

Revision of the world species of *Piogaster* Perkins (Hymenoptera, Ichneumonidae, Pimplinae), ectoparasitoids of jumping spiders (Araneae, Salticidae) with a description of one new species

Amber Bass¹, Andrew M. R. Bennett¹, Tamara Spasojevic², Marla Schwarzfeld¹

¹ Agriculture and Agri-Food Canada, Canadian National Collection of Insects, Arachnids and Nematodes, K.W. Neatby Building, 960 Carling Avenue, Ottawa, Ontario K1A 0C6, Canada ² 2nd Zoology, Museum of Natural History Vienna, Burgring 7, 1010 Vienna, Austria

Corresponding author: Andrew M. R. Bennett (andrew.bennett@agr.gc.ca)

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Abstract

The world species of *Piogaster* Perkins are revised including the description of a new species: *Piogaster variegata* Bass, Bennett & Schwarzfeld, **sp. nov.** from Alberta, Canada. The new species is described and the seven previously known species are redescribed, with an illustrated key to all eight world species. Species relationships are examined using molecular data, including DNA barcodes and ultra-conserved elements (UCEs). *Piogaster pilosator caucasica* Kasparyan, **syn. nov.** is newly synonymized under *Piogaster pilosator* (Aubert). *Piogaster pilosator* is newly recorded from Germany and Norway and a lectotype is hereby designated. *Piogaster albina* Perkins is newly recorded from Hungary and Sweden. We also include new generic records of *Piogaster* from Italy and new generic provincial records from British Columbia and Alberta, Canada. We report a new host genus for *Piogaster*, bringing the total host count to three genera of Salticidae. For the first time, a male *Piogaster* specimen is unequivocally associated with a female in *P. daisetsuzana* Kusigemati. Associating European and North American males with females based on morphology alone remains problematic.

Keywords

Dichotomous key, DNA barcodes, integrative taxonomy, morphology, new distribution record, *Polysphincta* group

Introduction

Piogaster Perkins, 1958 is a small Holarctic genus of parasitoid wasps of the family Ichneumonidae (Hymenoptera: Ichneumonidae: Pimplinae: Ephialtini). Four species are recorded from the western Palaearctic, two from the eastern Palaearctic and two from the Nearctic region (one of which is described in the current paper). See the species descriptions for references and/or specimens supporting species distributions (including new country records).

In terms of biology, Takasuka et al. (2018) reported observations of *Piogaster* sp. (cf. *pilosator* (Aubert, 1958)) ovipositing on the cephalothorax of *Salticus cingulatus* (Panzer, 1797) (Araneae: Salticidae) in the laboratory in Finland. Previous anecdotal studies had implicated Salticidae as the host of *Piogaster*. For example, Gauld and Dubois (2006) stated that they saw a North American specimen in the Canadian National Collection of Insects, Arachnids and Nematodes (CNC) reared from a species of *Habronattus* F.O. Pickard-Cambridge, 1901 (Salticidae). Shaw (2006) reported that a female of *P. albina* Perkins, 1958 was reared from an oak marble gall of *Andricus kollari* (Hartig, 1843) (Hymenoptera: Cynipidae) in southern England, with the presumption that it developed on a spider that had inhabited the gall. Fitton et al. (1987) stated that circumstantial evidence suggests that at least some species are arboreal, but did not elaborate. The putative sister genus to *Piogaster*, *Inbioia* Gauld & Ugalde, 2002 (see below), was recently reared from an unknown species of *Messua* Peckham & Peckham, 1896 (Salticidae) (Barrantes et al. 2019) which supports the close relationship of these two genera. These are the only two genera in the *Polysphincta* group of genera (see below) known to parasitize Salticidae (Gauld and Dubois 2006; Matsumoto 2016; Takasuka et al. 2018; Barrantes et al. 2019; Takasuka and Broad 2024) although the related genus *Clistopyga* Gravenhorst, 1829 has also been reared from Salticidae (Fritzén and Sääksjärvi 2016).

With respect to phylogeny, historically *Piogaster* was placed within the tribe Polysphinctini (Perkins 1958; Townes 1969). Wahl and Gauld (1998) found strong morphological support for the monophyly of Polysphinctini, but showed it was nested within Ephialtini and therefore synonymized the two tribes. Later, Gauld et al. (2002b) placed the genera of the former Polysphinctini within their *Sericopimpla* genus group that also included genera such as *Zaglyptus* Förster, 1868, *Tromatobia* Förster, 1869, and *Clistopyga* that have larvae that are predators of spider egg sacs (Austin 1985; Fitton et al. 1987; Fritzén and Sääksjärvi 2016). Later authors have used the term “*Polysphincta* group” to denote the genera formerly encompassing the Polysphinctini. Takasuka and Broad (2024) state that the *Polysphincta* group includes 25 genera and 294 species in the main text, but this is a miscount. The actual total from their supplemental data (appendix S1 and fig. S2) is 295 valid species (Takasuka and Broad 2024). Since then, an additional six species have been described: *Brachyzapus striatus* Humala, 2023 (Humala 2023); *Polysphincta sirena* Khalaim, 2024, *Polysphincta xena* Khalaim, 2024, *Flacopimpla oaxacana* Khalaim, 2024 (Khalaim et al. 2024); *Inbioia himalayensis* De Ketelaere & Maqbool, 2025 (Bhat et al. 2025), and *Zatypota orbitalis* Varga, 2025 (Varga 2025). In addition, *Eruga yehi* Gauld, 1991 is now considered a junior synonym of *Eruga lineata* Townes, 1960 (Khalaim et al. 2024), bringing the total count to 300 species in the *Polysphincta* group. Gauld and

Dubois (2006) performed a morphological cladistic analysis that placed *Piogaster* (based on *P. pilosator* and *P. sp. 1*) within their *Piogaster* clade which also included *Inbioia pivai* Gauld & Ugalde, 2002. *Inbioia* is a morphologically derived genus originally described from Costa Rica and recently with a second species described from India (Bhat et al. 2025). Gauld and Dubois (2006) stated that *Piogaster* and *Inbioia* formed a “very distinctive monophyletic clade” although its Bremer support was only 1 and the bootstrap value only 74. In their strict consensus tree, the three species were unresolved. Re-analysis using different weighting options always yielded a monophyletic *Piogaster* with *Inbioia* as the sister group. They did not state specifically what character(s) supported this grouping, but did mention the similarity of the metasoma that generally lacked any raised swellings (a relatively rare state in the *Polysphincta* group and its outgroups). Quicke et al. (2009) performed a phylogenetic analysis of Ichneumonidae using 28S rDNA, resulting in *Inbioia* and *Piogaster* as sister genera. Only one individual of each genus was included in this study, *P. sp.* from Korea and *I. sp.* from Sumatra, Indonesia (both DNA vouchers now lost). With respect to the placement of these two genera within the *Polysphincta* group, the unweighted analysis lacked resolution at the base of the tree; however, in their weighted analyses, these two genera were unequivocally the sister group to all other genera in the group. A more recent molecular phylogeny of the *Polysphincta* group (Matsumoto 2016) found that *P. daisetsuzana* Kusigemati, 1985 clustered with some species of *Schizopyga* Gravenhorst, 1829 within their *Schizopyga* subgroup which also included species of *Brachyzapus* Gauld & Dubois, 2006, *Iania* Matsumoto, 2016, *Dreischachia* Townes, 1962 and *Zabrachypus* Cushman, 1920. The *Schizopyga* subgroup was the sister group to all remaining genera of the *Polysphincta* group. Matsumoto (2016) did not include *Inbioia* in the analysis. Klopstein et al. (2019a) used hybrid capture data to study relationships within the Pimpliformes group of Ichneumonidae and found *P. pilosator* was consistently placed within the *Polysphincta* group as sister to *Schizopyga frigida* Cresson, 1870, and these two species were sister group to the other four genera of the *Polysphincta* group included in this analysis (*Acrodactyla* Haliday, 1838, *Zatypota* Förster, 1869, *Reclinervellus* He & Ye, 1998, and *Polysphincta* Gravenhorst, 1829). *Inbioia* was not included in this analysis. Spasojevic et al. (2021) recovered a strongly supported *Schizopyga* + (*Dreischachia* (= *Iania*) *pictifrons* (Thomson, 1877) + *Piogaster*) with an 11-gene analysis including all but *Dreischachia* and *Inbioia* from the *Schizopyga* subgroup. Kloss et al. (2024) included three genes and all genera from the *Schizopyga* subgroup except *Inbioia* and recovered *Dreischachia* + (*Iania* + *Piogaster*). In summary, *Piogaster* generally appears to belong to the *Schizopyga* subgroup which is a sister group of the remaining genera of the *Polysphincta* group, though the sister genus of *Piogaster* varies depending on the taxonomic sampling, loci, and analyses. On the basis of morphology it is very closely related to *Inbioia*.

The discovery of a unique specimen in Alberta, Canada, along with the absence of a comprehensive revision of the genus, highlights the need for a taxonomic reassessment. The purpose of this paper is to revise the species of *Piogaster* including describing a new species from Canada, and to discuss the interspecific relationships within the genus and its affinities within the *Polysphincta* group of genera. We examine a large proportion of the known *Piogaster* worldwide specimens, and thus redescribe all of the previously described species to incorporate variation within species not included

in original descriptions. In addition, we improve upon past descriptions by standardizing them for better comparison between species, incorporating new morphological characters, and providing detailed images of each species that were not included in any of the original descriptions. Additionally, we provide the first definitive association of a male *Piogaster* with its female based on multiple lines of evidence and provide a complete description of the male of this species. We address the challenge of associating males with females due to pronounced sexual dimorphism and limited morphological interspecific variation among males within the genus.

Materials and methods

Repositories

Specimens examined in this study originate from the following institutions. Standardized collection codes follow Evenhuis (2025), unless unavailable, in which case institutional abbreviations (marked with an asterisk) are used.

CNC	Canadian National Collection of Insects, Ottawa, Ontario, Canada (A. Bennett)
DNUE*	Daegu National University of Education, Daegu, South Korea (J-K. Choi)
EIHU	Hokkaido University Collection, Hokkaido, Japan (J. Okayasu)
EMUS	Utah State University Insect Collection, Logan, Utah, USA (D. Wahl)
EUMJ	Ehime University, Entomology, Matsuyama, Japan (H. Yoshitomi)
MNCN	Museo Nacional de Ciencias Naturales, Madrid, Spain (M. Paris)
MNHN	Muséum national d'Histoire naturelle, Paris, France (A. Guiguet)
MUCR	Ciudad Universitaria, Universidad de Costa Rica, Museo de Insectos (P. Hanson)
MZLS	Musée de Zoologie, Lausanne, Switzerland (A. Freitag)
MZLU	Lund University Biological Museum, Lund, Sweden (R. Bygebjerg)
NHMuK	National History Museum London, London, England (G. Broad)
NHMuW	Naturhistorisches Museum Wien, Vienna, Austria (T. Spasojevic)
NHRS	Naturhistoriska riksmuseet, Stockholm, Sweden (H. Vårdal)
NINA*	Norwegian Institute for Nature Research, Trondheim, Norway (A. Staverløkk)
NMBE	Naturhistorisches Museum Bern, Bern, Switzerland (H. Baur)
NMS	National Museums Scotland, Edinburgh, Scotland (M. Shaw)
NTNU*	Norwegian University of Science and Technology Museum, Trøndelag, Norway (T. Ekrem)
RMNH	Naturalis Biodiversity Centre, Leiden, Netherlands (F. Bakker)
USNM	National Museum of Natural History, Washington, DC, USA. (B. Kula)
ZFMK	Museum Koenig Bonn, Bonn, Germany (R. Peters)
ZIN	Russian Academy of Sciences, Zoological Institute, St. Petersburg, Russia (A. Khalaim)

Literature review and examined material

A literature review and inquiries to 40 entomological collections resulted in a list of 72 female specimens, 40 male specimens, and 16 additional specimens of unknown sex deposited in collections worldwide (Suppl. material 1: Specimen data). We examined 39 of the 72 female specimens to create our identification key, including six holotypes and the newly designated lectotype of *P. pilosator*. Among the 33 unexamined female specimens were three holotypes and one syntype. We were unable to examine the primary type of *Piogaster lucida* Constantineanu & Constantineanu, 1969, so the characters of this species are based only on descriptions (Constantineanu and Constantineanu 1969a; Constantineanu and Constantineanu 1969b). We were also unable to examine the primary type of *P. daisetsuzana*, but we examined photographs and the original description (Kusigemati 1985). One of the two syntypes of *P. pilosator* could not be found and is presumed lost, as is the holotype of *P. rugosa* Perkins, 1958 (= *P. pilosator*). We saw photographs of 13 of the remaining 33 unexamined female specimens.

Morphological analysis

There is no comprehensive key to the genus *Piogaster*. Species were identified with a combination of the original descriptions of each species (Aubert 1958; Perkins 1958; Townes and Townes 1960; Constantineanu and Constantineanu 1969a; Kusigemati 1985; Kasparyan and Khalaim 2007) and the following keys: Constantineanu and Pisica (1977), Kasparyan (1981), Fitton et al. (1988), and Kasparyan and Khalaim (2007). Measurements and structural terms follow Bennett et al. (2019) except for the differences listed below. The basal fore wing cross-vein of the areolet (Rs of Bennett et al. (2019)) is referred to as 2rs-m. The areas of the head referred to as the supraclypeal area and the supra-antennal area in Bennett et al. (2019) are referred to as the face and frons, respectively. The carina running from the base of the mandible to the junction of occipital carina and hypostomal carina (considered a continuation of the occipital carina in Bennett et al. (2019)) is called the genal carina here (as in Meier et al. (2022)). The genal index is the ratio of the length of the genal carina to the basal width of the mandible. The ocellar-ocular distance, not explicitly stated in Bennett et al. (2019) is the shortest distance from the outer margin of the eye to the lateral ocelli. The following abbreviations are used: **T1–T8**, metasomal tergites 1–8; **FW**, fore wing; **HW**, hind wing; **BWM**, basal width of the mandible; **MSL**, malar space length; **LOD**, lateral ocelli diameter; and **OOD**, ocellar-ocular distance. Microsculpture terms were based on Eady (1968). In the species descriptions, the primary type character state is within square brackets following characters with varied states. Colour variation within species was assessed using both physical specimens and high-resolution photographs, where colouration was clearly visible. Photographed specimens were included in the material examined only when reliable identification and colour assessment were possible and are indicated by (photo only) appearing after the label details. Most measurements were taken with a micrometer, but ovipositor sheaths were often twisted and therefore dif-

ficult to measure directly. These were imaged with a Keyence VHX-7000 (VH-Z20R lens, 200×) using the serial recording setting to generate a multi-image wide-view 2D stitch and measured with the multi-point plane measurement tool. When ovipositor sheaths were twisted in three dimensions such that accurate measurements were not possible, these specimens were excluded from measurement.

Species distribution maps

Specimen locality information was gathered from literature, email correspondence, loans from institutions listed above, iNaturalist records, and photographs of live specimens taken by Pierre Duhem (all data available in Suppl. material 1: Specimen data). For specimens without exact coordinates on the label or in the publication, approximations were obtained from Google Maps, rounded to four decimal places in decimal degree format. Maps were generated in R (R Core Team 2020) with the following packages: ggplot2 (Wickham 2016), rnatualearth (Massicotte and South 2023), and cowplot (Wilke 2020).

Photography

Specimen photographs were taken using three different imaging systems. First, a Leica MZ16 with a Leica DFC420 digital camera was used as previously described (Bennett et al. 2019). Second, a Canon 7D Mark II on a motorized focus rail controlled using a Stackshot (Cognisys Inc.) was used to create a stacked image. Images were stacked with Helicon Focus v8.2.0 (Helicon Soft, Kharkiv, Ukraine). Third, a Keyence VHX-7000 with a VH-Z20R (range 20–200×) lens was used to make a multi-image wide-view 2D stitch with the Serial Recording setting. Image plates were created with Adobe Photoshop Elements v21.0.

Molecular methods

Specimens were extracted with a modified DNeasy® Blood and Tissue kit protocol (Moreau 2014; Cruaud et al. 2019) using a middle leg. The barcoding region of COI was amplified with the following components: 2 µl 2.5 mM dNTPs, 0.2 µl Invitrogen™ Taq DNA Polymerase, 2.5 µl 10X Ex Taq buffer, 2 µl 25 mM MgCl₂, 1 µl of universal primers LCO1490 and HCO2198 (Folmer et al. 1994), 1–4 µl genomic DNA and water to 25 µl. Amplification was completed with an Eppendorf MasterCycler Pro S (Eppendorf, Hamburg, Germany) with the following protocol: 95 °C for 1 minute, 35 cycles of 95 °C for 1 minute, 49 °C for 1 minute, and 72 °C for 1 minute, then 72 °C for 4 minutes. The amplified product was viewed on a 2% agarose gel with Gel-Red, then cleaned with ExoSAP-IT (PE Applied Biosystems, Foster City, CA, USA). The BigDye Terminator v3.1 Cycle Sequencing kit (PE Applied Biosystems, Foster City, CA, USA) was performed in 10 µl reactions and Sanger sequencing was completed at the Agriculture & Agri-Food Canada Ottawa Research and Development Centre Core Sequencing Facility (Ottawa, ON, Canada) on a 3500xl DNA Genetic Analyzer (PE Applied Biosystems, Foster City, CA, USA).

Preliminary results showed little to no variation in the COI barcoding gene between *P. albina* and *P. pilosator*, species occurring in sympatry that are easily delimited by morphology. We expanded upon our gene sampling to assess whether other genes could better resolve these taxa. Because fresh *P. pilosator* material was unavailable, we depended on previously sequenced *P. pilosator* for this study. We expanded our gene sampling to include the nuclear locus Nasvi2EG013087, identified by Klopstein et al. (2019a) as a phylogenetically informative region. Klopstein et al. (2019a) identify eight genes that may provide additional resolution where mitochondrial markers fail. This region was already captured for *P. pilosator* in Klopstein et al. (2019a), enabling direct comparison with newly generated *P. albina* sequences. We attempted to amplify two additional loci (Nasvi2EG014339 and Nasvi2EG010812) from the same study but were unsuccessful. The primers and settings used for Sanger sequencing are included in Table 1.

Table 1. Primers used for Sanger sequencing. The following information about each primer pair is included: forward and reverse sequences, annealing temperature, number of cycles, and the final product length in bp.

Gene	Direction	Primer	Sequence 5'-3'	Annealing temp. (°C)	Cycles	Product (bp)
COI	Forward	LCO1490	GGTCAACAAATCATAAAGATATTGG	49	35	658
	Reverse	HCO2198	TAACTTCAGGGTGACCAAAAAATCA			
Nasvi2EG013087	Forward	013087F1	CTG AAG ACC ATT TCC CTG CG	51	35	389
	Reverse	013087R1	GCG ACC TTG GAA GCA TCT TG			

Extracting sequence data from UCEs

In addition to the Sanger sequencing data, we extracted COI, 18S, 28S, EF1a, and ITS2 from UCEs. UCE data from three *Piogaster* specimens (one *P. pilosator* and two *P. albina*) and one *Inbioia* specimen (see Suppl. material 2: Genetic data) were assembled with ABySS (Jackman et al. 2017), rnaSPAdes (Bushmanova et al. 2019), and SPAdes (Prjibelski et al. 2020) using an existing pipeline (<https://github.com/AAFC-BICoE/snakemake-partial-genome-pipeline>). Assembled contigs from each assembler were run through phyluce_assembly_match_contigs_to_barcode (Faircloth 2016) to look for matches to existing sequences (in Suppl. material 2: Genetic data). We used existing *Piogaster* sequences as the reference templates for this analysis, Genbank accession numbers as follows: LC145350.1 and KU753346.1 for COI, KU753135.1 for 18S, LC145412.1 and KU753534.1 for 28S, and LC145474.1 for EF1a. As no sequences for *Piogaster* were available for ITS2, we used *Scambus calobatus* (Gravenhorst, 1829), Genbank accession JN243123.1. The matches from this analysis were BLAST searched on GenBank and were retained if the top match from the BLAST search was a genus in Ephialtini (Pimplinae). If multiple short contigs for a single specimen had a BLAST result of Ephialtini they were aligned and a consensus sequence was created. The COI sequences mined from the UCEs were utilized in the phylogenetic analysis. Genetic sequences were aligned with existing *Piogaster* sequences with MUSCLE v5.1

to determine the genetic distances between the species of *Piogaster* and *Inbioia*. Two males of *Piogaster* (GMGM1875-14 and COLHH2702-19) were excluded from the evaluation of divergence, as their species identity could not be determined.

Identifying diagnostic signatures in COI

COI barcode sequences from *Piogaster* and *Inbioia* (Suppl. material 2: Genetic data) were combined with all available COI sequences from the *Polysphincta* group genera downloaded from GenBank (downloaded on 22 August 2025). Sequences were aligned with MUSCLE in Geneious 2025.0.3 and trimmed to the 658 bp Folmer region. Those shorter than 400 bp, with > 1% ambiguous bases, stop codons, or frameshifts were excluded. The final alignment (Suppl. material 3: Single locus alignments) included 359 sequences representing 22 of 25 genera, missing the following three genera: *Flacopimpla* Gauld, 1991, *Lamnatibia* Palacio & Sääksjärvi, 2007, and *Pterinopus* Townes, 1969. While sequences from non-*Piogaster* taxa were not filtered to include only authoritatively identified specimens, this is unlikely to introduce error into our analysis. First, all *Piogaster* sequences were authoritatively identified by the authors or by another expert. Second, we do not believe there are any false negatives (i.e., *Piogaster* specimens incorrectly labeled as other genera), as no non-*Piogaster* sequence falls within the range of pairwise genetic distances observed among *Piogaster* in the distance matrix, and none cluster within the *Piogaster* clade in a neighbor-joining tree of all 359 sequences. Third, any residual misidentifications among non-*Piogaster* sequences would tend to make the diagnostic signatures more conservative, potentially causing us to reject a site as diagnostic rather than accept an erroneous one. Finally, removal of sequences that are not authoritatively identified could create false positives by excluding sequences that would otherwise contradict a putative diagnostic site.

Diagnostic molecular characters for *Piogaster* and species within *Piogaster* were identified using DeSignate (Hütter et al. 2020). The nucleotides identified as diagnostic were viewed in Geneious 2025.0.3 to determine whether they corresponded to differences in amino acids. Amino acid positions are numbered according to the standard 658 bp COI barcode region defined by Folmer et al. (1994). Synonymous substitutions and isolated singletons were excluded, except where multiple singletons occurred in close proximity and together provided a consistent diagnostic signature. Diagnostic molecular characters are reported in the genus and species diagnoses (where applicable) in addition to the morphological characters in an integrative taxonomy approach.

Phylogenetic analysis

COI Phylogeny

Sequence assembly was completed with Geneious 2025.0.3. Additional COI sequences were mined from GenBank (Clark et al. 2016) and BOLD (Ratnasingham and Hebert 2007) (Suppl. material 2: Genetic data). In one case, for a *P. albina* specimen

with the specimen ID CNC842511, the specimen was both Sanger sequenced and extracted from UCE sequences with the above-described method, and the resulting COI sequence was a consensus of these two sequences. There were no ambiguities between overlapping regions of the Sanger and UCE extracted COI sequence, but combining the two increased the length of the sequence. Specimen limitations only allowed Palaearctic *Piogaster* to be included in this analysis. Two of the three examined Nearctic specimens are holotypes, and the third male specimen is: 1) likely too old to be successfully barcoded; and 2) potentially a future holotype specimen if further evidence justifies its description as a new species. The species *P. punctulata* Perkins, 1958 and *P. lucida* could not be included in this analysis because the only reliably identified material are the female holotypes (the latter of which we were not able to examine). Within the Palaearctic species, we were able to include *P. daisetsuzana*, *P. ussuriensis* Kasparyan & Khalaim, 2007, *P. pilosator*, and *P. albina*, and three male specimens in the COI analysis. One male specimen from Norway was excluded. It was part of a metabarcoding survey in Norway (Åström and Davey 2024) and was the only *Piogaster* in a sample collected at a window trap. However, metabarcoding of this window trap sample found two sequences with a BLAST hit of *Piogaster*, that varied by 14 nucleotides (3.33% difference). These were excluded as there was no way of knowing which sequence (if either) was correct. All specimen and sequence information is listed in Suppl. material 2: Genetic data. We aligned the sequences using MUSCLE v5.1 (Edgar 2022) with default settings. The last 11 nucleotides of an unknown *Piogaster* male (BOLD ID COLHH2702-19) and the last 14 nucleotides of *Acrotaphus wiltii* (Cresson, 1870) (Genbank ID MK959373) were removed as they were causing gaps in the alignment that led to frameshift mutations and stop codons. This may have been due to lower quality Sanger sequencing typically found at the ends of a sequence being retained. After removing these nucleotides, the sequences were realigned. Two COI gene trees were inferred with IQ-Tree (Nguyen et al. 2015), using ModelFinder Plus (Kalyaanamoorthy et al. 2017) to determine the best model based on the Bayesian information criterion (BIC). The first COI gene tree was based on a single substitution model (TIM2+F+I+G4), and a second partitioned analysis utilized a separate substitution model for each codon (TIM2+F+G4, F81+F+I, and HKY+F+R2 for codons 1, 2, and 3, respectively). Node support was evaluated with ultrafast bootstrapping (Hoang et al. 2018) with 1000 replicates. Trees were annotated in R (R Core Team 2020) with the following packages: ape (Paradis and Schliep 2019), ggplot2 (Wickham 2016), and ggtree (Yu et al. 2017).

UCE phylogeny

UCE data from fourteen pipelines including three *Piogaster* specimens (Suppl. material 2: Genetic data) were assembled with ABySS, SPAdes, and rnaSPAdes in an existing pipeline (<https://github.com/AAFC-BICoE/snakemake-partial-genome-pipeline>) as discussed above. This pipeline trims and matches the assembled contigs with the UCE probes from the myBaits UCE Hymenoptera 2.5Kv2P bait set using the PHYLUCE

(Faircloth 2016) program `phyluce_assembly_match_contigs_to_probes`. The contigs were aligned with `phyluce_align_seqcap_align` using `mafft` and internally trimmed with `phyluce_align_get_gblocks_trimmed_alignments_from_untrimmed` using less stringent settings ($b1 = 0.5$, $b2 = 0.5$, $b3 = 12$, $b4 = 7$, Branstetter and Longino (2022)). Loci with 100% completeness were retained for downstream analysis with `phyluce_align_get_only_loci_with_min_taxa`, leaving 346 loci. The filtered loci were assessed for outlier sequences and alignment issues with Spruceup (Borowiec 2019) using the weibull min criterion and a 0.98 cutoff. The final UCE dataset (Suppl. material 4: UCE alignment) included 346 loci shared by all 14 taxa in the dataset, for a total alignment length of 100,115 containing 9,721 parsimony informative sites and 17.67% missing data. We used Sliding-Window Site Characteristics entropy method (SWSC-EN) (Tagliacollo and Lanfear 2018) to partition each loci either to include the entire locus or split it into a left, right, and core partition. These partitions were used as input for IQ-TREE 2 (Minh et al. 2020b). We ran IQ-TREE 2 with ModelFinder Plus (Kalyaanamoorthy et al. 2017), ultra-fast bootstrapping (Hoang et al. 2018) and 1000 replicates. We ran this analysis with `symtest` which assesses and removes partitions that do not meet the phylogenetic assumptions of stationarity and homogeneity (Naser-Khdour et al. 2019). We assigned *Clistopyga* sp. as the outgroup taxon. We produced individual locus trees and calculated gene and site concordance factors for each node (Minh et al. 2020a) in IQ-TREE 2 to evaluate nodal support in conjunction with bootstrap values.

Results and discussion

Genetic distances of sequences

Alignments used for genetic distances are available as Suppl. material 3: Single locus alignments. The genetic distances matrices of all loci are available as Suppl. material 5: Genetic distances.

The 780 bp alignment of COI (658 barcoding region and available flanking nucleotides) showed a maximum interspecific variation of 6.89% among *Piogaster* specimens. Divergence between *Piogaster* and *Inbioia* ranged from 11.74–14.86%. Interspecific divergence (reported as a range) and maximum intraspecific divergence, respectively, were as follows: *P. daisetsuzana*, 3.13–6.28%, 0.14%; *P. ussuriensis*, 1.97–6.89%, 4.52%; *P. albina*, 0–6.29%, 0.14%; *P. pilosator*, 0–6.89%, 0.23%. One *P. ussuriensis* specimen ([KU753347.1](#)) was highly divergent from the other three accounting for the 4.52% genetic distance. Among the remaining three *P. ussuriensis* specimens, the maximum intraspecific divergence was only 0.48%. *Piogaster albina* and *P. pilosator* diverged by 0–0.23%.

The 771 bp alignment of 28S included six specimens (four *Piogaster* species and one *Inbioia* from Sumatra, Indonesia). The divergence within *Piogaster* ranged from 0.32–0.94%, while the divergence between *Piogaster* and *Inbioia* ranged from 2.35–2.99%.

The 918 bp alignment of 18S included five specimens (three *Piogaster* species and one *Inbioia*). The divergence within *Piogaster* ranged from 0–0.44%, while the

variation between *Piogaster* and *Inbioia* ranged from 0.44–0.54%. The two *P. albina* and single *P. pilosator* sequences were 100% identical.

The 448 bp alignment of the Nasvi2EG013087 was successfully sequenced for five specimens (four *Piogaster* species). *Piogaster albina* and *P. pilosator* had low divergence (0–0.3%). *Piogaster ussuriensis* was 1.29–1.79% divergent from *P. albina*, 1.31% divergent from *P. pilosator*, and 2.94% divergent from *P. daisetsuzana*. *Piogaster daisetsuzana* was 2.56% divergent from both *P. albina* and *P. pilosator*, and 2.94% divergent from *P. ussuriensis*.

The 819 bp alignment of ITS2 included two *P. albina* specimens and one *P. pilosator* specimen. There was 0% divergence between these sequences.

EF1a was only successfully mined from one *P. albina* UCE specimen (CNC842511). When compared to the existing *P. daisetsuzana* sequence, they had a divergence of 0.19%.

Phylogenetic analysis

The COI phylogenies (Figs 1, 2) and the UCE phylogeny (Fig. 3) recovered a strongly supported monophyletic *Piogaster*. The node supporting *Piogaster* as a monophyletic group in the UCE phylogeny had 100% bootstrap support and also strong gene and site concordance factors (70.5 and 86.7, respectively).

