Jun. 1959; CNC, CNCHYM 01523.

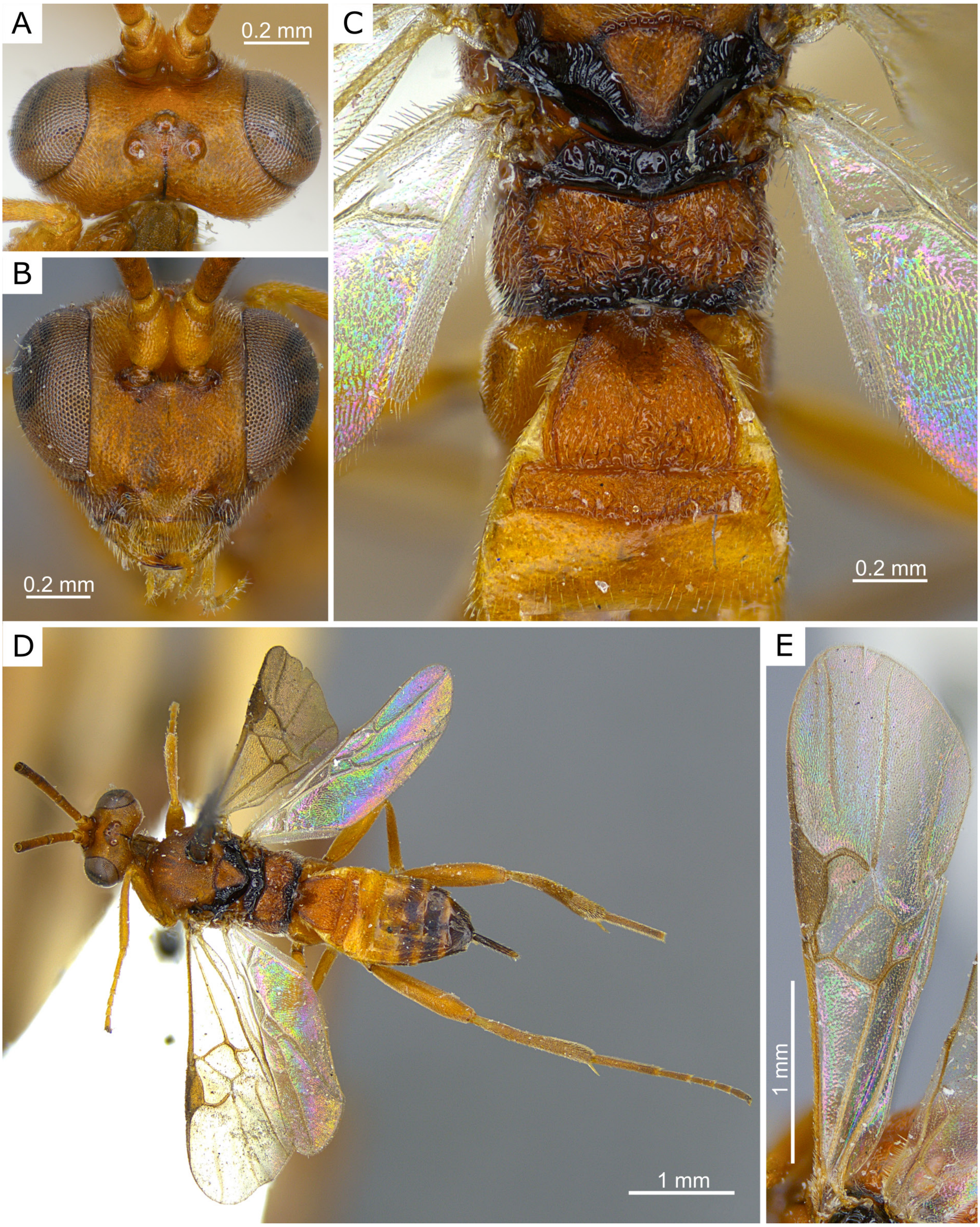

Fig. 53. *Illidops suffectus* (Tobias & Kotenko, 1986), holotype, ♀ (SIZK). **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Partial meso- and metasoma, dorsal view. **D**. Dorsal view. **E**. Fore wing. Body length of the specimen: 3.8 mm.

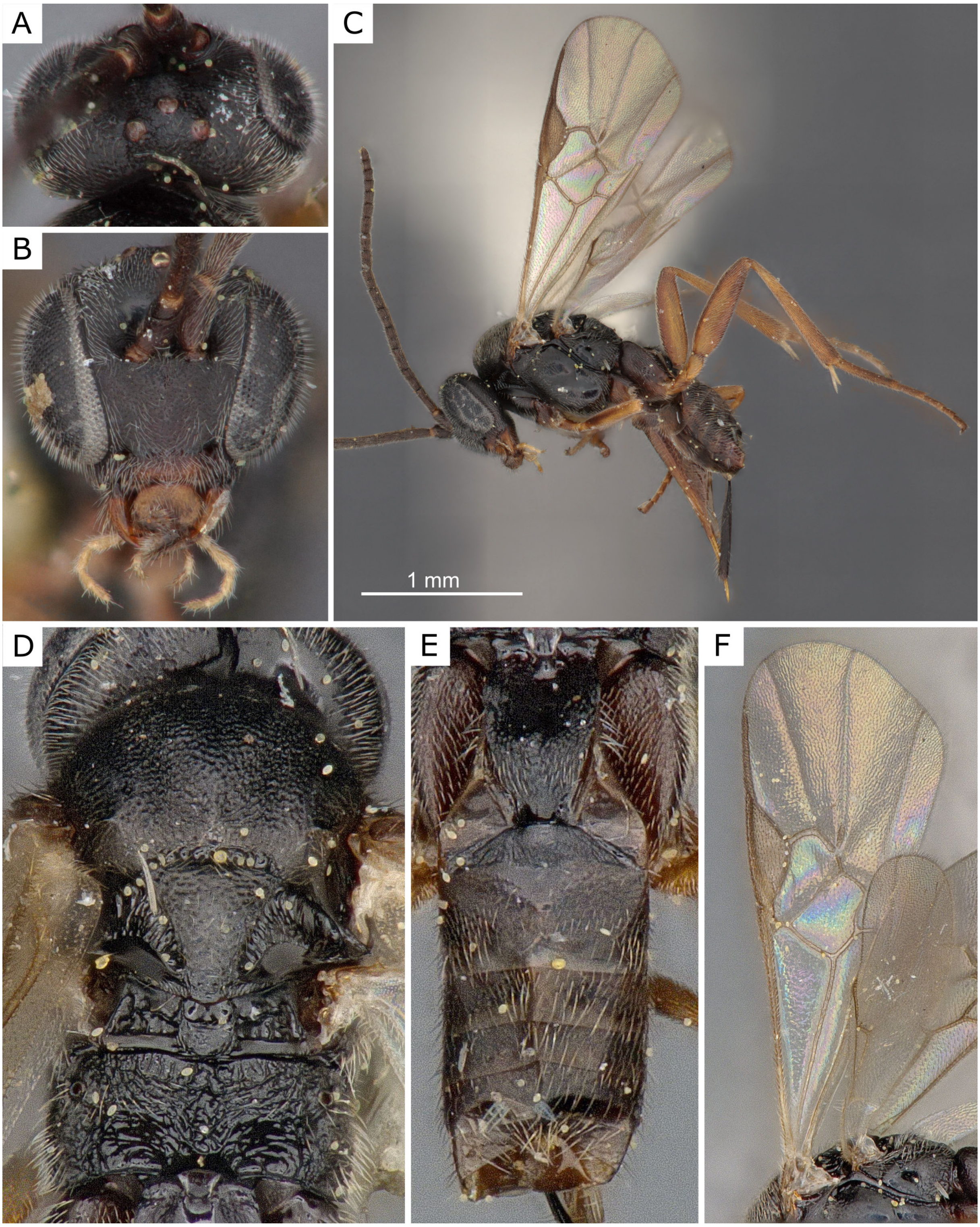

Fig. 54. *Illidops terrestris* Wharton, 1983, paratype, ♀ (CNCHYM 01522). **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Habitus, lateral view. **D**. Mesosoma, dorsal view. **E**. Metasoma, dorsal view. **F**. Fore wing. Body length of the specimen: 2.5 mm.

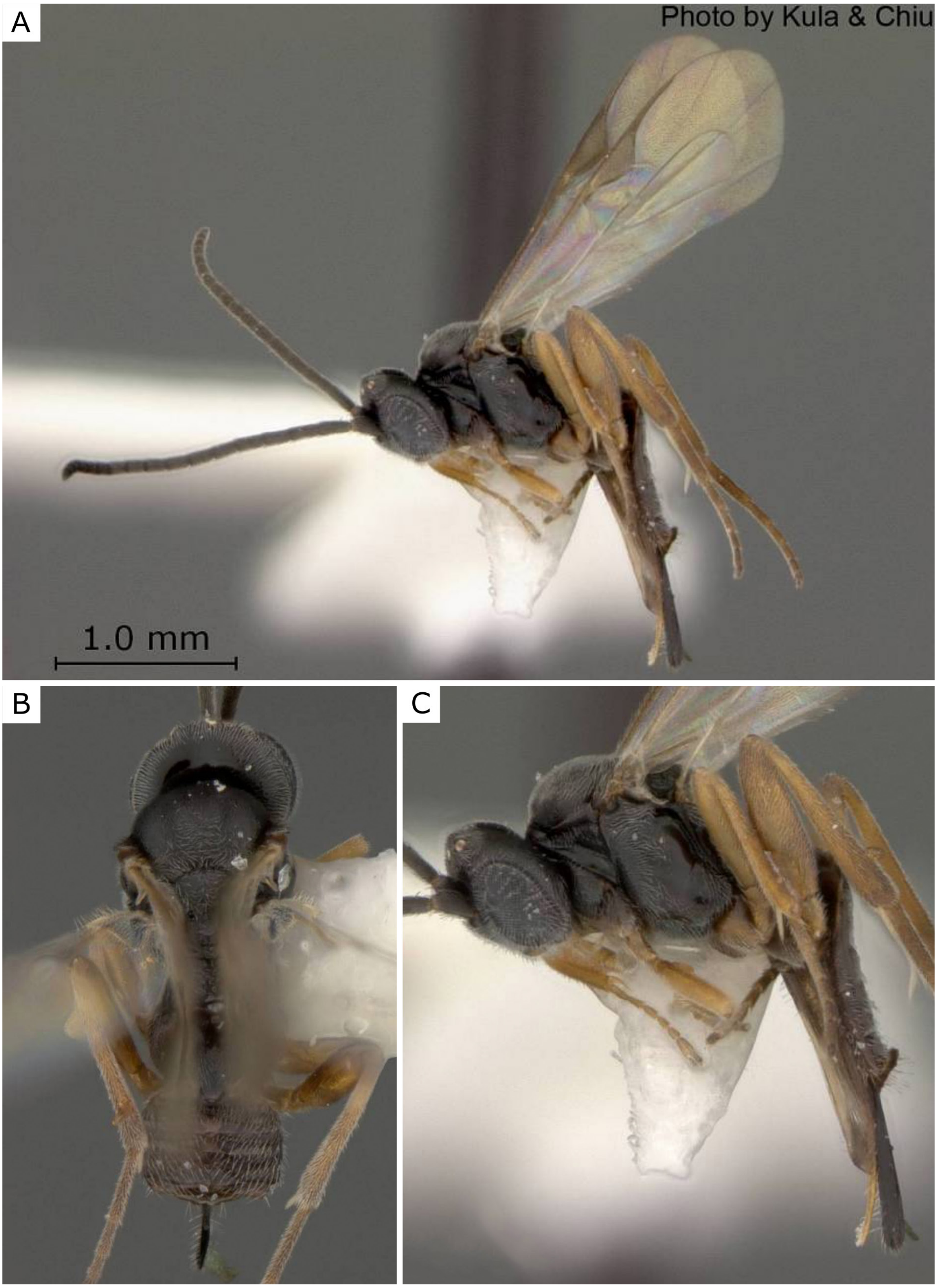

Fig. 55. *Illidops terrestris* Wharton, 1983, holotype, ♀ (USNM type number 100719). **A**. Habitus, lateral view. **B**. Habitus, dorsal view. **C**. Detail lateral view. Photos downloaded from the USNM online type catalogue (http://n2t.net/ark:/65665/3538962a5-a0fd-48e8-b3ea-20bf31e926b4) available under CC0 license.

Species concept

Our species concept is based on our examination of habitus photos of the holotype (available via the Smithsonian Website), our examination of a female paratype stored at the CNC, and the information available in Wharton (1983). → ***.

Ecology / host information

Parts of the type series (including holotype) reared from Pyralidae: *Elasmopalpus lignosellus* (Zeller, 1848). For more details see Wharton (1983).

Distribution

NEA: United States (CA, FL, GA, TX).

Molecular data

Currently, only a very short fragment of COI (164 bp) of a female paratype CNCHYM 01520 stored at the CNC is available for this species. When blasted, it matches a public sequence with the Specimen-ID BIOUG02764-D01 in BIN BOLD:ABY3260 at a similarity of 99.33%. Specimen BIOUG02764-D01 was collected in Florida and all four sequences in the BIN were obtained from specimens collected in the United States, which matches the known distribution range of the species. We consider it likely that these specimens are representatives of *I. terrestris* but have not seen the material to confirm our hypothesis.

