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North-Western Palaearctic species of the *Pristiphora ruficornis* group (Hymenoptera, Tenthredinidae)

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Abstract

The *Pristiphora ruficornis* group, defined here based on the structure of the penis valve and the genetic data, includes morphologically and genetically highly similar species that remain taxonomically challenging. Study of most of the relevant type material, examination of female saws and male genitalia, some rearing experiments, and genetic data enabled us to solve most of the taxonomic problems involving northern European taxa. As a result, 17 species are recognised in northern Europe. The following synonymies are proposed: *Pristiphora aterrima* Lindqvist, 1977, **syn. n.** is synonymised with *P. albitibia* (Costa, 1859), *P. brunniapex* Lindqvist, 1960, **syn. n.** and *P. coniceps* Lindqvist, 1955, **syn. n.** both with *P. subopaca* Lindqvist, 1955, *Nematus vitreipennis* Eversmann in Kawall, 1864, **syn. n.** (**nomen oblitum**) with *P. leucopus* (Hellén, 1948) (**nomen protectum**), and *Nematus* (*Pristiphora*) *ruficornis* var. *integer* Hellén, 1948, **syn. n.** with *P. ruficornis* (Olivier, 1811). Lectotypes are designated for the following taxa: *Nematus appendiculatus* Hartig, 1837, *Nematus cathoraticus* Förster, 1854, *Nematus* (*Pristiphora*) *bifidus* Hellén, 1948, *Nematus frigidus* Boheman, 1865, *Pristiphora adelungi* Konow, 1902, *Nematus vitreipennis* Eversmann in Kawall, 1864, *Nematus melanocarpus* Hartig, 1840, *Nematus wuestneii* Stein, 1885, *Pristiphora pusilla* Malaise, 1921, and *Nematus fraxini* Hartig, 1837. An illustrated electronic key made with Lucid and a traditional dichotomous key are provided to facilitate identification of the species. In addition we report the first occurrence of distinctly asymmetrical penis valves in *Pristiphora* (in *P. pusilla*), a condition rarely observed in Hymenoptera.

Keywords

Sawflies, lectotypes, new synonyms, nomenclature, taxonomy, identification key, phylogeny, asymmetrical genitalia, triose-phosphate isomerase, cytochrome oxidase subunit I, DNA barcoding

Introduction

Pristiphora Latreille, 1810 contains several species groups, within which identification of species is difficult because of high similarity in external morphology, the need to study female saws and male genitalia, and the lack of reliable keys and recent revisions (Lindqvist 1952; 1953; 1955; Benson 1958; Lindqvist 1962; Zhelochovtsev [and Zinovjev] 1988). One of the species groups is the *ruficornis* or *melanocarpa* group (Lindqvist 1955), within which species are externally very similar, although males generally show good differences in genitalia (penis valves). Based on genetic data and penis valves, we delimit this group more precisely and call it the *ruficornis* group (based on the oldest species name within the group: *ruficornis* Olivier in Olivier & Manuel, 1811). Studies by Vikberg (1978; 2006) solved some of the problems within the group, but many gaps and deficits remain, such as the validity of many nominal species, association of males and females, and the lack of reliable keys to identify species. Here, we revise the group in northern Europe, recognising 17 species as valid. An illustrated electronic key (Lucid) and a traditional dichotomous key are provided together with high resolution photos of female lancets and male penis valves to enable identification of species more reliably than previously.