This is the first phylogenetic analysis of the relationships within *Piogaster*. *Piogaster daisetsuzana* formed a highly supported monophyletic clade and was the sister species to all others (Figs 1, 2). *Piogaster ussuriensis* is recovered as monophyletic with 98% bootstrap support in the single model phylogeny (Fig. 1) but poorly supported with 60% bootstrap support in the codon model phylogeny (Fig. 2). *Piogaster albina* and *P. pilosator* are recovered in a mixed clade with high bootstrap support in both COI phylogenies (Figs 1, 2), rendering both species paraphyletic. In contrast, the UCE phylogeny recovered *P. albina* and *P. pilosator* as sister species with strong support (Fig. 3: bootstrap = 100; gCF = 70.5; sCF = 86.7). Despite the low sequence divergence in both the COI and UCE analyses, females of *P. pilosator* and *P. albina* are morphologically distinct (see key and species descriptions). Although COI remains useful, its gene tree is not always congruent with the species tree (Klopfstein et al. 2016), and in *Piogaster* it showed limited power in delimiting species, particularly between *P. albina* and *P. pilosator*. The inclusion of broader genomic data from UCEs helped to clarify their relationship and supports recognizing *P. albina* and *P. pilosator* as distinct species, although UCEs from additional specimens of both species are required to support their separate status further.

The COI phylogeny only helped associate one of the three males included in the analysis. A male from Japan was recovered within the *P. daisetsuzana* clade in both phylogenies (Figs 1, 2). A male specimen from Germany was recovered within the *P. albina* + *P. pilosator* clade and thus could not be definitively placed with either species. A second male specimen was recovered in different places in the phylogeny depending on the analysis. In the single model analysis (Fig. 1), it was recovered as the sister group to *P. ussuriensis* and + the *P. albina*/*P. pilosator* clade, while in the partitioned analysis

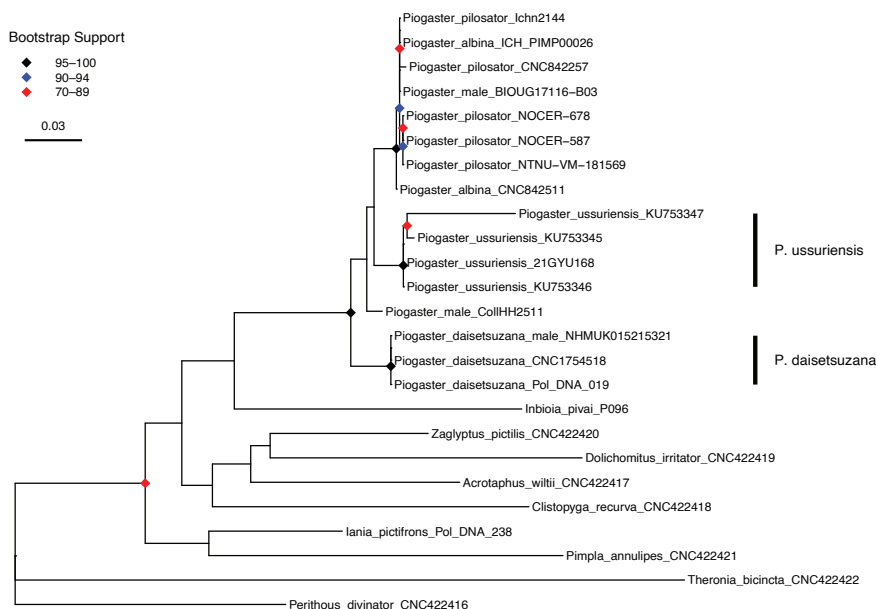


Figure 1. Phylogeny of *Piogaster* based on the COI barcoding gene in IQTree with a single substitution model assigned with ModelFinder Plus. Tip labels are the taxon name and the unique ID, BOLD Sample ID, or Genbank Accession number listed in Suppl. material 1: Specimen data. In cases where *Piogaster* specimens are male, sex is also included in the tip label (otherwise all specimens are female). Bootstrap support is indicated by colour, as shown in the legend on the top right. Unlabelled nodes have less than 70% bootstrap support.

(Fig. 2) it was the sister group of the *P. albina*/*P. pilosator* clade. This species could also not be associated with conspecific females.

Inbioia was recovered as the sister genus of *Piogaster* in all analyses (Figs 1–3). This relationship was not well supported in the COI trees (bootstrap of 55 and 61 in the single model and codon-partitioned phylogenies, respectively). In the UCE analysis, this node had 100% bootstrap support and low to moderate gene and site concordance factors (34.1 and 54.1, respectively). While *Inbioia* and *Piogaster* are morphologically similar, many of the apomorphies of *Piogaster* and *Inbioia* discussed by Gauld et al. (2002a) no longer apply upon examination of additional specimens (see Comments following *Piogaster* generic description), prompting Bhat et al. (2025) to contemplate synonymizing *Inbioia*. Overall, the combination of a barcode gap between *Piogaster* and *Inbioia* in COI and 28S and our phylogenetic results agree with those of Gauld and Dubois (2006) and Quicke et al. (2009) that *Piogaster* and *Inbioia* are sister taxa. Based on molecular analyses, we found no evidence that the two genera should be synonymized as contemplated by Bhat et al. (2025). On the contrary, the long branch lengths, genetic divergence results, and strong nodal support of the *Piogaster* clade as monophyletic support that *Piogaster* and *Inbioia* are distinct. The inclusion of additional *Inbioia* specimens,

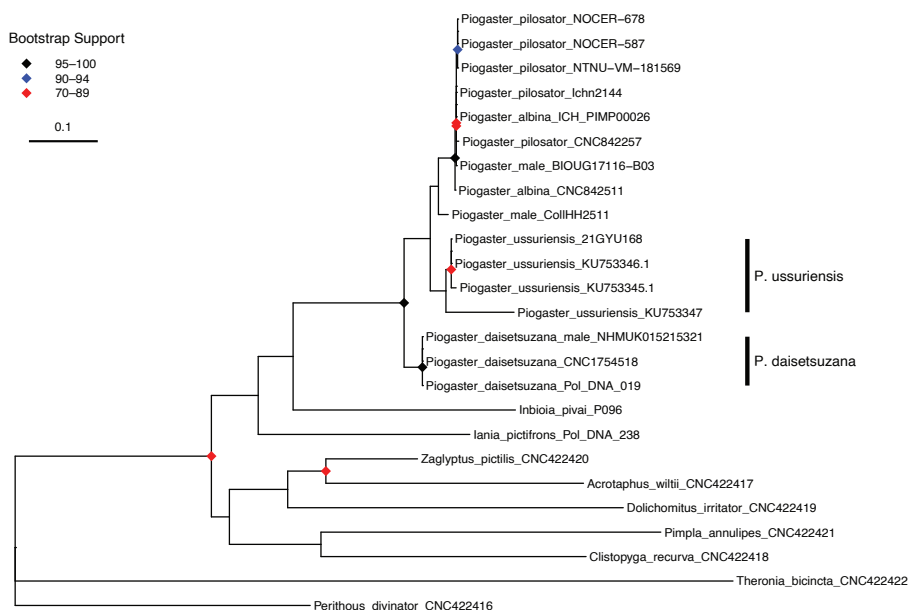


Figure 2. Phylogeny of *Piogaster* based on the COI barcoding gene in IQTree with a separate substitution model assigned to codons 1, 2 and 3 with ModelFinder Plus. Tip labels are the taxon name and the unique ID, BOLD Sample ID, or Genbank Accession number listed in Suppl. material 1: Specimen data. In cases where *Piogaster* specimens are male, sex is also included in the tip label (otherwise all specimens are female). Bootstrap support indicated by colour, as shown in the legend on the top right. Unlabelled nodes have less than 70% bootstrap support.

particularly the newly described *I. himalayensis* from India, and the discovery of new morphological features to diagnose these taxa may strengthen these findings.

Neither COI phylogeny rendered the *Polysphincta* group monophyletic as *Iania* (Fig. 1) and *Acrotaphus* (Figs 1, 2) did not cluster with *Piogaster* + *Inbioia* without inclusion of genera outside of the *Polysphincta* group (*Clistopyga*, *Dolichomitius* Smith, 1877, *Pimpla* Fabricius, 1804 and *Zaglyptus*). This was likely due to the type of data utilized, as COI is fast evolving and thus useful at resolving recent relationships but performs poorly at resolving older divergences. In the UCE phylogeny (Fig. 3) the *Polysphincta* group was monophyletic with moderate bootstrap support but low gene and site concordance factors. The three subgroups within the *Polysphincta* group (*Schizopyga*, *Polysphincta*, and *Acrodactyla* subgroups) proposed by Matsumoto (2016) were also monophyletic, each with 100% bootstrap but with low to moderate gene and site concordance factors. Matsumoto (2016) did not include *Eruga* Townes, 1960 in their analysis but presumed it was in the *Acrodactyla* subgroup, and this was supported here. *Piogaster* was placed within the *Schizopyga* group and the *Schizopyga* group was sister to all other genera in the *Polysphincta* group as in Matsumoto (2016) and Klopstein et al. (2019a).

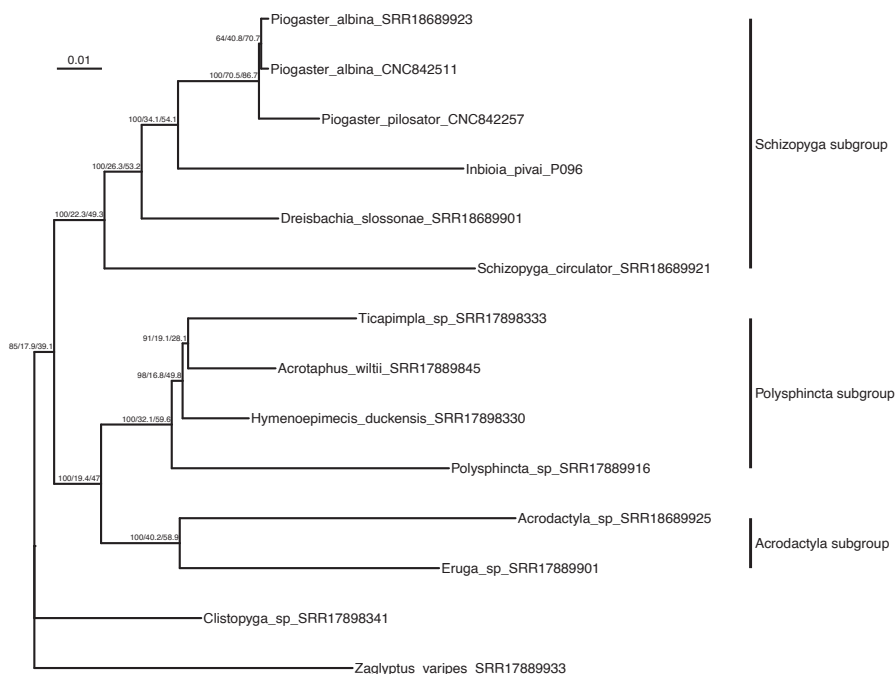


Figure 3. Phylogeny of the *Polysphincta* group utilizing 346 UCE loci in IQTree. Subgroups within the *Polysphincta* group are labelled on the left. Nodes are labelled with bootstrap support, gene concordance factor, and site concordance factor in that order.

Taxonomy

ICHNEUMONIDAE Latreille, 1802

PIMPLINAE Wesmael, 1845

EPHIALTINI Hellén, 1915

***Piogaster* Perkins, 1958**

Figs 4–25

Piogaster Perkins, 1958: 263. Type species: *Piogaster rugosa* Perkins (= *Polysphincta pilosator* Aubert), by original designation.

Diagnosis. *Piogaster* can be distinguished from all other genera of the *Polysphincta* group of genera by combination of the following: 1) notauli absent (Fig. 4E); 2) female metasomal T8 without paired, lateral, three-branched setose appendages (present in *Inbioia*; Barrantes et al. 2019; Bhat et al. 2025). Within the *Polysphincta* group of genera, the complete lack of notauli is only known in *Piogaster* and *Inbioia*. However,

some species in other genera in the Holarctic region, especially *Eriostethus* Morley, 1914, *Eruga*, *Flacopimpla*, *Polysphincta*, and *Zatypota* have notauli that are incomplete, weak, and/or only indistinctly impressed anteriorly, therefore the following additional characters are included should the presence/absence of the notauli be uncertain: 3) palp formula 5 : 4 (4 : 3 in *Eriostethus*); 4) two mandibular teeth subequal in breadth (upper tooth broader than lower tooth in *Eruga*); 5) T2 without anterolateral and posterolateral oblique grooves forming rhombic shape (present in *Zatypota* and *Flacopimpla*); and 6) clypeus convex (flat clypeus in *Polysphincta*).

In addition to these morphological characters, *Piogaster* has diagnostic molecular characters in the COI barcode region: a binary character at site 377 (G in *Piogaster*, T in all other *Polysphincta* group genera), corresponding to amino acid 126 (Alanine in *Piogaster*, Serine in others); and an asymmetric character at site 416 (T in *Piogaster*, A or G in other genera), corresponding to amino acid 139 (Serine or Tryptophan in *Piogaster*, Methionine, Alanine, or Threonine in other genera).

Description. Adult. Female. Body length 4.2–6.8 mm. Fore wing 2.5–5.1 mm long. **Head.** Antenna with 22–25 flagellomeres. Flagellomere 2 0.6–0.9× length of flagellomere 1 and subequal to flagellomere 3. Eye without long, dense setae between ommatidia (Fig. 13C). Clypeus convex, separated from face by groove (Fig. 7C). Mandible with upper tooth longer than lower; upper and lower tooth with similar breadth. Palp formula 5 : 4. Genal index 0.7–1.6. **Mesosoma.** Epomia usually absent, sometimes present across pronotal groove, but absent dorsal to groove (Fig. 10A). Mesoscutum lacking notauli (Fig. 4E). Epicnemial carina complete ventrally, extending dorsally to 0.3–0.5× height of posterior pronotum (Figs 5A, 14A), curving anteriorly towards anterior edge of mesopleuron in most specimens (Fig. 14B), but sometimes mostly straight (Fig. 5B). Submetapleural carina strong anteriorly to 0.6–0.8, weakening posteriorly. Juxtacoxal carina usually completely absent, rarely present posteriorly, or very rarely complete (if present, weak and sinuous (Fig. 5C)). Propodeum with pleural carina ranging from absent to strong and complete (Fig. 14C); other carinae absent except lateral longitudinal carinae present posteriorly (Figs 5D, 8D, 12A, 22G). **Wings. Fore wing.** Vein 2m-cu weakly inclivous with two bullae. Vein 3rs-m absent. Vein Rs&M basal to 1cu-a by 0.2–0.7 length of 1cu-a. **Hind wing.** Vein M+Cu moderately curved medially (Figs 5E, 14E). **Legs.** Hind femur 3.2–4.2× as long as wide. Hind tarsal dimensions 1:0: 0.5–0.7: 0.3–0.5: 0.2–0.3: 0.5–0.7. **Metasoma.** T1 0.6–1.3× as long as wide; 1.0–1.5× as long as T2. T1 spiracle at 0.3–0.5× length of T1. T2 0.5–0.8× as long as wide. T3 0.4–0.7× as long as wide. Tergites variable, without oblique, anterolateral and posterolateral grooves or tubercles in most species, T2–T5 with weak submedial to sublateral ovoid tubercles and transverse grooves in one species (Figs 19E, F). Ovipositor straight (Fig. 7A) to slightly upcurved (Fig. 20A).

Male. As described above for females, but with more variation in the propodeal carina. Males may have the same propodeal carina as described for females, or have longer lateral longitudinal carinae (to 0.8× length of propodeum), and may have the median longitudinal carinae present, albeit weak (Fig. 25E). Tergites variable, T2–4 without grooves or tubercles or with transverse grooves medially to posteriorly in some specimens.

Species included. Eight in total, seven previously described and one described in the current study (see introduction and key below).

Distribution. Holarctic. Four species are recorded from the western Palearctic, two from the eastern Palearctic and two from the Nearctic region (see distributional maps in Figs 26–32).

Piogaster albina is widespread throughout Europe, *P. daisetsuzana* is from Japan, *P. lucida* is from Romania, *P. maculata* Townes, 1960 is from western USA (California), *P. pilosator* is widespread through Europe, *P. punctulata* is from the United Kingdom, *P. ussuriensis* is from the Russian Far East (Primorsky Krai) and Korea, and *P. variegata* sp. nov. is from Canada (Alberta).

Biology. Ectoparasitoids of jumping spiders (Araneae: Salticidae). Three genera within the family Salticidae (from subfamily Salticinae, tribes Salticini and Dendryphantini) have been recorded as hosts. An unidentified *Piogaster* male from British Columbia, Canada was reared from *Habronattus* (specimen described below). An unidentified *Piogaster* female from Finland was recorded parasitizing *Salticus* Latreille, 1804 in a laboratory setting (Takasuka et al. 2018). Finally, iNaturalist records made by Christine Evers (profile name: cae1) show both a salticid host with a larval exoparasite (Evers 2019a) collected near Brisbane, California on May 11, 2019 and an adult *Piogaster* reared from that salticid host (Evers 2019b). This *Piogaster* specimen shares the spotted legs and lack of hind wing 2/Cu of other North American females, but could not be identified to species from the images. This *Piogaster* specimen was not retained, so it could not be examined further. The spider was identified as a subadult male of the subtribe Dendryphantina, and based on the location, it was most likely *Metaphidippus manni* (G. & E. Peckham, 1901) (Wayne Maddison, pers. comm.).

Comments. Gauld and Dubois (2006) list uniformly convex tergites without tubercles and grooves as diagnostic of *Piogaster*. However, there are paired convex tubercles on tergites 2–4 of *P. ussuriensis* (Fig. 19E, F) as well as weaker tubercles on some *P. pilosator* specimens, and some male *Piogaster* have transverse grooves on some of the metasomal tergites (Fig. 25H). Except for the presence of the paired, branching appendages on T8 in female *Inbioia* (absent in female *Piogaster*), these two genera are difficult to differentiate. One of the previously listed diagnostic features differentiating *Piogaster* from *Inbioia* is the lack of an epomia in *Piogaster* (Gauld and Dubois 2006). However, Kusigemati (1985) reported that *P. daisetsuzana* has a “very short and weak” epomia. We have examined *P. daisetsuzana* female specimens that appear to have a short, weak epomia (Fig. 8A), but in others we cannot see an epomia or it may be obscured by the head position. *Piogaster daisetsuzana* males have a more distinct epomia (Fig. 10A). In other species, interpretation is further complicated because the anterodorsal pronotum has longitudinal rugae, which may obscure or mimic a weak epomia (as in Figs 14A, 19A, 25B). In contrast, females of some species, such as *P. albina*, clearly lack an epomia entirely (Fig. 5A). Characters listed as diagnostic for *Inbioia* by Gauld et al. (2002a) include a straight 1/Cu+cu-a vein and lack of a 2/Cu vein, a straight epicnemial carina, and the presence of an epomia, however each of these characters appears in a *Piogaster* specimen examined as part of this study (Figs 21E, 5B, and 10A, respectively). Furthermore, the recently described *Inbioia himalayensis* has a

bend in the 1/Cu+cu-a vein with an intercepting 2/Cu vein (Bhat et al. 2025) so this character is no longer diagnostic for *Inbioia*. While *I. piva* has a long T8 (Gauld et al. 2002a), this is not shared by *I. himalayensis* (Bhat et al. 2025) meaning this character is also not diagnostic. Thus, the only diagnostic character is the branched process on metasomal T8. The male of *Inbioia* is not known, but it is assumed that the branching structure near the apex of the metasoma is only present in the female. If and when the male is discovered, the diagnosis of *Piogaster* will need to be updated accordingly.

Key to the world species of *Piogaster* Perkins, females

- 1 Mesoscutum polished, smooth to weakly coriaceous, impunctate or rarely punctate anteriorly, with at most a few sparse setae located laterally and anteriorly (Fig. 4E) **2**
- Mesoscutum matte, moderately to densely setose, and pustulate (Fig. 20E), granulate (Fig. 11D), rugose to rugose-punctate (Figs 7E, 13E, 18E), or matte to subpolished and punctate (Fig. 16E) **3**
- 2(1) Metasomal T2–T5 coarsely, densely punctate (Fig. 5H). Western Palearctic ***P. albina* Perkins**
- Metasomal T2–T5 sparsely punctate anteriorly and laterally but otherwise impunctate. Romania ***P. lucida* Constantineanu & Constantineanu**
- 3(1) Mesopleuron polished with shallow, setiferous punctures, punctures becoming rugose-punctate dorsal to mesopleural fovea (Fig. 17A). Frons matte, granulate laterally, granulations becoming transversely strigose laterally (Fig. 16C, D). United Kingdom ***P. punctulata* Perkins**
- Mesopleuron matte, granulate (Fig. 11F), pustulate (Fig. 21B), rugulose, or rugose (Fig. 19A), not polished with clearly separated punctures. Frons matte, granulate (Fig. 20D), rugulose to rugose (Fig. 18D), rugose punctate or densely punctate. Holarctic **4**
- 4(3) Metasoma with T2–T5 granulate (Figs 12D, 21H). HW vein 1/Cu&cu-a gently curved, without a strong angle distinguishing 1/Cu from cu-a, abscissa 2/Cu absent (Fig. 21F). Nearctic **5**
- Metasoma with T2–T5 punctate to punctate reticulate (Fig. 14H); HW vein 1/Cu&cu-a with a strong angle distinguishing 1/Cu from cu-a, abscissa 2/Cu present, intercepting 1/Cu&cu-a in the lower half as a tubular, spectral, or nebulous vein (Figs 8E, 19C). Palearctic **6**
- 5(4) Metasoma with T2–T6 uniformly dark brown (Fig. 12D); coxae brown with some patches of yellow (Fig. 11A). MSL equal to BWM. FW vein 2rs-m 0.4× as long as M between 2rs-m and 2m-cu (Fig. 12B). USA: California ***P. maculata* Townes**
- Metasoma with T2–T6 variegated, anterior 0.8 of each segment pale brown with dark brown spots, the posterior 0.2 white (Fig. 21H); coxae white, with some brown markings (Fig. 20A). MSL 1.3× as long as BWM. FW vein 2rs-m 0.6× as long as M between 2rs-m and 2m-cu (Fig. 21E). Canada: Alberta ***P. variegata* Bass, Bennett & Schwarzfeld, sp. nov.**

- 6(4) Propodeum medially with transverse striations (Fig. 8D). FW vein Rs+M with ramellus present (Fig. 8F). FW vein 2m-cu slightly thickened and angulate between bullae (Fig. 8F). Japan ***P. daisetsuzana* Kusigemati**
- Propodeum rugose without transverse striations (Figs 14D, 19B). FW vein Rs+M with ramellus absent (Figs 14F, 19C); FW vein 2m-cu straight or slightly bent, not thickened between bullae (Figs 14F, 19C). Palaearctic (Europe, southwestern and eastern Russia, Korea) 7
- 7(6) Head primarily dark brown to black with metasoma white to very pale yellow (Fig. 18A). Ovipositor sheath at most 0.5× as long as hind tibia (Fig. 18A). Korea and Eastern Russia ***P. ussuriensis* Kasparyan & Khalaim**
- Head and metasoma colour variable, from pale yellow to black, but never with contrasting dark brown to black head and pale metasoma as described above (Figs 13A, 15A–C). Ovipositor sheath at least 0.7× as long as hind tibia (Figs 13A, 15A, C). Western Palaearctic ***P. pilosator* (Aubert)**

***Piogaster albina* Perkins, 1958**

Figs 4–6

Piogaster albina Perkins, 1958: 264.

Diagnosis. *Piogaster albina* can be distinguished from its congeners by possession of the combination of the following: 1) mesoscutum polished, impunctate in most specimens (Fig. 4E) or punctate anteriorly with at most a few sparse setae laterally and anteriorly; 2) metasomal T2–T5 coarsely, densely punctate (Fig. 5H) to moderately punctate (Fig. 6B). *P. albina* closely resembles *P. lucida*, however *P. albina* T2–T5 are coarsely densely to moderately punctate, whereas *P. lucida* T2–T5 are sparsely punctate anteriorly and laterally and otherwise smooth.

Redescription. Adult. Female. Body length 4.4–6.8 [5.4] mm. FW length 3.5–4.9 [3.9] mm. **Head.** Antennae with 20–23 [21] flagellomeres (Fig. 4A). Clypeus 1.5–2.2 [1.65]× as wide as high, polished, weakly rugulose, with sparse long light brown setae (Fig. 4C). Face polished, sculpture variable from completely smooth, to smooth laterally and ventrally and weakly rugulose punctate mediodorsally [as in holotype, (Fig. 4C)], to entirely weakly rugulose punctate, with sparse medium length yellow-white setae. Frons and vertex polished, smooth [as in holotype, (Fig. 4B)] to coriaceous (Fig. 4D) but finely densely punctate in some specimens, with sparse to moderately dense short to medium length yellow-white to medium brown setae (Fig. 4D). Occipital carina complete (Fig. 4B). MSL 0.7–1.0 [1.0]× as long as BWM. OOD 1.3–1.7 [1.3]× as long as LOD. **Mesosoma.** Pronotum with epomia absent; polished, smooth (Fig. 6), weakly coriaceous (Fig. 5A), or weakly rugulose punctate [as in holotype, (Fig. 4A)], lacking setae or with sparse, medium length yellow setae. Mesoscutum polished, smooth to weakly coriaceous, anterolaterally smooth (Fig. 5A) to densely punctate, sometimes posteriorly sparsely setose, medially with at most 10 sparse medium to long brown setae

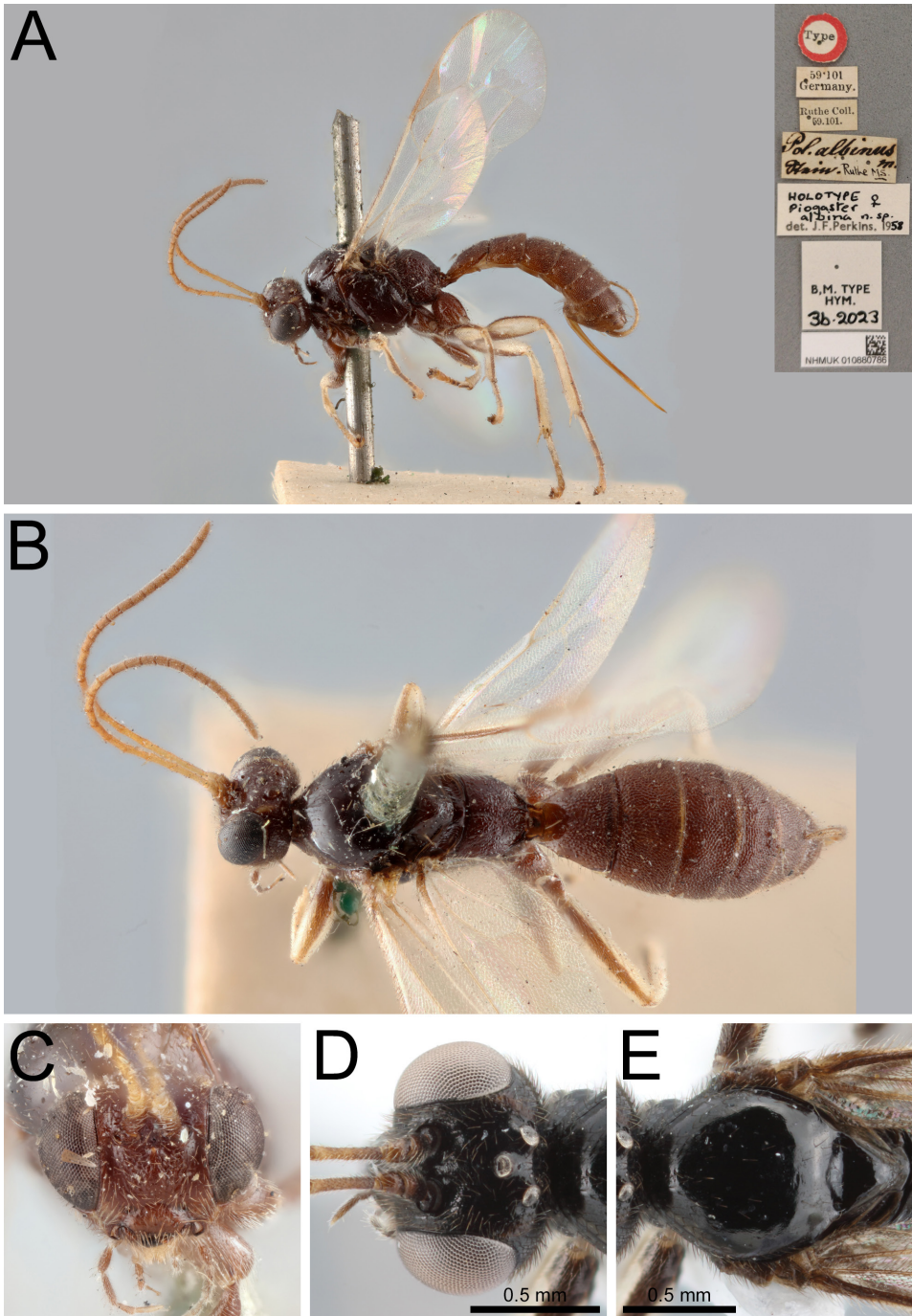


Figure 4. *Piogaster albina* female. Figures A–C of holotype (NHMUK) and D and E of non-type specimen CNC1754425 (NMS). **A** habitus, lateral view with holotype labels inset **B** habitus, dorsal view **C** head, anterior view **D** head, dorsal view **E** mesoscutum, dorsal view. Figures A and B were taken by Gavin Broad (© Trustees of the Natural History Museum, CC-BY).