Remarks

Holotype female, USNM. Country of type locality: United States. The type was examined by Fernandez-Triana *et al.* (2020). This species was reared from a Pyralidae host, *Elasmopalpus lignosellus*, associated with peanut (holotype) and from *Elasmopalpus* sp. associated with cowpea (some paratypes).

Illidops tigris (Kotenko, 1986)
Fig. 56

Apanteles tigris Kotenko in Tobias & Kotenko, 1986: 754–755 [424].

Type material

Holotype

TAJIKISTAN – **[Khatlon Province]** • ♀; Tigrovaya Balka Nature Reserve; [37.27° N, 68.47° E]; [331 m]; 2 Apr. 1981; Plyushch leg.; SIZK.

Species concept

Our species concept is based on our examination of photos of the holotype and the information available in Tobias & Kotenko (1986) → ***.

Ecology / host information

Host unknown.

Distribution

PAL: Tajikistan, Turkmenistan.

Molecular data

No molecular data available.

Remarks

In addition to the holotype, there are 12 female and 1 male paratypes stored at SIZK (Zerova *et al.* 2006).

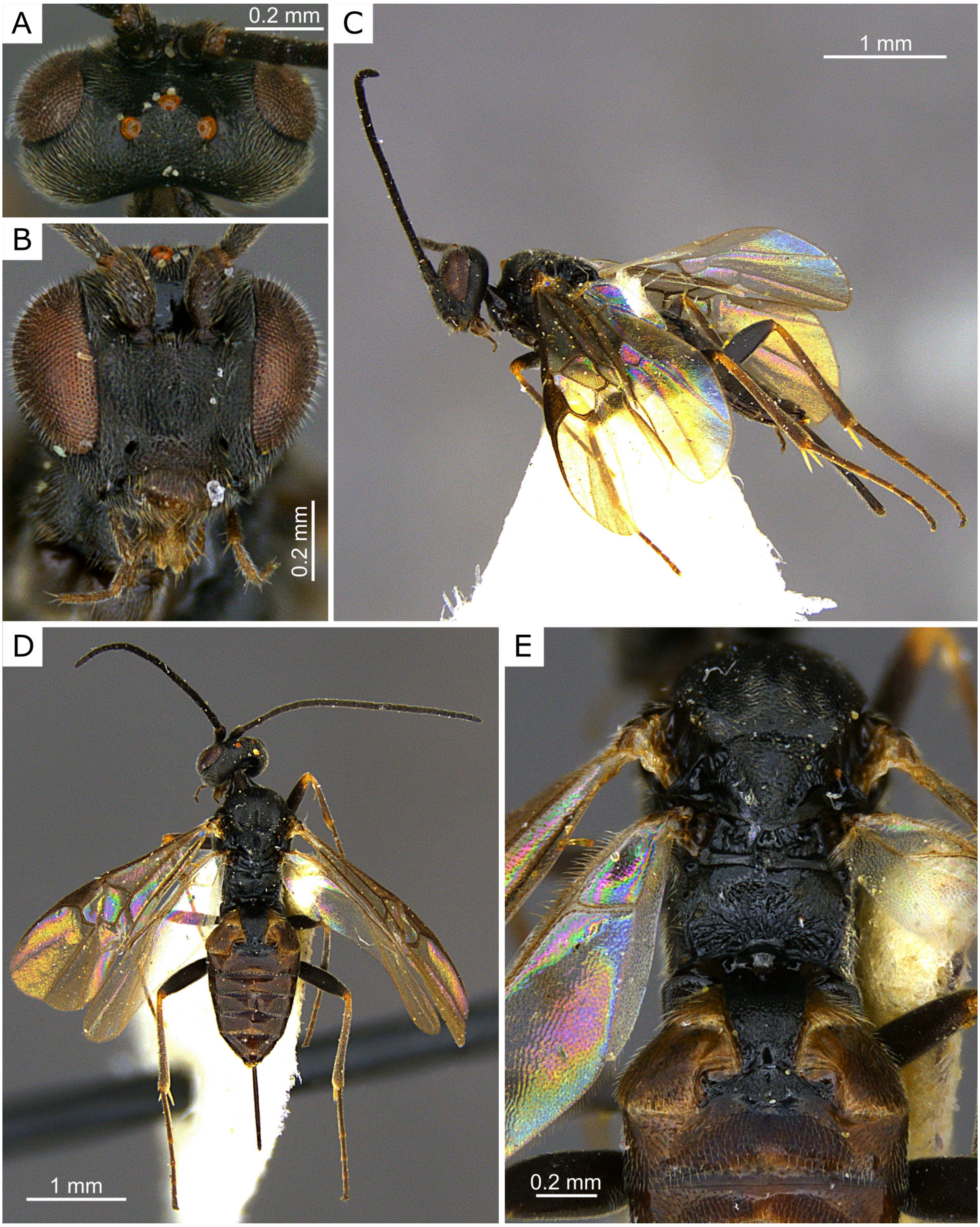

Fig. 56. *Illidops tigris* (Kotenko, 1986), holotype, ♀ (SIZK). **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Lateral view. **D**. Dorsal view. **E**. Partial meso- and metasoma, dorsal view. Body length of the specimen: 3.3 mm.

Illidops toreicus Kotenko, 2007
Fig. 57

Illidops toreicus Kotenko, 2007: 178–179, pl. 79 figs 1–2, pl. 80 fig. 23.

Type material

Holotype

RUSSIA – **[Zabaykalsky Krai]** • ♀; [Ononsky District], Chitinsk Province, Daurskiy Nature Reserve, north side of Zun-Torey Lake, tract Irel'zhin; [50.23° N, 115.78° E]; [738 m]; gully; 7 Jul. 1990; A. Kotenko leg.; SIZK.

Species concept

Our species concept is based on our examination of photos of the holotype and the information available in Kotenko (2007). → ***.

Ecology / host information

Host unknown.

Distribution

PAL: Russia (ZAB).

Molecular data

No molecular data available.

Original description sensu Kotenko (2007) (translated from Russian and with updated morphological terminology and comments in brackets when our observations did not match Kotenko's)

[Diagnosis: Similar to *I. kostjuki*, but differs in the following characters:] T2 wider, width ~3 × central length. T2 1.5 × shorter than T3, posterior margin weakly arcuately curved. Ovipositor sheaths shorter, about 0.5 × metatibia length. Pterostigma uniformly colored, dark brown. Fore wing vein R1 2.3–2.5 × longer than the distance from it to apex of 3RS. Anteromesoscutum with less noticeable setae and denser punctation, mostly matte, posteriorly with smooth sheen. Smaller: 2.5 [mm].

Head 1.7 × as wide as long, slightly narrower than mesosoma width, roundly narrowed behind eyes. Gena 1.5 × shorter than the eye width (laterally). Ocelli in obtuse triangle [ocelli in low triangle], its base 1.9–2.0 × as long as OOL [POL 1.2 × OOL]. POL 1.4 × greater than OD [POL 2.2 × OD]. Tangent to anterior edge of the posterior ocelli crossing posterior edge of the front ocellus [imaginary tangent posterior to the anterior ocellus touches the posterior ocelli]. Eyes noticeably converging downwards, their longitudinal diameter 1.7 × the transverse diameter and 1.6 × the height of the face. Upper width of face 1.2 × more than the lower width, and 1.6 × its height. Front margin of the clypeus convex, its height 3.2 × less than face height. Gena height 3.7 × shorter than longitudinal eye diameter. Antenna slightly longer than body, F15 length 1.3 × its width. Mesosoma barely shorter than metasoma. Mesosoma length 1.6 × more than its height. Fore wing 1.2 × as long as hind wing, and slightly shorter than body. Pterostigma 2.6 × as long as wide, slightly shorter than vein R1. Vein r slightly shorter than 2RS. Vein 1cu-a arising at around middle of the 1st discal cell length; hind wing vein cu-a almost straight; metafemur length 3.2–3.3 × its width and 1.3 × less than the length of the metatibia. Metatarsus 1.2 × as long as metatibia, Ratio of holotype metatarsomere lengths as follows 3.5:1.9:1.4:1.0:1.2. T1 slightly widened posteriorly, 1.3 × longer than maximum width.

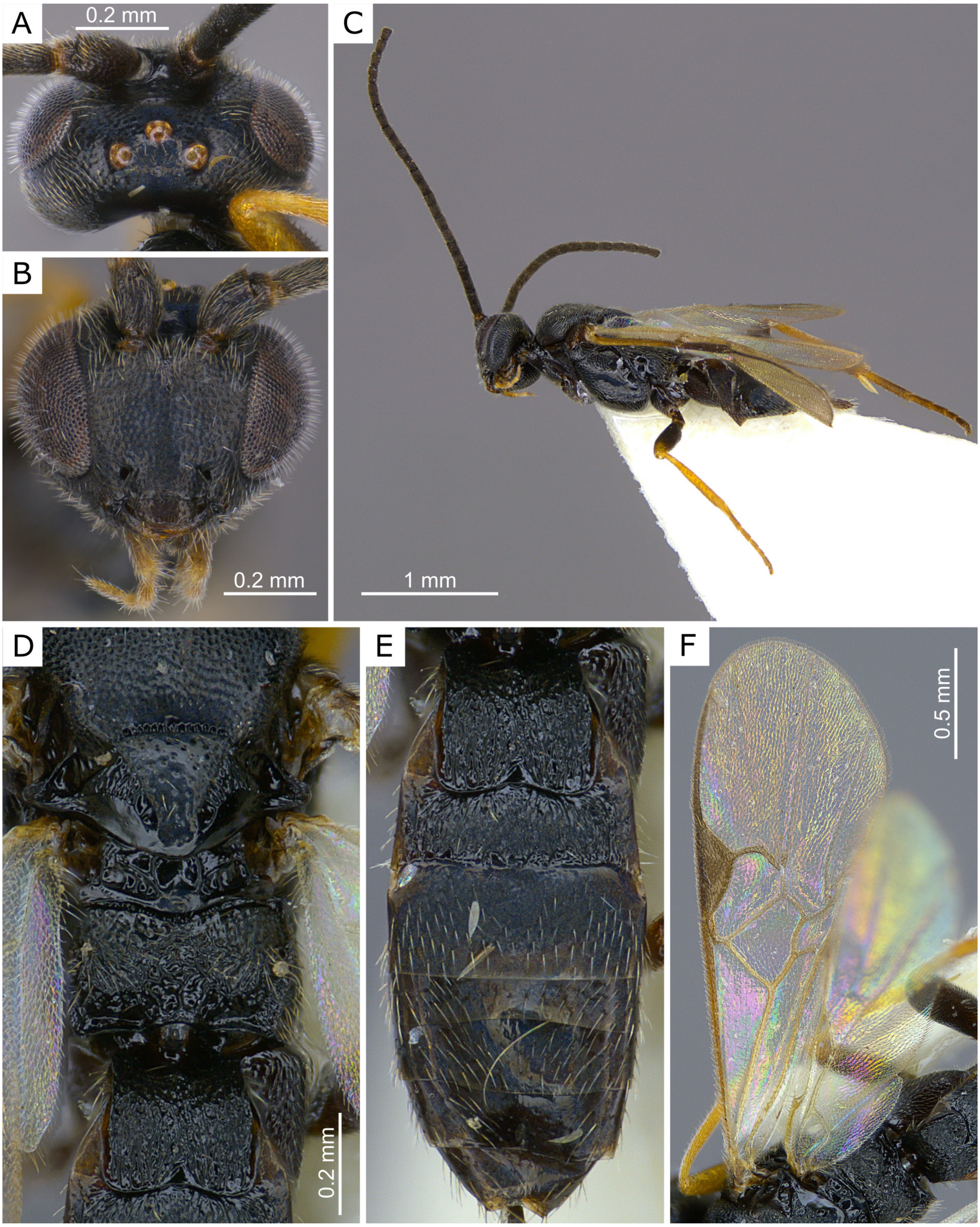

Fig. 57. *Illidops toreicus* Kotenko, 2007, holotype, ♀ (SIZK). **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Lateral view. **D**. Partial mesosoma, dorsal view. **E**. Metasoma, dorsal view. **F**. Fore wing. Body length of the specimen: 2.5 mm.

Sculpture. Head dorsally, clypeus and frontal part of gena (narrow stripe behind eyes) with sparser punctures, more or less shiny. Face and posterior side of gena densely punctured, matte. Scutoscutellar suture narrow, crenulated. Scutellum with punctation less dense than mesoscutum, shiny. Propodeum, T1, T2 densely and softly wrinkled (except for posterior part of propodeum), matte. Metacoxa densely punctated apically, matte, their outer side more sparsely punctured, with satin sheen.

Coloration. Body black. Antennae almost black. Palps and tibial spurs yellowish. Tegulae, R1 and most veins in the middle of the fore wing dark brown. Wings slightly smoky. Legs mostly black. Apices of the front and middle femorae and all of tibiae reddish-brown, apex of metatibia and all tarsi slightly darkened.

Holotype – ♀, Chit. [Chitinsky District, Zabaykalsky Krai, Russia], Daursky Reserve, N[orth] shore of Lake Zun-Torey, tract Irel’zhin, beam, 7.VII 1990 (A.K.) [SIZK].

Illidops urgens Kotenko, 2004

Fig. 58

Illidops urgens Kotenko, 2004: 119–121, fig. 7.

Type material

Holotype

KAZAKHSTAN – **[Aktobe Region]** • ♀; Aktyubinsk Province, Mugodzhary, 25 km north of the settlement Borly, locality of Baymen; [49.44° N, 58.90° E]; 13 Jun. 1985; A. Kotenko leg.; SIZK.