(Fig. 4E). Scutellum polished, smooth, with only a few very sparse, short yellow-white to medium brown setae (Fig. 4E). Mesopleuron polished, smooth [as in holotype] (Fig. 6A) or weakly coriaceous (Fig. 5B), lacking setae centrally, with sparse, medium length, yellow-white setae dorsally, posteriorly and especially ventrally (Fig. 5B). Metapleuron polished, weakly rugulose, moderately densely punctate with medium length white setae (Fig. 5C). Propodeum polished, variable sculpture from almost completely smooth (Fig. 6B) to mostly rugulose [as in holotype] (Fig. 5D), with sparse long yellow-white setae, setae absent medially. Propodeum with pleural carina complete in most specimens, present and strongly indicated anteriorly (Fig. 5C), but indistinct and/or sinuous medially to posteriorly in some specimens [including holotype] (Fig. 4A); lateral longitudinal carina present in posterior 0.2–0.5 [0.5], all other propodeal carina absent (Figs 5D, 6B). **Wings. Fore wing.** Vein Rs+M without ramellus extending conspicuously anteriorly into cell 1M + 1R1 (Fig. 5F) (at most indicated by a small stub where these two veins meet). Vein 2rs-m 0.5–1.0 [1.0]× as long as M between 2rs-m and 2m-cu (Fig. 5F). Vein 2m-cu not thickened or angulate between bullae (Fig. 5F). **Hind wing.** Vein 1/Cu&cu-a inclivous, strongly angled where 2/Cu intercepts in lower 0.3–0.4 [0.3] (Fig. 5E), with 2/Cu ranging from completely tubular to tubular at extreme base and nebulous more apically [as in holotype] to completely nebulous. **Metasoma.** T1 polished, anteriorly smooth [as in holotype] to sparsely punctate, medially to posteriorly punctate (Figs 5G, 6B), sometimes posterolaterally punctate reticulate, punctures with dense medium length yellow-white setae. T1 median dorsal carina absent (Fig. 6B), or present anteriorly but short and weak (rounded) [as in holotype] (Fig. 5G), 0.1–0.2 [0.2]× length of T1; dorsolateral carinae variable, completely absent in some specimens, present anteriorly for 0.2–0.4× length of T1 [as in holotype], present in posterior 0.3× length of T1 in some specimens, absent medially in all specimens (Fig. 5C). T2–T5 polished, densely to moderately densely punctate, with sparse to dense medium length white setae, T2 and T3 laterally punctate reticulate in some specimens (Figs 4B, 5H, 6A, B). T6 polished, with punctures varying from sparse (Fig. 6A) to moderately dense (Figs 5H, 6C) to dense [dense] (Fig. 4A), with medium length white setae (Figs 5H, 6A, C). T7 and T8 polished, smooth (impunctate), with a few short to medium length white to medium brown setae anteriorly and laterally (Figs 4A, 5H, 6A, C). Tergites without grooves or tubercles (Figs 4A, 5H, 6A, C). Ovipositor sheath 0.8–1.0 [0.9]× as long as hind tibia (Fig. 6C). **Colour.** Face, frons, and gena medium brown [as in holotype (Figs 4A–C)] to black (Fig. 4D). Clypeus medium brown [as in holotype, (Fig. 4C)] to black, some specimens yellow-brown medially. Malar space medium brown to black, some specimens with yellow-brown spot [as in holotype]. Vertex and occiput medium brown to black [medium brown, (Fig. 4B)], vertex with long thin irregular shaped yellow [as in holotype (Fig. 4B)] to red-brown mark (Fig. 4D). Mandible black with thin transverse basal red-brown stripe or brown basally, red-brown apically with medial transverse black stripe [as in holotype]. Maxillary and labial palps medium to dark brown [medium brown, Fig. 4C]. Antenna colour uniformly brown-black or with scape and pedicel light to dark brown with pale to medium brown flagellomeres [as in holotype, Figs 4A, B] (Fig. 4B). Pronotum uniform medium brown [as

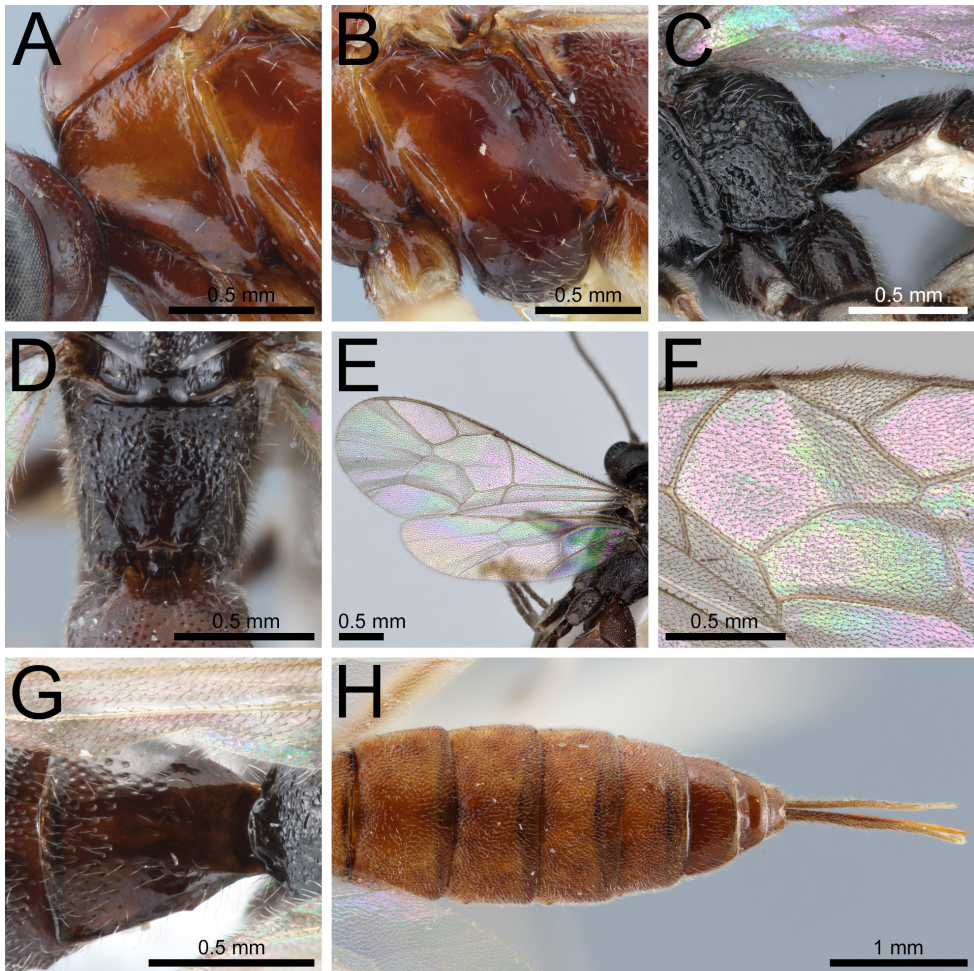


Figure 5. *Piogaster albina* female. Figures A, B, and H from non-type specimen NHMUK012850730 (NHMUK), figure C of non-type specimen CNC1754425 (NMS), figures D–G from non-type specimen CNC310408 (NMS). **A** pronotum **B** mesopleuron **C** metapleuron, propodeum and T1, lateral view **D** propodeum, dorsal view **E** wings **F** fore wing **G** tergite 1, dorsal view **H** metasoma, T2–T8 and ovipositor, dorsal view.

in holotype, (Fig. 4A)] to black (Fig. 6A), sometimes lighter dorsally (Figs 6C, 5A). Tegula light [as in holotype, Fig. 4B] to medium brown (Fig. 4E). Mesoscutum medium brown [as in holotype, (Fig. 4B)] to black (Fig. 4E), sometimes with yellow to red-brown lateral margins (Fig. 5A) and yellow to red-brown posteriorly. Scutellum, post-scutellum and axillary troughs uniform medium brown [as in holotype, (Fig. 4B)] to black (Fig. 4E). Mesopleuron medium brown [as in holotype, (Fig. 4A)] to black, sometimes with yellow-brown or red-brown area anteriorly (Fig. 6C). Metapleuron uniform medium brown [as in holotype] to black. Propodeum uniformly medium

brown [as in holotype, (Fig. 4B)] to black (Fig. 6B). Wings hyaline, veins light brown transparent, SC+R medium brown, stigma variable from light brown transparent [as in holotype, (Fig. 5E)] to medium brown. Fore, middle and hind coxae medium brown [as in holotype] to black, white apically in some specimens, trochanters medium brown [as in holotype, (Fig. 4A)] to black (Fig. 5C), white apically in most specimens, femur and tibia yellow-white with medium brown to black longitudinal stripe on dorsal and ventral surfaces, fore tibia without ventral stripe in most specimens, tarsi yellow-white, light brown to black on dorsal surface (Fig. 4A). Metasomal tergites variable, uniform yellow-brown (Fig. 5H), medium brown [as in holotype, (Figs 4A, B)] (Fig. 4B) or brown-black (Fig. 6A). Ovipositor sheath variable, medium brown with a yellow-white band from 0.2–0.4 [as in holotype, (Fig. 4A)], uniform medium to dark brown (Fig. 6A), or medium brown fading to white at apical 0.2 (Fig. 6C).

Male. A male was described by Aubert (1963) as *P. albina* because it was collected in the same locality on the same day as four female *P. albina*. We have examined this male and whereas we could not refute Aubert's identification, we also could not find any characters that would associate it unequivocally with females of *P. albina*.

Distribution. Fig. 26. Western Palaearctic: England (Shaw 2006), France (Aubert 1963), Germany (Perkins 1958), Hungary (current study, new record), Poland (Sawoniewicz 1978), Romania (Pisica 2002), Spain (del Castillo 1994), Sweden (personal communication, Harald Havnås, new record). A male *Piogaster* specimen from Austria was listed as *P. albina* in Kazmierczak (1990), but this specimen was not examined. With so little known about males of *Piogaster* and no justification for identification of this male as *P. albina*, this record cannot be confirmed.

Biology. Host unknown. Reared from an oak marble gall, *A. kollari* (Hymenoptera: Cynipidae) in southern England (Shaw 2006), with the assumption that the host of *P. albina* had entered the gall after being parasitized.

Material examined. Holotype. GERMANY • 1 ♀; B.M. Type Hym. 3b.2023; Ruthe Coll. 59.101; NHMUK010880786; [NHMUK].

Condition of type: Metasoma detached and glued to a separate point, otherwise intact.

Paratype. ENGLAND • 1 ♀; Norfolk, King's Lynn; viii.1911; Atmore; [NHMUK].

Other material. ENGLAND • 1 ♀; Leicester; vi.1973; Jennifer Owen; [EMUS] • 1 ♀; Goblin Combe, vc6, Somerset ST 47 65; 5.iii.2000; D. Gibbs; Em. 6.v.2000; Emerged from oak marble gall; CNC310408; [NMS] • 1 ♀; Kent, VC16, Halling, St. Andrews Lakes centroid; v-vii.2022, M. C. Townsend; CNC1754425; [NMS] • 1 ♀; same data as for preceding; [NMS] • 1 ♀; Norfolk, Holme Dunes, site ENDURE_MARRAM_INVERT_12_UK; 13.vii.2019; 52.97528°N, 0.54713°E; Ruben Van De Walle; Sweep on *Ammophila arenaria*; coastal dune, marram dominated; [RBINS] (photo only). FRANCE • 1 ♀; Vendée, Longeville; 19–26.ix.1965; J. A. J. Clark; B.M. 1965-489; NHMUK012850730; [NHMUK] • 1 ♀; FR44, Notre-Dame-des-Landes, La Freusière (WGS84); 47.3487°N, 1.7709°W; 16.vii.2013; Naturalistes en lutte - PM1; Genbank: [SRX14790939](#); ICH_PIMP_00026; [USNM] (photo only) • 2 ♀; Bouches-du-Rhône, Fos-sur-Mer; 13.ix.1962; J. A. Aubert; [MZLS] (photo only) • 1 ♀; Pont du Gard; 4.vi.1967; Matile; [MZLS] (photo only).

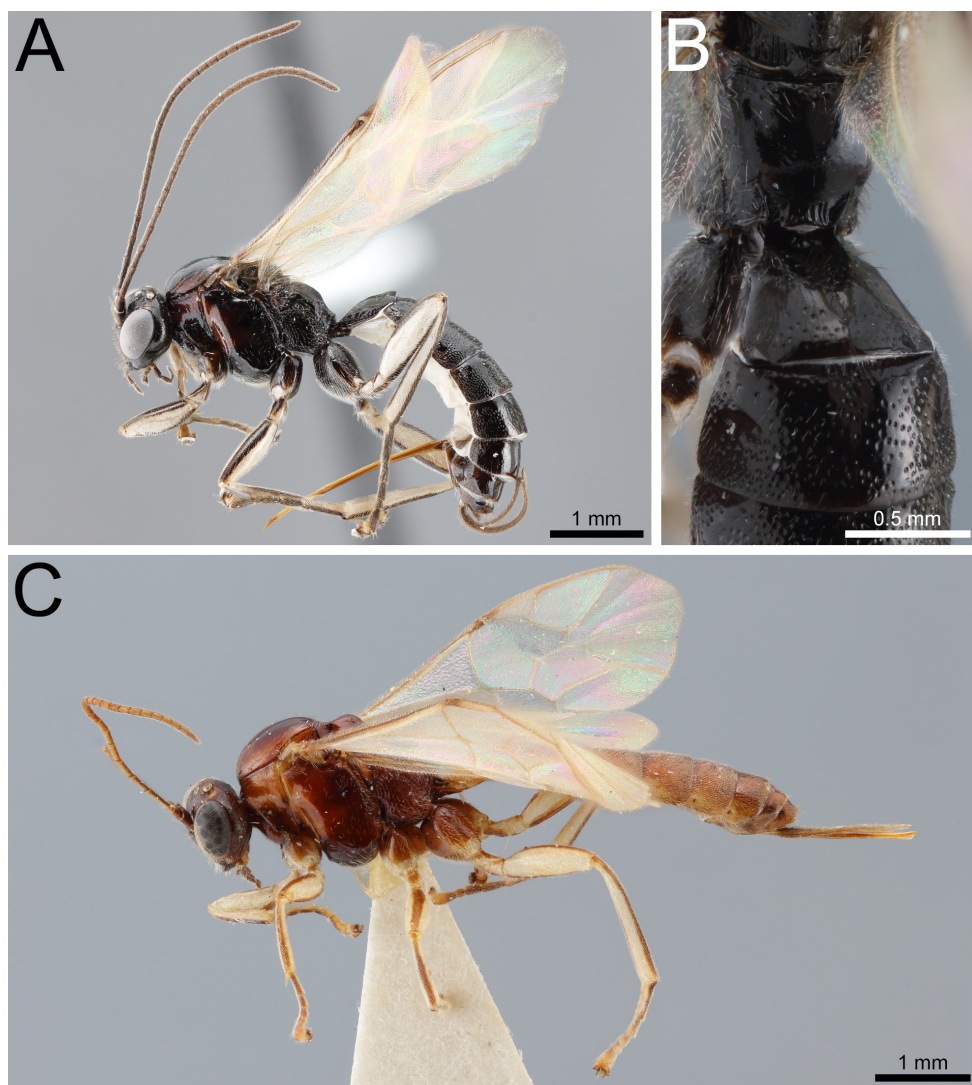


Figure 6. Colour and microsculpture variation within *Piogaster albina*, to be compared to the holotype specimen in Figs 4A–C. **A** habitus, lateral view of specimen from Hungary (CNC842511; CNC) **B** propodeum, T1, and T2 of specimen from Hungary (CNC842511; CNC) showing sculptural variation **C** habitus, lateral view of specimen from France (NHMUK012850730; NHMUK).

HUNGARY • 1 ♀; Vas Co., Kétvölgy; 46.88333°N, 16.21667°E; 18.v.2001; G. Gibson; CNC842511; [CNC]. SPAIN • 1 ♀; Cantabria, Trillayo; 20.viii.1991; Carmen Rey del Castillo; Yellow pan trap; MNCN_Ent 203194; [MNCN]. SWEDEN • 1 ♀; Gotlands kommun, Roleks; 57.53678°N, 18.33788°E; 10.iv–6.vi.2005; The Swedish Malaise Trap Project; Malaise trap ID 28; Border between mixed pine forest and open grazed calcareous pasture; [NHRS].

Comments. There is a great variation in the degree of rugosity of parts of the head, mesosoma and metasoma, especially the face, pronotum and propodeum, from highly rugose as in the specimen from England, Goblin Combe (Fig. 5D showing propodeum) to highly smooth and polished in the specimen from Hungary (Fig. 6B). The holotype tends towards more rugosity in these areas (Figs 4A, B).

Aubert named two new forms, form *alboclypeata* (Aubert 1963) and form *rufa* (Aubert 1969a). We examined the specimen Aubert (1969a) references for form *rufa* and the morphological variation found in this specimen is included in the above description. We examined two of the four females collected at Fos-sur-Mer on September 13, 1962 (the locality where form *alboclypeata* was collected), but neither of these had a white clypeus, so they were not likely the specimen assigned to form *alboclypeata* by Aubert (1963). As we did not see this specimen, and Aubert (1963) does not provide a detailed description of the morphology of the form, the morphological variation of this form is not captured in our description. As both were published after 1960, they are considered infrasubspecific categories rather than subspecies (see ICZN 1999: Art. 45.6).

Piogaster daisetsuzana Kusigemati, 1985

Figs 7–10

Piogaster daisetsuzana Kusigemati, 1985: 583.

Diagnosis. *Piogaster daisetsuzana* females can be distinguished from congeners by any of the following: 1) propodeum with medial transverse striations (Fig. 8D) (absent in all other species), 2) FW vein Rs+M with ramellus extending anteriorly into cell 1M + 1R1, tubular for 0.1–0.6× as long as vein 2rs-m, and extending farther as nebulous or spectral vein (Figs 7A, 8F) (absent or present as only a very short stub in other species), and 3) FW vein 2m-cu slightly thickened and angulate between bullae (Fig. 8F) (of uniform thickness and lacking angulation in all other species). Males can be distinguished from other male congeners by a combination of the following: 1) propodeum with medial transverse striations (Fig. 10D), and 2) presence of a polished, smooth medial part of metapleuron without microsculpture or setae (Fig. 10C) (some sculpture and/or setae in this region in other males, e.g., Fig. 25D).

In addition to these morphological characters, there is a binary diagnostic molecular character in the COI barcode sequence of *P. daisetsuzana* at site 290 (T in *P. daisetsuzana*, A in other *Piogaster*), corresponding to amino acid 97 (Leucine in *P. daisetsuzana*, Methionine in other *Piogaster*).

Redescription. Adult. Female. Body length 4.7–6.0 [5.0] mm. FW length 4.1–4.8 [4.1] mm. **Head.** Antennae with 23–24 [23] flagellomeres. Clypeus 1.6–2.0 [1.7]× as wide as high, subpolished (Fig. 7C), weakly rugulose in most specimens [smoother in holotype] and sparse, setiferous punctures with long white setae. Face, frons and vertex matte and granulate, with dense, short, yellow-white setae (Figs 7C, D). Occipital carina weak but complete in some specimens (Fig. 7D), apparently obsolete dorsally

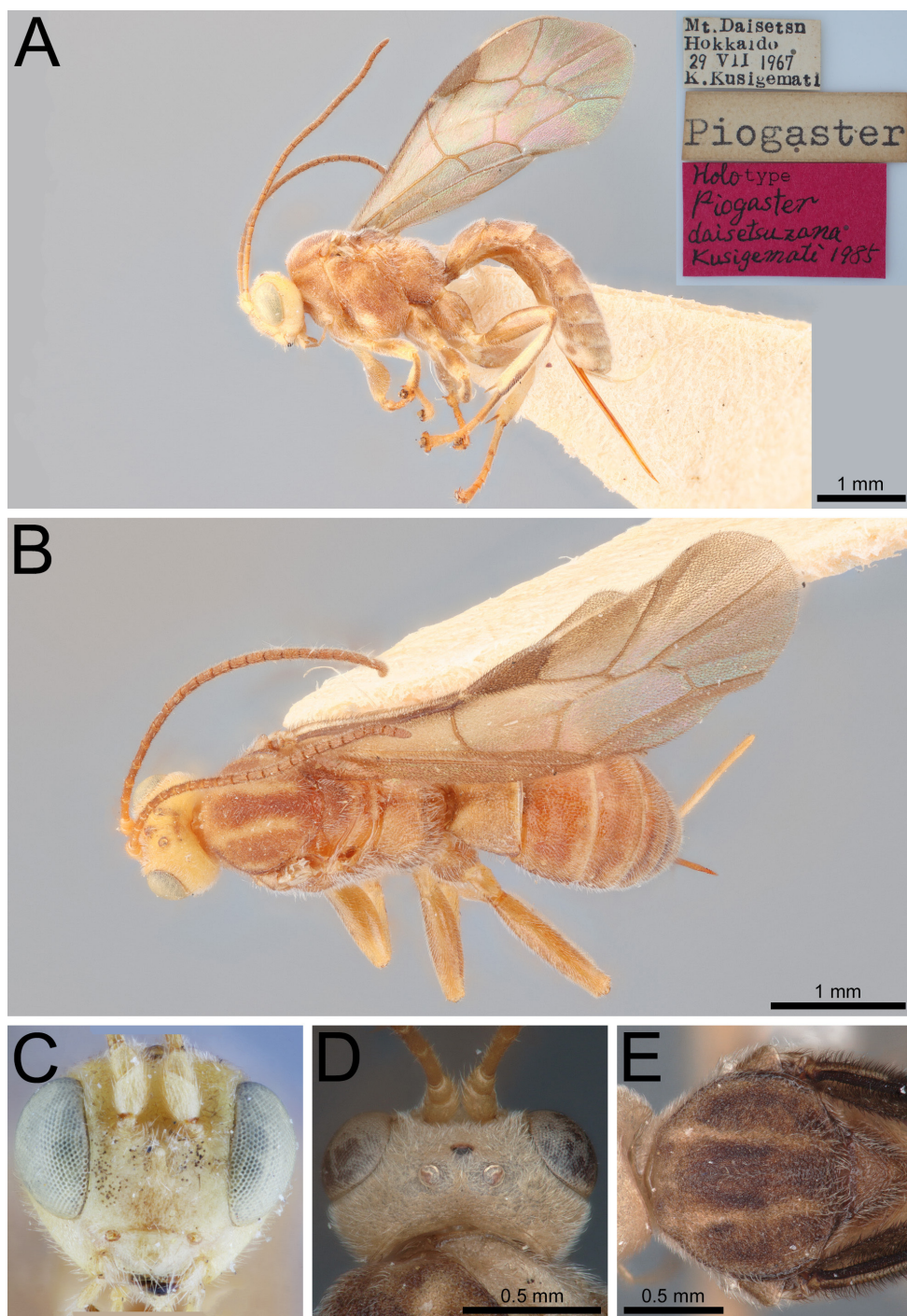


Figure 7. *Piogaster daisetsuzana* female. Figures A–C are the holotype, D–E are of non-type specimen CNC1754518 (EUMJ). **A** habitus, lateral view with holotype labels inset **B** habitus, dorsal view **C** head, anterior view **D** head, dorsal view **E** mesoscutum, dorsal view. Figures A–C © Juriya Okayasu.

in some specimens [based on original description of holotype] (Fig. 7B). MSL 0.8–1.1 [1.1]× as long as BWM. OOD 1.7–2.3 [2.3]× as long as LOD. **Mesosoma.** Pronotum with epomia as a short, low, vertical carina in dorsolateral pronotal groove (Fig. 8A). Pronotum (Fig. 8A) and scutellum (Fig. 7B) matte and rugose, with dense short yellow-white setae. Mesoscutum matte, densely rugulose-punctate to rugose-punctate, with dense short yellow-white setae (Fig. 7B). Mesopleuron and metapleuron matte, rugose with dense medium length yellow-white setae (Fig. 7A). Propodeum matte, rugose with medial transverse striations, with dense long yellow-white setae (Fig. 8D). Propodeum with pleural carina complete, but weak; lateral longitudinal carinae present in posterior 0.3–0.4, all other propodeal carinae absent. **Fore wing.** Vein Rs+M with ramellus extending into 1M+1R1 (discocubital) cell as a tubular vein for 0.1–0.6× as long as 2rs-m, and then continuing further as nebulous or spectral vein. Vein 2rs-m 0.5–0.6 [0.6]× as long as M between 2rs-m and 2m-cu. Vein 2m-cu thickened and angulate between bullae (Fig. 8E). **Hind wing.** Vein 1/Cu&cu-a inclivous, angled apically where 2/Cu intercepts (Fig. 8E), 2/Cu intercepting in lower 0.3–0.5 [0.5], 2/Cu tubular or nebulous at least 0.7 length to posterior edge of wing, reaching posterior edge of wing in some specimens. **Metasoma.** T1 matte, with dense, setiferous punctures, punctate reticulate laterally and in some specimens medially, with dense, short, yellow setae (Figs 7B, 8G). T1 median dorsal carina present anteriorly, but weak and short, 0.1–0.3 [0.2]× length of T1; dorsolateral carinae complete (Fig. 8C). T2–T5 subpolished, with dense, setiferous punctures, space between punctures less than 0.5× puncture diameter, laterally punctate reticulate with dense short to medium length yellow-white setae (Figs 7B, 8H). T6 subpolished, finely punctate, with dense short white setae. T7 and T8 subpolished, sparsely, finely punctate with dense medium length white setae. Tergites without grooves or tubercles. Ovipositor sheath 0.9–1.2 [1.2]× as long as hind tibia. **Colour.** Head (Figs 7A–D) yellow to yellow-white, lighter ventrally (clypeus and face and gena), frons tinged with light brown in some specimens. Vertex uniformly yellow, lacking sublateral lighter-coloured mark present in other *Piogaster* species (Figs 7B, D). Occiput yellow near occipital carina, light brown medially. Mandible basally yellow, apically dark brown-black. Maxillary and labial palps uniformly pale yellow. Antenna uniform yellow-brown or yellow basally and dark brown apically [as in holotype] (Fig. 7A). Pronotum yellow-white to yellow dorsally, tinged with pale brown medially and ventrally in most specimens [including holotype] (Fig. 7A). Tegula yellow to light brown [light brown] (Fig. 7A). Mesoscutum medium brown, with yellow submedial and sublateral longitudinal stripes (Fig. 7E). Scutellum light to medium brown, pale yellow to light brown anteriorly, axillary troughs medium brown (Fig. 7E). Post-scutellum light to medium brown, axillary troughs yellow. Mesopleuron yellow-white/yellow to brown-yellow, paler in ventral third in most specimens, especially anteriorly [“pale yellow spot on anterior lower corner”] (Fig. 7A). Metapleuron and propodeum uniformly yellow to brown-yellow. Wings hyaline to subhyaline, veins light to medium brown, SC+R medium to dark brown. Legs yellow to yellow brown, with medium brown longitudinal stripe on dorsal and/or ventral of fore, mid-

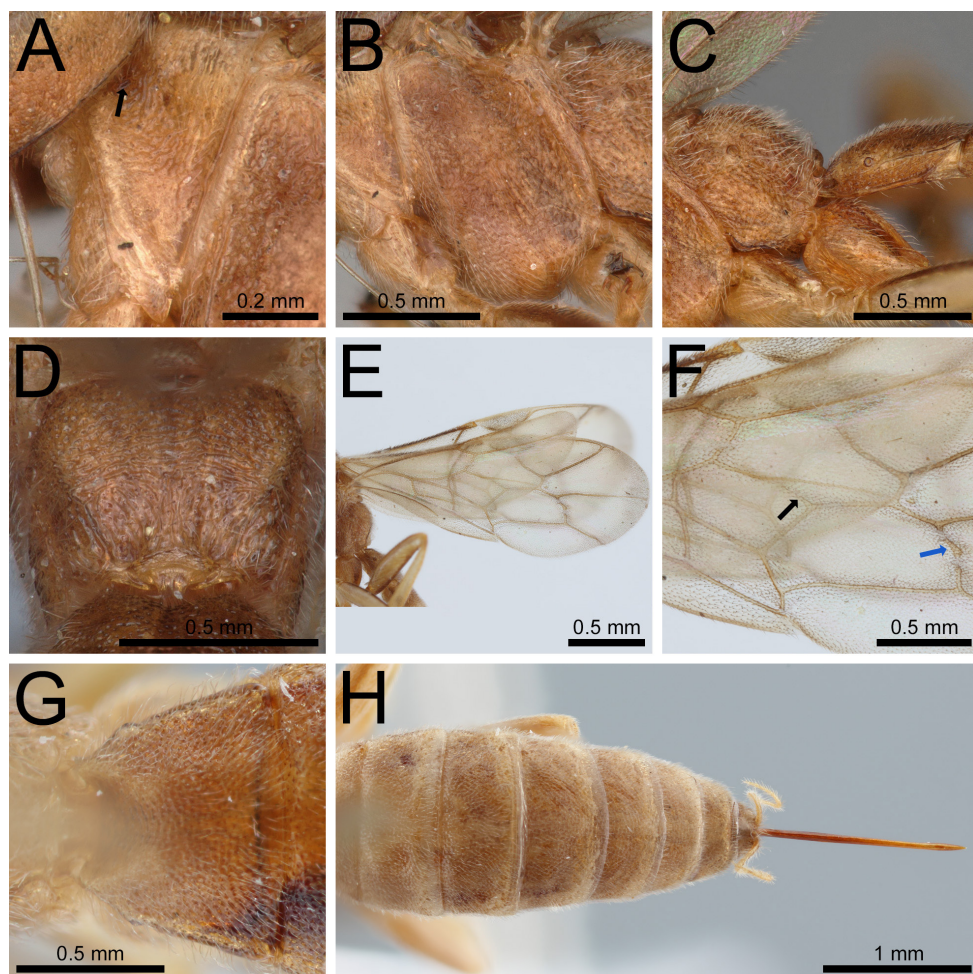


Figure 8. *Piogaster daisetsuzana* female. Figures A–F are of non-type specimen NHMUK012850731 (NHMUK), figure G is of non-type specimen NHMUK015215320 (NHMUK), and figure H is of non-type specimen CNC1754518 (EUMJ). **A** pronotum **B** mesopleuron **C** metapleuron, propodeum and T1, lateral view **D** propodeum, dorsal view **E** wings **F** fore wing **G** tergite 1, dorsal view **H** metasoma, T2–T8 and ovipositor, dorsal view. Arrow in A indicates the epomia. Black arrow in F indicates the ramellus, and blue arrow in F indicates the thickened 2m-cu vein between bullae

dle, and/or hind femora and tibiae, these longitudinal stripes ranging from poorly to well-defined [holotype with femoral stripes poorly defined, tibial stripes well defined (Figs 7A, B)]; all leg segments paler on anterior and posterior surfaces; tarsi a bit darker than other segments. Metasomal tergites yellow to medium brown, T2–T6 pale yellow posteriorly in most specimens [including holotype (Fig. 7A)]. Ovipositor sheaths uniform yellow-white.