Species concept

Our species concept is based on our examination of photos of the holotype and the information available in Kotenko (2004, 2007). In addition, the species is morphologically very distinct and unlikely to be confused. → ***.

Ecology / host information

Host unknown.

Distribution

PAL: Kazakhstan, Russia (SAR).

Molecular data

No molecular data available.

Remarks

In addition to the holotype, there are at least 5 female paratypes stored at SIZK (Zerova *et al.* 2006).

Original description sensu Kotenko (2004) (translated from Russian and with updated morphological terminology and comments in brackets when our observations did not match Kotenko’s)

Diagnosis. The new species is close to *I. urgo*, from which it differs in having a matte anteromesoscutum, the smooth band posterior to the scutellum interrupted in the middle by a wrinkled area, smooth posterolateral part of scutellum, darkly colored legs, black or dark reddish-brown metacoxa, comparatively more long and narrow T1, and ovipositor almost as long as metatibia [ovipositor and sheaths appearing shorter than metatibia in holotype photos].

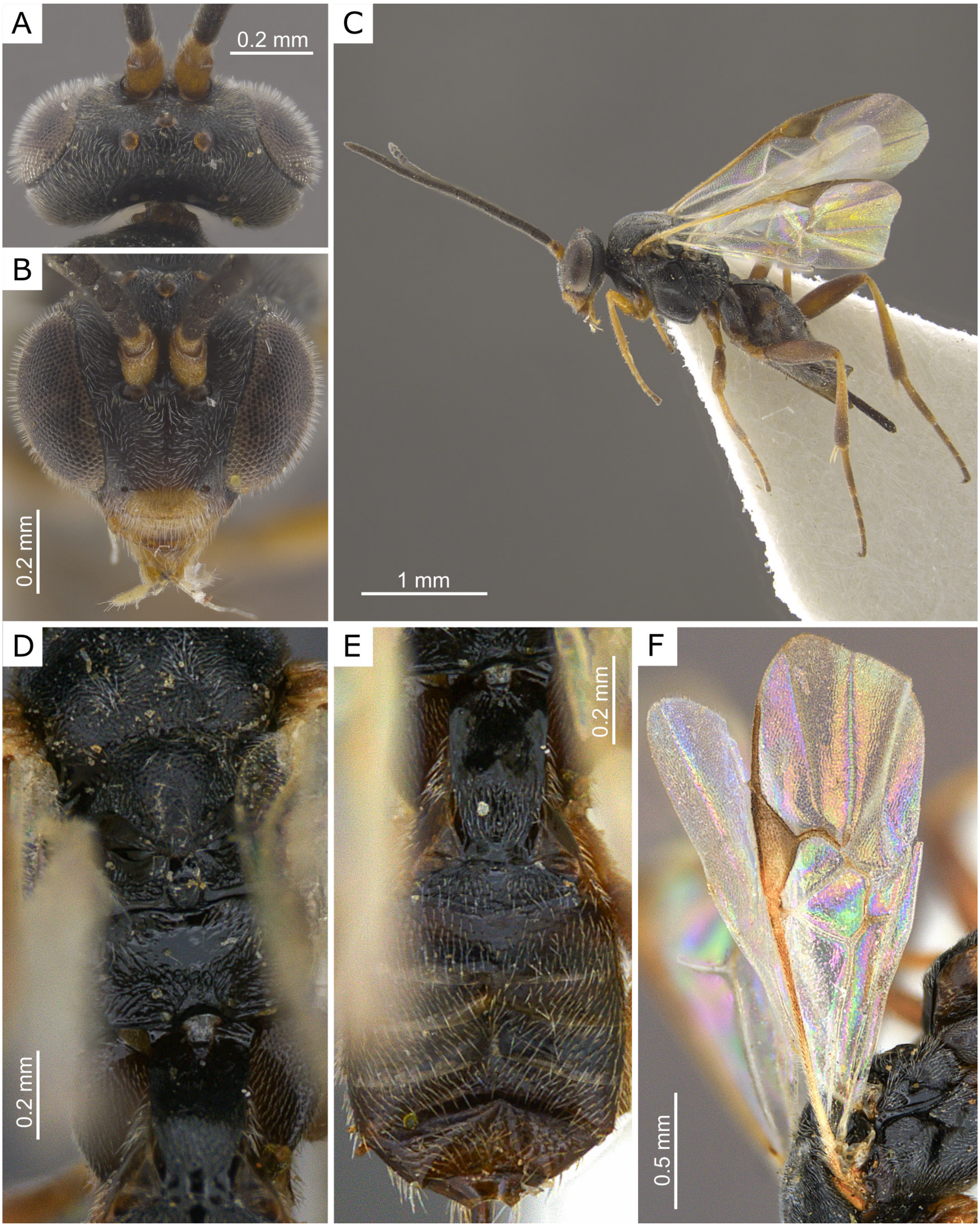

Fig. 58. *Illidops urgens* Kotenko, 2004, holotype, ♀ (SIZK). **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Lateral view. **D**. Partial mesosoma, dorsal view. **E**. Metasoma, dorsal view. **F**. Fore wing. Body length of the specimen: 2.6 mm.

Description. Female. Body length 2.3–2.5 mm. Width of head twice its length [dorsal head width and length], slightly greater than width of anteromesoscutum; head roundly narrowed behind eyes. Ocelli in strongly obtuse triangle [ocelli in high triangle]; tangent to anterior margin of posterior ocelli running along posterior margin of anterior ocellus [imaginary tangent posterior to the anterior ocellus does not touch or cross the posterior ocelli]; POL distinctly greater than OD. Eyes strongly converging downwards, their transverse diameter 1.6 × less than longitudinal diameter and almost twice as long as gena width laterally. Face height with the clypeus slightly more than lower face width. Clypeus shortened, slightly incised along anterior margin, almost straight. Antennae shorter than body; length of F15 around 1.3 × its width. Mesosoma noticeably shorter than metasoma, its length 1.5 × its height. Fore wing equal to or slightly shorter than body; length of pterostigma 2.4 × its width; vein R1 slightly shorter than pterostigma and only slightly longer than distance from its apex to wing apex; vein 1cu-a arising at around middle length of 1st discal cell [vein 1cu-a arising at around basal third of length of 1st discal cell]; hind wing vein cu-a nearly straight. Metatibia noticeably shorter than metatarsus; inner spur of metatibia only slightly longer than outer spur, distinctly shorter than half length of basitarsus; Ratio of metatarsomere lengths as follows 4.3 : 2.1 : 1.4 : 1.0 : 1.3. T1 long and narrow, distinctly narrowed towards apex in posterior (sculpted) part, its length almost twice its maximum width; T2 comparatively large and wide. Ovipositor sheaths equal or slightly shorter than metatibia [ovipositor and sheaths appearing shorter than metatibia in holotype photos].

Sculpture. Face, gena, head dorsally, mesoscutum and scutellum with dense punctures, matte or with slight satin shine. Propodeum weakly sculptured, shining [sculptured, with smooth, shining area anteriormedially]. Basal half of T1 almost smooth and shining, its apical half and most of T2 with identical dense sculpture, with satin sheen; tubercle at base of median field of T2 with smoothed sculpture, shining.

Coloration. Body black, often metasoma (except T1 and T2) dark reddish-brown; antennal flagellomeres black or dark reddish-brown; visible mouthparts, clypeus, scapes and usually pedicels, tegulae, fore and often middle legs light-colored, yellowish-brown or brown; metacoxae black, rarely dark reddish-brown; metafemur brown or dark brown; metatibia brown with darkened apical third [metatibia light/yellow-brownish with darker apical third]; metatibial spurs whitish. Wings slightly milky; pterostigma brown, in basal half and usually along the anterior margin light; vein R1and veins in middle part of fore wing brown.

The male is unknown.

Material. Holotype: ♀, Kazakhstan, Aktobe region, Mugodzhary, 25 km N of Borly settlement, tract Baymen, 13 VI 1986 (A. Kotenko). Paratypes. Kazakhstan, Aktobe region: 1 ♀, labeled as holotype; 1 ♀, Mugodzhary, Shevchenko village, steppe, on spurge [Euphorbia], 14 VI 1986 (A. Kotenko); 1 ♀, Mugodzhary, 25 km W of Yubileyny settlement, 16 VI 1986 (A. Kotenko); 1 ♀, Mugodzhary, western slope of Dva Brata [Екі ағайынды] mountain, 17 VI 1986 (A. Kotenko). Russia: 1 ♀, Saratov Region, vicinity of Ozinki, Blue Mountains, 27 V 1986 (A. Kotenko).

Illidops urgo (Nixon, 1965)
Figs 59–60

Apanteles urgo Nixon, 1965: 182, fig. 204.

Other material examined

GREECE – **Crete** • 1 ♂; Canea; 6 Jul. [year unknown]; Biró leg.; J. Papp det. 1974; CNC, CNCHYM 01529.

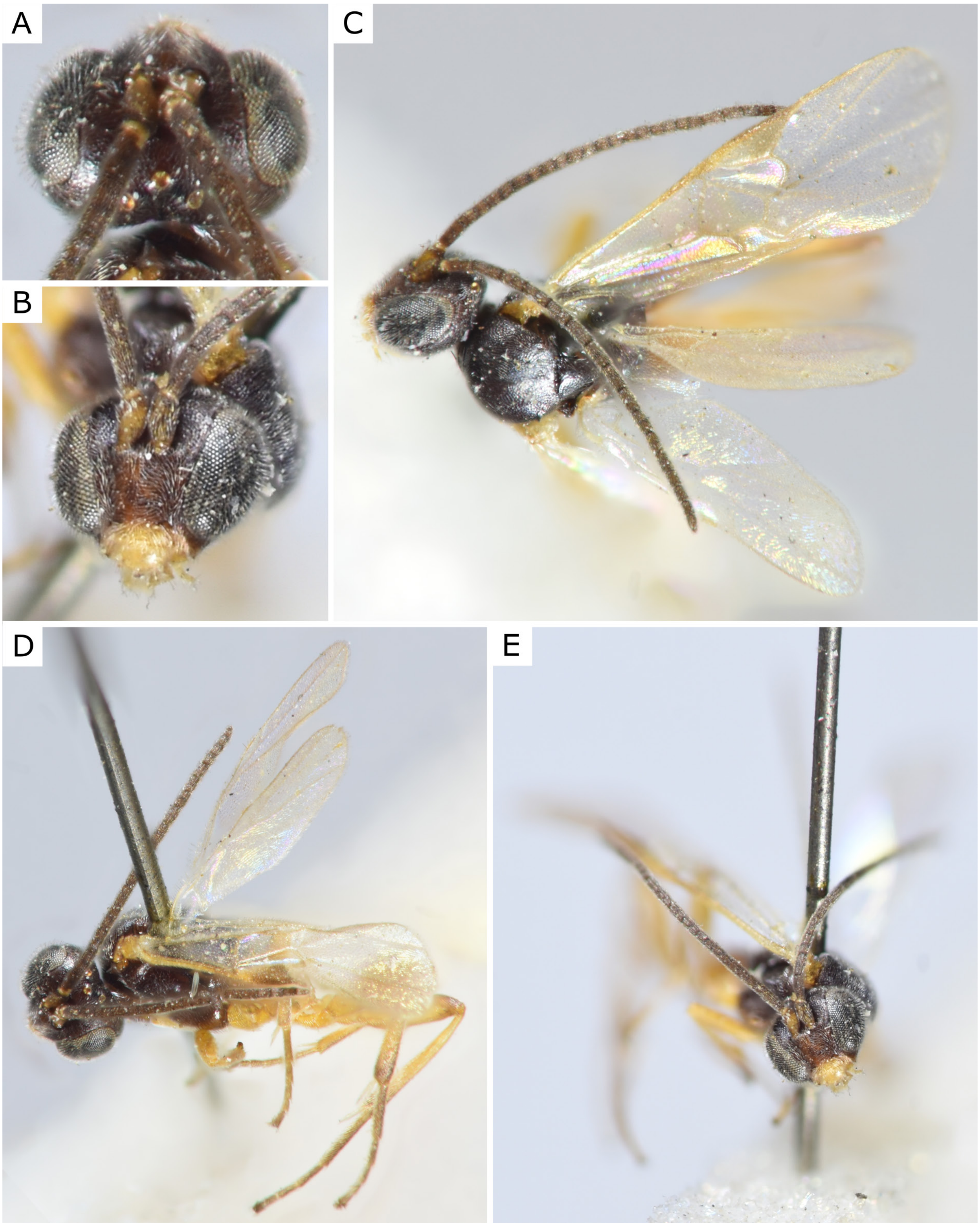

Fig. 59. *Illidops urgo* (Nixon, 1965), holotype, ♀ (HNHM). **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Wing and mesosoma, dorsal view. **D**. Head, dorsal view. **E**. Head and antennae, frontal view. Body length of the specimen [from original description]: ca 2.3 mm.

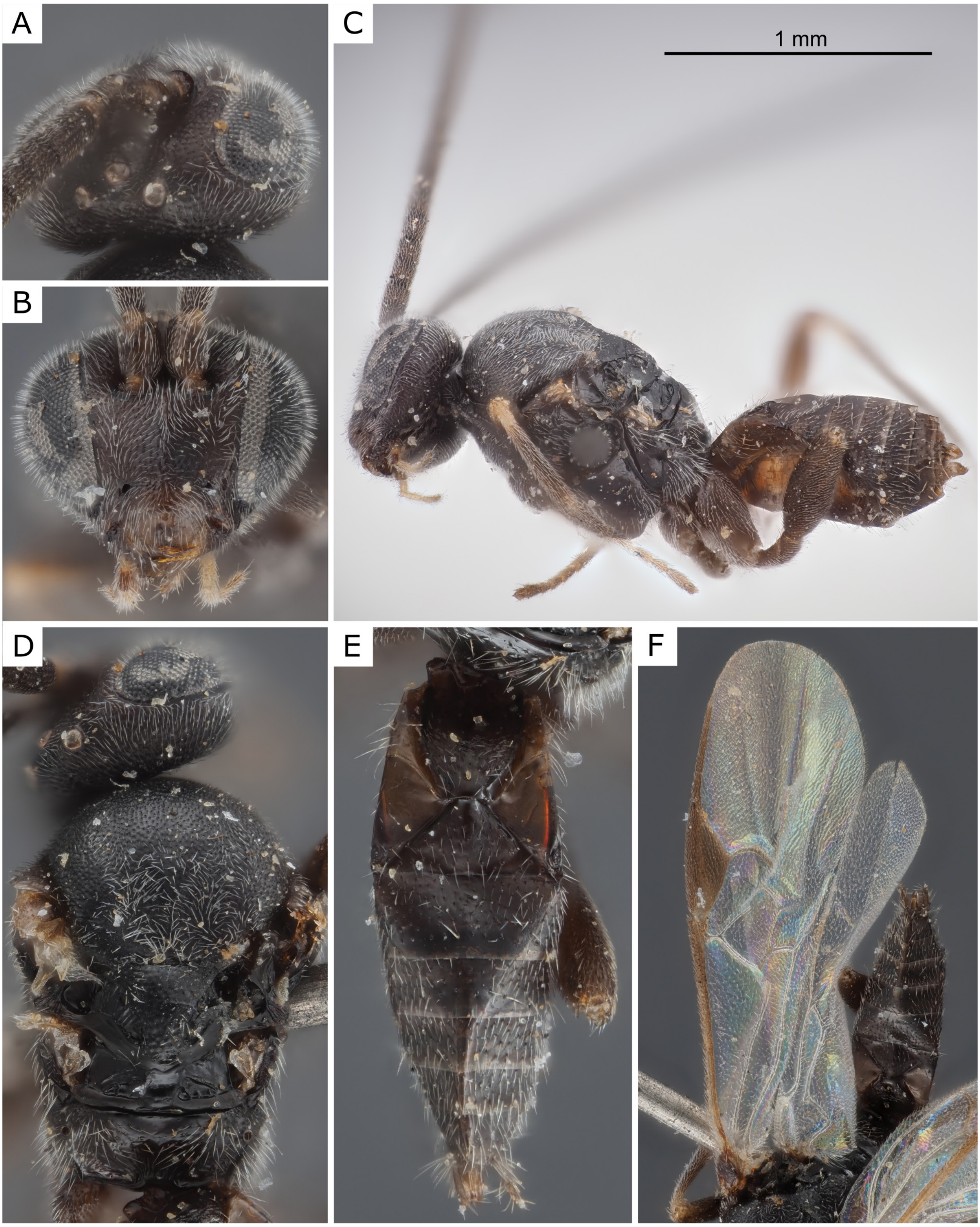

Fig. 60. *Illidops urgo* (Nixon, 1965), ♂ (CNCHYM 01529), det. J. Papp. **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Lateral view. **D**. Partial mesosoma, dorsal view. **E**. Metasoma, dorsal view. **F**. Fore wing. Body length of the specimen: 2.3 mm.

Species concept

Our species concept is based on our examination of habitus photos of the female holotype and the information available in Nixon (1965, 1976), Papp (1981), Kotenko (2007), and Tobias & Kotenko (1986). In addition, the species is morphologically very distinct and unlikely to be confused → ***.

Ecology / host information

Host unknown.

Distribution

PAL: Armenia, Azerbaijan, Croatia, Greece, Hungary, Iran, Mongolia, Russia (S), Slovakia, Turkey.

Molecular data

One sequence was retrieved via sequencing of a male specimen available at the CNC which was identified by Papp. When entering the sequence into the BOLD identification engine, the sequence most closely matches (maximum 94.7% barcode similarity) some sequences of specimens from Canada collected in British Columbia. These specimens cluster in BIN BOLD:ACL9661 but the single female specimen with photos available does not at all show any of the rather distinct coloration of *I. urgo*. First, it should be noted that the match between the low-quality sequence of CNCHYM01529 and the Canadian specimens is quite low and both might very well represent different species. Specimens of no other barcoding cluster were found to match the morphology of *I. urgo*. Secondly, the male specimen identified by Papp may very well be misidentified as sexual dimorphism in *Illidops* is quite strong. It might be the case that Papp identified the specimen based on its collection locality from Crete (Biró), which is where the holotype of *I. urgo* was collected. For another such case where Papp apparently matched male and female specimens mostly based on the collection locality, compare the remarks section for *I. barcinonensis*. Summarizing this, we currently cannot match this species reliably with any DNA sequences, but as reference our sequence of CNCHYM01529 mapped to ZSM-HYM-33161-C11 is provided as a fasta file in Supp. file 11. It should be noted that this sequence is of very poor quality and we are not certain about its accuracy and the accuracy of the identification of the male specimen as *I. urgo*.

Remarks

Holotype female, HNHM. Country of type locality: Greece.

Illidops vitobiasi Kotenko, 2004

Fig. 61

Illidops vitobiasi Kotenko, 2004: 119, figs 1–6.

Type material

Holotype

TURKMENISTAN – **[Lebap Region]** • ♀; Repetek [Repetek Biosphere State Reserve?]; [38.61° N, 63.21° E]; sands; 27 Apr. 1992; A. Kotenko leg.; SIZK.

Species concept

Our species concept is based on our examination of photos of the holotype and the information available in Kotenko (2004, 2007) → ***.

Ecology / host information

Host unknown.

Distribution

PAL: Turkmenistan.

Molecular data

No molecular data available.

Remarks

In addition to the holotype, there are 5 female and 2 male paratypes stored at SIZK (Zerova *et al.* 2006).

Original description sensu Kotenko (2004) (translated from Russian and with updated morphological terminology and comments in brackets when our observations did not match Kotenko's)

Diagnosis. The new species is most similar to *Illidops electilis*, but differs from it by eyes more strongly converging downwards, usually more articulated sculpture of the propodeum, short and wide T1 and shorter ovipositor sheaths.

Description. Female. Body length 2.3 mm. Width of head almost 2 × its length [in dorsal view head width versus head length], slightly wider than width of mesonotum; head behind eyes comparatively sharply roundly narrowed [in dorsal view head behind eyes comparatively narrow]. The occiput is rather strongly concave. Ocelli arranged in a strongly obtuse triangle [ocelli in high triangle]; tangent to the anterior margin of the posterior ocelli passing along the posterior margin of the anterior ocellus [imaginary tangent posterior to the anterior ocellus does not touch or cross the posterior ocelli]; POL distinctly greater than OD. Eyes noticeably converging downwards, their transverse diameter 1.6 × less than longitudinal diameter, and almost 2.0 × longer than length of gena (laterally). Face with longitudinal median elevation, which is more distinct before frons. Height of the face with the clypeus approximately equal to its width at its lower part. Clypeus well separated, shortened, with dense setae, almost straight along the front margin. Antennae shorter than the body; length of F15 1.5 × as long as its width. Mesosoma slightly shorter than metasoma, its length 1.3 × its height. Fore wing length 1.3 × hind wing length, approximately equal in length to the body; length of pterostigma 2.3 × its width; vein R1 shorter than pterostigma length and noticeably shorter than the distance from the apex of the R1 to the apex of the wing; vein 1cu arising around the middle of the 1st discal cell; hind wing vein cu-a almost straight. Metatibiae slightly shorter than metatarsi; inner spur of metatibia not longer than outer, distinctly shorter than half of basitarsus; Ratio of metatarsomere lengths as follows 4.4 : 2.1 : 1.4 : 1.0 : 1.3. T1 short and wide, its length 1.2 × its maximum width; T2 large and wide. Ovipositor sheaths relatively short, their visible part barely longer than half length of metatibia.

Face, gena, and head dorsally with shallow sculpture, slightly shiny; occiput densely wrinkly-sculptured, matte. Mesoscutum and scutellum densely punctured, with slight satin shine, almost matte. Propodeum along anterior margin and in postero-lateral corners sculptured, matte, in middle part with smoothed sculpture and more or less shiny; propodeum often softly sculpted and matte. T1 and T2 equally densely sculptured, matte.

Body black; antennae and palps reddish-brown or brown; tegulae and legs (except mostly black metacoxa) yellowish-brown or brown; metatibial spurs whitish; wings very faintly yellowish; pterostigma light brown, usually in the basal half and along the anterior margin lighter; vein R1 and veins in the middle part of the fore wing light brown or brownish-yellow.

Male. It differs from female by longer (longer than body) antennae and darker coloration of legs (metafemur, apical half of middle and metatibiae, and metatarsus darkened).

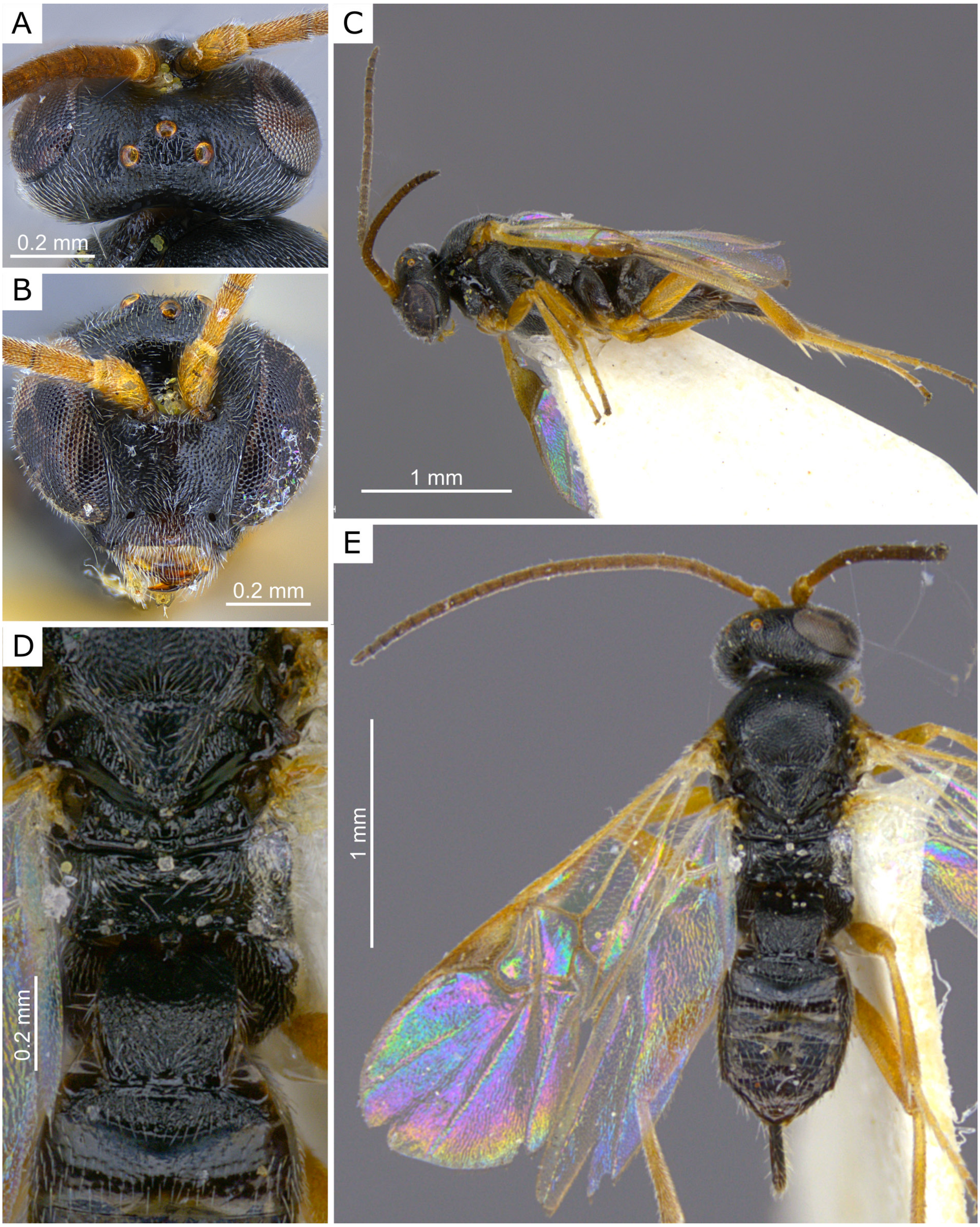

Fig. 61. *Illidops vitobiasi* Kotenko, 2004, holotype, ♀ (SIZK). **A**. Head, dorsal view. **B**. Head, frontal view. **C**. Habitus, lateral view. **D**. Partial meso- and metasoma, dorsal view. **E**. Habitus, dorsal view. Body length of the specimen: 2.3 mm.

Material. Holotype: ♀, Turkmenistan, Repetek, sands, 27 IV 1992 (A. Kotenko). Paratypes. Turkmenistan: 5 ♀♀, 2 ♂♂, labeled as in the holotype; 1 ♀, Repetek, ridge sands, white saxaul, ephedra, 9 IV 1993 (V. Perepechaenko).