Male. Body length 5.4–6.1 mm. FW length 4.5–5.2 mm. **Head.** Antennae with 24 flagellomeres. Clypeus 1.6–2.0× as wide as high, smooth, polished with sparse setiferous punctures, with medium brown long setae. Face polished, smooth with sparse setiferous punctures, with sparse short yellow setae (Fig. 9C). Frons and vertex polished, with moderately dense setiferous punctures, short yellow-white setae (Figs 9C, D). Occipital carina complete (Fig. 9D). MSL 0.7× as long as BW. OOD 1.2–1.7× as long as LOD. **Mesosoma.** Pronotum with epomia present in dorsolateral pronotal groove, short (Fig. 10A); polished, punctate dorsally with dense medium length white setae, smooth ventrally and lacking setae (Fig. 10A). Mesoscutum subpolished, densely punctate, with dense medium length white setae (Fig. 9E). Scutellum polished, punctate, with dense long white setae (Fig. 9E). Mesopleuron polished, punctate with moderately dense medium length white setae, posterodorsally smooth without setae (Fig. 10B). Metapleuron polished, margins with sparse, setiferous punctures and moderately dense long white setae, medially smooth and lacking setae (Fig. 10C). Propodeum rugose punctate with medial transverse striations, with dense long white setae (Fig. 10D). Propodeum with pleural carina complete (Fig. 10C); lateral longitudinal carina present posteriorly, extending anteriorly to 0.8× length of propodeum; median longitudinal carinae present anteriorly (Fig. 10D), extending posteriorly to 0.5–0.6× length of propodeum. **Wings. Fore wing.** Vein Rs+M with ramellus extending into 1M+1R1 (discocubital) cell as a tubular vein for 0.8–1.1× length of 2rs-m, continuing across 1M+1R1 cell as a nebulous and/or spectral vein (Fig. 10E). Vein 2rs-m 0.5× as long as M between 2rs-m and 2m-cu (Fig. 10E). Vein 2m-cu not thickened or angulate between bullae (Fig. 10G). **Hind wing.** Vein 1/Cu&cu-a slightly inclivous, in most specimens angled apically where 2/Cu intercepts in lower 0.3–0.4, tubular basally and nebulous apically, extending 0.7–0.8 to edge of wing (Fig. 10F). One wing of one specimen with vein 1/Cu&cu-a inclivous, not angled, vein 2/Cu present, but not intercepting vein 1/Cu&cu-a. **Metasoma.** T1 polished, strongly, densely punctate reticulate, with dense, medium length, white setae (Fig. 10H). T1 median dorsal carinae present, 0.4× length of T1, bordering the medial basal sulcus; dorsolateral carina complete. T2–T4 each with a weak medial to posterior transverse groove; coarsely, densely punctate reticulate with dense, medium length, yellow setae anterior to groove, sparsely punctate and polished with sparse, medium length, yellow setae posterior to groove. T5 more polished than anterior tergites, densely punctate to punctate reticulate anteriorly, densely, finely punctate with dense medium length yellow setae posteriorly (Fig. 10H). T6–T8 polished with sparse punctuation with dense, medium length, yellow setae (Fig. 10H). **Colour.** Frons and gena dark brown to black, with clypeus and medial face medium brown (Figs 9C, D). Vertex and occiput uniformly black (Fig. 9D) or vertex black with white-yellow small ovoid mark (Fig. 9B). Mandible brown-yellow with longitudinal dark brown stripe or dark brown and apically brown-yellow. Maxillary and labial palps yellow basally, light to medium brown apically (Fig. 9A). Antenna dark brown, first 13–14 antennomeres pale yellow ventrally (Figs 9A, B). Mesosoma (Figs 9E, 10A–D) dark brown to black except for the following: pronotum with brown-yellow dorsoposterior corner (Fig. 10A), tegula yellow-white (Fig. 10A). Wings hyaline, veins medium brown (Figs 10E, F). Fore and middle leg including coxa pale yellow, except tibiae with dorsal, longitudinal, pale brown stripe. Apical three tarsomeres of

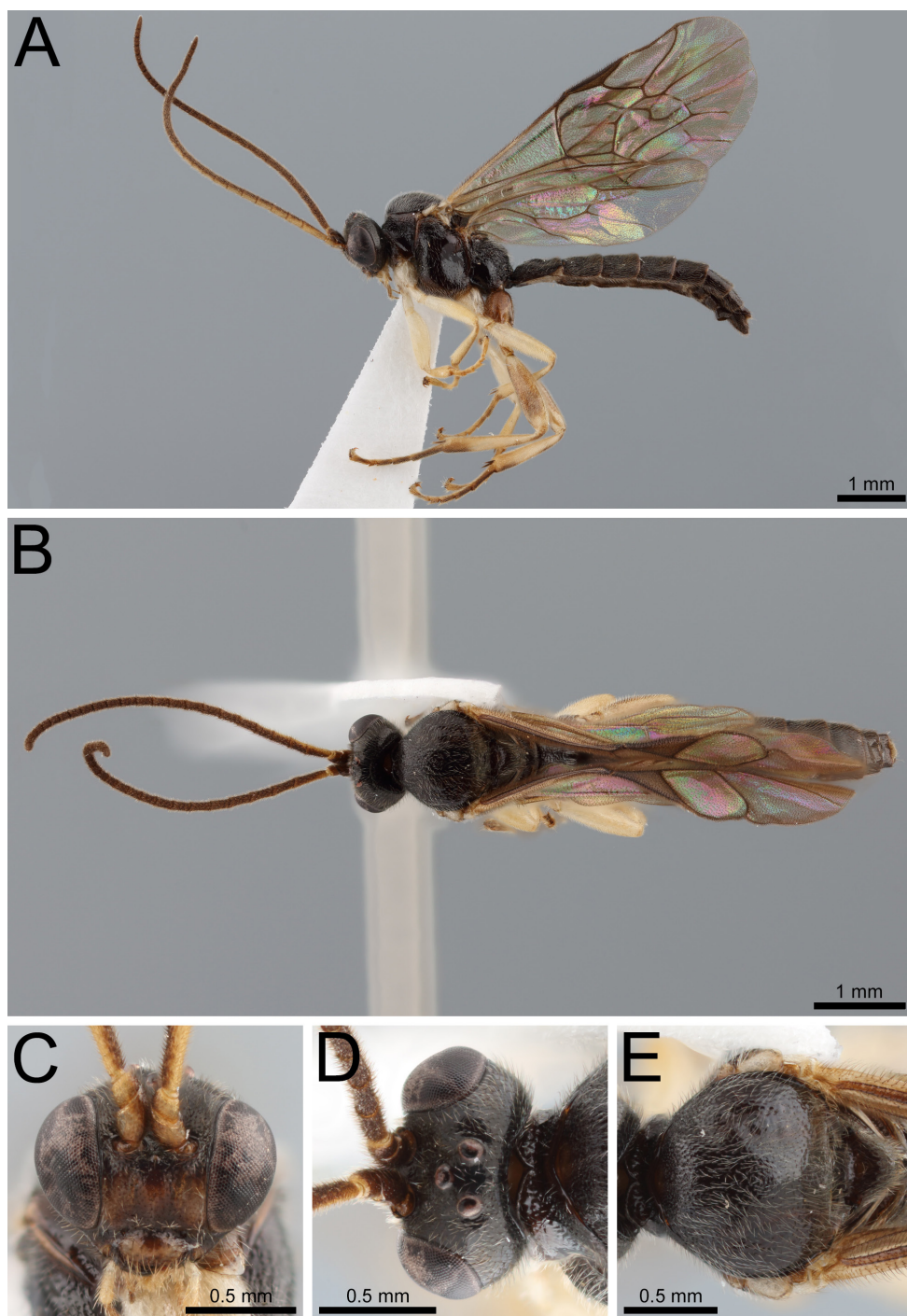


Figure 9. *Piogaster daisetsuzana* male. All figures of non-type specimen NHMUK015215321 (NHMUK). **A** habitus, lateral view **B** habitus, dorsal view **C** head, anterior view **D** head, dorsal view **E** mesoscutum, dorsal view.

fore leg yellow brown, middle tarsus dark yellow brown, except basal tarsomere yellow laterally. Hind leg yellow brown, except coxa light brown, trochanter and trochantellus light brown dorsally, femur laterally between 0.1–0.8 light brown, tibia with brown, dorsal stripe in basal 0.2 and apical 0.3, tarsus brown dorsally, yellow brown ventrally (Fig. 9A). Metasomal tergites uniformly dark brown to black (Figs 9A, 10H).

Distribution. Fig. 27. Japan: Hokkaido (Kusigemati 1985), Kyushu (Matsumoto 2016), and Honshu (Watanabe and Yamauchi 2018).

Biology. Host unknown.

Material examined. Holotype. JAPAN • ♀; Hokkaido, Mt. Daisetsu [Mt. Daisetsu]; 29.vii.1967; K. Kusigemati; [EIHU].

Condition of holotype: Missing left fore wing and hind wing, otherwise intact (Digital images analyzed, Figs 7A–C).

Other material. JAPAN • 1 ♀; Hokkaido, Chitose, stream near Shikotsu-tunnel; 42.7048°N, 141.2910°E; 17.viii–1.ix.2012; N. Kuhara; Malaise trap; CNC1754518; [EUMJ] • 1 ♀; Kyushu, Fukuoka, Sefuriyama c.; 6.vi.1995; R. Matsumoto; NHMUK015215320; [NHMUK] • 1 ♀; same data as for preceding; NHMUK012850731; [NHMUK] • 1 ♀; same data for preceding; 16.vi.1995; R. Matsumoto; CNC310409; [NMS] • 1 ♀; Kameya, Toyama City; 1–8.ix.2009; [Kanagawa Prefectural Museum of Planet Earth and Life] (photo only) • 1 ♂; Honshu, Kansai, Osaka, Kishiwada, near Izumi-Katsuragisan; 30.vi–13.vii.2002, R. Matsumoto; Malaise Trap 3 (A); CNC310410; [NMS] • 1 ♂; same data for preceding; 2–13.v.2002; R. Matsumoto; Malaise Trap 2 (C); NHMUK015215321; [NHMUK].

Comments. In the original description of *P. daisetsuzana*, Kusigemati (1985) states that the diagnostic features of this species are the presence of an epomia, a wide malar space, and antennae with 25 segments. In this study, four additional female specimens and two additional male specimens were examined that have made these features no longer diagnostic. Malar space and antennal segments now overlap with other species. While we have not examined the holotype specimen in person and thus have not seen the epomia on that specimen, we have seen what appears to be a short, weak to indistinct epomia in two specimens (as in Fig. 8A). Verification of its presence in other species is complicated by the presence of rugose sculpture in this area (Fig. 14A) and the angle of the head which obscures the area in several specimens. As such, we have not included it as a diagnostic character for *P. daisetsuzana*. The male *P. daisetsuzana* we examined have a short epomia (Fig. 10A), but other males from Europe (example: BOLD ProcessID [BIOUG17116-B03](#)) have been examined with a similar epomia, so this is not diagnostic for male *P. daisetsuzana*.

This is the first time the male of *P. daisetsuzana* has been described. Two *P. daisetsuzana* males were examined morphologically, and one was barcoded and included in the COI phylogeny. This male clustered in a monophyletic clade with two female *P. daisetsuzana* (Figs 1, 2) and its COI sequence was only 0.11–0.14% divergent from these two females. In addition, males and females share diagnostic morphological features (see Diagnosis). Finally, *P. daisetsuzana* is geographically isolated from all other *Piogaster* species (only recorded from Japan: Fig. 27).

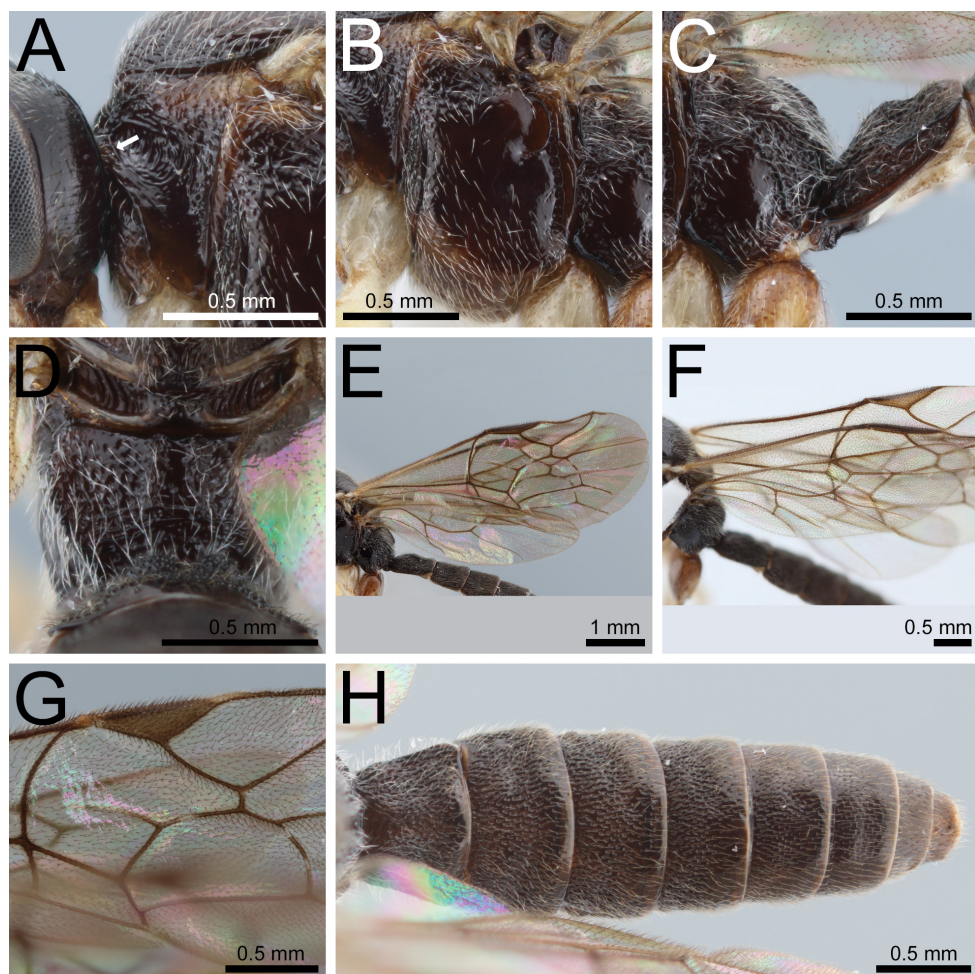


Figure 10. *Piogaster daisetsuzana* male. Figures E and F of non-type specimen NHMUK015215321 (NHMUK), all others of non-type specimen CNC310410 (NMS). **A** pronotum **B** mesopleuron **C** metapleuron, propodeum and T1, lateral view **D** propodeum, dorsal view **E** wings **F** hind wing **G** fore wing close up **H** metasoma, dorsal view. Arrow in A indicates the epomia.

Sexes differ in some diagnostic characters. First, males do not have a FW 2m-cu slightly thickened and angulate between bullae (Fig. 10E) as in females (Fig. 8E). Second, while male *P. daisetsuzana* have a longer extension of the FW ramellus than females (tubular and $0.75\text{--}1.1\times$ length of 2rs-m) (Fig. 10E) we have examined two males from Italy (presumably not *P. daisetsuzana* because of the locality) that have an extension of the FW ramellus up to $0.9\times$ as long as 2rs-m, so this character is also not diagnostic for male *P. daisetsuzana*.

In the original description, Kusigemati (1985) reported T3 of the female as $2.2\times$ as long as wide. However, this is an error, as T3 is much wider than long in all female

specimens examined including the holotype based on the photos of this specimen (Fig. 7A, B). Additionally, Kusigemati (1985) described the head as pale yellow and the mesosoma as yellowish-brown to light infusate. The photos of the holotype (Fig. 7A, B) appear to have a brighter yellow head and the mesosoma has areas of orange, but this is likely an artifact of the photographic settings (e.g., lighting, white balance) which produced a more saturated image. In Fig. 7C, however, the head of the holotype appears closer to the pale yellow from the original description.

***Piogaster lucida* Constantineanu & Constantineanu, 1969**

Piogaster lucida Constantineanu & Constantineanu, 1969a: 157 [Romanian].

Piogaster lucida Constantineanu & Constantineanu, 1969b: 173 [French].

Diagnosis. *Piogaster lucida* can be distinguished from its congeners by possession of the combination of the following: 1) mesoscutum impunctate and polished and 2) metasomal T2–T5 smooth with very sparse punctation anteriorly and laterally. This species is most similar to *P. albina* which shares the highly polished, impunctate mesoscutum (Fig. 4E), but can be distinguished by the densely punctate metasomal T2–T5 of *P. albina* (Fig. 5H).

Redescription. Adult. Female. Body length 5.0 mm. FW length 4.0 mm. **Head.** Number of flagellomeres unknown [antenna about half length of body]. Clypeus width to height ratio and microsculpture unknown. Face and vertex microsculpture and setation unknown. Frons polished and smooth, setation unknown. Occipital carina complete. Ratio of MSL to BWM unknown. Ratio of OOD to LOD unknown. **Mesosoma.** Pronotum with epomia absent; sculpture and setation unknown. Mesoscutum polished, smooth with sparse white setae. Scutellum sculpture unknown. Mesopleuron sculpture unknown. Metapleuron medially to posteriorly smooth. Propodeum rugulose or rugose [wrinkled] (original description *zbîrcit*) and sparsely punctate. Propodeum with pleural carina complete but weak, other propodeal carina unknown. **Wings. Fore wing.** Vein Rs+M not specifically mentioned or drawn as having ramellus extending greatly into cell 1M + 1R1 (only a rudimentary stub of ramellus indicated in habitus drawing). Vein 2rs-m slightly shorter than M between 2rs-m and 2m-cu, but not measured. Vein 2m-cu not thickened or angulate between bullae (based on habitus drawing). **Hind wing.** Vein 1/Cu&cu-a angled where 2/Cu intercepts, 2/Cu intercepting in lower 0.5, 2/Cu extending almost to wing margin. **Metasoma.** T1 polished and smooth, without setae. T1 with median dorsal carina only present in anterior half of anteromedial furrow; T1 dorsolateral carinae present anteriorly for 0.5× length of T1. T2–T5 polished, smooth, sparsely punctate anteriorly and laterally with whitish setae. T6–T8 polished, smooth, sparsely punctate anteriorly, setae unknown. Tergites without grooves or tubercles. Ovipositor sheath 1.5 mm, hind tibia not measured. **Colour.** Head black. Vertex with oblong yellowish spot. Mandible colour unknown. Maxillary and labial palps colour unknown. Antenna brown with black scape. Mesosoma black except for the following:

tegula red-brown, mesopleuron with some areas dark red to brown (see Constantineanu and Constantineanu 1969a, 1969b). Wing colour and transparency unknown, veins including stigma pale yellow, C+Sc+R brown. Femora white with black-brown longitudinal stripes on dorsal and ventral surface, fore and middle femur stripes larger than hind femur. Tibiae white with black-brown longitudinal stripe on dorsal surface. Tarsi with dorsal surface brown, anteroventral and posteroventral surfaces red-white. Fifth tarsomere apically red. Metasomal tergites black. Ovipositor sheath brown.

Male. Unknown.

Distribution. Fig. 28. Romania.

Biology. Unknown.

Material examined. None. *Piogaster lucida* is known only from the holotype in the Constantineanu collection (Iași, Romania) and was unavailable for examination.

Comments. *Piogaster lucida* was originally described both in Romanian (Constantineanu and Constantineanu 1969a) and French (Constantineanu and Constantineanu 1969b) in the same year. We were unable to determine a date of publication for either. The date of the Romanian publication is listed as 1969 on the cover of the issue, but 1968 on the first page inside. The French publication is listed as received on August 16, 1968 but it does not include a publication date; another paper in the same issue was received on January 28, 1969 so it had to be published after this date. As no precise publication dates are available, ICZN Article 21.3.2 requires adoption of 31 December 1969 for both, making them simultaneous. Both descriptions together constitute the original description. As we were unable to see the holotype, the diagnosis and description provided here are based on these descriptions.

Constantineanu and Constantineanu (1969b) describe *P. albina* and *P. lucida* as differing by: 1) ovipositor sheath colour, with *P. albina* having a white band on the sheath and *P. lucida* having a completely brown ovipositor sheath, and 2) trochanter colour, with *P. albina* having trochanters with white apically, versus *P. lucida* in which the trochanters lack the white apically. However, we have seen multiple specimens of *P. albina* with completely brown ovipositor sheaths, and with trochanters completely dark brown-black.

We examined one *Piogaster* specimen from Hungary (Fig. 6A) that we identify and treat here as *P. albina*, although it shows morphology intermediate between *P. albina* and *P. lucida*. In this specimen, the metasomal tergites have reduced punctation compared to other *P. albina* specimens (Figs 4B, 5H). The specimen also differs in the sculpture of the propodeum, which is almost completely smooth (Fig. 6A), rather than wrinkled as in other examined specimens of *P. albina* (Figs 4B, 5D) and in the original description of *P. lucida*. This variation raises the possibility that if the propodeal sculpture in *P. albina* can be completely smooth while the specimen otherwise conforms to *P. albina*, then similar variation might also occur in the sculpture of the metasomal tergites. If so, *P. lucida*, which is diagnosed from *P. albina* primarily by the smooth sculpture of tergites T2–T5, may represent a morphological variant of *P. albina* rather than a distinct species. However, because we were unable to examine the holotype of *P. lucida* or locate additional material matching the *P. albina* holotype condition, we could not investigate this.

***Piogaster maculata* Townes, 1960**

Figs 11, 12

Piogaster maculata Townes, 1960: 241.

Diagnosis. *Piogaster maculata* can be distinguished from its congeners by possession of the combination of the following: 1) mesoscutum matte and granulate (Fig. 11D); 2) T1–T5 matte and granulate (Figs 12C, D); and 3) metasomal tergites primarily dark brown, with only posterior edges of some tergites light brown (Fig. 12D).

Piogaster maculata is most similar to *P. variegata* in that these two species both have the metasoma with T2–T5 granulate (Figs 12D, 21H) and HW vein 1/Cu&cu-a gently curved, without a strong angle distinguishing 1/Cu from cu-a and with abscissa 2/Cu absent (Fig. 21F). They can be differentiated by colour, with *P. variegata* having variegated tergites (Figs 21G, H), mesopleuron (Fig. 21B) and propodeum (Fig. 21D). The sculpture of the mesoscutum also differs with *P. maculata* granulate, whereas *P. variegata* is pustulate (Fig. 20E).

Redescription. Adult. Female. Body length about 5 mm. FW length 3.4 mm. **Head.** Antennae with 21 flagellomeres. Clypeus width to height ratio about 2× as wide as high, matte and granulate with sparse white setae. Face (Fig. 11B), frons and vertex (Fig. 11C) matte, granulate, with dense, short, white setae (slightly less dense on face). Occipital carina complete. MSL 1.0× as long as BWM. OOD 1.5× as long as LOD. **Mesosoma.** Pronotum with epomia absent (Fig. 11E). Mesosoma matte, granulate, with dense, white setae that are short on mesoscutum (Fig. 11D) and scutellum, medium-length on pronotum and long on mesopleuron (Fig. 11F), metapleuron (Fig. 11G) and propodeum (Fig. 12A) (slightly less dense on pronotum, mesopleuron and metapleuron). Propodeum with pleural carina indistinct anteriorly to medially, absent posterior to this; lateral longitudinal carina present in posterior 0.2, all other propodeal carinae absent (Fig. 12A). **Wings. Fore wing.** Vein Rs+M without ramellus extending into cell 1M+1R1 (Fig. 12B). Vein 2rs-m 0.4× as long as M between 2rs-m and 2m-cu. Vein 2m-cu not thickened or angulate between bullae (Fig. 12B). **Hind wing.** Vein 1/Cu&cu-a slightly inclivous but not strongly angulate (Fig. 11A), vein 2/Cu absent. **Metasoma.** T1 matte, anteromedially smooth, remainder granulate, with dense short white setae (Fig. 12C). T1 median dorsal carina present anteriorly but short, 0.2× length of T1; dorsolateral carinae present anteriorly to 0.4× length of T1. T2–T7 matte, granulate, with dense short white setae (Fig. 12D). T8 smooth to alutaceous and lacking setae anteriorly, posteriorly with sparse long white setae. Tergites without grooves or tubercles. Ovipositor sheath 0.7× as long as length of hind tibia. **Colour.** Frons and clypeus dark brown (Figs 11B, C) with red-brown gena. Face dark brown and yellow laterally (Fig. 11B). Vertex dark brown with yellow triangular elongate mark (Fig. 11C). Occiput not visible, but likely same colour as posterior of vertex and gena (medium to dark brown). Mandible medium brown with black medial transverse stripe. Maxillary and labial palps uniformly medium brown. Antenna with scape dark brown, pedicel white-yellow, flagellomeres yellow-brown (Fig. 11B). Pronotum red-brown (Fig. 11E). Tegula yellow-white

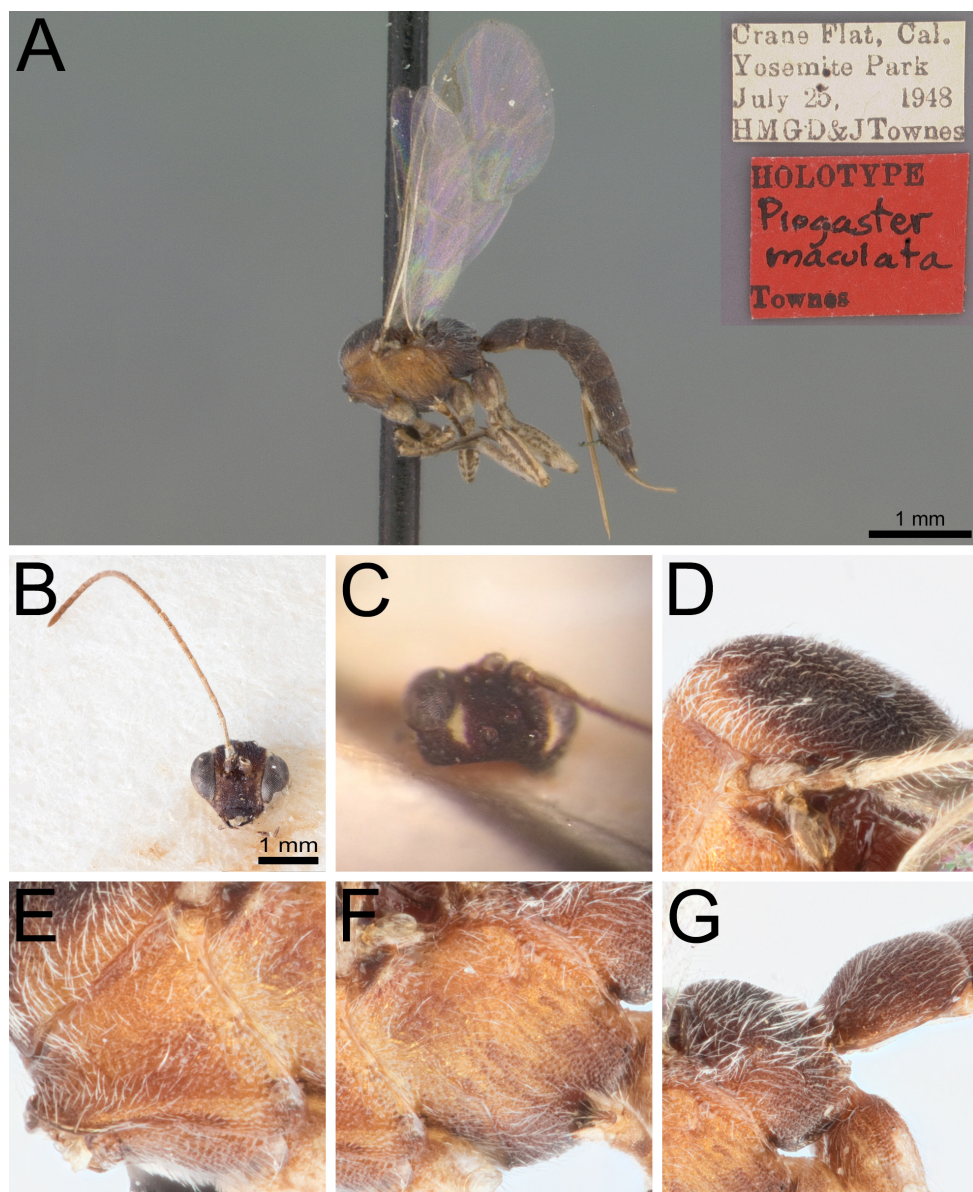


Figure 11. *Piogaster maculata* female. All figures are of the holotype (EMUS). **A** habitus, lateral view with holotype labels inset **B** head and antenna, anterior view **C** head, dorsal view **D** mesoscutum, lateral view **E** pronotum **F** mesopleuron **G** metapleuron, propodeum and T1, lateral view.

with brown margins (11D). Mesoscutum dark brown, red-brown anteriorly and on lateral margins (Fig. 11D). Scutellum dark brown with yellow-white spot on medioposterior margin, axillary troughs medium brown. Post-scutellum dark brown, yellow-white posteriorly, with axillary troughs dark brown (Fig. 12A). Mesopleuron red-brown, dark

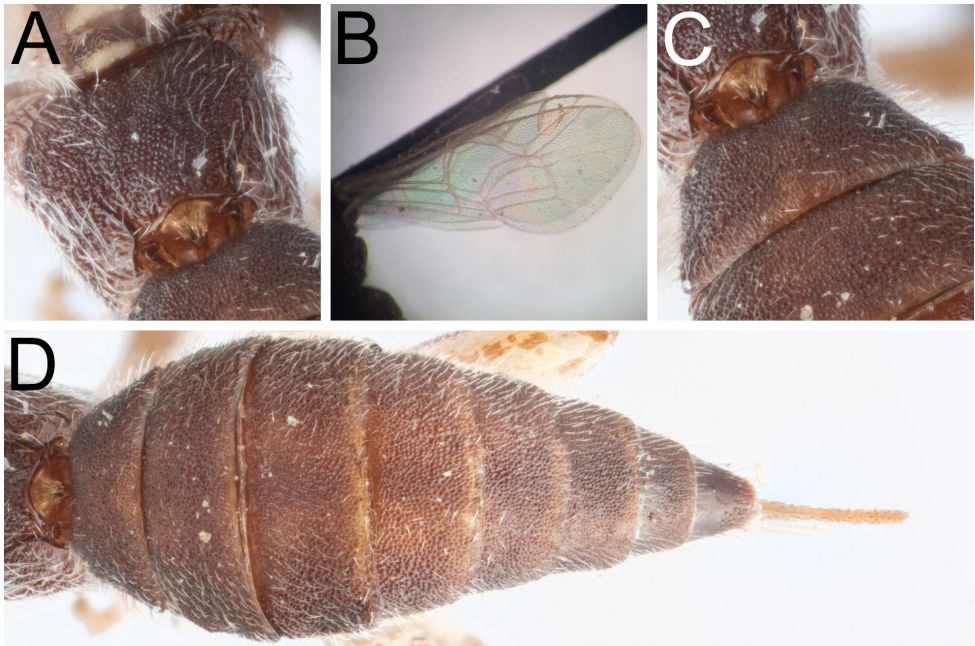


Figure 12. *Piogaster maculata* female holotype (EMUS). **A** propodeum, dorsal view **B** wings **C** tergite 1, dorsal view **D** metasoma, dorsal view.

brown ventrally (Fig. 11F). Metapleuron dark brown, anterodorsally red-brown (Fig. 11G). Propodeum uniformly dark brown (Fig. 12A). Wings hyaline, veins pale brown transparent, costa and apical stigma white (Fig. 12B). Fore coxa medium brown basally, white with brown spots apically; trochanter yellow with brown anterodorsal and posterodorsal stripes, femur yellow-white with scattered brown spots laterally and two brown subdorsal longitudinal stripes; tibia yellow-white with a brown stripe dorsally and scattered brown spots ventrally, tarsus brown, paler ventrally, apical tarsomeres lighter than basal ones. Middle and hind leg similar to fore leg with brown areas generally darker and more extensive (Fig. 11A). Metasomal tergites medium brown, posterior margin of T3–T6 light brown (Fig. 12D). Ovipositor sheath white-yellow.

Male. Unknown.

Distribution. Fig. 29. United States of America (California).

Biology. Unknown.

Material examined. *Holotype.* USA • ♀; California, Yosemite National Park, Crane Flat; 25.vii.1948; H. M. G. D. and J. Townes; edge of mountain meadow, swept from shoulder-high branches of conifer; USNM63703; [EMUS].