Hosts of Illidops

Only a few species of *Illidops* have associated host information. We went through all of the literature available to us and collected the information in Table 9. This information needs to be interpreted carefully (Shaw 2023).

DNA barcoding and COI sequence analysis of Illidops

A total of 13 out of 32 Holarctic species of *Illidops* are currently linked to DNA barcode sequences. From these, eight show significant cryptic diversity and are only tentatively associated with one or several barcoding clusters, and one additional sequence is of very low quality (*I. urgo*). We performed a NJ analysis of the Holarctic COI sequences of Microgastrinae in BOLD, including only the longest sequence per BIN. With this method, we found a larger cluster which we associate with *Illidops* and another cluster which contains *I. albostigmalis* and *I. mutabilis* (see Supp. file 10). In total, 50 different BINs in the Holarctic were associated with *Illidops* in the BOLD database. Of these, 29 BINs include sequences linked to voucher specimens stored in the collections accessible to us, 14 BINs include sequences which are publicly available, often with associated images, and 7 BINs include only private data. By reviewing the BIN pages and the information on Nearest Neighbors (NN), we found nine additional BINs potentially linked to *Illidops*, but we do not have access to these sequences and BINs. For most of the BINs listed below, we were able to observe voucher specimens, or at least photos of the vouchers, but we did not have access to voucher specimens of all BINs.

BIN distances in *Illidops*

In general, we observed that the overall COI divergence between the BINs of *Illidops* is higher than in other genera of Microgastrinae (see Table 10 for p-distances). The distance to the NN in our dataset ranges between 10.18% in *I. albostigmalis* and 1.18% in *I. doreenae* sp. nov. However, the low distance in *I. doreenae* sp. nov. represents the distance between both BINs currently associated with this species.

Neighbor-Joining topology of *Illidops*

Our Neighbor Joining (NJ) analyses of the partial cytochrome c oxidase subunit I (COI) gene for the Holarctic diversity of microgastrinae wasps show *Illidops* as potentially polyphyletic, with *I.* cf. *mutabilis* and *I. albostigmalis* clustering apart from a different, larger cluster of other species of *Illidops* (e.g., Supp. file 10). Neighbor Joining analyses of our *Illidops* data (Fig. 62, Supp. file 4) supports the results of the BIN approach as most species and BINs show high bootstrap values. *Illidops stefanschmidti* Höcherl & Fernandez-Triana sp. nov. and *I. scutellaris* appear as sister taxa, as well as *I. butalidis* and an unidentified BIN BOLD:AAK1598 from Canada, and *I. mutabilis* and *I. albostigmalis*. The NJ topology also clearly shows the most divergent species, with *I. butalidis* and *I. sophrosine* (pink coloration) showing high intraspecific divergence and being represented by various BINs. The same is true for the clusters tentatively associated with *I. naso* (blue) and *I. suevus* (green), which do not appear as sister taxa to each other.

Discussion

This study provides the first comprehensive revision of the genus *Illidops* in the Holarctic in over 35 years, including an updated generic concept and a key to the species. In addition, many species concepts are updated, DNA barcodes, type localities, citations and translations of original descriptions are provided in a single manuscript, primary types and many additional specimens illustrated, and three new species are described.

Table 9. Hosts of different species of *Illidops* Mason, 1981, including the source of the information and comments regarding the reliability of the information.

Parasitoid species	Host family	Host species	Reference	Comments
Illidops albostigmalis	Crambidae	*Prophantis* sp.	Fernandez-Triana & van Achterberg (2017: 297) original description	Two male specimens from Yemen (Hammam ‘Ali) reared from *Prophantis* sp. (Crambidae), ‘coffee berry moth’. Both are not types.
Illidops butalidis	Scythrididae	*Scythris fuscoaenea*	Wilkinson (1945: 196), redescription	Holotype reared from this host.
		Scythris picaepennis	Wilkinson (1945: 196), redescription	Many specimens (>100) reared by R.L.E. Ford.
Illidops kostjuki	Tortricidae	*Aphelia stigmatana*	Tobias & Kotenko (1986: 56), original description	This information likely refers to type material, but no details are provided.
Illidops mutabilis	?Pyralidae	*?Etiella zinckenella*	Tobias & Kotenko (1986: 753)	This is not a record from type material. The association first appears here and it is unclear how it was made.
Illidops cf. naso BOLD:AEI9858	?Gelechiidae	*?Aroga velocella*	Specimen ZSM-HYM-42448-E05	Host not preserved as voucher, but reared by Tina Schulz, a lepidopterist.
Illidops planiscapus	?Crambidae	*?Talis quercella*	Tobias (1976: 49) original description	Question mark in front of Tobias’ identification, this association is very uncertain.
Illidops scutellaris	Gelechiidae	*Phthorimaea operculella*	Muesebeck (1921: 534), original description, plus host info on paratype.	“Four female and three male specimens bred by J.E. Graf [...]”.
Illidops suevus	Psychidae	*Rebelia* sp.	Papp (1984: 288)	Based on rearing experiments by Dr L. Gozmány in Montenegro.
		?Epichnopterix sp.	Nixon (1976: 713)	Information on junior synonym *A. dion*, non-type material.
Illidops terrestris	Pyralidae	*Elasmopalpus lignosellus*	Wharton (1983: 669)	Holotype reared ex. *E. lignosellus* on peanuts, other specimens ex. *Elasmopalpus* sp. on cowpeas.

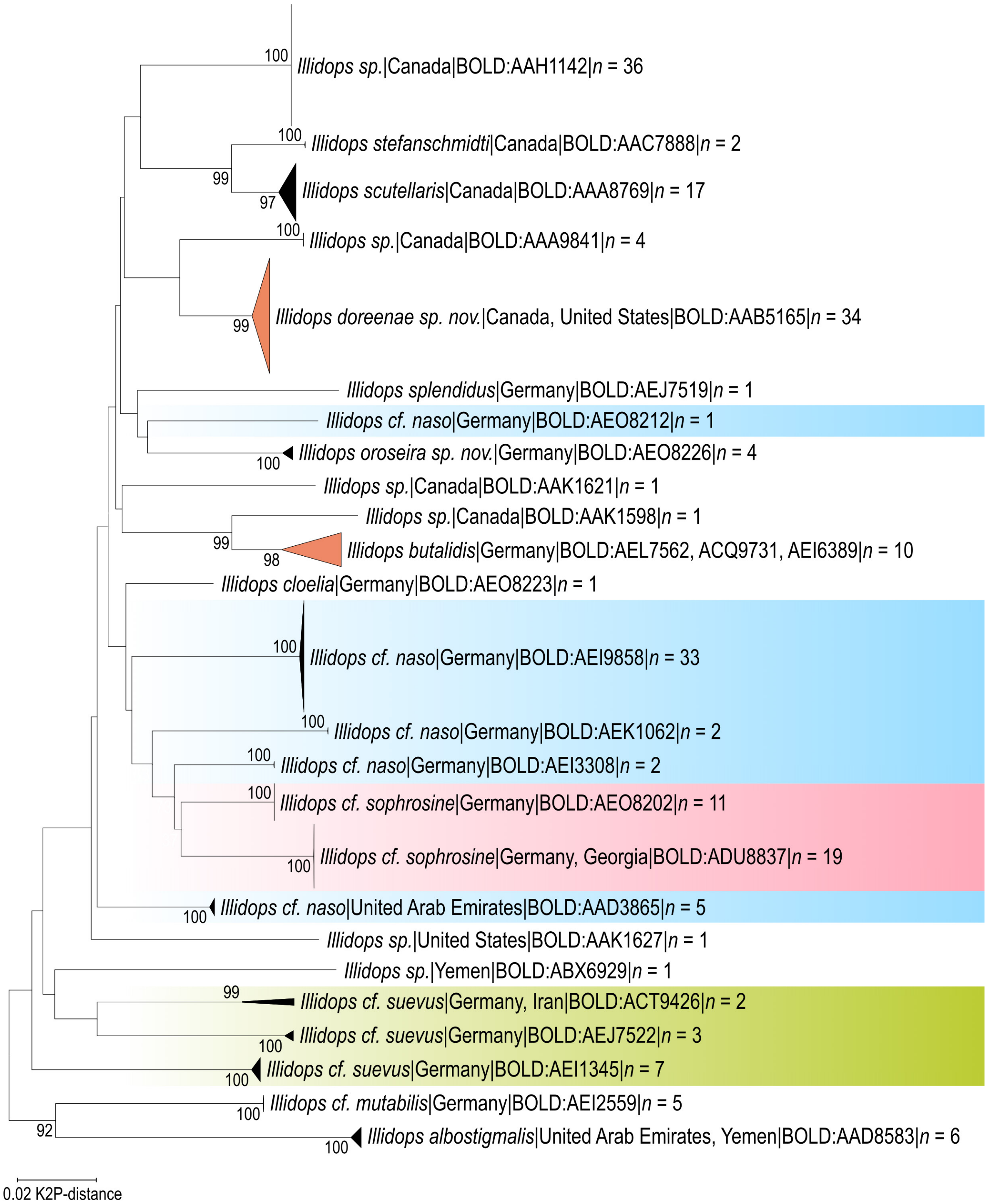

Fig. 62. Neighbor Joining (NJ) topology of the COI barcoding region of our dataset based on Kimura 2-parameter distances and with 1000 bootstrap replicates. The topology includes all sequences from specimens morphologically identified as members of *Illidops* Mason, 1981. Triangles show the relative number of individuals sampled (height) and sequence divergence (width). Orange coloration indicates species associated with sequences that have a maximum within-cluster distance > 2.2%. Numbers next to nodes represent non-parametric bootstrap values > 90% (10 000 replicates). The aligned sequences and NJ complete topology can be reviewed in Supp. file 3 and Supp. file 4.

Table 10 (continued on next page). Publicly available Holarctic BINs from the BOLD database which we associated with *Illidops* Mason, 1981 and their Nearest Neighbor BINs (NN). P-distances and number of specimens (n) of the BINs treated here, retrieved on 19 Dec. 2024. Entries are ordered from highest to lowest minimum NN p-dist. BINs retrieved only from publicly available sequences are marked by an asterisk (*). For public BINs where the identification differed but which we consider to be part of *Illidops*, the identification in the database is added in brackets.

Identification	BIN [BOLD:]	Number of specimens (n)	Average p-dist.	Max. within-BIN p-dist.	minimum NN p-dist.	NN	Number of specimens (n)	NN max. within-BIN p-dist
Illidops albostigmalis	AAD8583	53	0.53	1.89	10.18	ADG0707	1	n/a
Illidops sp.	ABX6929	1	n/a	n/a	10	ADZ9328	3	0.64
Illidops cf. *mutabilis*	AEI2559	5	0	0	8.86	ACV4289	23	2.44
Illidops cf. *terrestris*	ABY3260	4	0.32	0.64	8.51	ABA4355	1	n/a
Illidops sp.	AAK1627	1	n/a	n/a	8.29	AAD3865	5	1.44
Illidops cf. *suevus*	AEJ7522	3	0.21	0.32	7.53	AFN8552	9	1.61
Illidops sp.	AAK1621	1	n/a	n/a	7.37	ACL9661	5	1.42
Illidops sp. [*Rhygoplitis* sp.]	ACA6442	1	n/a	n/a	7.07	AAC0735	261	1
Illidops cf. *naso*	AEK1062	2	0	0	7.05	AEO8223	2	0
Illidops cf. *naso*	AEO8212	2	0	0	6.89	AFN9174	3	0
Illidops cf. *naso*	AEI9858	34	0.18	0.96	6.73	AEO8223	2	0
Illidops splendidus	AEJ7519	1	n/a	n/a	6.58	ABA4355	1	n/a
Illidops oroseira sp. nov.	AEO8226	4	0.16	0.32	6.56	ACP4312	1	n/a
Illidops sp. [Microgastrinae]	AAH1025	2	1.38	1.38	6.41	AEV8845	4	1.12
Illidops sp.	AAH1142	37	0.15	0.94	6.41	AET9368	2	1.45
Illidops sp.	ACP4312	1	n/a	n/a	6.27	AEA1257	7	0
Illidops sp.	AAK1598	1	n/a	n/a	6.09	AEI6389	5	0.78
Illidops sp.	AAH1044	4	0	0	5.77	AAF9897	11	0.78
Illidops sp. [Microgastrinae]	ACO0671	4	0	0	5.61	AAK4166	24	0.72
Illidops sp. [Microgastrinae]	ADY9461	1	n/a	n/a	5.54	ACT9426	2	2.03
Illidops cloelia	AEO8223	2	0	0	4.81	AEI3308	2	0
Illidops cf. *suevus*	ACT9426	2	2.03	2.03	4.8	ADZ9328	3	0.64
Illidops cf. *sophrosine*	AEO8202	12	0.03	0.16	4.3	AAK4166	24	0.72
Illidops sp.	AAK4166	24	0.13	0.72	3.76	AEI3308	2	0
Illidops cf. *naso*	AEI3308	2	0	0	3.76	AAK4166	24	0.72
Illidops sp.	AEA1257	7	0	0	3.37	AAD3865	5	1.44
Illidops sp.	AAA9841	5	0.13	0.32	3.24	ACL9661	5	1.42
Illidops sp. [Microgastrinae]	AAZ8761	1	n/a	n/a	3.09	AEI1345	5	1.12
Illidops cf. *suevus*	AEI1345	5	0.5	1.12	3.09	AAZ8761	1	n/a
Illidops sp.	AFB2959	4	0	0	2.88	AFN9174	3	0
Illidops butalidis	AEI6389	5	0.27	0.78	2.72	ACQ9731	7	0.17
	AEL7562	2	0	0	1.34	ACQ9731	7	0.17
	ACQ9731	7	0.05	0.17	1.34	AEL7562	2	0

Table 10 (continued). Publicly available Holarctic BINs from the BOLD database which we associated with *Illidops* Mason, 1981 and their Nearest Neighbor BINs (NN). P-distances and number of specimens (n) of the BINs treated here, retrieved on 19 Dec. 2024. Entries are ordered from highest to lowest minimum NN p-dist. BINs retrieved only from publicly available sequences are marked by an asterisk (*). For public BINs where the identification differed but which we consider to be part of *Illidops*, the identification in the database is added in brackets.