Condition of type: head detached from body and glued to a card, left antenna missing beyond scape, left fore and middle legs detached after coxa. Two legs are glued to a card with the head, but these legs are not conspecific with the specimen, as one of the legs glued to the point still has the coxa attached, and neither legs have the characteristic spots of the legs remaining attached to the specimen.

Comments. The original description lists the depository as the United States National Museum, Washington, but the specimen is in the Townes Collection, at Utah State University, Logan, Utah. Townes and Townes (1983) explain that listing the holotype depository as the United States National Museum, Washington was an error.

***Piogaster pilosator* (Aubert, 1958)**

Figs 13–15

Polysphincta pilosator Aubert, 1958: 79. Transferred to *Piogaster* by Aubert (1960b).

Piogaster rugosa Perkins, 1958: 266. Synonymized by Aubert (1965). Type lost.

Piogaster punctulata Perkins, 1958, (syn. by Aubert, 1967 with doubt, indicated by “?”; not adopted by subsequent authors).

Piogaster pilosator caucasica Kasparyan, 1981: 70. syn. nov.

Diagnosis. *Piogaster pilosator* can be distinguished from its congeners by possession of the combination of the following: 1) mesopleuron rugose (Fig. 14B); 2) propodeum rugose to rugose punctate (Figs 13B, 14D); 3) in specimens with head primarily dark brown to black (Figs 15C), metasoma is not pale yellow to white.

This species is most similar to *P. daisetsuzana*, *P. punctulata*, and *P. ussuriensis*. *Piogaster pilosator* can be distinguished from *P. daisetsuzana* by the absence of medial transverse striations on the propodeum (present in *P. daisetsuzana*, Fig. 8D) and the absence of the elongated fore wing vein ramellus (Fig. 14F) or ramellus present only as a short stub (Fig. 13A) (ramellus present and long in *P. daisetsuzana*, Fig. 8F). *Piogaster pilosator* can be differentiated from *P. ussuriensis* by the colour of the head and metasoma and the lengths of the ovipositor sheaths (see couplet 7 of key). *Piogaster ussuriensis* has a primarily dark brown to black head and a contrasting pale yellow-white metasoma (Fig. 18A) whereas *P. pilosator* specimens have the head and metasoma colour variable, from pale yellow to black (Figs 15A–C), but never with contrasting dark brown to black head and pale metasoma as found in *P. ussuriensis*. *Piogaster ussuriensis* has ovipositor sheaths that range from 0.4–0.5× as long as hind tibia (Fig. 18A), while *P. pilosator* has ovipositor sheaths that range from 0.7–0.9× as long as hind tibia (Figs 13A, 15A, C). *Piogaster pilosator* can be differentiated from *P. punctulata* by the sculpture of the mesopleuron: rugose in *P. pilosator* (Fig. 14B), and punctate in *P. punctulata* (Fig. 17A).

Redescription. Adult. Female [values in square brackets are from lectotype]. Body length 4.0–6.4 [6.4] mm. FW length 3.2–4.8 [4.6] mm. **Head.** Antenna with 20–24 [22] flagellomeres. Clypeus 1.9–2.4 [2.3]× as wide as high, matte to subpolished, weakly rugulose with fine, dense, setiferous punctation located mainly ventrally and dorsally, medially sparse to absent, with long white setae. Face, frons and vertex (Figs 13C, D) matte with short to long white to yellow setae, sculpture highly variable: all regions can be partly or completely rugulose, rugose, rugose punctate, granulate or punctate [rugose punctate]. Gena matte to subpolished, strigose ventrally, strigose to irregularly rugose medially and dorsally, with short to medium length white to yellow

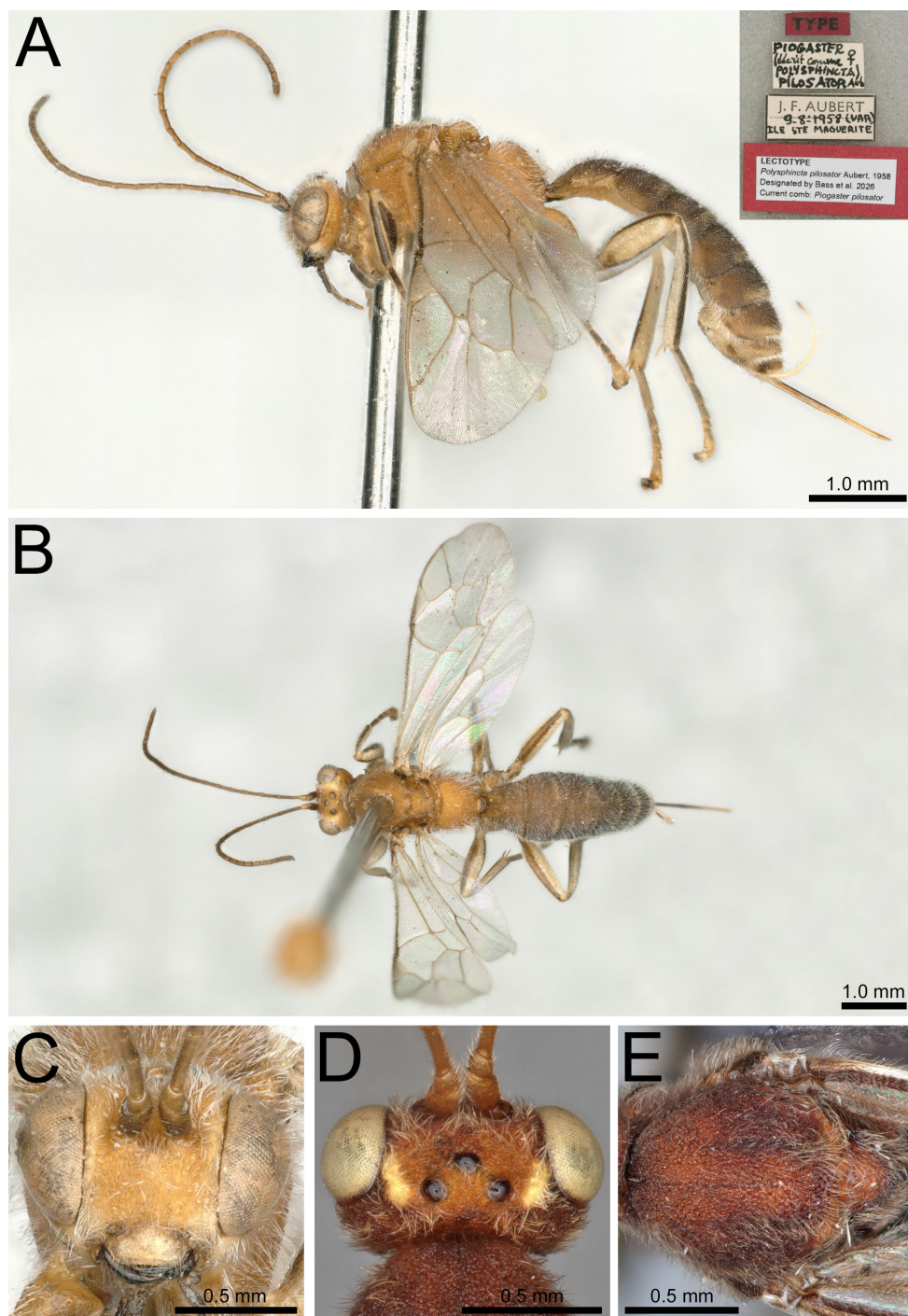


Figure 13. *Piogaster pilosator* female. Figures A–C of lectotype (MZLS), figure D of NOCER-678 (NINA), figure E of CNC1754423 (NINA). **A** habitus, lateral view **B** habitus, dorsal view **C** head, anterior view **D** head, dorsal view **E** mesoscutum, dorsal view.

setae. Occipital carina complete (Figs 13A, 14A). MSL 0.8–1.0 [1.0]× as long as BW. OOD 1.2–2.0 [1.6]× as long as LOD. **Mesosoma.** Pronotum with epomia absent; matte, rugulose to rugose to rugose punctate [rugose punctate], with sparse to dense short to medium length white setae. Mesoscutum matte, densely punctate to densely rugose punctate [densely rugose punctate], with dense short to medium length white to yellow setae. Scutellum matte, rugulose to rugose, with dense short to long white setae. Mesopleuron matte to subpolished, rugulose to rugose [rugose] with sparse to dense medium to long white setae (Figs 14B, 15). Metapleuron matte to subpolished, rugose, with dense long white to yellow setae, sometimes setae absent medially (Fig. 14C). Propodeum matte to subpolished, rugose to rugose punctate [rugose punctate], with dense long white setae (Fig. 14D). Propodeum with pleural carina variable, absent to complete (Fig. 14C), sometimes partially complete anteriorly or posteriorly [complete but weak]; lateral longitudinal carina present in posterior 0.2–0.5 [0.2], all other carinae absent. **Wings.** *Fore wing.* Vein Rs+M without ramellus extending significantly into cell 1M+1R1 (Fig. 14F), at most, a stub of ramellus present (Fig. 13B). Vein 2rs-m 0.5–0.9 [0.8]× as long as M between 2rs-m and 2m-cu (Figs 14E, F). Vein 2m-cu not thickened or angulate between bullae (Fig. 14F). *Hind wing.* Vein 1/Cu&cu-a inclivous and strongly angled apically where 2/Cu intercepts, 2/Cu intercepting in lower 0.3–0.4 [0.3], 2/Cu long, tubular to spectral (Fig. 14E). **Metasoma.** T1 matte to subpolished, densely punctate to punctate reticulate [punctate reticulate] with dense long white setae anteriorly, dense medium to long white setae posteriorly (Figs 13B, 14G). T1 median dorsal carina absent (lateral margin of dorsomedial sulcus rounded), or bordering sulcus at extreme base or entire length of sulcus, 0.1–0.4× length of T1; dorsolateral carinae present anterior to spiracle, or complete to almost complete but medially and/or posteriorly weak [complete to 0.9 length of T1] (Fig. 14C). T2–T5 matte to subpolished, densely punctate to punctate reticulate, with dense medium length white setae (Fig. 14H). T6 subpolished, densely shallowly punctate, with dense medium length white setae (Fig. 14H). T7 and T8 subpolished, densely finely punctate, with dense medium length white setae (Fig. 14H). Tergites either without grooves and tubercles or with weak paired anterior tubercles and a weak medial transverse groove on T2–T3 (Fig. 14H). Ovipositor sheath 0.7–0.9 [0.8]× as long as hind tibia (Figs 13A, 15A, C). **Colour.** Head, mesosoma and metasoma highly variable, yellow-white (Fig. 15A) to yellow/orange-brown (Fig. 13A) to red-brown (Fig. 15B) to dark brown-black (Fig. 15C), paler specimens generally darker dorsally and ventrally than laterally. Clypeus yellow-white (Fig. 15A), orange-yellow, orange-brown or dark brown-black (Fig. 15C), [yellow white (Fig. 13C)]. Face pale yellow (Fig. 15A), pale to dark orange, completely brown-orange, dark brown medially and brown-orange laterally, or dark brown-black (Fig. 15C); ventrolaterally paler (light brown, yellow or white) in some of the predominantly orange specimens [orange, paler ventrolaterally (Fig. 13C)]. Frons pale yellow, pale to dark brown-orange (Fig. 13D), medium brown or dark brown-black; ventral orbit may be same colour as medially or paler, dorsal orbit is paler in all specimens (pale region contiguous with pale marking laterally on vertex) [pale brown-orange (Figs 13B, C)]. Vertex medially

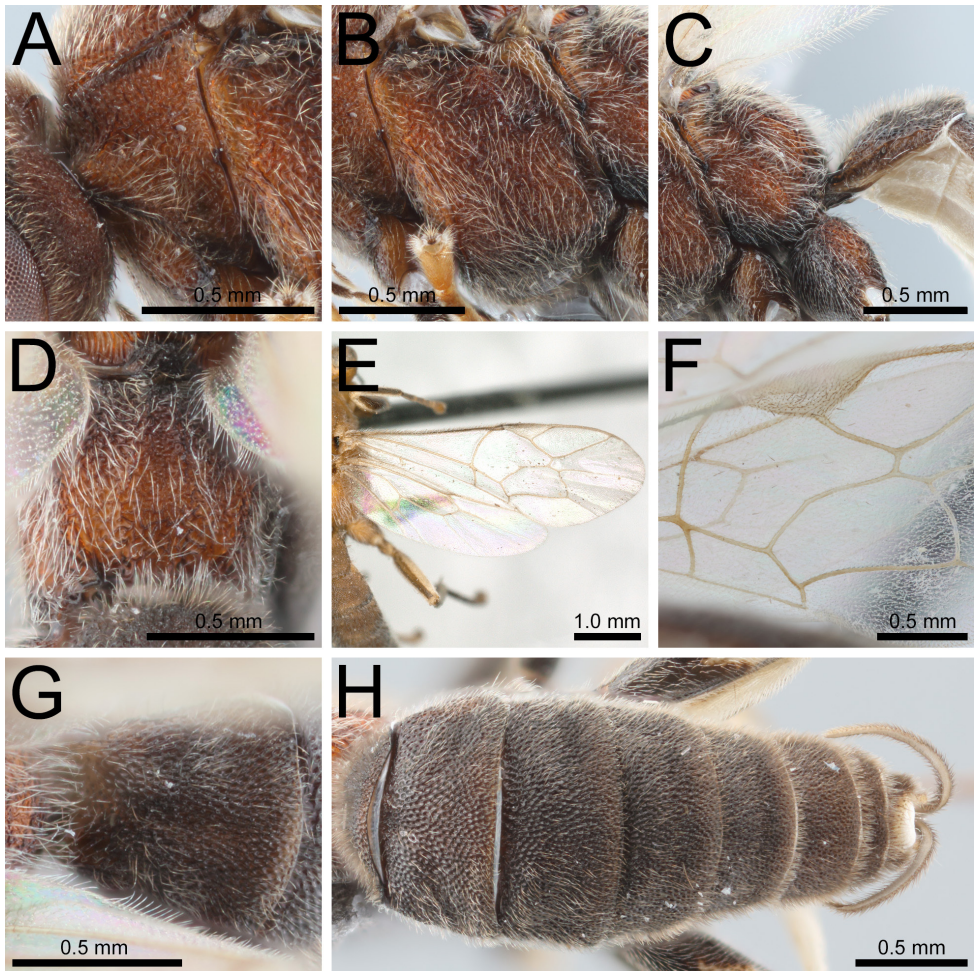


Figure 14. *Piogaster pilosator* female. Figure E of lectotype (MZLS), figures A–D, G and H of CNC1754423 (NINA), figure F of NTNU-VM-181569 (NTNU). **A** pronotum **B** mesopleuron **C** metapleuron, propodeum and T1, lateral view **D** propodeum, dorsal **E** wings **F** fore wing **G** tergite 1, dorsolateral view **H** metasoma, T2–T8, dorsal view.

pale yellow, pale to dark brown-orange, medium to dark brown (Fig. 13D) or brown-black; anterolaterally with white-yellow to yellow longitudinal ovoid, crescentic or sub-rectangular markings (Figs 13B, D), darker markings may also be present, especially posteriorly and in ocellar triangle [pale brown orange medially with crescentic yellow-white markings laterally (Fig. 13B)]. Gena except ventral to eye yellow white (Fig. 15A), light to dark orange brown (Fig. 15B) to brown-black (Fig. 15C), posteriorly and ventrally darker in some specimens; area ventral to eye (posterior of malar space) with white to yellow marking in form of vertical stripe (Fig. 15B) or complete area paler (Fig. 13A), this marking apparently absent in holotype of *Piogaster pilosator*

caucasica Kasparyan, 1981 (Fig. 15A) and Dagestan specimen (Fig. 15C) [light orange-brown except yellow-white ventral to eye (Fig. 13A)]. Occiput generally concolourous with posterior of vertex and gena or a bit darker. Mandibles except teeth yellow, light brown, orange-brown, medium to dark brown or black, teeth brown/black [dark brown (Fig. 13C)]. Maxillary and labial palps yellow (Fig. 15A), medium brown (Fig. 15B) to brown/black (Fig. 15C), darker basally than apically [medium brown (Fig. 13A)]. Antenna light yellow to light brown basally, light to medium brown apically (Fig. 13B). Mesosoma including pronotum, mesoscutum, scutellum, mesopleuron, mesosternum, post-scutellum, metapleuron and propodeum highly variable (see start of colour description and Figs 13–15). Palest (Fig. 15A) and darkest (Fig. 15C) specimens uniformly coloured; specimens with intermediate darkness (yellow-brown including holotype, orange or red-brown) with lateral areas (pronotum, mesopleuron, metapleuron, lateral propodeum) generally paler than dorsal and ventral areas (mesoscutum, scutellum, post-scutellum, anterior, dorsal propodeum and mesosternum) (Figs 13A, B, 15B); yellow-brown and orange-brown specimens may have mesoscutum with paler, longitudinal markings where notauli would be and/or anteriorly and medioposteriorly in some specimens. Tegula white to pale brown [pale brown (Fig. 13A)] in specimens with mesosoma predominantly yellow, yellow-brown or orange-brown; tegula brown to black in specimens with mesosoma predominantly red-brown to brown-black (Fig. 13E). Wings hyaline, veins including stigma pale brown to transparent, Sc+R medium to dark brown. Legs highly variable, coxae yellow-white (Fig. 15A), yellow-brown, orange, light brown to dark brown-black (Fig. 15C) [orange (Fig. 13A)], trochanters similar to coxae (yellow-white to dark brown), trochanters can be unicolorous with coxae in palest (Fig. 15A) or darkest (Fig. 15C) specimens, or have some dark and light colour in specimens of intermediate darkness [as in holotype, Fig. 13B]; femora of holotype of *P. p. caucasica* completely yellow (Fig. 15A), all other specimens have femora predominantly white to yellow with light to dark brown longitudinal stripe on dorsal and/or ventral surfaces and laterally at base in most specimens (especially darker ones) (Figs 13A, B, 15B, C), tibiae with dorsal and in most specimens, ventral surface dark with light to dark brown longitudinal stripe (holotype of *P. p. caucasica* with light brown dorsally near apex only); tarsi from pale brown to dark brown, generally paler ventrally than dorsally and apically compared to basally [pale brown (Fig. 13A)]. Metasomal tergites yellow-white, pale yellow (Fig. 15A), orange-yellow (Fig. 13B) or dark brown-black (Figs 15B, C); specimens with dark mesosoma (red-brown to brown-black) have dark metasoma (brown to brown-black) (Figs 15B, C); whereas specimens with pale mesosoma (yellow to orange-brown) can have metasomas ranging from yellow-white to orange-brown. Most specimens have the metasoma uniformly coloured, although it may be somewhat paler laterally on some segments and paler in posterior segments; however, some specimens have the posterior of T2–5 with pale transverse bands [orange-brown, slightly paler medioposteriorly on T5, posteriorly and laterally on T6–7 (Fig. 13A, B)]. Ovipositor sheath white or yellow (Figs 13B, 15A) to medium/dark brown (Fig. 15C), uniformly coloured, darker apically or paler apically [yellow, light brown apically (Fig. 13A)].

Male. Unknown. Male specimens have been collected at the same localities as females of *P. albina* and *P. pilosator*; however, European males are morphologically cryptic and therefore species identifications of male specimens of both these species cannot be confirmed.

Distribution. Fig. 30. Western Palaearctic: Austria (Kazmierczak 1990), Belgium (Verheyde et al. 2021), Bulgaria (Kolarov 1989, 1997), Finland (Koponen et al. 1995), France (Aubert 1960b; Aubert 1960a), Germany (new record), Norway (new record), Poland (Kazmierczak 2004), Russia (Kasparyan 1981), Sweden (Perkins 1958), Switzerland (Klopfstein et al. 2019b), Ukraine (Varga 2021). Aubert (1969b) listed a record of *P. pilosator* from England. However, this record references Perkins (1958) and therefore it is most likely referring to the holotype of *P. punctulata* which was from England as Aubert (1969b) synonymized *P. punctulata* under *P. pilosator* (see more about this synonymy in the Comments of the *P. punctulata* description).

Biology. *Piogaster* sp. (cf. *pilosator* (Aubert)) oviposited on the cephalothorax of *S. cingulatus* (Salticidae) in a laboratory setting (Takasuka et al. 2018). We were unable to locate these two specimens for identification; however, given that this was a European species, it seems very likely it was *P. pilosator* considering the clear morphological distinction from females of *P. albina* and *P. lucida* and the fact that the author who observed these interactions (N. Fritzén) had previously examined the type of *P. punctulata* (G. Broad, pers. comm.).

Material examined. Primary types.

Polysphincta pilosator pilosator Aubert, 1958 lectotype (hereby designated):

FRANCE • ♀; Alpes-Maritimes, Ile Ste. Marguerite; 9.viii.1958; J.A. Aubert; [MZLS] (Figs 13A–C).

Condition of type: Intact, pinned through mesoscutum.

Piogaster pilosator caucasicus Kasparyan, 1981 holotype:

RUSSIA • 1 ♀; Caucasus, Krasnodar Krai Lazarevskoye, Sochi; 1.vi.1976; Kasparyan; [ZIN] (Fig. 15A).

Condition of type: Metasoma detached from body and glued to point. Left hind leg missing. Distal three right maxillary palpomeres missing.

Other material. AUSTRIA • 1 ♀; Tirol, Zillertal Alps, Schlegeisgrund; 5.vii.1967; NHMW-HYM0022253; [NHMW]. BELGIUM • 1 ♀; West Flanders; Ruiselede, Gulke Putten; 51.07528°N, 3.34472°E; 22.v.2020; A. De Ketelaere; Light trap; [Personal collection of Augustijn De Ketelaere] (photo only). FRANCE • 1 ♀; Orléans, Ardon, Institut National de la Recherche agronomique, 2163 Avenue de la pomme de pin, 45075 Ardon; 12.iii.1991; D. Rougon; Emerged 6.v.1991; host unknown; MNHN-EY-EY51; [MNHN] • 1 ♀; St. Tropez; vi.1980; Z. Boucek; [NHMUK] • 1 ♀; same data for proceeding; NHMUK012850732 [NHMUK] • 1 ♀; Lot-et-Garonne, Bernac; 26.vi–3.vii.1991; R. R. Askew; Malaise trap; [NMS] • 1 ♀; St. Tropez; 13.viii.1980; Boucek; [NHMUK]. GERMANY • 1 ♀; Bayern, Berchtesgaden-Schönau, Königsbachalm; 47.5693°N, 13.01144°E; 1222 m; 30.vii–9.viii.2018; D. Doczkal & V. Voith; [private collection of H. Haraldseide] (photo only). NORWAY

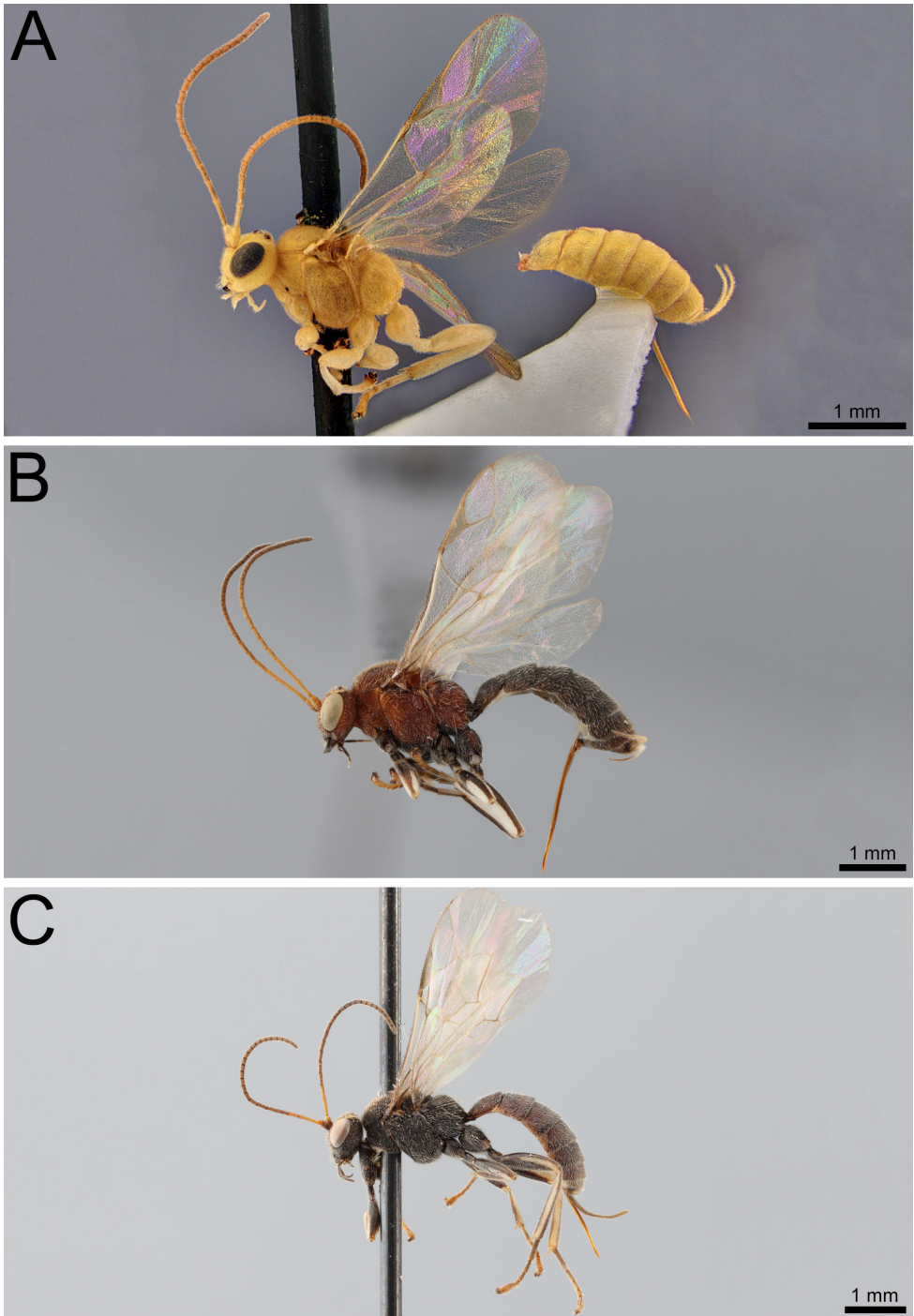


Figure 15. *Piogaster pilosator* female colour variation, to be contrasted to Figs 13A–C (lectotype specimen). **A** holotype of *Piogaster pilosator caucasica* (ZIN); **B** specimen from Norway (NOCER-678; NINA); **C** specimen from Russia: Dagestan (CNC310411; ZIN).

• 1 ♀; Sør-Trøndelag, Malvik, Skjeltjønnbekken; 63.37499°N, 10.67403°E; 8.vii–5.viii.2019; Arnstein Staverløkk; Malaise trap; NOCER-678; [NINA] • 1 ♀; Innlandet, Vågå, Lye-Fellese, EIS 71, ON; 61.86734°N, 9.05867°E; 30.vi–4.viii.2018; Frode Ødegaard; Malaise trap; NOCER-587; [NINA] • 1 ♀; Telemark, Vinje, Vådalen, Lauvheim; 59.74674°N, 7.84290°E; 28.iii–11.v.2022 [date interpreted, date listed verbatim as 28.iv–11.iiv.2022]; NINA/Arnstein Staverløkk; seminatural habitat; Malaise trap sample 2; CNC1754423; [NINA] • 1 ♀; Sør-Trøndelag, Trondheim, Sommerlystvegen 22; 63.40531°N, 10.38222°E; 29.vi–6.vii.2014; E. Stur and T. Ekrem; 75 moh, Malaise trap; NTNU-VM-181569 [NTNU]. RUSSIA • 1 ♀; Dagestan, Rutul; 29.vi–1.vii.2018; 1400–1500 m; Astafurova; CNC310411; [ZIN]. SWEDEN • 1 ♀; Västergötland, Hisingen, Säve s:n, Sävholmen; 57.84333°N, 11.90667°E; 11–20.vii.1996, Michael Sporrang; Malaise trap; damp to marshy meadows with *Salix*; [EUMJ] • 1 ♀; Gothenburg; 57.67907°N, 11.92913°E; 12.vi.2020; Sweep net; garden; [Private collection of Johan Ennerfelt] (photo only) • 1 ♀; Västergötland, Västra Götaland, Härryda, Råda portar 60, Råda portar, Råda, Vg; 57.66816°N, 12.09508°E; 25.v.2023; Oscar Josefsson; [SLU Artdatabanken] (photo only). SWITZERLAND • 1 ♀; Jura, Delémont, CABI; 47.37306°N, 7.32472°E; 26.v–19.vi.2014; J. Squire; Malaise trap; forest edge; CNC842257; [CNC] • 1 ♀; Engiadina Bassa/Val Müstair; iv.2015; Marc Neuman; Ichn-2144; [NMBE] • 1 ♀; Grisons/Graubünden, Tschier; 18.vii.1951; J. de Beaumont; [MZLS]. UKRAINE • 1 ♀; Odesa Region; Prymorske; 5.vi.1996; Anatoly Kotenko; [SIZK] (photo only). UNKNOWN • 1 ♀; 1915; J. Perez; [MNHN].

Comments. Aubert (1958) did not assign a holotype in the original description of *P. pilosator*, but listed two type specimens (syntypes) which were acquired by the Musée de Zoologie in Lausanne, Switzerland. These specimens were assumed loaned and lost (Klopfstein and Baur 2011), but one of the two syntypes was located and examined for this study. This specimen has been designated as the lectotype. The type specimen of *P. rugosa* (now synonymized with *P. pilosator*) was also lost. It should have been at the Lund University Museum. The archives at the Lund University Museum list one ichneumonid of a new genus, according to Dr. Henry Townes, loaned to J. F. Perkins in 1958. The material was not returned after the specimen was described as *Piogaster rugosa* in Perkins (1958). The Natural History Museum in London, where J. F. Perkins was employed, has been searched and this specimen was not located.

Piogaster pilosator caucasica was briefly described only in a key and the only characters of note are colour related, based on a single pale specimen collected in southcentral Russia (Kasparyan 1981) (Fig. 15A). Upon examination of 18 *P. pilosator* specimens (including the *P. p. caucasica* specimen) and seeing photos of an additional 10 specimens, it is clear *P. pilosator* has a wide range of colour variation (Figs 15A–C). We have seen another similarly pale yellow specimen from Bernac, France, which is geographically isolated from the type of *P. p. caucasica*. As we could find no further morphological characters distinguishing the holotype of *P. p. caucasica* from other *P. pilosator*, the subspecies *caucasica* is here placed in synonymy with *P. pilosator*.

***Piogaster punctulata* Perkins, 1958**

Figs 16, 17

Piogaster punctulata Perkins, 1958: 264.*Polysphincta pilosator* Aubert, 1958: 79; Synonymized with *P. pilosator* by Aubert (1967); synonymy not adopted by Fitton (1976), Fitton et al. (1988), Yu and Horstmann (1997), Shaw (2006), Broad (2016) and the current study.

Diagnosis. The female of *Piogaster punctulata* can be distinguished from all female congeners by possession of the combination of the following: 1) mesopleuron polished with shallow punctures (Fig. 17A) (polished and impunctate to weakly coriaceous, matte and rugulose to rugose, or matte and granulate to pustulate in all other species); 2) mesoscutum subpolished and punctate (Fig. 16E) (polished and impunctate, mat and granulate, matte and rugose, or matte and punctate in all other species); and 3) frons matte, granulate laterally, granulations become transversely strigose laterally (Fig. 16D) (polished and smooth, coriaceous, punctate, matte and granulate (not transversely strigose laterally), rugulose to rugose, rugose punctate or punctate in other species).

Redescription. Adult. Female. Body length 4.8 mm. FW length 4.1 mm. **Head.** Antennae with 22 flagellomeres. Clypeus 1.5× as wide as high, polished with sparse punctures, with yellow-white setae (Fig. 16C). Face matte, rugose-punctate, with moderately dense medium length yellow setae (Fig. 16C). Frons matte, granulate laterally, granulations become transversely strigose laterally, with dense short light brown setae (Fig. 16D). Vertex matte and densely punctate, punctures small and touching, with dense medium length yellow setae (Fig. 16D). Occipital carina complete. MSL 0.7× as long as BWM. OOD 1.5× as long as LOD. **Mesosoma.** Pronotum with epomia absent; subpolished, coarsely, densely punctate dorsally, rugose-punctate antero-medially, with dense medium length yellow setae. Mesoscutum subpolished, densely punctate, dense medium length light brown setae (Fig. 16E). Scutellum punctate, punctures nearly touching, with dense medium length white-brown setae (Fig. 16E). Mesopleuron polished, shallowly punctate with less than width of a puncture between punctures, rugose-punctate dorsal to mesopleural fovea, with moderately dense long white-brown setae (Fig. 17A). Metapleuron subpolished, densely, deeply punctate, with dense long light brown setae (Fig. 17B). Propodeum subpolished, coarsely deeply punctate, medially longitudinally rugose-punctate, with dense long white setae (Fig. 17C). Propodeum with pleural carina weak but complete (Fig. 17B); lateral longitudinal carina present in posterior 0.3, all other propodeal carina absent. **Wings. Fore wing.** Vein Rs+M without ramellus extending into cell 1M+1R1. Vein 2rs-m 0.6× as long as M between 2rs-m and 2m-cu. Vein 2m-cu not thickened or angulate between bullae. **Hind wing.** Vein 1/Cu&cu-a inclivous and strongly angled apically (Fig. 17D), 2/Cu intercepting in lower 0.3, 2/Cu basally tubular then nebulous. **Metasoma.** T1 subpolished, densely punctate, punctures nearly touching, lateroposteriorly punctate reticulate with dense medium length white setae. T1 median dorsal carina indistinct

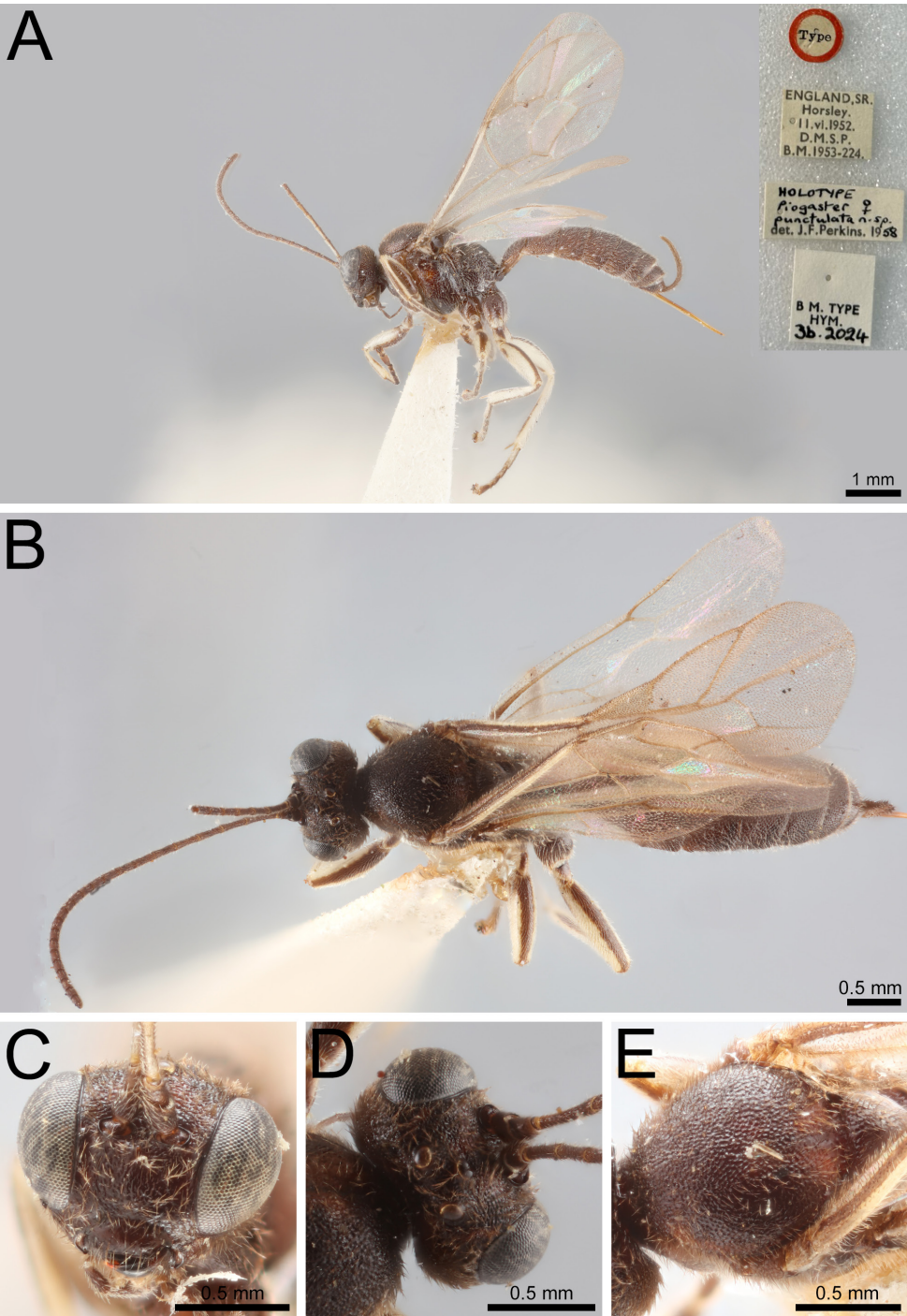


Figure 16. *Piogaster punctulata* female. All figures are of the holotype (NHMUK). **A** habitus, lateral view, with holotype labels inset **B** habitus, dorsal view **C** head, anterior view **D** head, dorsal view **E** mesoscutum, dorsal view. Figure A was taken by Gavin Broad (© Trustees of the Natural History Museum, CC-BY).

to absent; dorsolateral carinae present to spiracle, absent (rounded) just posterior to spiracle, present posteriorly (Fig. 17B). T2–T6 subpolished, coarsely, densely punctate with anterior and medial areas punctate reticulate, with dense short white setae (Fig. 17E). T7 polished, shallowly punctate, with moderately dense short white setae. T8 polished, smooth with sparse short white setae (Fig. 17E). Tergites without grooves or tubercles. Ovipositor sheaths $0.8\times$ as long as hind tibia (Fig. 15A). **Colour.** Clypeus, face, frons, gena and occiput predominantly medium brown (Figs 16A, C, D). Vertex medium brown with faint, thin linear brown-orange mark extending from posterior 0.3 of eye, roughly longitudinally to level of middle of lateral ocellus. Mandible red-brown with medial black transverse stripe. Maxillary and labial palps dark brown. Antenna brown, basal 12 flagellomeres yellow ventrally. Pronotum brown-orange on dorsal 0.7, brown on ventral 0.3. Tegula dark brown (Fig. 16A). Mesoscutum brown-black, brown-orange anteriorly (Fig. 16E). Scutellum, post-scutellum and axillary troughs dark brown-black. Mesopleuron dark brown-black, brown-orange anteriorly (Fig. 17A). Metapleuron black (Fig. 17B). Propodeum uniformly black (Fig. 17C). Wings hyaline, veins light brown to translucent (Fig. 17D). Legs with coxae dark brown, remainder of legs white with the following dark brown: dorsal surface of trochanters, longitudinal stripe on dorsal and/or ventral surface of femora and/or tibiae, dorsal of tarsi (Fig. 16A). Metasomal tergites brown, T5–7 darker than T1–T4 (Figs 16A, 17E), T8 brown-orange medially. Ovipositor sheath brown.

Male. Unknown. Perkins (1958) described a specimen from Germany he said was possibly a male *P. punctulata*, but we were unable to locate this specimen (see Comments). The description of this specimen is consistent with all other European male *Piogaster* specimens we examined.

Distribution. Fig. 28. England.

Biology. Unknown.

Material examined. Holotype. ENGLAND • ♀; Surrey, Horsley; 11.vi.1952; D. M. S. Perkins; Hym. 3b. 2024; [NHMUK].

Comments. The holotype specimen is the only female of *P. punctulata* known to us. Considering that the type locality is in a very well-collected part of the world in close proximity to NHMUK, this is surprising, suggesting that the species may be very rare. Alternatively, the holotype of *P. punctulata* could be a variant of *P. pilosator* with an exceptionally polished mesopleuron with reduced punctation and lacking the extensive rugulose/rugose sculpture of *P. pilosator*. This idea was considered by Perkins (1958) who said that *P. punctulata* “may prove to be only a form of *P. rugosa*” which is now a junior synonym of *P. pilosator*. *Piogaster punctulata* was synonymized under *P. pilosator* by Aubert (1967), but there was uncertainty in this synonymy and it was not adopted by subsequent authors (Fitton 1976; Fitton et al. 1988; Yu and Horstmann 1997; Shaw 2006; Broad 2016). The hypothesis that sculpture could have intraspecific variation is supported by observed variation in the sculpture of other species of *Piogaster*, for example, the propodeum of *P. albina* can be moderately rugose to almost completely smooth (compare Figs 5D, 6A). However, we have examined or seen photos of more than 30 females of *P. pilosator* from all over continental Europe

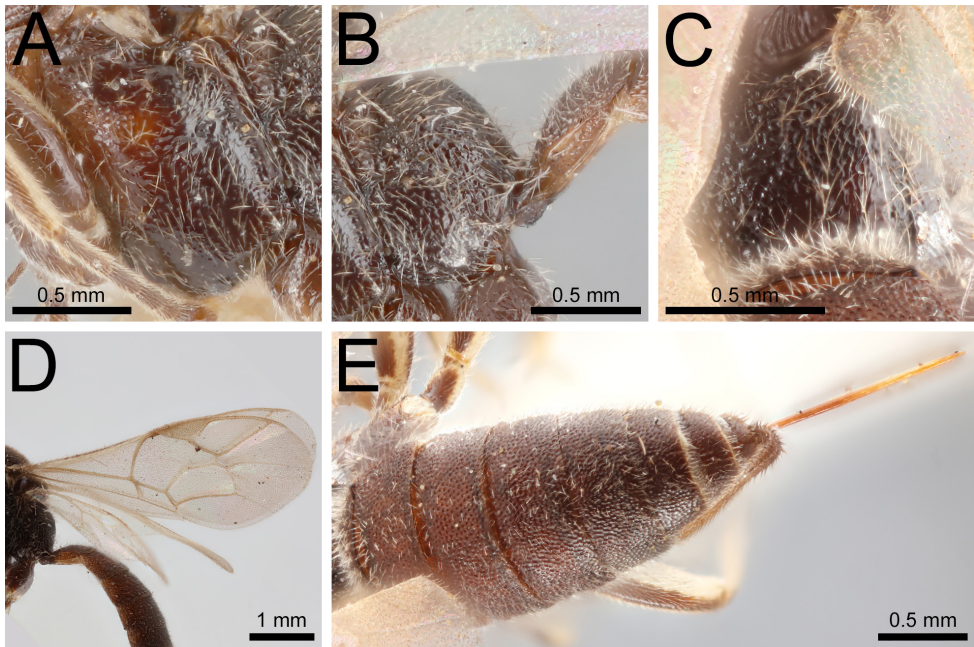


Figure 17. *Piogaster punctulata* female. All figures are of the holotype (NHMUK). **A** mesopleuron **B** metapleuron, propodeum and T1, lateral view **C** propodeum, dorsal view **D** wings **E** metasoma, T2–T8 and ovipositor, dorsal view.

(Fig. 30) and none of them have highly polished mesopleura (Figs 14B, 15) and all of them have extensive rugosity that differs greatly from the mostly smooth sculpture of the holotype of *P. punctulata* (Fig. 17A). For now, we maintain *P. punctulata* as a distinct species and hope additional material will be collected to clarify its status.

As noted above, we were unable to locate the male *Piogaster* specimen that Perkins (1958) tentatively associated with the female of *P. punctulata*. The only information provided about this specimen was that it was collected in Germany and is part of the Ruthe collection. Johann Friedrich Ruthe's (1778–1860) collection was acquired by the NHMUK upon his death, as indicated in his eulogy (Kraatz 1860). A female *Piogaster* specimen from the Ruthe collection is present in NHMUK, designated by Perkins (1958) as the holotype of *P. albina*, but the male *Piogaster punctulata* could not be located. Other males of *P. punctulata* have been mentioned in the literature (Fitton et al. 1988; Shaw 2006). We examined the male from Fitton et al. (1988) and the Santon Downham specimen from Shaw (2006). Both of these males most closely resemble the holotype of *P. punctulata* in that they have a punctate mesoscutum and a relatively polished, impunctate mesopleuron. However, all European males share these sculptural characters (Figs 24, 25), and we were unable to find characters that can be used to associate male specimens to their female counterparts in Europe.

***Piogaster ussuriensis* Kasparyan & Khalaim, 2007**

Figs 18, 19

Piogaster ussuriensis Kasparyan & Khalaim, 2007: 306.

Diagnosis. *Piogaster ussuriensis* can be distinguished from its congeners by possession of a combination of the following: 1) mesoscutum matte and rugose (Fig. 18E); 2) head primarily dark brown to black with pale yellow to white metasoma (Fig. 18A). In addition, the following character is diagnostic for distinguishing *P. ussuriensis* from other Palaearctic species: ovipositor sheath short, no more than 0.5× as long as hind tibia (Fig. 18A).

The metasoma of *P. ussuriensis* may have the most prominent tubercles of any female *Piogaster* species (Figs 19E, F). Other species lack tubercles or have weak tubercles, although this distinction is hard to quantify between species and individuals, so we do not include this character in the diagnosis above.

In addition to these morphological characters, *P. ussuriensis* has two binary molecular characters in the COI barcoding region at nucleotides 226 and 229, such that 226–229 are CATG in *P. ussuriensis*, and TATA in other *Piogaster*.

Piogaster ussuriensis is most likely to be confused with *P. pilosator*. *Piogaster pilosator* can be differentiated by having longer ovipositor sheaths, which are at least 0.7× as long as hind tibia. Ovipositor sheaths are often twisted and difficult to measure, so colour works best for differentiating these species. While *P. pilosator* is colour variable ranging from completely dark (Fig. 15C) to completely pale (Fig. 15A), we have not seen a specimen of *P. pilosator* or any other species with a dark brown to black head and a contrasting pale metasoma as is seen in *P. ussuriensis*. To be precise, *Piogaster ussuriensis* is the only species with the metasoma white (Fig. 19A) or pale yellow (Fig. 19E) (all other specimens with pale metasomas have theirs yellow (Fig. 15A) or orange (Fig. 7A)). *Piogaster ussuriensis* also tends to have stronger (higher) rugosity than *P. pilosator* which is weaker (lower). This is most easily seen in the mesosoma. It is a subjective comparison and therefore difficult to judge when examining only one specimen; however, differences in the relative strength of the rugosity can be judged by comparing photos of the propodeum and metapleuron of these two species (Fig. 19A, B to Figs 14C, D) as well as the pronotum and mesopleuron (compare Fig. 19A to Figs 14A, B).

Redescription. Adult. Female. Body length 4.2–5.0 [5.0] mm. FW length 3.3–3.9 [3.9] mm. **Head.** Antennae with 21–22 [21] flagellomeres. Clypeus 1.6–1.8 [1.8]× as wide as high, clypeus matte, with fine sparse setiferous punctations, with sparse to dense, medium to long white setae (Fig. 18C). Face and frons matte, coarsely rugose, with dense short white setae (Fig. 18C). Vertex matte, coarsely punctate, punctures small and touching, with dense short white setae (Fig. 18D). Occipital carina complete. MSL 0.8–1.0 [1.0]× as long as BWM. OOD 1.3–1.6 [1.4]× as long as LOD. **Mesosoma.** Pronotum with epomia absent; matte, coarsely rugose, with sparse short white setae (Fig. 19A). Mesoscutum matte with dense, short, white setae, coarsely,

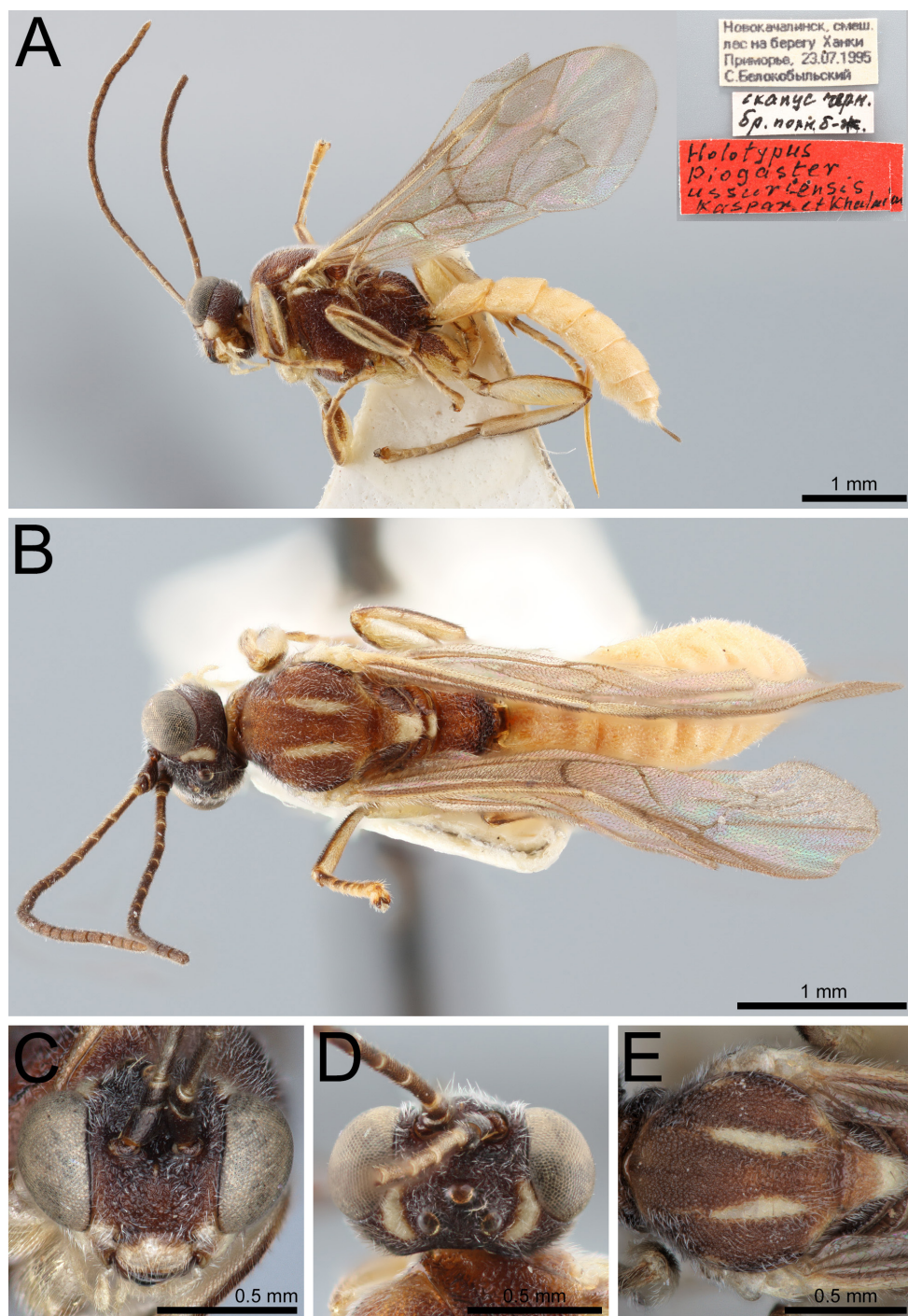


Figure 18. *Piogaster ussuriensis* female. Figures A–C of holotype (ZIN), figures D and E of CNC1754423 (NINA). **A** habitus, lateral view, with holotype labels inset **B** habitus, dorsal view **C** head, anterior view **D** head, dorsal view **E** mesoscutum, dorsal view.

densely punctate, punctures small and touching, with rugose sculpture anterolaterally where notauli would be and medioposteriorly to scuto-scutellar groove (Fig. 18E) [holotype a bit less strongly rugose in these areas (Fig. 18B)]. Scutellum matte, rugose-punctate with dense short white setae (Figs 18B, E). Mesopleuron, metapleuron, and propodeum matte, coarsely densely rugose, with sparse to dense short white setae (Figs 19A, B). Propodeum with pleural carina variable, absent in some specimens (Fig. 19A), present anteriorly but absent posteriorly, or present anteriorly and posteriorly, but not complete and not present medially [indistinct anteriorly and posteriorly, absent medially (Fig. 19B)], difficult to see in the high rugose sculpture. Propodeum with lateral longitudinal carina present in posterior 0.3–0.5 but difficult to see among the high rugae (Fig. 19B), all other propodeal carina absent. **Wings. Fore wing.** Vein Rs+M without ramellus extending into cell 1M+1R1 (Fig. 19C). Vein 2rs-m 0.6–0.9 [0.9]× as long as M between 2rs-m and 2m-cu (Figs 18A, 19C). Vein 2m-cu not thickened or angulate between bullae (Fig. 19C). **Hind wing.** Vein 1/Cu&cu-a inclivous and angled apically, 2/Cu intercepting in lower 0.3, 2/Cu present but spectral to nebulous (Fig. 19C). **Metasoma.** T1 subpolished and densely punctate, with dense short white setae (Fig. 19D). T1 dorsal medial carina absent, or present anteriorly but weak and short [present], 0.1–0.3 [0.3]× length of T1; dorsolateral carinae complete, weak posteriorly and sinuous throughout length in most specimens (Fig. 19F). T2–T5 subpolished in most specimens or polished [subpolished], densely punctate with dense short white setae (Fig. 19E). T6 subpolished in most specimens or polished [subpolished], densely shallowly punctate, with moderately dense short white setae. T7–T8 subpolished in most specimens or polished [subpolished], smooth, sparsely weakly punctate with sparse short white setae. T2–T5 anteriorly with weak ovoid tubercles, located submedially to sublaterally, remaining tergites without grooves or tubercles (Fig. 19E, F). Ovipositor sheath 0.4–0.5 [0.4]× length of hind tibia (Fig. 18A). **Colour.** Head predominantly dark brown to black except the following areas white: face ventrolaterally (lateral and a little dorsal to clypeal foveae) (Fig. 18C), clypeus except dorsolaterally near foveae in most specimens, malar space except stained with brown in malar sulcus in some specimens, ventral 0.2 of gena (Fig. 18A), a crescent-shaped region laterally on vertex extending from eye to level of posterior of lateral ocellus (Fig. 18D) or to occipital carina. Face may be light brown in some specimens. Mandible medium to dark brown with dark black transverse medial band. Maxillary and labial palps white. Antenna light to dark brown (Fig. 18B), with basal 2–4 flagellomeres ventrally white to pale brown (Fig. 18A). Pronotum brown-yellow, medium brown or dark brown [medium brown] with posterodorsal corner white (Fig. 19A). Tegula white. Mesoscutum brown-yellow to dark brown [medium brown] with yellow-white submedial longitudinal stripes (Fig. 18B) and lateral spots (Fig. 18A). Scutellum anteriorly brown orange to dark brown [medium brown], medially to posteriorly white, with axillary troughs medium to dark brown [medium brown] (Fig. 18B). Post-scutellum white with axillary troughs medium to dark brown [medium brown] (Figs 18B, E). Mesopleuron variable, predominantly brown-yellow (Fig. 19A) to dark brown [medium brown (Fig. 18A)]. White subtegular ridge, and white spot dorsal to mesopleural

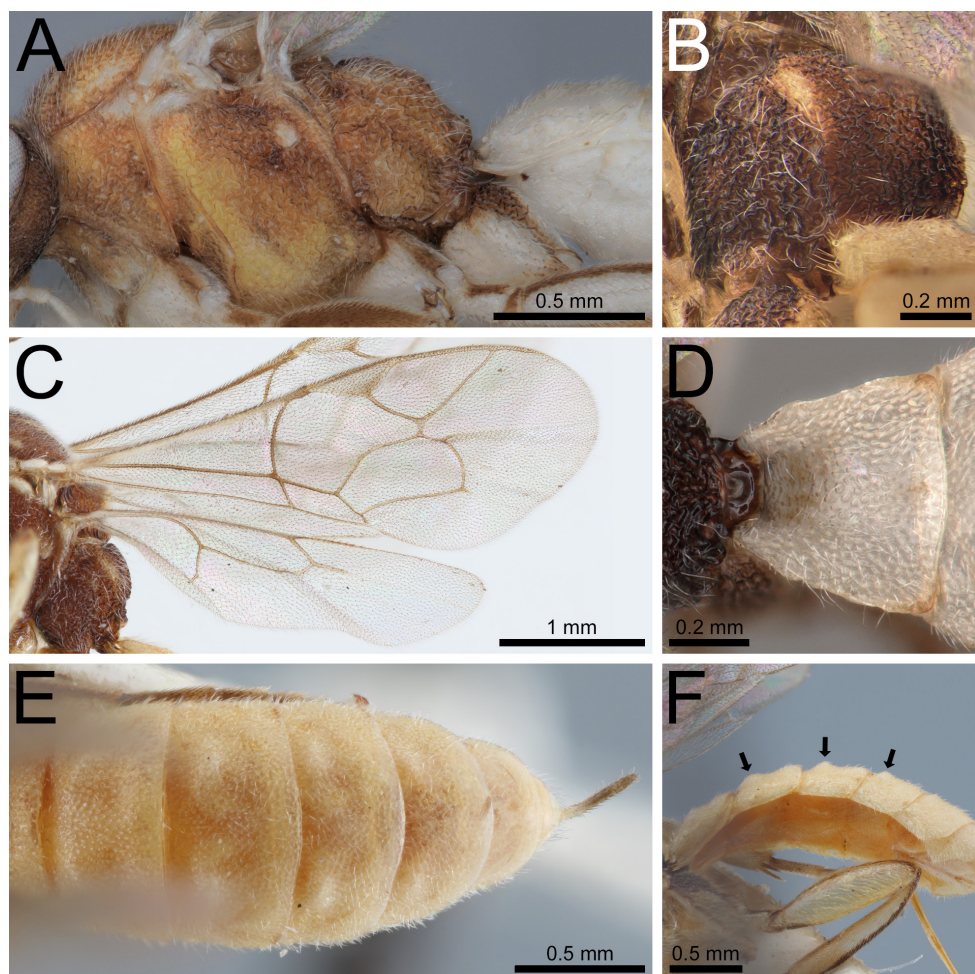


Figure 19. *Piogaster ussuriensis* female. Figures B, E and F of holotype (ZIN), A of specimen NHMUK012850733 (NHMUK), C of non-type specimen CNC310413 (ZIN), D of 21GYU168 (DNUE). **A** mesosoma and T1, lateral view **B** propodeum, dorsolateral view **C** wings **D** T1, dorsal view **E** metasoma, dorsal view **F** metasoma, T1–T5, ventrolateral view. Arrows in F point to the left tubercle of the paired tubercles on T2–T4.

fovea present in some specimens (Fig. 19A). Metapleuron variable, yellow-brown (Fig. 19A) to dark brown [medium brown (Fig. 18A)]. Propodeum variable, yellow-brown to dark brown [medium brown], with paler white to medium brown area anterior to lateral longitudinal carina and dorsal to spiracle (Fig. 19B). Wings hyaline, veins including stigma pale brown to transparent, Sc+R medium brown. Legs predominantly white to yellow-white [yellow-white (Fig. 18A)], coxae with medium brown spot or stripe dorsally, trochanters medium brown on dorsal surface, femora with medium brown longitudinal stripe on dorsal and/or ventral surface [holotype with both stripes on fore leg, middle and hind leg dorsal stripe complete, but only partial stripe ventrally

at base], tibia with dark brown complete stripe on dorsal surface, light to dark brown complete or incomplete stripe on ventral surface [incomplete, light brown], tarsi with dorsal surface medium to light brown [light brown], basal tarsomeres darker on dorsal surface than apical ones. Metasomal tergites pale yellow to white [pale yellow], with small brown dot present on tubercles of T2–T5 in some specimens [absent, (Fig. 18A)]. Ovipositor sheaths white to pale yellow basally [pale yellow], light brown to medium brown apically [medium brown (Fig. 18A)].

Male. Unknown.

Distribution. Fig. 31. Eastern Russia: Primorsky Krai (Kasparyan and Khalaim 2007) and Amur Oblast (this study), and South Korea (Choi et al. 2015).

Biology. Unknown.

Material examined. Holotype. RUSSIA • ♀; Primorsky Krai, Novokachalinsk; 23.vii.1995; C. Belokobylskiy; mixed forest on the shore of the lake Khanka; [ZIN].

Condition of type: Missing one ovipositor sheath, and right antenna broken off after flagellomere 14, otherwise intact.

Other material. KOREA • 1 ♀; Gangwon-do, Goseong, Ganseong, Heulri (Shinseonbong); 2.viii–19.ix.2002; D-S. Ku; Malaise trap; NHMUK012850733; [NHMUK] • 1 ♀; Gangwon-do, Wonju-si, Heungeop-myeon, Maeji-ri, Yonsei University; 37.28180°N, 127.89848°E; 5–18.vii.2015; H. Y. Han; 21GYU168; [DNUE] • 1 ♀; Gyeonggi-do, Namyangju-si, Choan-myeon, Songcheon-ri, Mt. Ungilsan; 37.57867°N, 127.31042°E; 26.vi–16.vii.2009, J. O. Lim; 21GYU169; [DNUE]. RUSSIA • 1 ♀; Amur Oblast, 30 km south of Arkhara, Barge on the Arkhara river; 22.vii.2003; C. Belokobylskiy; mixed forest; CNC310413; [ZIN].

Comments. One specimen (NHMUK012850733) is more polished in the metasoma and has a paler face which shows morphological variation as noted in the description above.