Identification	**BIN [BOLD:]**	**Number of specimens (n)**	**Average p-dist.**	**Max. within-BIN p-dist.**	**minimum NN p-dist.**	**NN**	**Number of specimens (n)**	**NN max. within-BIN p-dist**
Illidops sp.	AAF9897	11	0.4	0.78	2.69	AAH1052	3	1.18
Illidops sp.	AAH1052	3	0.79	1.18	2.69	AAF9897	11	0.78
Illidops sp.	ABA4355	1	n/a	n/a	2.46	ACL9661	5	1.42
Illidops sp.	ACL9661	5	0.6	1.42	2.46	ABA4355	1	n/a
Illidops cf. *naso*	AAD3865	5	0.71	1.44	2.37	AEA1257	7	0
Illidops stefanschmidti sp. nov.	AAC7888	3	0	0	1.85	AET9368	2	1.45
Illidops cf. *sophrosine*	ADU8837	20	0.16	0.8	1.76	AEI2994	2	0
Illidops sp.	AAA8769	21	0.2	1.33	1.44	AFQ9589	1	n/a
Illidops doreenae sp. nov.	AAB5165	26	0.6	2.14	1.18	ACL9543	13	1.02
	ACL9543	13	0.5	1.02	1.18	AAB5165	26	2.14

Hosts of *Illidops*

Only a few species of *Illidops* have host information associated and the information available needs to be interpreted very carefully as we were unable to verify the material ourselves in most cases (Shaw 1994, 2023). We consider some of the information of the following records as relatively trustworthy, for example the Scythrididae host for *I. butalidis*, the Psychidae host for *I. suevus*, the Pyralidae host for *I. terrestris*, and the Gelechiidae host for *I. scutellaris*. All host records indicate quite a broad general host spectrum for *Illidops* (although that could also be a reflection of our poor understanding of the genus). The host species in question have no ecological similarities that we were able to observe. Some of them (*Phthorimaea operculella*, *Elasmopalpus lignosellus*) are agricultural pests, indicating that *Illidops* species may have some relevance in pest control.

Molecular analyses using the COI barcoding gene in *Illidops*

In general, we found a high overall divergence between the BINs of *Illidops* (up to 10% p-distance or more), even among morphologically very similar specimens (e.g., *Illidops suevus* and *I. naso*). In other genera, we often observe much lower interspecific p-distances (minimum p-distance of a BIN to NN), e.g., *Cotesia risilis* (1.12%), *Cotesia eulipis* (1.18%), and *Glyptapanteles vitripennis* and *G. liparidis* (2.13%, Höcherl *et al.* 2024). Since many BINs we associate with *Illidops* currently remain unidentified, it is difficult to make conclusions about the interspecific and intraspecific variability. We can only speculate on whether this due to the rather reduced morphology of the genus, poor taxon sampling in *Illidops* compared to other genera of Microgastrinae, or if it represents a true effect. Potential issues caused by *Wolbachia* infections or mitochondrial heteroplasmy should also be investigated and additional, nuclear markers should be tested in this context (e.g., Hurst & Jiggins 2005; Kaczmarczyk-Ziemba *et al.* 2025). Significantly varying COI distances between taxa have been observed for other groups (Schmidt *et al.* 2017; Schütte *et al.* 2023) and it may be of relevance to consider this for future efforts in this genus.

We attempted phylogenetic analyses using our data of the partial COI gene, but our analyses were inconclusive and with low support. Taking our attempts, the high p-distances in our sample as well as known factors limiting this marker's usefulness in phylogenetic analyses into account (Ballard & Whitlock 2004; Hurst & Jiggins 2005; Simon *et al.* 2006; Kaltenpoth *et al.* 2012; Mutanen *et al.* 2016; Hebert *et al.* 2023; Kaczmarczyk-Ziemba *et al.* 2025), COI seems to be ill-suited for phylogenetic inference here. Overall, additional genetic markers, deeper taxon sampling and phylogenetic methods will be required to resolve these open questions.

***Illidops* as a dark taxon**

With an estimated overall diversity of more than 50 species for the genus compared to the 37 described species listed in the latest catalogue (Fernandez-Triana *et al.* 2020), *Illidops*, by numbers alone, would not qualify as a dark taxon sensu Hartop *et al.* (2022). Nonetheless, it meets several typical criteria of dark taxa: being small, morphologically cryptic, taxonomically neglected (in terms of larger-scale revisions, Hausmann 2020; Chimeno *et al*. 2022), and, in particular, having the majority of DNA-barcode sequences available in databases not linked to any species names (Page 2016). It also exemplifies additional challenges that are partially unique to the European and Palearctic fauna. First, the concept of the genus is still weak and is likely going to be subject to change in the future. This is probably due to historical reasons, such as the genus being described based on only three species, as well as the fact that some related genera such as *Dolichogenidea* are not resolved. *Dolichogenidea* appears polyphyletic not only in COI-based analyses (Fernandez-Triana *et al.* 2025), but also in ongoing analyses based on UCEs (ultraconserved elements) (Fernandez-Triana, pers. obs.). This is also the case in other genera of Microgastrinae, such as *Sathon*, *Glyptapanteles* and *Parapanteles* (Fernandez-Triana *et al.* 2020; Parks *et al.* 2020), pointing out the dire need of a robust molecular phylogeny of Microgastrinae.

Additional factors complicate taxonomic progress: *Illidops* is also affected by fragmented and incomplete keys in various languages, which include 8–12 (Nixon 1965, 1976; Papp 1981; Kotenko 2007) and at most 20 (Tobias & Kotenko 1986) out of 30 previously known Holarctic species at once. In addition, original descriptions are often incomplete and type material is scattered or potentially lost. Most species of *Illidops* are only known from the holotype or the type series and from a narrow geographic range, meaning we often know little about intraspecific variation of the morphological characters used for species' identification. In addition, some species of *Illidops*, such as *I. naso* or *I. suevus*, show significant morphologically cryptic diversity, in combination with these particular species having many junior synonyms. This complicates linking freshly collected material to existing names and makes it particularly challenging to untangle these complexes.

The lack of host data and rearing records in *Illidops* is quite significant and difficult to resolve. Although DNA-based methods for recovering host-parasitoid-interactions are available (Wolz *et al.* 2024), they are still expensive and not as exact as accurate rearing experiments. Reliable historical parasitoid-host data used in an integrative taxonomy approach has proven very efficient in connecting historical names with DNA barcodes in the past (Shaw 2023) and also contributed to more reliable associations of male and female specimens in historical species descriptions, such as in *I. butalidis* (Wilkinson 1945). This showcases the value of host information for parasitoid taxonomy and the impact which the lack of this has on our understanding of *Illidops* and similar taxa. Sexual dimorphism is quite strongly developed in *Illidops*, which has likely affected nomenclature due to dubious synonymization in several cases, such as *A. rhamphus* as a junior synonym of *I. barcinonensis*. Some names in *Illidops* are linked to non-reared male holotypes, one particularly problematic case being *I. naso* with its many synonyms and cryptic diversity. Linking recently collected specimens to these names or verifying synonyms will be a considerable challenge in the future.

In our opinion, *Illidops* is not one of the darkest taxa in terms of undiscovered diversity. There are likely more new species to be discovered in the Holarctic region in the future, but probably around half of the Holarctic diversity is already described. In contrast to other dark taxa, the main challenge for *Illidops* lies not in the diversity (Hartop *et al.* 2022), specimen size, or even the crypsis (Hausmann *et al.* 2020; Chimeno *et al.* 2022) of the taxon. The main challenge in tackling this taxon is the existence of often incomplete and convoluted historical information which impedes linking historical names to freshly collected material and modern methodologies, such as DNA barcoding. This 'historical backlog' is mostly unique to Europe, the Palearctic and Holarctic regions – all with relatively well-studied faunas – and comprises a dimension of dark taxa that represents an additional major hurdle to overcome which cannot be solved alone by making species descriptions or specimen processing more efficient.

Potential directions for future work

Evidently, many other authors have encountered similar problems in other European and Western Palearctic taxa and explored different ways, including enormous efforts in integrative taxonomy, to deal with this historical backlog (e.g., Awad *et al.* 2023; Johansson 2024; Vogel *et al.* 2024; Johannson & Astafurova 2025). In addition to locating and studying historical material morphologically, sequencing type material, including holotypes, may be the key to linking historical names to molecular data. We tested a shotgun-sequencing approach for historical specimens (partially male paratypes) and were able to retrieve reliable sequences for the COI barcoding region for three out of four specimens. Other protocols for sequencing historical specimens have been successful in retrieving complete mitochondrial genomes and/or partial mitochondrial and nuclear genes (Raxworthy & Smith 2021; Chang *et al.* 2024). Large-scale species discovery protocols (Hartop *et al.* 2022; Meier *et al.* 2024) also enhance progress in taxa such as *Illidops* even in regions with better documented diversity. By efficiently producing a large number of specimens available for study, these protocols improve our grasp on sexual dimorphism, rare MOTUs, and intraspecific variability. This could also open the doors for additional morphological approaches, which were so far unavailable due to requiring a higher number of sequenced specimens per MOTU. These include morphometrics, wing interference patterns (e.g., Vogel *et al.* 2024), or morphological characters of male specimens, including male genitalia (Nixon 1965; Williams 1988; Maetô 1996), which might provide useful information in differentiating cryptic species.

With this study, we hope to provide a first step in improving the understanding of *Illidops* by using all of the information available to us and assembling a key to the species of the Holarctic region. Some of our species concepts are very weak or only based on literature and we attempted to account for this by using a system which points out the more poorly or very poorly understood species to the user at first glance. While this is a rather preliminary and rudimentary system, more sophisticated, standardized and detailed scoring systems, as employed by other authors (e.g., Shaw 2023 for quality of host data) will be necessary in the future. Examining all primary types and additional specimens in person is usually regarded as the gold standard in taxonomic revisionary work; however, this approach is not always possible due to limited resources and time, and often considerably slows taxonomic progress. We aimed to responsibly find a pragmatic solution for *Illidops* by using type images, compiling all the information available, as well as highlighting problematic taxa at first glance, but including them anyway and proceeding to publish our collected insights without having access to all relevant information. We hope that our pragmatic yet detailed approach will be a first step and facilitate future work and advances in the knowledge about this challenging group of parasitoid wasps.

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References

Abdoli P., Talebi A.A., Kavallieratos N.G., Khosravi R. & Bidari F. 2024. Contribution to the phylogeny of Microgastrinae (Hymenoptera: Braconidae) based on mitochondrial COI and nuclear 28S rDNA genes, with comments on the identity of *Pholetesor circumscriptus* (Nees, 1834). *Journal of Insect Biodiversity and Systematics* 10 (4): 965–981. https://doi.org/10.61186/jibs.10.4.965

Awad J., Krogmann L. & Talamas E. 2023. Taxonomic history and review of the Förster genera of Platygastridae (Hymenoptera: Platygastroidea). *European Journal of Taxonomy* 875: 1–46. https://doi.org/10.5852/ejt.2023.875.2137

Ballard J.W.O. & Whitlock M.C. 2004. The incomplete natural history of mitochondria. *Molecular Ecology* 13 (4): 729–744. https://doi.org/10.1046/j.1365-294X.2003.02063.x

Banks J.C. & Whitfield J.B. 2006. Dissecting the ancient rapid radiation of microgastrine wasp genera using additional nuclear genes. *Molecular Phylogenetics and Evolution* 41 (3): 690–703. https://doi.org/10.1016/j.ympev.2006.06.001

Beaudin M., Höcherl A., Boudreault C., Cullingham C.I., Lapen D. & Fernandez-Triana J. 2025. A research hotspot for Microgastrinae parasitoid wasps (Hymenoptera, Braconidae) in North America: DNA barcoding reveals the need for increased taxonomic efforts in dark taxa. *Frontiers in Sustainable Food Systems* 9: e1457055. https://doi.org/10.3389/fsufs.2025.1457055

Chang J.J.M., Raupach M.J., Cheng L., Damgaard J., Hongjamrassilp W., Ip Y.C.A., Ng M.H.-C., Chan W.W.R., Kunning I., Liang B.J.Y., Maggioni D., Mana R.R., Mishra H., Mowe M.A.D., Wainwright B.J., Whitney J.L., Wolfe K., Yeo D.C.J. & Huang D. 2024. Skimming the skaters: genome skimming improves phylogenetic resolution of Halobatinae (Hemiptera: Gerridae). *Insect Systematics and Diversity* 8 (4): 3. https://doi.org/10.1093/isd/ixae015

Chimeno C., Hausmann A., Schmidt S., Raupach M.J., Doczkal D., Baranov V., Hübner J., Höcherl A., Albrecht R., Jaschhof M., Haszprunar G. & Hebert P.D.N. 2022. Peering into the darkness: DNA barcoding reveals surprisingly high diversity of unknown species of Diptera (Insecta) in Germany. *Insects* 13 (1): 82. https://doi.org/10.3390/insects13010082

Clement M., Snell Q., Walker P., Posada D. & Crandall K. 2002. TCS: estimating gene genealogies. *Proceedings 16th International Parallel and Distributed Processing Symposium*. https://doi.org/10.1109/IPDPS.2002.1016585

Fahringer J. 1936. *Palaearktische Region*. Opuscula braconologica 3, Fritz Wagner, Vienna.