***Piogaster variegata* Bass, Bennett & Schwarzfeld, sp. nov.**

<https://zoobank.org/A4647326-B4BE-4315-ADFF-FB4580A46C6D>

Figs 20, 21

Diagnosis. *Piogaster variegata* can be distinguished from its congeners by possession of a combination of the following: 1) mesoscutum matte and pustulate (Fig. 20E); 2) HW 2/Cu absent with no angulation in 1/Cu&cu-a, only a very weak curve posterior to midheight present (Fig. 21F); 3) T1–T5 matte and granulate (Figs 21G, H); 4) metasomal T2–T6 variegated: anterior 0.8 of each segment pale brown with dark brown spots, posterior 0.2 white (Fig. 21H). *Piogaster variegata* is similar to other North American specimens (*P. maculata* and undescribed male *Piogaster* from British Columbia) as T1–T5 of the metasoma are granulate and the abscissa 2/Cu of the hind wing is absent. It can be distinguished by the variegated white and brown colour of the metasoma (Figs 21G, H) (tergites unicolorous with only narrow, posterior lighter bands in the other Nearctic specimens) (Figs 12D, 23C).

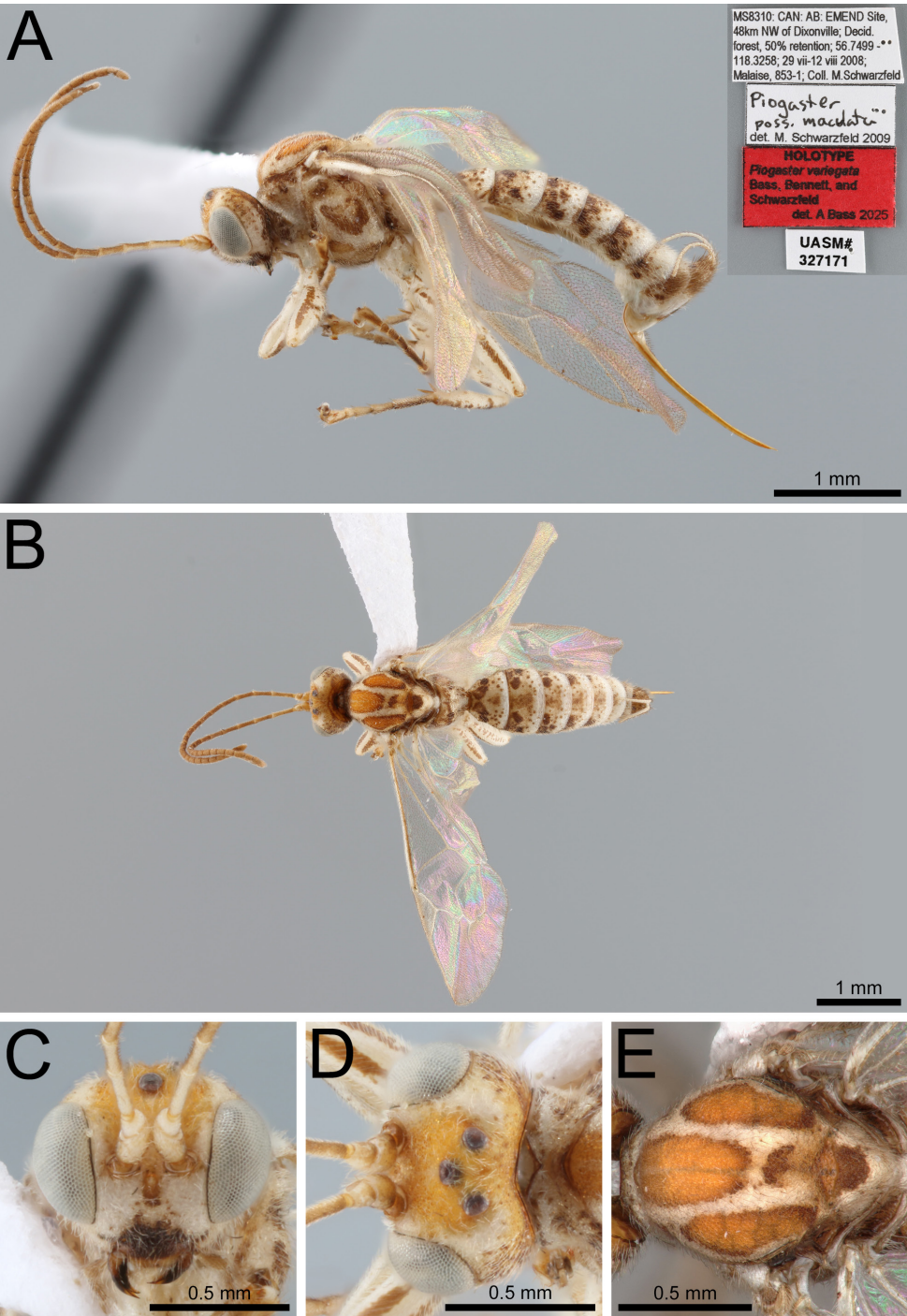


Figure 20. *Piogaster variegata* sp. nov. female. All photos are of the holotype specimen (CNC). **A** habitus, lateral view, with holotype labels inset **B** habitus, dorsal view **C** head, anterior view **D** head, dorsal view **E** mesoscutum, dorsal view.

Description. Adult. Female. Body length 4.3 mm. FW length 3.8 mm. **Head.** Antennae with 21 flagellomeres. Clypeus 2.0× as wide as high, matte, granulate with sparse long white setae (Fig. 20C). Face, frons and vertex matte, granulate with dense short white setae (Figs 20C, D). Occipital carina complete (Fig. 20D). MSL 1.3× as long as BWM. OOD 1.6× as long as LOD. **Mesosoma.** Pronotum with epomia absent; matte, granulate, with dense medium length white setae (Fig. 21A). Mesoscutum (Fig. 20E), mesopleuron (Fig. 21B), metapleuron, and propodeum (Fig. 21D) matte, pustulate, with sparse to dense short to medium length white setae. Scutellum matte, granulate, with dense short white setae (Fig. 20E). Propodeum with pleural carina complete; lateral longitudinal carina present in posterior 0.6, all other propodeal carina absent (Fig. 21D). **Wings. Fore wing.** Vein Rs+M without ramellus extending into cell 1M+1R1 (Fig. 21E). Vein 2rs-m 0.6× as long as M between 2rs-m and 2m-cu (Fig. 21E). Vein 2m-cu not thickened or angulate between bullae (Fig. 21E). **Hind wing.** Vein 1/Cu&cu-a slightly inclivous, slightly curved posteriorly, but not angulate, 2/Cu absent (Fig. 21F). **Metasoma.** T1 matte, granulate with dense short white setae (Fig. 21G). T1 median dorsal carina present anteriorly but short, 0.1× length of T1; dorsolateral carina present anteriorly, 0.6× length of T1, absent posteriorly (Fig. 21C). T2–T5 matte, granulate with dense medium length white setae (Fig. 21H). T6 matte, granulate, with dense long white setae. T7 matte, granulate and sparsely punctulate with dense long brown setae (Fig. 21H). T8 subpolished, punctulate with dense long brown setae. Tergites without grooves or tubercles (Fig. 21H). Ovipositor sheath 0.6× as long as hind tibia. **Colour.** Face white except stained with light brown near medial tubercle (Fig. 20C). Clypeus dark brown basally, yellow apically (Fig. 20C). Frons yellow-orange except white in orbits (Fig. 20D). Vertex orange medially between lateral ocelli and posteriorly near occipital carina, these areas with a few small scattered light brown dots, sublaterally with white, subtriangular mark that is contiguous with white inner orbits of frons, laterally light brown with brown dots (Fig. 20D). Gena white with dense, medium brown dots in dorsal half and posteriorly medium brown (Fig. 20A). Occiput dark orange (Fig. 20B). Mandible medium brown with transverse dark brown median band. Maxillary palps with segment 1 white, remaining segments light brown. Labial palps uniform white. Antenna light brown, scape, pedicel and flagellomeres 1–2 white anteriorly (Figs 20A–C). Pronotum variegated white and medium brown. Tegula white. Mesoscutum predominantly orange, with a white H-shaped mark in the location where the notauli would be, the shape formed by sublateral, longitudinal white stripes joined by a transverse white mark just posterior to middle, lateral edges of mesoscutum narrowly white, posteromedially medium brown (Fig. 20E). Scutellum white with anteromedial medium-brown spot (Fig. 20E), axillary troughs orange-yellow in anterior half, white in posterior half (Fig. 20E). Post-scutellum white, axillary troughs medium brown anteriorly, light brown posteriorly (Fig. 21D). Mesopleuron variegated white and medium brown, ventrally light brown, area of sternaulus brown-orange. Metapleuron and propodeum (Fig. 21D) variegated white and medium brown. Mesosternum light brown. Wings hyaline, veins including stigma white, Sc+R yellow-orange. Legs predominantly white. Fore and middle coxae with some small brown spots (two near

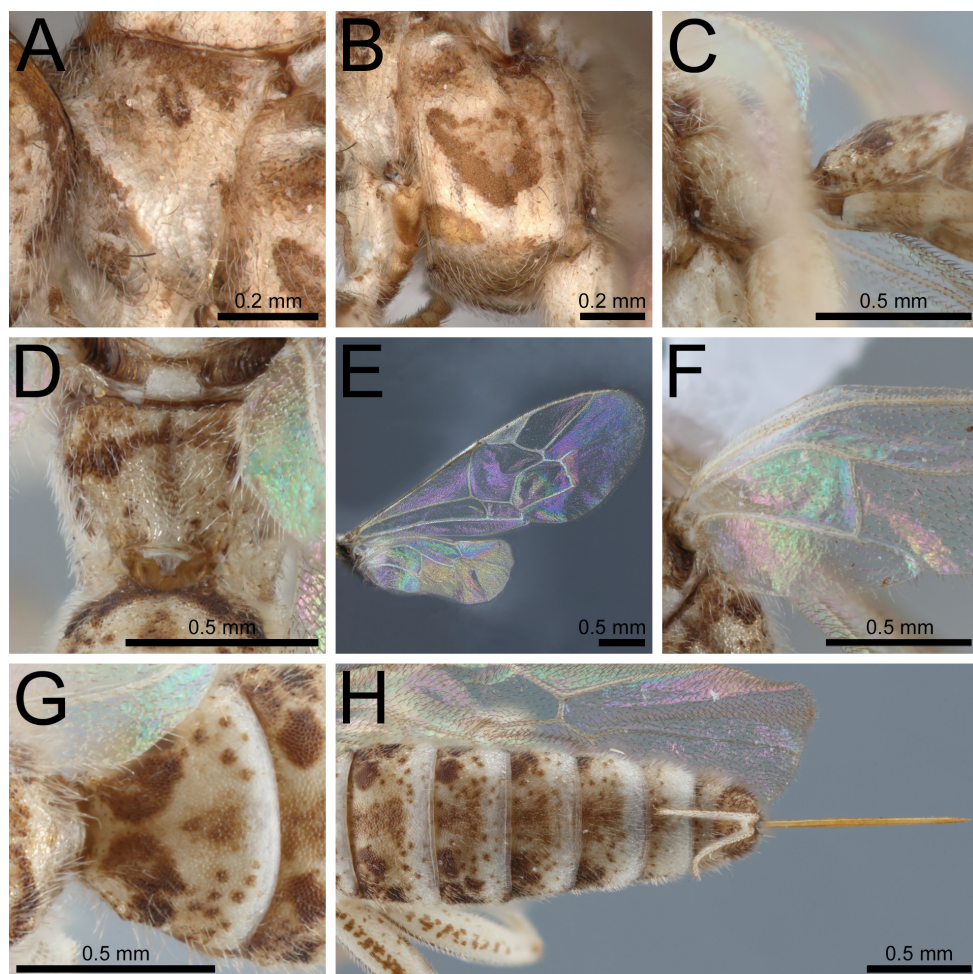


Figure 21. *Piogaster variegata* sp. nov. female. All photos are of the holotype specimen (CNC). **A** pronotum **B** mesopleuron **C** metapleuron and T1, lateral view **D** propodeum, dorsal view **E** wings **F** fore wing **G** tergite 1, dorsal view **H** metasoma, T2–T8 and ovipositor, dorsal view.

base, one near apex), hind coxa with more extensive brown spots, laterally coalescing into a longitudinal band. Trochanters with small brown spots anteriorly and posteriorly that coalesce into longitudinal bands, trochantellus white with a small brown spot basally. Femora with small medium brown spots ventrally and laterally, dorsally coalescing into two longitudinal stripes anterodorsally and posterodorsally (Fig. 20A). Fore tibia with a medium brown stripe on dorsal surface, and middle and hind tibiae with brown spots partly coalesced into longitudinal stripe dorsally. Tarsi medium brown dorsally, yellow-white ventrally. Metasomal tergites variegated white, yellow-white, and medium brown, most noticeably, round, slightly darker brown spots sublaterally near anterior margin of T1–5 (Fig. 21H). Ovipositor sheath white (Fig. 21H).

Male. Unknown.

Distribution. Fig. 29. Canada (Alberta). This is the first record of *Piogaster* in both Canada and Alberta.

Biology. Unknown.

Material examined. Holotype. CANADA • ♀; Alberta, EMEND site, 48 km NW of Dixonville; 56.7499°N, 118.3258°W; 29.vii–12.viii.2008; M. Schwarzfeld; Malaise trap, 853-1; deciduous forest, 50% retention; UASM327171; [CNC].

Condition of type: Intact.

Etymology. The epithet *variegata* is a descriptive name referring to the variegated colour patterns on the body, particularly the metasomal tergites, that are unique to this species in the genus *Piogaster*.

Comments. The holotype of *P. variegata* is probably the most distinctive specimen of *Piogaster* known, with its predominantly variegated white and brown colouration and H-shaped white marking on the mesoscutum. These variegated spots are only known in some other specimens on the legs (as in *P. maculata*), not the body. With respect to distribution, this specimen and the unidentified male from British Columbia represent a huge range extension (2900 km distant between the type localities of *P. maculata* and *P. variegata*). This demonstrates the great range of the genus *Piogaster* within the Holarctic region and highlights the need for much more collecting of wasps and jumping spiders which will hopefully fill in gaps in the current species ranges and likely discover many more undescribed species.

Unidentified North American *Piogaster* male

Figs 22, 23

There is one male specimen collected in 1938 in British Columbia. This male could not be associated with a female or unequivocally determined to be a new species. Geographically, this male is more supported as *P. variegata* as it was collected ~380 km from the type locality of this species in contrast to ~1700 km from *P. maculata*. However, given how little we know about the distribution of North American species, this alone is not evidence enough to associate it. Identification utilizing molecular data was not possible due to the age of the specimen and the lack of DNA of the two other North American *Piogaster* species which are known only from the holotype. To confidently associate this male with either *P. variegata* or *P. maculata*, multiple shared morphological characters are required and were not observed in this study and thus it remains identified only to genus. Nevertheless, we provide a diagnosis and description of this specimen to aid future researchers should additional material be found that will allow clarification with respect to its status. This is the specimen mentioned in Gauld and Dubois (2006) as *Piogaster* sp. 1. It was reared from *Habronattus*, providing a new generic host record for *Piogaster* and, to our knowledge, is the only specimen with associated host remains (Figs 23E, F).

Diagnosis. This specimen can be distinguished from congeners by possession of the combination of the following: 1) Metasoma with T1–T5 weakly granulate (Fig. 23C), 2) HW 2/Cu absent with no apparent bend in 1/Cu&cu-a (Fig. 23A);

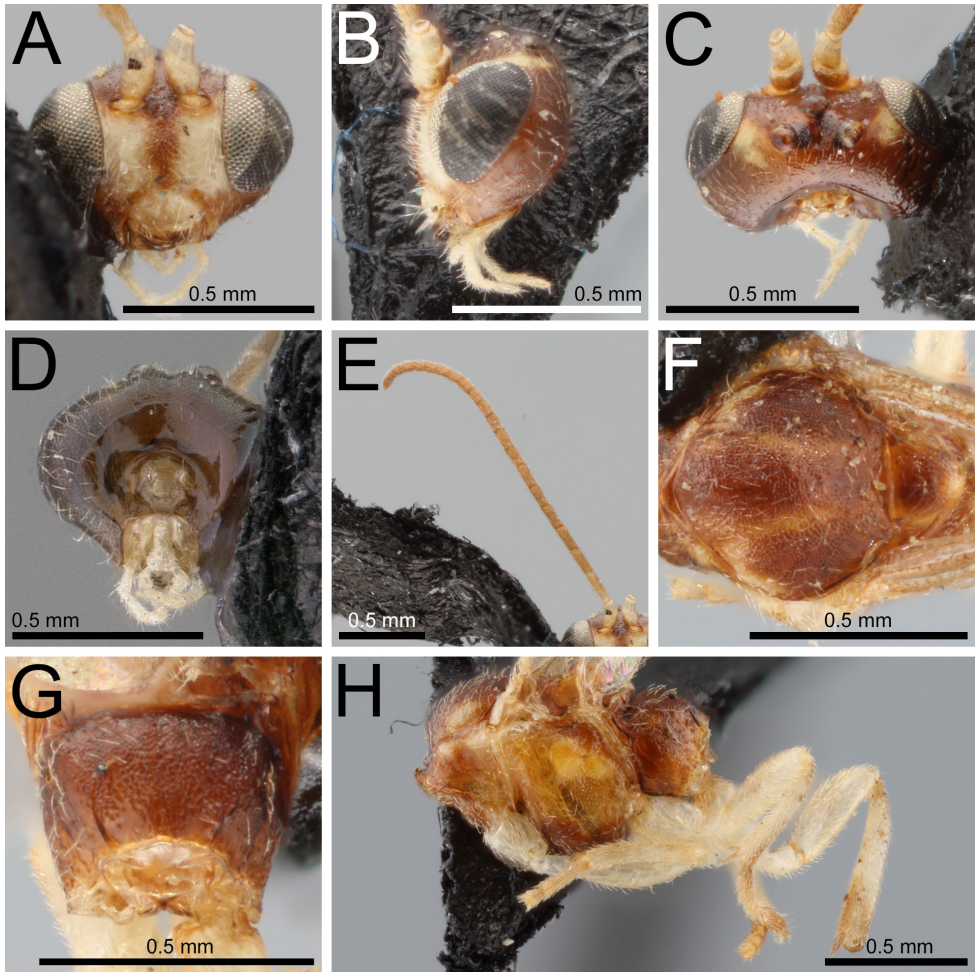


Figure 22. Male *Piogaster* sp. from British Columbia, Canada. All photos are of CNC1754420 (CNC). **A** head, anterior view **B** head, lateral view **C** head, dorsal view **D** head, posterior view **E** antenna **F** mesoscutum, dorsal view **G** propodeum, dorsal view **H** mesosoma, lateral view.

3) T6–T8 smooth, subpolished (Fig. 23C); 4) FW vein 2rs-m short, ratio of 2rs-m to M between 2rs-m and 2m-cu 0.3 (Fig. 23A). This specimen is most similar to *P. variegata* and *P. maculata* with respect to the granulate metasoma and the unbent HW vein 1/Cu&cu-a, but differs in T6–T8 being smooth and subpolished rather than granulate and matte, and the 2rs-m vein being short.

Description. Adult. Male. Body length estimated at about 3 mm (specimen in multiple pieces). FW length 2.5 mm. **Head.** Antenna with 20 flagellomeres. Clypeus 1.9× as wide as high, matte and granulate, with long white setae. Face and vertex matte and granulate, with sparse (vertex) to moderately dense (face) short white setae (Fig. 22A). Frons matte and granulate with sparse short yellow-white setae

(Fig. 22C). Occipital carina complete (Fig. 22D). MSL 1.0× as long as BWM. OOD 1.3× as long as LOD. **Mesosoma.** Pronotum with epomia absent; granulate, with weak longitudinal striations dorsoposterior to the pronotal groove, with sparse medium length yellow setae (Fig. 22H). Mesoscutum matte, granulate medially, pustulate laterally, with sparse short white setae (Fig. 22F). Scutellum matte, granulate, with sparse short white setae. Metapleuron subpolished, granulate, with a few sparse short white setae (Fig. 22H). Propodeum matte, pustulate with sparse long white setae; with pleural carina complete; lateral longitudinal carina present in posterior 0.3, all other propodeal carina absent (Fig. 22G). **Wings.** **Fore wing.** Vein Rs+M with ramellus absent (Fig. 23A). Vein 2rs-m 0.3× as long as M between 2rs-m and 2m-cu (Fig. 23A). Vein 2m-cu not thickened or angulate between bullae (Fig. 23A). **Hind wing.** Vein 1/Cu&cu-a slightly inclivous, not angulate, with 2/Cu absent (Fig. 23A). **Metasoma.** T1 matte, granulate, with sparse short yellow-white setae. T1 dorsal medial carina present anteriorly but weak and short, 0.3× length of T1 (Fig. 23B); dorsolateral carina present anteriorly, 0.3× length of T1 (Fig. 23D). T2–T5 matte to subpolished, weakly granulate, with sparse medium length white setae (Fig. 23C). T6–T8 subpolished, smooth. T6–T7 with sparse medium length yellow setae, T8 with sparse medium length medium brown setae. Tergites without grooves or tubercles (Fig. 23D). **Colour.** Head primarily medium brown, except the following: clypeus yellow-white; face white with medium brown vertical stripe extending from area between antenna to dorsal edge of clypeus (Fig. 22A); vertex with triangular pale yellow-white mark (Fig. 22C). Malar space and ventral gena not paler than rest of gena (dark brown), except just dorsal to base of mandible (Fig. 22C). Mandible light brown-yellow basally, dark brown apically (Fig. 22A). Maxillary and labial palps yellow-white. Antenna with scape medium brown dorsally, yellow-white ventrally (Fig. 22A), pedicel yellow-white, flagellum light brown (Fig. 22E), slightly darker dorsally than ventrally. Pronotum medium brown anteriorly, pale yellow posteriorly (Fig. 22H). Tegula white. Mesoscutum medium brown with thin submedial yellow longitudinal stripes (Fig. 22F) and two anterior sublateral yellow spots (Fig. 22H). Scutellum medium brown, yellow posteriorly (Fig. 22F), with axillary troughs yellow-brown. Post-scutellum medium brown and white posteriorly, axillary troughs brown-yellow. Mesopleuron orange-yellow, medium brown ventrally and postero-dorsally (Fig. 22H). Mesosternum medium brown. Metapleuron medium brown dorsoanteriorly, paler ventroposteriorly (Fig. 22H). Propodeum medium brown (Fig. 22G). Wings hyaline, veins light brown to transparent (Fig. 23A). Legs uniformly yellow white, with hind tibia brown-white basally and apically, tarsomeres brown-white, (hind tarsomere not viewed, broken off specimen) (Fig. 22H). Metasomal tergites medium brown, posterior margins of T1–T6 yellow (Figs 23C, D). Hypopygium medium brown. Gonoforceps medium brown (Fig. 23D).

Female. Unknown.

Distribution. Fig. 29. Canada (British Columbia). This is the first record of *Piogaster* in British Columbia.

Biology. Reared from *Habronattus* sp. (Araneae: Salticidae).

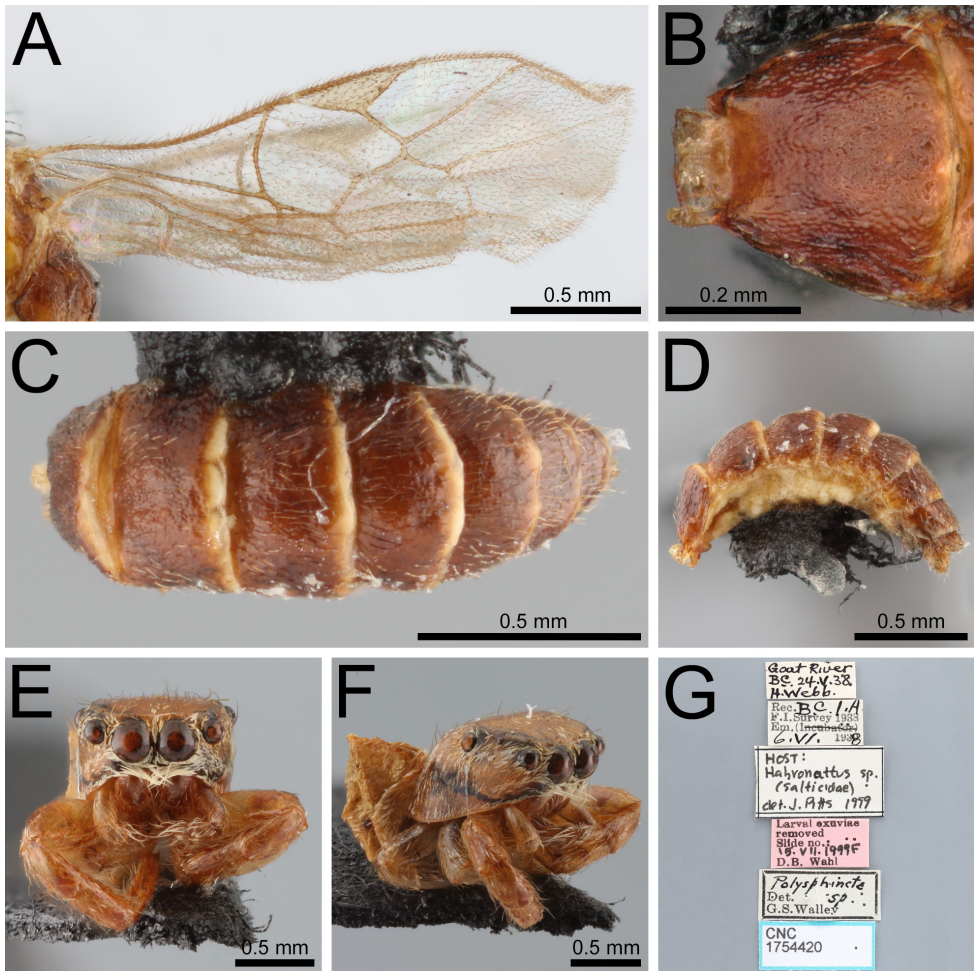


Figure 23. Male *Piogaster* sp. from British Columbia, Canada. All photos are of CNC1754420 (CNC). **A** wings **B** tergite 1, dorsal view **C** metasoma, dorsal view **D** metasoma, lateral view **E** host, *Habronattus* sp., anterior view **F** host, *Habronattus* sp., anterolateral view **G** labels.

Material examined. CANADA • 1 ♂; BC, Goat River; 24.v.1938; H. Webb; Rec. B.C.I.A. F.I. Survey 1938; Em. 6.vi.1938; host: *Habronattus* (Salticidae) det. J. Pitts 1999; larval exuviae removed slide no. 15.vii.1999 D. B. Wahl; CNC1754420; [CNC].

Condition of specimen: Body on three points. First point has head glued to point on right side (Fig. 22A). Right antennae is intact, left antennae is glued to same point. Second point has mesosoma glued to point on right side (Fig. 22H). Third point has metasoma glued to the point on right side (Fig. 23D). Host on fourth point, glued to point ventrally (Figs 23E, F).

Comments. This specimen was collected as part of the Forest Insect Survey, a project that ran from 1936–1961 (and continued until 1995 as the Forest Insect

and Disease Survey) with the goal of documenting Canadian forest insect fauna (van Sickle et al. 2001). The specimen locality is listed as Goat River, BC. According to the Canadian Geographical Names Database there are three Goat Rivers in British Columbia (Natural Resources Canada 2021). In 1938, 345 of the 442 insect samples collected in British Columbia as part of the Forest Insect Survey were collected by the BC Forest Service (Dominion Forest Service 1939). By accessing archival records of BC Forest Service staff, we determined that the collector of the specimen, H. Webb, was an assistant ranger stationed at Goat River in the Prince George Forest District from April 30 until September 30 in 1938 (British Columbia Forest Service 1920–1964). Therefore, the specimen was almost certainly collected at the Goat River that drains into the Fraser River near McBride, British Columbia, as it is the only Goat River in the Prince George Forest District (Fig. 29). An attempt was made to slide mount the exuvia; however, the resulting preparation appears to be from a sub-mature instar (D. Wahl, pers. comm.). Therefore, the last larval cephalic sclerites of *Piogaster* remain unknown.

Unidentified European *Piogaster* males

Figs 24, 25

While there have been at least 37 male specimens collected in Europe (Fig. 32), we were unable to associate any of them with the females of any of the four described European species (*P. albina*, *P. pilosator*, *P. lucida*, and *P. punctulata*). This difficulty appears to result from two factors: strong sexual dimorphism between males and females and the morphological similarity among male specimens.

Sexual dimorphism complicates these associations. *Piogaster* males and females of the same species vary in colour and sculpture (see *P. daisetsuzana* female and male specimens in Figs 7–10), with males tending have darker bodies and legs lacking the stripes that are typical of females, as one example. A similar pattern appears to occur in European species. Although at least 31 female *P. pilosator* are known from collections, and additional photos of female specimens exist online, to our knowledge there are no male specimens that have similar morphology to these females.

In addition to sexual dimorphism, European males appear to be morphologically cryptic. Male *Piogaster* have been collected from a wide geographic distribution in Europe (Fig. 32), yet we found very little morphological variation between these specimens. The few characters that do vary (e.g., colour of the face and coxae, strength of metasomal grooves, and presence of a short epomia) may represent intraspecific variation rather than species-level differences. In addition, much of the variation that exists between male specimens is likely not species level variation, as highlighted in the comments detailing variation between six males collected at the same locality in Italy on 25–28 May 1990. Consequently, we were unable to identify diagnostic characters that would allow reliable differentiation of European males or their association with known females.