Felsenstein J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39 (4): 783–791. https://doi.org/10.1111/j.1558-5646.1985.tb00420.x

Fernández-Triana J. & van Achterberg C. 2017. Order Hymenoptera, family Braconidae Subfamily Microgastrinae from the Arabian Peninsula. *Arthropod fauna of the UAE* 6: 275–321.

Fernandez-Triana J., Shaw M.R., Cardinal S. & Mason P. 2014a. Contributions to the study of the Holarctic fauna of Microgastrinae (Hymenoptera, Braconidae). I. Introduction and first results of transatlantic comparisons. *Journal of Hymenoptera Research* 37: 61–76. https://doi.org/10.3897/jhr.37.7186

Fernandez-Triana J., Whitfield J., Rodriguez J., Smith M.A., Janzen D., Hallwachs W., Hajibabaei M., Burns J., Solis A., Brown J., Cardinal S., Goulet H. & Hebert P. 2014b. Review of *Apanteles* sensu stricto (Hymenoptera, Braconidae, Microgastrinae) from Area de Conservación Guanacaste, northwestern Costa Rica, with keys to all described species from Mesoamerica. *ZooKeys* 383: 1–565. https://doi.org/10.3897/zookeys.383.6418

Fernandez-Triana J., Shaw M.R., Boudreault C., Beaudin M. & Broad G.R. 2020. Annotated and illustrated world checklist of Microgastrinae parasitoid wasps (Hymenoptera, Braconidae). *ZooKeys* 920: 1–1089. https://doi.org/10.3897/zookeys.920.39128

Fernandez-Triana J.L., Boudreault C., Whitfield J.B., Höcherl A., Smith M.A., Hallwachs W. & Janzen D. 2025. A revision of the parasitoid wasp genus *Dolichogenidea* Viereck (Hymenoptera, Braconidae) in the Neotropical region, with the description of 102 new species. *ZooKeys* 1237: 1–250. https://doi.org/10.3897/zookeys.1237.141007

Ghafouri Moghaddam M., Rakhshani E., van Achterberg C. & Mokhtari A. 2021. Revision of the genus *Napamus* Papp (Hymenoptera, Braconidae, Microgastrinae). *International Journal of Tropical Insect Science* 41 (4): 2529–2542. https://doi.org/10.1007/s42690-021-00433-7

Haris A. 2016. *Hymenoptera Research in the Carpathian Basin (Hymenoptera: Aculeata)*. Natura Somogyiensis. Rippl-Rónai Town Museum, Kaposvár. https://doi.org/10.24394/NatSom.2016.29.2

Hartop E., Srivathsan A., Ronquist F. & Meier R. 2022. Towards large-scale integrative taxonomy (LIT): Resolving the data conundrum for dark taxa. *Systematic Biology*: 77 (6): 1404–1422. https://doi.org/10.1093/sysbio/syac033

Hausmann A., Krogmann L., Peters R., Rduch V. & Schmidt S. 2020. GBOL III: Dark Taxa. *iBOL Barcode Bulletin*. https://doi.org/10.21083/ibol.v10i1.6242

Hebert P.D.N., Bock D.G. & Prosser S.W.J. 2023. Interrogating 1000 insect genomes for NUMTs: A risk assessment for estimates of species richness. *PLoS ONE* 18 (6): e0286620. https://doi.org/10.1371/journal.pone.0286620

Heraty J. & Hawks D. 1998. Hexamethyldisilazane - A chemical alternative for drying Insects. *Entomological News* 109 (5): 369–374.

Höcherl A., Shaw M.R., Boudreault C., Rabl D., Haszprunar G., Raupach M.J., Schmidt S., Baranov V. & Fernández-Triana J. 2024. Scratching the tip of the iceberg: integrative taxonomy reveals 30 new species records of Microgastrinae (Braconidae) parasitoid wasps for Germany, including new Holarctic distributions. *ZooKeys* 1188: 305–386. https://doi.org/10.3897/zookeys.1188.112516

Hurst G.D.D. & Jiggins F.M. 2005. Problems with mitochondrial DNA as a marker in population, phylogeographic and phylogenetic studies: the effects of inherited symbionts. *Proceedings of the Royal Society B: Biological Sciences* 272 (1572): 1525–1534. https://doi.org/10.1098/rspb.2005.3056

Johansson N. 2024. *Revision of the Swedish Species of Lissonota Gravenhorst (Hymenoptera: Ichneumonidae: Banchinae) with an Illustrated Key to the Females of the Western Palaearctic*. *Supplement*. Swedish Entomological Society, Uppsala.

Johansson N. & Astafurova Y. 2025. *Revision of the Swedish Species of Exochus Gravenhorst, 1829 (Hymenoptera: Ichneumonidae: Metopiinae) with an Illustrated Key to the Species of the Western Palaearctic*. *Supplement*. Swedish Entomological Society, Uppsala.

Kaczmarczyk-Ziemba A., Halabowski D., Berchi G.M., Rewicz T., Boda P., Krepski T., Višinskienė G., Stoianova D., Tończyk G., Momotko A., Chylińska J. & Raupach M.J. 2025. Evidence for mitochondrial heteroplasmy in the freshwater bug *Aphelocheirus aestivalis* (Fabricius, 1794) (Insecta: Heteroptera): a challenge for future studies based on mtDNA markers. *Hydrobiologia* 852 (4): 927–940. https://doi.org/10.1007/s10750-024-05737-6

Kaltenpoth M., Corneli P.S., Dunn D.M., Weiss R.B., Strohm E. & Seger J. 2012. Accelerated evolution of mitochondrial but not nuclear genomes of Hymenoptera: New evidence from crabronid wasps. *PLoS ONE* 7 (3): e32826. https://doi.org/10.1371/journal.pone.0032826

Kimura M. 1980. A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution* 16 (2): 111–120. https://doi.org/10.1007/BF01731581

Kotenko A. 2004. Two new species of *Illidops* Mason (Hymenoptera: Braconidae, Microgastrinae) from Turkmenia, Kazakhstan and Russia. *Trudy Russkogo Entomologicheskogo Obshchestva* 75 (1): 118–121.

Kotenko A. 2007. Microgastrinae. *In*: Lelej A. (ed.) *Neuropteroidea, Mecoptera, Hymenoptera*: 134–192. Dalnauka, Vladivostok.

Kotenko A.G., Tolkanitz V.I. & Nuzhna A.D. 2014. The type material of Ichneumonoidea (Hymenoptera) described after 2006 which is deposited in collection of Schmalhausen Institute of Zoology NAS of Ukraine. *Fauna and Systematics* 477: 29–36.

Laetsch D.R. & Blaxter M.L. 2017. BlobTools: Interrogation of genome assemblies. *F1000Research* 6:1287. https://doi.org/10.12688/f1000research.12232.1

Leigh J.W. & Bryant D. 2015. PopART: Full-feature software for haplotype network construction. *Methods in Ecology and Evolution* 6 (9): 1110–1116. https://doi.org/10.1111/2041-210x.12410

Maetô K. 1996. Inter-generic variation in the external male genitalia of the subfamily Microgastrinae (Hymenoptera, Braconidae), with a reassessment of Mason's tribal system. *Journal of Hymenoptera Research* 5: 38–52.

Mardulyn P. & Whitfield J.B. 1999. Phylogenetic signal in the COI, 16S, and 28S genes for inferring relationships among genera of Microgastrinae (Hymenoptera; Braconidae): Evidence of a high diversification rate in this group of parasitoids. *Molecular Phylogenetics and Evolution* 12 (3): 282–294. https://doi.org/10.1006/mpev.1999.0618

Marshall Rev. T.A. 1885. I. Monograph of British Braconidae. Part I. *Transactions of the Royal Entomological Society of London* 33 (1): 1–280. https://doi.org/10.1111/j.1365-2311.1885.tb00886.x

Marshall T.A. 1898. Les Braconides (Supplément). *In*: André E. (ed.) *Tome 5: Espèces des Hyménoptères d'Europe et d'Algérie*: 145–288. Beaune.

Mason W.R.M. 1981. The polyphyletic nature of *Apanteles* Foerster (Hymenoptera: Braconidae): A phylogeny and reclassification of Microgastrinae. *Memoirs of the Entomological Society of Canada* 113 (S115): 1–147. https://doi.org/10.4039/entm113115fv

Meier R., Lawniczak M.K.N. & Srivathsan A. 2024. Illuminating entomological dark matter with DNA Barcodes in an era of insect decline, deep learning, and genomics. *Annual Review of Entomology* 70: 185–204. https://doi.org/10.1146/annurev-ento-040124-014001

Muesebeck C. 1921. A revision of the North American species of ichneumon-flies belonging to the genus *Apanteles*. *Proceedings of the United States National Museum* 58: 483–576. https://doi.org/10.5479/si.00963801.2349.483

Mutanen M., Kivelä S.M., Vos R.A., Doorenweerd C., Ratnasingham S., Hausmann A., Huemer P., Dincă V., van Nieukerken E.J., Lopez-Vaamonde C., Vila R., Aarvik L., Decaëns T., Efetov K.A., Hebert P.D.N., Johnsen A., Karsholt O., Pentinsaari M., Rougerie R., Segerer A., Tarmann G., Zahiri R. & Godfray H.C.J. 2016. Species-level para- and polyphyly in DNA barcode gene trees: strong operational bias in European Lepidoptera. *Systematic Biology* 65 (6): 1024–1040. https://doi.org/10.1093/sysbio/syw044

Niezabitowsky E. 1909. Materyaly do fauny Braconidów Polski. *Sprawozdanie Komisyi Fizyograficznej* 44: 47–106.

Nixon G. 1965. A reclassification of the tribe Microgasterini (Hymenoptera: Braconidae). *Bulletin of the British Museum (Natural History). Entomology. Supplement* 2: 1–284. https://doi.org/10.5962/p.144036

Nixon G. 1973. A revision of the north-western European species of the *vitripennis*, *pallipes*, *octonarius*, *triangulator*, *fraternus*, *formosus*, *parasitellae*, *metacarpalis* and *circumscriptus*-groups of *Apanteles* Förster (Hymenoptera, Braconidae). *Bulletin of Entomological Research* 63 (2): 169–230. https://doi.org/10.1017/S0007485300039006

Nixon G. 1976. A revision of the north-western European species of the *merula*, *lacteus*, *vipio*, *ultor*, *ater*, *butalidis*, *popularis*, *carbonarius* and *validus*-groups of *Apanteles* Förster (Hymenoptera, Braconidae). *Bulletin of Entomological Research* 65 (4): 687–735. https://doi.org/10.1017/S0007485300006386

O'Hara J.E., Shima H. & Zhang C. 2009. Annotated catalogue of the Tachinidae (Insecta: Diptera) of China. *Zootaxa* 2190 (1): 1–236. https://doi.org/10.11646/zootaxa.2190.1.1

Page R.D.M. 2016. DNA barcoding and taxonomy: dark taxa and dark texts. *Philosophical Transactions of the Royal Society: Biological Sciences* 371: e20150334. https://doi.org/10.1098/rstb.2015.0334

Papp J. 1972. New *Apanteles* Först. species from Hungary (Hymenoptera, Braconidae: Microgasterinae), I. *Annales Historico-Naturales Musei Nationalis Hungarici* 64: 335–345.

Papp J. 1974. New *Apanteles* Först. species from Hungary (Hymenoptera, Braconidae: Microgasterinae), III. *Annales historico-naturales Musei nationalis hungarici* 66: 325–337.

Papp J. 1976. Braconidae (Hymenoptera) from Mongolia, V. *Annales Historico-Naturales Musei Nationalis Hungarici* 68: 227–249.

Papp J. 1977. Braconidae (Hymenoptera) from Mongolia, VII. *Annales Historico-Naturales Musei Nationalis Hungarici* 69: 219–240.

Papp J. 1981. A survey of the European species of *Apanteles* Först. (Hymenoptera, Braconidae: Microgastrinae), V. The *lacteus*-, *longipalpis*-, *ultor*-, *butalidis*- and *vipio*-group. *Annales Historico-Naturales Musei Nationalis Hungarici* 73: 263–291.

Papp J. 1984. A survey of the European species of *Apanteles* Först. (Hymenoptera, Braconidae: Microgastrinae), VIII. The *metacarpalis*-, *formosus*-, *popularis*- and *suevus*-group. *Annales Historico-Naturales Musei Nationalis Hungarici* 76: 265–295.

Papp J. 1986. Redescription of *Apanteles barcinonensis* Marshall, 1898 (Hymenoptera, Braconidae: Microgastrinae). *Revista Española de Entomología* 62 (1–4): 167–173.

Papp J. 1988. A survey of the European species of *Apanteles* Först. (Hymenoptera, Braconidae: Microgastrinae) XI. 'Homologization' of the species-group of *Apanteles* s. l. with Mason's generic taxa. Checklist of genera. Parasitoid host list 1. *Annales Historico-Naturales Musei Nationalis Hungarici* 80: 145–175.

Papp J. 1993. New braconid wasps (Hymenoptera, Braconidae) in the Hungarian Natural History Museum. *Annales Historico-Naturales Musei Nationalis Hungarici* 84: 155–188.

Parks K.S., Janzen D.H., Hallwachs W., Fernández-Triana J., Dyer L.A., Rodriguez J.J., Arias-Penna D.C. & Whitfield J.B. 2020. A five-gene molecular phylogeny reveals *Parapanteles* Ashmead (Hymenoptera: Braconidae) to be polyphyletic as currently composed. *Molecular Phylogenetics and Evolution* 150: e106859. https://doi.org/10.1016/j.ympev.2020.106859

Patzold F., Zilli A. & Hundsdoerfer A.K. 2020. Advantages of an easy-to-use DNA extraction method for minimal-destructive analysis of collection specimens. *PLoS ONE* 15 (7): e0235222. https://doi.org/10.1371/journal.pone.0235222

Prjibelski A., Antipov D., Meleshko D., Lapidus A. & Korobeynikov A. 2020. Using SPAdes de novo assembler. *Current Protocols in Bioinformatics* 70 (1): e102. https://doi.org/10.1002/cpbi.102

Ratnasingham S. & Hebert P.D.N. 2007. BOLD: The Barcode of Life Data System *Molecular Ecology Notes* 7 (3): 355–364. https://doi.org/10.1111/j.1471-8286.2007.01678.x

Ratnasingham S. & Hebert P.D.N. 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

Raxworthy C.J. & Smith B.T. 2021. Mining museums for historical DNA: advances and challenges in museomics. *Trends in Ecology & Evolution* 36 (11): 1049–1060. https://doi.org/10.1016/j.tree.2021.07.009

Reinhard H. 1880. Beiträge zur Kenntniss einiger Braconiden-Gattungen. Fünftes Stück. XVI. Zur Gattung *Microgaster*, Latr. *Deutsche Entomologische Zeitschrift* 24: 353–370.

Rennwald E., Rodeland J. & Guggemoos T. 2023. Lepiforum's checklist of European Lepidoptera. Available from: https://lepiforum.org/wiki/page/Downloads#Lepiforums-Europaliste_der_Schmetterlinge-Lepiforums_Checklist_of_European_Lepidoptera [accessed 21 Jul. 2023].

Schmidt S., Taeger A., Morinière J., Liston A., Blank S.M., Kramp K., Kraus M., Schmidt O., Heibo E., Prous M., Nyman T., Malm T. & Stahlhut J. 2017. Identification of sawflies and horntails (Hymenoptera, 'Symphyta') through DNA barcodes: successes and caveats. *Molecular Ecology Resources* 17 (4): 670–685. https://doi.org/10.1111/1755-0998.12614

Schütte A., Stüben P. & Astrin J. 2023. Molecular weevil identification project: A thoroughly curated barcode release of 1300 Western Palearctic weevil species (Coleoptera, Curculionoidea). *Biodiversity Data Journal* 11: e96438. https://doi.org/10.3897/BDJ.11.e96438

Shaw M.R. 1994. Parasitoid host ranges. *In*: Hawkins B.A. & Sheehan W. (eds) *Parasitoid Community Ecology*: 111–144. Oxford University Press, Oxford. https://doi.org/10.1093/oso/9780198540588.003.0007

Shaw M.R. 2023. Obtaining, recording and using host data for reared parasitoid wasps (Hymenoptera). *British Journal of Entomology & Natural History* 36: 205–213.

Shaw M.R., Höcherl A. & Fernandez-Triana J. 2024. An illustrated key to European genera of Microgastrinae parasitoid wasps (Hymenoptera, Braconidae) with a recent historical and biological perspective and a guide to available species-level identification resources. *ZooKeys* 1212: 285–316. https://doi.org/10.3897/zookeys.1212.126155

Simon C., Buckley T.R., Frati F., Stewart J.B. & Beckenbach A.T. 2006. Incorporating molecular evolution into phylogenetic analysis, and a new compilation of conserved polymerase chain reaction primers for animal mitochondrial DNA. *Annual Review of Ecology, Evolution, and Systematics* 37 (1): 545–579. https://doi.org/10.1146/annurev.ecolsys.37.091305.110018

Smith M.A., Fernández-Triana J.L., Eveleigh E., Gómez J., Guclu C., Hallwachs W., Hebert P.D.N., Hrcek J., Huber J.T., Janzen D., Mason P.G., Miller S., Quicke D.L.J., Rodriguez J.J., Rougerie R., Shaw M.R., Várkonyi G., Ward D.F., Whitfield J.B. & Zaldívar-Riverón A. 2013. DNA barcoding and the taxonomy of Microgastrinae wasps (Hymenoptera, Braconidae): impacts after 8 years and nearly 20 000 sequences. *Molecular Ecology Resources* 13 (2): 168–176. https://doi.org/10.1111/1755-0998.12038

Szépligeti G. 1896. Beiträge zur Kenntnis der Ungarischen Braconiden. (Zweiter Theil). *Természetrajzi Füzetek* 19: 285–321 [In Hungarian.], 359–386 [In German.].

Tamura K., Stecher G. & Kumar S. 2021. MEGA11: Molecular evolutionary genetics analysis version 11. *Molecular Biology and Evolution* 38 (7): 3022–3027. https://doi.org/10.1093/molbev/msab120

Telenga N.A. 1955. Braconidae, subfamily Microgastrinae, subfamily Agathinae. Fauna USSR, Hymenoptera. *Zoological Institute of the Academy of Science of the U.S.S.R.* 5 (4): 1–311.

Tobias V. 1964. New species and genus of Braconids (Hymenoptera, Braconidae) from Kazakhstan. *Trudy Zoologicheskogo Instituta* 34: 177–234.

Tobias V. 1976. Braconids of the Caucasus (Hymenoptera, Braconidae). *Opredelitel Faune SSSR*: 1–286. Nauka Press, Leningrad.

Tobias V. & Kotenko A. 1986. Subfamily Microgasterinae. *In*: Medvedev G.S. (ed.) *Key to the Insects of the European Part of the USSR III*: 605–815. Insitute of Zoology, Academy of Sciences of the USSE, Leningrad. Available from https://www.biodiversitylibrary.org/page/32124963 [accessed 22 Oct. 2025].

van Achterberg C. 2002. Western Palaearctic genera of the subfamily Microgastrinae: a reappraisal of the generic and tribal division (Hymenoptera: Braconidae). *In*: Melika G. & Thuróczy C. (eds) *Parasitic Wasps: Evolution, Systematics, Biodiversity and Biological Control*: 19–35. Agroinform, Budapest.

Vogel J., Forshage M., Bartsch S.B., Ankermann A., Mayer C., Falkenhausen P. von, Rduch V., Müller B., Braun C., Krammer H.-J. & Peters R.S. 2024. Integrative characterisation of the Northwestern European species of *Anacharis* Dalman, 1823 (Hymenoptera, Cynipoidea, Figitidae) with the description of three new species. *Journal of Hymenoptera Research* 97: 621–698. https://doi.org/10.3897/jhr.97.131350

Wharton R.A. 1983. New species of *Illidops* and *Bracon* (Hymenoptera: Braconidae) of potential use in biological control. *The Canadian Entomologist* 115 (6): 667–672. https://doi.org/10.4039/Ent115667-6

Whitfield J.B. 1997. Subfamily Microgastrinae. *In*: Wharton R.A., Marsh P.M. & Sharkey M.J. (eds) *Manual of the New World Genera of the Family Braconidae (Hymenoptera)*: 333–364. International Society of Hymenopterists, Washington, DC.

Whitfield J.B. & Kjer K.M. 2008. Ancient rapid radiations of insects: Challenges for phylogenetic analysis. *Annual Review of Entomology* 53: 449–472. https://doi.org/10.1146/annurev.ento.53.103106.093304

Whitfield J.B., Mardulyn P., Austin A.D. & Dowton M. 2002. Phylogenetic relationships among microgastrine braconid wasp genera based on data from the 16S, COI and 28S genes and morphology. *Systematic Entomology* 27 (3): 337–359. https://doi.org/10.1046/j.1365-3113.2002.00183.x

Whitfield J.B., Austin A.D. & Fernandez-Triana J.L. 2018. Systematics, biology, and evolution of Microgastrine parasitoid wasps. *Annual Review of Entomology* 63 (1): 389–406. https://doi.org/10.1146/annurev-ento-020117-043405

Wilkinson D. 1945. Description of Palearctic species of *Apanteles* (Hymen., Braconidae). *Transactions of the Entomological Society of London* 95: 35–226. https://doi.org/10.1111/j.1365-2311.1945.tb00436.x

Williams D. 1988. Classification, phylogeny and zoogeographic studies of species of *Sathon* Mason (Hymenoptera: Braconidae). *Quaestiones Entomologicae* 24 (4): 529–639.

Wolz M., Höcherl A., Hübner J., Tschorsnig H.-P., Whitmore D., Leroy B.M.L., Weisser W.W., Mitesser O., Zakharov E.V., Hebert P.D.N., Liebhold A.M. & Müller J. 2024. Response of parasitoid communities to insecticide application during a *Lymantria dispar* outbreak in mixed oak forests. *Journal of Applied Ecology* 61 (11): 2774-2785. https://doi.org/10.1111/1365-2664.14791

Yu D., van Achterberg C. & Horstmann K. 2016. Taxapad 2016, Ichneumonoidea 2015. Database on flash-drive. Nepean, Ontario, Canada.

Zerova M.D., Tolkanitz V.I., Kotenko A., Dyakonchuk L.A., Melika Z.G., Gumovsky A.V., Fursov V.N., Simutnik S.A., Narolsky N.B. & Stetsenko I.T. 2006. The types of Ichneumonoidea, Cynipoidea and Chalcidoidea (Hymenoptera, Apocrita) deposited in the collection of the Schmalhausen Institute of Zoology of National Academy of Sciences of Ukraine. *Bulletin of Zoology* 20: 1–136.

Printed versions of all papers are deposited in the libraries of three of the institutes that are members of the *EJT* consortium: Muséum national d'Histoire naturelle, Paris, France; Royal Museum for Central Africa, Tervuren, Belgium; Royal Belgian Institute of Natural Sciences, Brussels, Belgium. The other members of the consortium are: Meise Botanic Garden, Meise, Belgium; Natural History Museum of Denmark, Copenhagen, Denmark; Naturalis Biodiversity Center, Leiden, the Netherlands; Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; Leibniz Institute for the Analysis of Biodiversity Change, Bonn – Hamburg, Germany; National Museum of the Czech Republic, Prague, Czech Republic; The Steinhardt Museum of Natural History, Tel Aviv, Israël.

Supplementary files

Supp. file 1. Material examined for this study, file format based on BOLD specimen data with additonal specimens not included in the database. Table in .xslx format.
https://doi.org/10.5852/ejt.2025.1031.3133.13941

Supp. file 2. Measurements of the newly described species. Table in .xslx format with each species in a separate tab. https://doi.org/10.5852/ejt.2025.1031.3133.13947

Supp. file 3. Sequence alignment of the barcoding region of the COI gene used as a basis for the NJ analysis depicted in Fig. 62. Sequences in FASTA-format.
https://doi.org/10.5852/ejt.2025.1031.3133.13949

Supp. file 4. Complete Neighbor Joining (NJ) topology of the COI barcoding region of our dataset based on Kimura 2-parameter distances and with 1000 bootstrap replicates. The topology includes all sequences from specimens morphologically identified as members of *Illidops* Mason, 1981. Numbers next to nodes represent non-parametric bootstrap values > 90% (10 000 replicates).
https://doi.org/10.5852/ejt.2025.1031.3133.13951

Supp. file 5. Neighbor Joining (NJ) topology of the COI barcoding region. The topology includes all sequences from specimens morphologically identified as members of *Illidops* Mason, 1981, and, in addition, publicly available sequences from BOLD which we consider likely to represent species of *Illidops*. Triangles show the relative number of individuals sampled (height) and sequence divergence (width). Orange coloration indicates species associated with sequences that have a maximum within-cluster distance > 2.2%. Numbers next to nodes represent non-parametric bootstrap values > 90% (10 000 replicates). https://doi.org/10.5852/ejt.2025.1031.3133.13953

Supp. file 6. Sequence alignment of the barcoding region of the COI gene used as a basis for the NJ analysis depicted in Supp. file 5. Sequences in FASTA-format.
https://doi.org/10.5852/ejt.2025.1031.3133.13955

Supp. file 7. Sequence alignment of the barcoding region of the COI gene of *I. butalidis* (Marshall, 1889) used in the haplotype network in Fig. 11. Sequences in nexus format.
https://doi.org/10.5852/ejt.2025.1031.3133.13957

Supp. file 8. Sequence alignment of the barcoding region of the COI gene of *I. doreenae* Höcherl & Fernandez-Triana sp. nov. used in the haplotype network in Fig 11. Sequences in nexus format.
https://doi.org/10.5852/ejt.2025.1031.3133.13959

Supp. file 9. Original descriptions in Russian, translated here. Text and screenshots in .docx format.
https://doi.org/10.5852/ejt.2025.1031.3133.13961

Supp. file 10. BOLD output, intermediate step. NJ topology of all publicly available holarctic sequences related to clusters considered likely to include species of *Illidops* Mason, 1981.
https://doi.org/10.5852/ejt.2025.1031.3133.13963

Supp. file 11. Low-quality contig of *I. urgo* Nixon, 1965 (CNCHYM 01529). Sequence in FASTA format. https://doi.org/10.5852/ejt.2025.1031.3133.13965