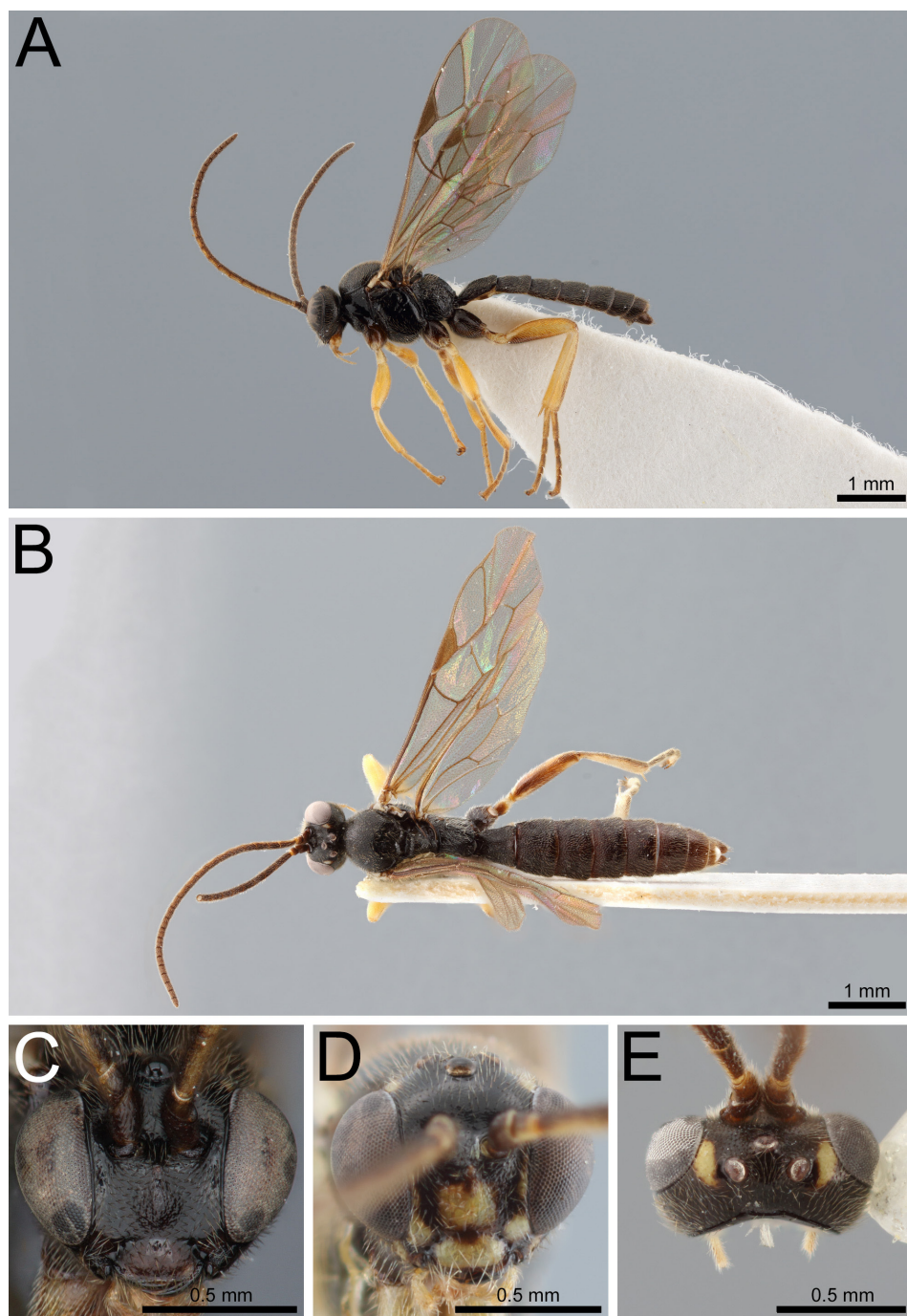


Figure 24. Male European *Piogaster* specimens. Figure A and C are of specimen RMNH1561210 (RMNH), figure B is specimen MNHN-EY-EY36003 (MNHN), figure D is of specimen RMNH1561213 (RMNH), figure E is specimen CNC1754569 (NMS). **A** habitus, lateral view **B** habitus, dorsal view **C** head, anterior view **D** head, anterior view **E** head, dorsal view.

Molecular data have so far not resolved these associations. Two European male specimens have been DNA barcoded (Figs 1, 2, Suppl. material 2), but neither could be confidently linked to females. One specimen collected in Norway showed unstable (rogue-like) placement in both COI phylogenies (Figs 1, 2) with low bootstrap support and did not cluster within a species clade in either case. A portion of this specimens COI sequence was removed prior to phylogenetic analysis due to frame shift mutations in the alignment. Chromatograms were not available, but the unstable placement of this specimen may reflect lower-quality sequencing or base-calling errors. Another specimen collected in Germany clustered within the *P. albina* + *P. pilosator* mixed clade, but morphological examination could not link it definitively to either species.

We examined 16 European male specimens, and the description of those specimens is included below. This description is provided to detail the similarity of these male specimens, highlight the differences between males and females, and provide characters to distinguish these males from the Nearctic male specimen and the two *P. daisetsuzana* males.

Description. Adult. Male. Clypeus subpolished to polished, smooth with sparse setaceous punctation (Fig. 24C, D). Face subpolished to polished, weakly rugulose and densely, weakly punctate (Fig. 24C, D). Frons (Fig. 24D) and vertex (Fig. 24E) subpolished to polished, punctulate. Occipital carina complete (Fig. 24E). **Mesosoma.** Pronotum with epomia usually absent, sometimes present in the dorsal pronotal groove but weak and short; polished, ventrally smooth without setae, dorsally punctate with dense setae (Fig. 25B). Mesoscutum subpolished to polished, densely punctate, with dense setae (Fig. 25A). Scutellum subpolished, densely shallowly punctate, with dense setae (Fig. 25A). Mesopleuron polished, with fine sparse setiferous punctation, dorsoposterior area smooth, without setae (Fig. 25C). Metapleuron polished, weakly punctate, with sparse setae (Fig. 25D). Propodeum subpolished, rugose, rugose punctate, or rugulose punctate, with dense setae (lacking transverse striations as in male of *P. daisetsuzana*), with a longitudinal groove medially, especially anteriorly in most specimens (Fig. 25E). Propodeum with pleural carina complete, sometimes weak and/or sinuous posterior to spiracle; lateral and medial longitudinal carinae (Fig. 25E) variable, present in posterior, anterior, or complete. **Wings. Fore wing.** Vein Rs+M usually with ramellus absent, sometimes ramellus present for $0.1 \times$ length of 2rs-m (Fig. 25F). Vein 2rs-m $0.5\text{--}0.7 \times$ as long as M between 2rs-m and 2m-cu (Fig. 25F). Vein 2m-cu not thickened or angulate between bullae (Fig. 25F). **Hind wing.** Vein 1/Cu&cu-a inclivous, angled apically where 2/Cu intercepts, 2/Cu intercepting in lower $0.2\text{--}0.4$, 2/Cu long and nebulous or spectral, sometimes with short tubular section basally (Fig. 25F). **Metasoma.** T1 subpolished, punctate reticulate with dense setae (Fig. 25G). T1 median dorsal carina $0.8\text{--}1.0 \times$ length of T1 (Fig. 25G); dorsolateral carina complete (Fig. 25G). T2–T5 subpolished, T2–T4 punctate reticulate, T5–T6 punctate, with dense setae (Fig. 25H). T7–T8 subpolished to polished, finely punctate, with dense long yellow setae (Fig. 25H). Tergites often with weak medial to posterior grooves (Fig. 25H) on T2, T3, and/or T4, sometimes grooves deep, sometimes without grooves, sometimes with weak anterior submedial tubercles on T2 and T3. **Colour.** Head dark brown to black, except for the

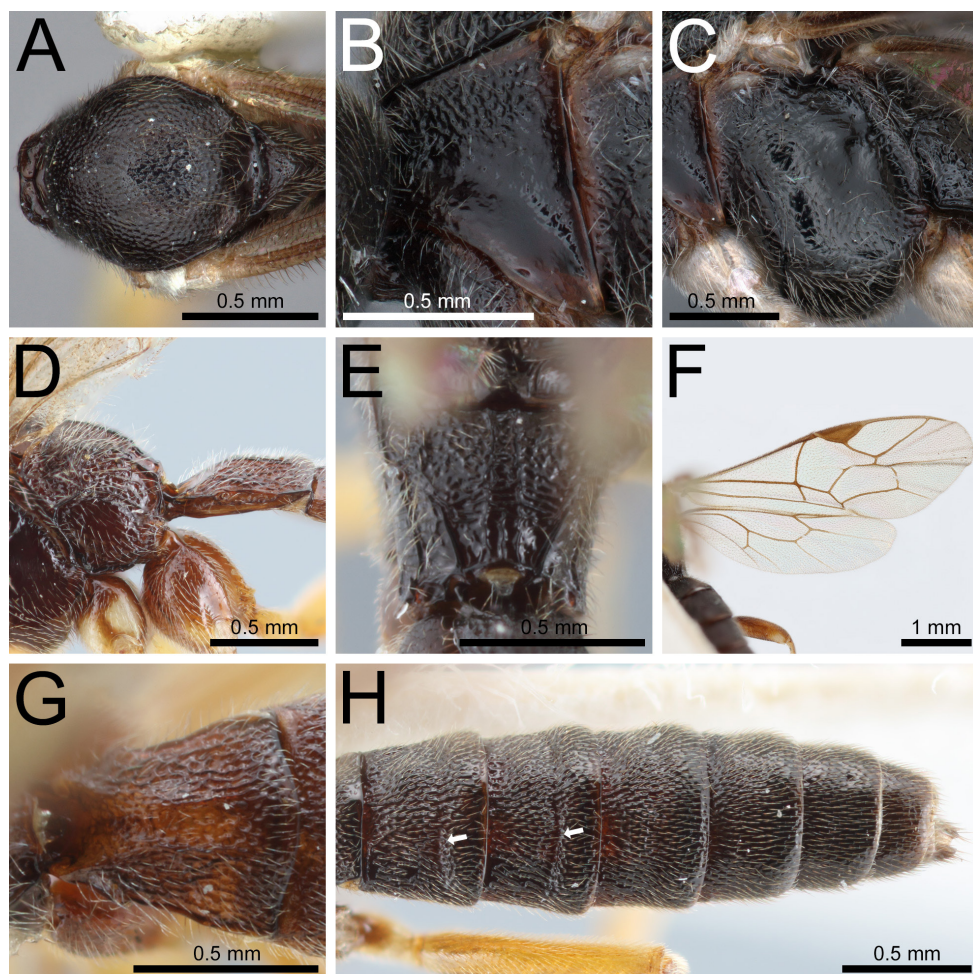


Figure 25. Male European *Piogaster* specimens. Figure A is CNC1754569 (NMS), figures B and C are of BIOUG17116-B03 (ZFMK), figure D and G are of CNC310414 (NMS), Figure E is specimen RMNH. INS.1561209 (RMNH), Figure F is MNHN-EY-EY36003 (MNHN), Figure H is RMNH. INS.1561210 (RMNH). **A** mesoscutum **B** pronotum, lateral view **C** mesopleuron, lateral view **D** metapleuron and T1, lateral view **E** propodeum, dorsal view **F** wings **G** tergite 1, dorsal view **H** metasoma, T2–T8, dorsolateral view. Arrows in H point to grooves on T2 and T3.

following areas: face variable from fully dark brown to black (Fig. 24C) to primarily dark brown to black with yellow to white markings (Fig. 24D), malar space yellow to white, clypeus white to yellow to dark brown to black. Vertex dark brown to black, usually with yellow to white mark in varying shapes and sizes (Fig. 24E). Mandible dark brown to black, apically red-brown on ventral and/or dorsal tooth, with or without basoventral yellow to brown-red spot. Maxillary and labial palps yellow to brown yellow (Fig. 24A).

Antenna medium brown, pedicel and basal 10–14 flagellomeres white to yellow ventrally (Fig. 24A). Mesosoma dark brown to black except for the following: tegula white to pale yellow (Fig. 25C), mesopleuron sometimes with white to yellow subtegular ridge (Fig. 25C). Wings hyaline, veins light brown (Fig. 25F). Fore leg coxa yellow-white (Fig. 25C) to medium brown (Fig. 24A), remaining leg yellow (Fig. 24A). Middle coxa primarily yellow-white and medium brown basally to completely dark brown, remaining leg yellow (Fig. 25A). Hind leg coxa primarily medium to dark brown, femur yellow to medium brown, tibia white to yellow with medium brown longitudinal stripe dorsally, tarsi yellow with medium brown longitudinal stripe dorsally (Fig. 25A). Metasomal tergites uniformly medium brown to black (Fig. 25H).

Material examined. ENGLAND • 1 ♂; South East England, Theydon Bois; 30.viii.1954; J.A & D.J. Clark; B.M. 1954-539; NHMUK015215322; [NHMUK] • 1 ♂; Norfolk, Santon Downham; 2–11.vi.1983; J.P. Field; Malaise trap; heath with birch and pine; RMSNH 1986.021; CNC310414; [NMS]. FRANCE • 1 ♂; Bouches-du-Rhone/Provence, Fos-sur-Mer; 13.ix.1962; Aubert; [MZLS] • 1 ♂; Corse Piriò, Vallée du Fango; 25.v–3.vi.1997; Claire Villemant; Malaise trap; holm oak grove; MNHN-EY-EY36003; [MNHN] • 2 ♂♂; Lot-et-Garonne, Bernac; 27–31.v.1991; R.R. Askew; Malaise trap; CNC1754569, CNC1754570 [NMS] • 3 ♂♂; same data for preceding; 26–30.v.1986; *Quercus/Juniperus/Cornus*; CNC1754546, CNC1754547, CNC1754548 [NMS]. GERMANY • 1 ♂; Rhineland-Palatinate, Kreis Ahrweiler, Landskrone; 50.552°N, 7.17°E; 194 m; 16.v.2014; B. Rulik; Malaise trap; BOLD: [GMGMI875-14](#); BIOUG17116-B03; [ZFMK]. ITALY • 4 ♂♂; Trento, Riva del Garda; 250 m; 25.v.1990; C.J. Zwakhals; RMNH. INS.1561208, RMNH. INS.1561209, RMNH. INS.1561212, RMNH. INS.1561213; [RMNH] • 2 ♂♂; same data for preceding; 28.v.1990; RMNH. INS.1561210, RMNH. INS.1561211; [RMNH]. NORWAY • 1 ♂; Telemark, Drangedal, Gjeskefjell Mountain; 59.00275°N, 8.91627°E; 26.v–11.vi.2020; Arnstein Staverløkk; window trap; [NINA] (photo only) • 1 ♂; Hordaland, Sveio, Moelstre; 59.5161°N, 5.27878°E; 15–30.vi.2019; Håkon Haraldseide; Malaise trap; BOLD: [COLHH2702-19](#); [private collection of H. Haraldseide] (photo only).

Comments. The male *Piogaster* from Italy represent the first record of the genus for Italy. Fourteen male specimens were collected at the same locality between May 25 and 31, 1990, and therefore likely represent the same species. However, the six specimens of these fourteen examined as part of this study vary in the colour of the clypeus, malar space, and face (compare Fig. 24C with uniform colour to Fig. 24D with the maximal yellow markings found in these specimens), colour of the fore and middle coxae (primarily yellow-white versus entirely medium brown), strength of metasomal grooves (weak versus strong on T2 and T3), and presence or absence of a short epomia. If these specimens are conspecific, this indicates that the variable characters listed above are not reliable for diagnosing species based on males. We attempted to sequence the COI barcoding region of three of these specimens but were unsuccessful.

Two historical male-female associations have been suggested based on collection data but lack morphological support. First, Perkins (1958) described a male as possibly being *P. punctulata* based on superficial resemblance to the female. Male *Piogaster* specimens are commonly identified as *P. punctulata* as they are most similar morphologically to the female holotype of *P. punctulata* (Figs 16, 17), particularly the polished, sparsely punctate mesopleuron. We were unable to locate this male to examine it as part of this study. Second, Aubert (1963) described a male *Piogaster* from southern France (Fos-sur-Mer) as *P. albina* based on its collection alongside multiple females of that species (Aubert 1965). Our examination found no morphological evidence supporting (or refuting) this identification and *P. pilosator* has also been collected in close proximity (Fig. 30), including a syntype collected at Èze (Aubert 1958) and three specimens collected in St. Tropez (Suppl. material 1: Specimen data). This specimen is old and would be unlikely to result in an extraction with a high enough concentration to successfully amplify the COI barcoding gene using a standard PCR protocol, so we did not attempt this.

In addition to these historical published associations, we examined two male specimens collected in Lot-et-Garonne, France (May 27–31, 1991) that were likely associated with a female *P. pilosator* collected at the same site a month later. While these males are likely *P. pilosator*, we could not find anything morphological in our examination of these males that connects them to the *P. pilosator* female.

Study limitations and future directions

Revising *Piogaster* was hampered by the rarity of this genus as well as lack of access to some critical specimens. Though *Piogaster* is Holarctic, we found 128 specimens held in institutions (Suppl. material 1: Specimen data). Of these, we were able to examine 58 specimens physically and another 15 specimens through photographs. Some publications including *Piogaster* did not include deposition information (Kazmierczak 1988; Kolarov 1989; Kazmierczak 1990; Kazmierczak 2004; Quicke et al. 2009; Matsumoto 2016), and attempts to locate these specimens were unsuccessful. Molecular approaches were also restricted as four of the eight *Piogaster* species are singletons, and many specimens were collected decades ago and did not amplify successfully. A morphometrics analysis and/or examination of male genitalia may reveal differences that went unnoticed and help differentiate male specimens which may eventually help them be associated with females. Collection of more specimens, including targeting rearing of salticids, particularly in type localities of species known only from the holotypes, would allow a more extensive molecular and morphological analysis to be conducted. UCE sequencing often has a higher success rate than Sanger sequencing for older specimens with degraded DNA (Prosser et al. 2016) which is important given that many known *Piogaster* were collected prior to 1980. This technique could increase the pool of usable material. Additional genes and broader UCE sampling across multiple specimens per species would help refine relationships further, resolve gene-tree discordance, and better associate male and female specimens.

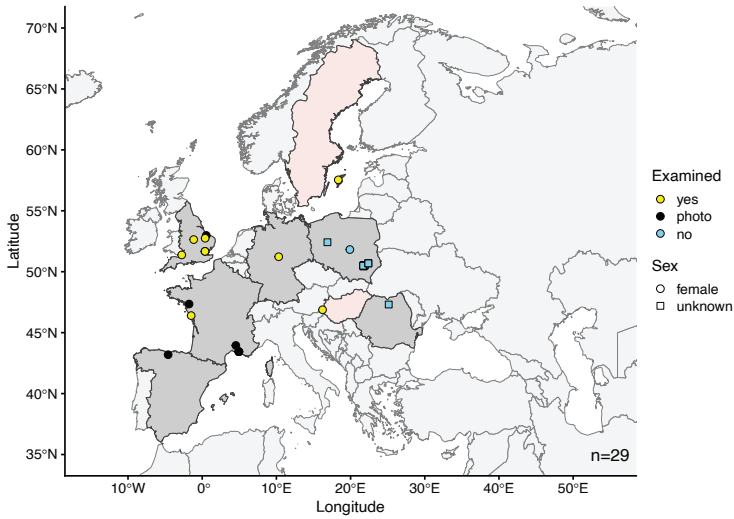


Figure 26. Localities of all known *P. albina* specimens. Dark grey shading indicates countries with collection records, and pink shading indicates new records of *P. albina*. As shown in the legend, colour indicates whether the species was examined as part of this study and shape indicates sex. In some cases, the sex of the specimens is unknown as this information was not included in the publication and the specimens were not seen to confirm sex. The total number of specimens included in this map is indicated in the bottom right corner. Two specimens identified in publications as male *P. albina* (Kązmierczak 1990; Aubert 1963) are included in Fig. 32 (unidentified European males) as identification of *Piogaster* males is difficult and the identification of these specimens is uncertain.

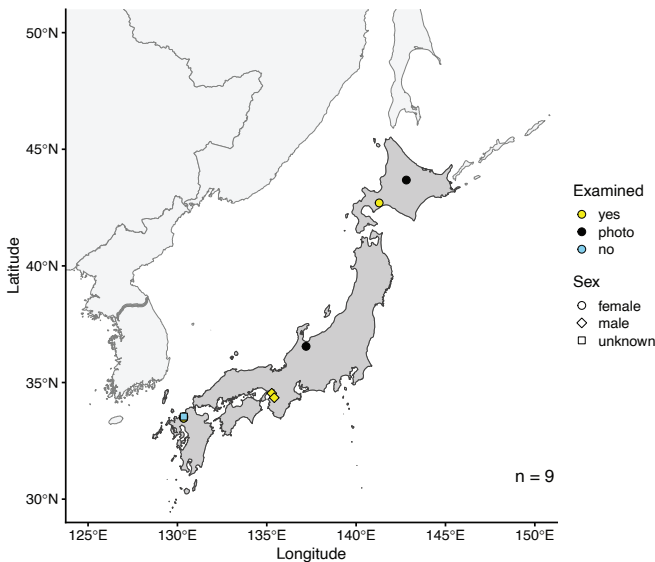


Figure 27. Localities of all known *P. daisetsuzana* specimens. Dark grey shading indicates countries with collection records of *P. daisetsuzana*. As shown in the legend, colour indicates whether the species was examined as part of this study and shape indicates sex. The total number of specimens appears in the bottom right corner.

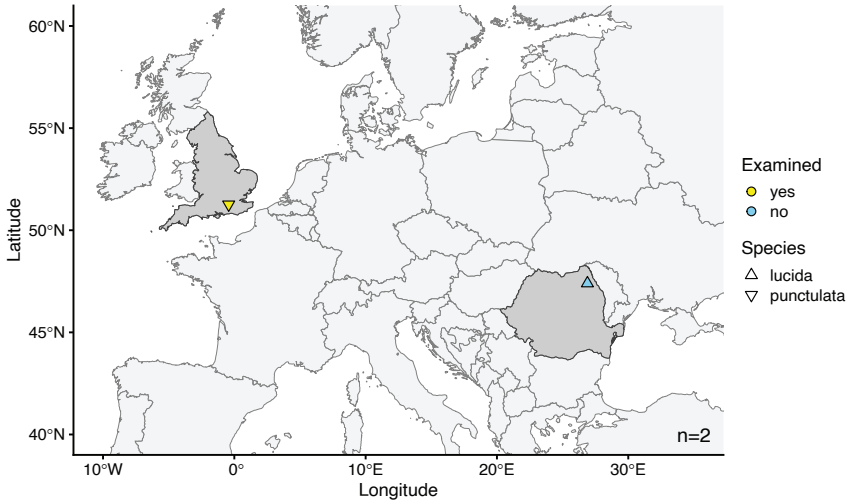


Figure 28. Localities of the singleton species *P. lucida* and *P. punctulata*. Both species are known only from the holotype specimen. Dark grey shading indicates countries with collection records. As shown in the legend, colour indicates whether the species was examined as part of this study and shape indicates species. The total number of specimens included in this map is indicated in the bottom right corner.

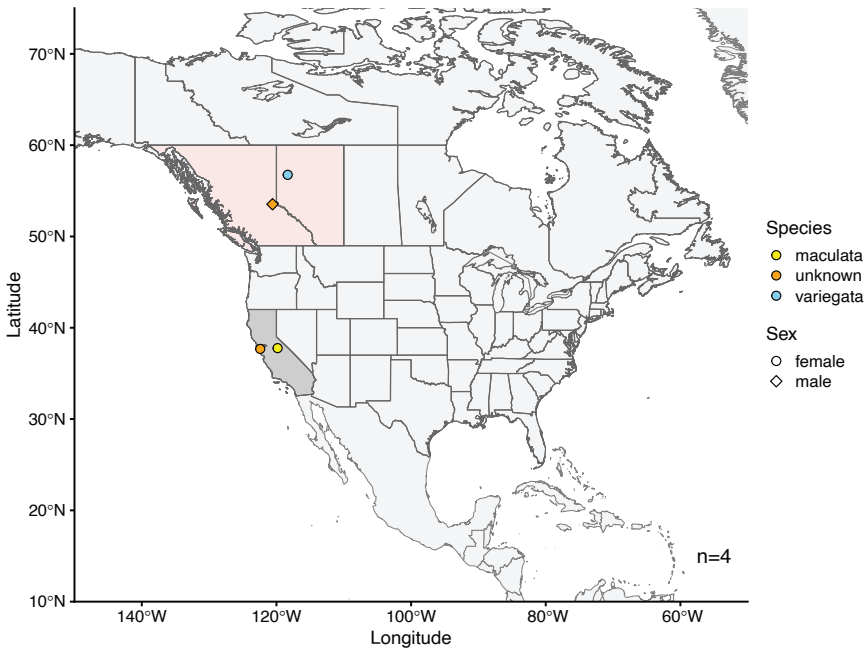


Figure 29. Localities of all known record of *Piogaster* specimens in North America. Dark grey shading indicates states and provinces with collection records of *Piogaster*. New generic provincial records are shaded in pink. As shown in the legend, colour indicates species and shape indicates sex. The unidentified female specimen from California was an iNaturalist record (Evers 2019b). The remaining three specimens are deposited in collections.

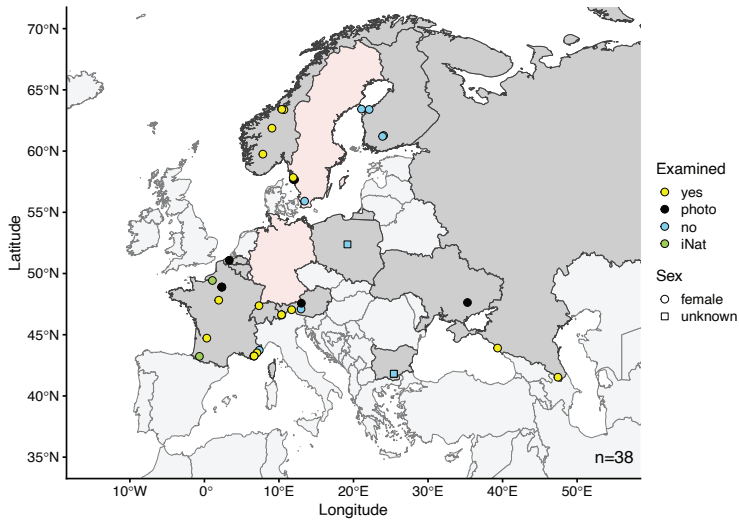


Figure 30. Localities of all known *P. pilosator* specimens. Dark grey shading indicates countries with collection records, and pink shading indicates new records of *P. pilosator*. As shown in the legend, shape indicates sex and colour indicates whether the species was physically examined as part of this study (yes: yellow, no: blue), is an iNaturalist record (iNat, green), or is from photographs of specimens. In some cases, the sex of the specimens is unknown as this information was not included in the publication and the specimens were not examined to determine sex. The total number of specimens included in this map is indicated in the bottom right corner. There is one additional *P. pilosator* specimen deposited at NHMUK but lacking locality information, so it does not appear on this map.

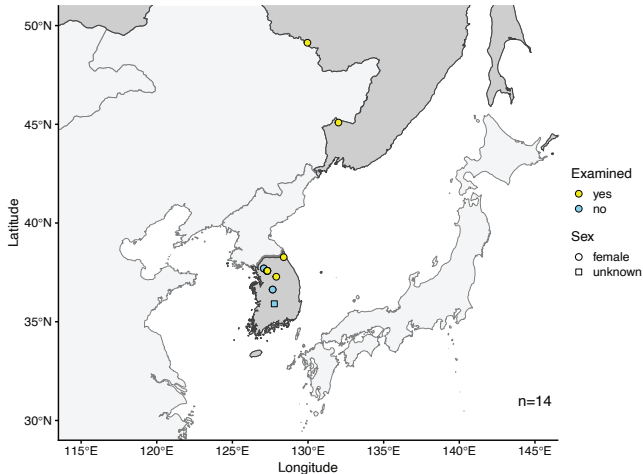


Figure 31. Localities of all known *P. ussuriensis* specimens. Dark grey shading indicates countries with collection records of *P. ussuriensis*. As shown in the legend, colour indicates whether the species was examined as part of this study and shape indicates sex. In one case, the sex of the specimen is unknown as this information was not included in the publication and the specimen was not seen to confirm sex. A *Piogaster* specimen from Quicke et al. 2009 but not identified to species is included in the map as it is most likely *P. ussuriensis*. The total number of specimens is indicated in the bottom right corner.

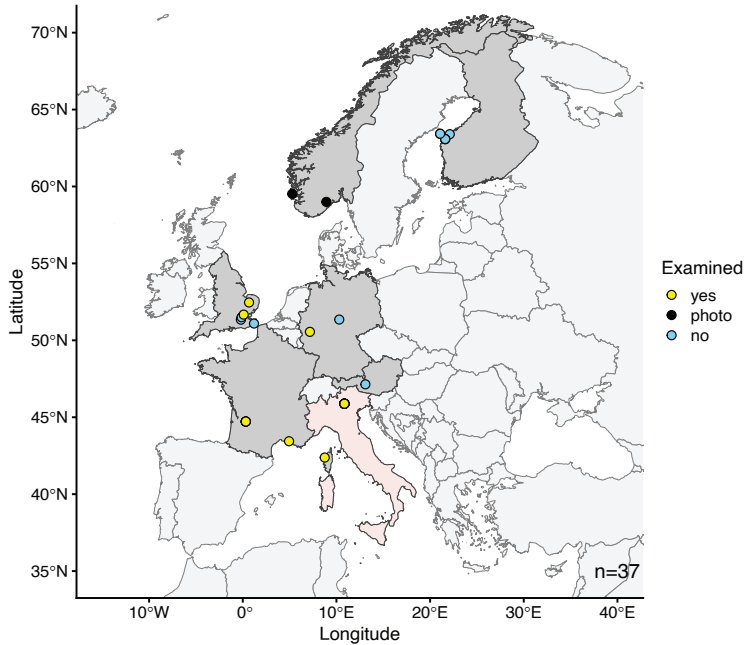


Figure 32. Localities of all known unidentified male *Piogaster* specimens in Europe. Dark grey shading indicates countries with collection records. Pink shading indicates new generic records. As shown in the legend, colour indicates whether the species was examined as part of this study (yes: yellow, no: blue) or if they were examined only from one or more photographs (photo: black). The total number of specimens included in this map is indicated in the bottom right corner.

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Supplementary material 1

Piogaster specimen data

Authors: Amber Bass, Andrew M. R. Bennett, Tamara Spasojevic, Marla Schwarzfeld

Data type: csv

Explanation note: All known records of *Piogaster* from literature, collections, and online sources including detailed collection data.

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Link: <https://doi.org/10.3897/jhr.99.184465.suppl1>

Supplementary material 2

Piogaster genetic data

Authors: Amber Bass, Andrew M. R. Bennett, Tamara Spasojevic, Marla Schwarzfeld

Data type: xlsx

Explanation note: Specimen metadata and sequence accession information for all taxa included in the molecular analyses. The table lists species name, country of origin, sex, repository, voucher identifier, and availability of sequence data for UCE, COI, 28S, 18S, Nasvi2EG013087, ITS2, and EF1 α .

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Link: <https://doi.org/10.3897/jhr.99.184465.suppl2>

Supplementary material 3

Piogaster single locus alignments

Authors: Amber Bass, Andrew M. R. Bennett, Tamara Spasojevic, Marla Schwarzfeld

Data type: nexus

Explanation note: Nexus alignments of COI, 18S, 28S, ITS2, EF1a, and Nasvi2EG013087 used for phylogenetic analyses and calculating genetic distances, and alignment of COI for determining diagnostic molecular characters.

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Link: <https://doi.org/10.3897/jhr.99.184465.suppl3>

Supplementary material 4

Piogaster UCE alignment

Authors: Amber Bass, Andrew M. R. Bennett, Tamara Spasojevic, Marla Schwarzfeld

Data type: phy

Explanation note: Alignment of 346 UCE loci for 14 taxa in PHYLIP format followed by the partitioning scheme in nexus format.

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Link: <https://doi.org/10.3897/jhr.99.184465.suppl4>

Supplementary material 5

***Piogaster* genetic distance matrices**

Authors: Amber Bass, Andrew M. R. Bennett, Tamara Spasojevic, Marla Schwarzfeld

Data type: xlsx

Explanation note: Genetic distance matrices for COI, 28S, 18S, Nasvi2EG013087, ITS2, and EF1 α .

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