The host plant associations, details of larval morphology, and bionomy of only a few species of the *ruficornis* group have been recorded in detail. Because its larvae sometimes defoliate cultivated *Ribes*, particularly *R. uva-crispa* (gooseberry), biological observations on *P. appendiculata* are included in numerous publications, including many general and popular works on plant "pests" (e.g. Meitzner 1985; Alford 2014). As a result of its status as a "pest", this is the only species in the *ruficornis* group that has vernacular names in several languages, such as "small gooseberry sawfly" in English, and "Schwarzen Stachelbeerblattwespe" in German. This species is normally thelytokous, with very rare males (Comrie 1938). Males of several other species of the *ruficornis* group are unknown or very rare (*P. aphantoneura*, *P. astragali*, populations of *P. luteipes* in northern and middle Europe, and *P. sootryeni*: Vikberg 1978; 2006), or occur at a low ratio (e.g. *P. leucopus*: Grearson and Liston 2012), whereas the sex ratio of others appears to be about normal. Voltinism differs between species, and probably also according to climate. The group shows a broad spectrum of phenological patterns: particularly the boreo-alpine species, e.g. *P. staudingeri*, are probably univoltine, based on collection dates of adults, while others are apparently bivoltine (e.g. *P. bifida*: Liston and Burger 2009), or plurivoltine, with four generations per year, or even more in optimal conditions (e.g. *P. appendiculata*, *P. leucopus*: Miles 1932, Grearson and Liston 2012). So far unique in the species group, and a rare phenomenon in the Tenthredinidae, is the seasonal dimorphism detected in adult *P. leucopus* (Grearson and Liston 2012). In all species, as far as observations have been made: oviposition is in the leaf-blade margin (Vikberg 2006, Grearson and Liston 2012), in *P. appendiculata* also infrequently in the interior, near a vein (Miles 1932); only one egg is laid per leaf, and the larvae are normally solitary, feeding from the leaf-edge (Grearson and Liston 2012, Meitzner 1985, personal observations on *P. bifida*). Exceptionally, more eggs are laid per leaf at high population levels in *P. appendiculata*, but density of larvae is probably regulated by egg cannabilism: Rahoo and Luff 1988). There are four or five larval instars and no prepupal ecdysis ("extra moult") (Miles 1932, Vikberg 2006). Cocoons of the overwintering generation are made in the soil, but those of some the summer generations may be made above ground, often between leaves or on the underside of leaves (Miles 1932, Grearson and Liston 2012).

Larvae are cryptically coloured, with a largely green body (http://dx.doi.org/10.6084/m9.figshare.3486341.v1). Only the head and coxae of the thoracic legs are more or less dark-marked. The dark pattern on the head of the final instar larva, composed of spots of brown pigment that to the naked eye appear confluent and blackish, is similar in all species of the *ruficornis* group: a stripe along the coronal suture, branching ventrally to run along upper edges of frons; upper frons more or less dark marked; an approximately vertical stripe on each orbit that does not connect with the coronal stripe. The anal tergum of the abdomen is entirely green in some species of the group of which the larva is known, but yellow in *P. appendiculata*, and extensively red in *P. aphantoneura*, *P. luteipes*, *P. sootryeni* (Vikberg 2006), *P. staudingeri* (Vikberg 1978) and possibly *P. armata* (Lorenz and Kraus 1957: who wrote under the name *P. ruficornis* that larvae, which they collected from *Crataegus* and were presumably therefore *P. armata*, had an extensive red patch on the dorsum of the last abdominal segment). Differences in setation can apparently be used to distinguish the larvae of some species, according to the descriptions in Lorenz and Kraus (1957) and Vikberg (2006), but detailed descriptions of many species are lacking. It is not clear to which species the description of *P. melanocarpa* by Lorenz and Kraus (1957) belongs: according to the list of host plants (Pflanzenliste) they examined larvae collected from both *Betula* and *Salix cinerea*. Because detailed studies on immature stages of most species are still lacking, we only summarize and complement data on host plants of the *ruficornis* group species.

Material and methods

Specimens examined or mentioned are deposited in the following collections:

ANSP	Academy of Natural Sciences of Drexel University, Philadelphia, USA;
BMNH	The Natural History Museum, London, United Kingdom;
CEH	Collection of Erik Heibo, Lierskogen, Norway;
COL	Collection of Ole Lønnve, Oslo, Norway;
CVV	Collection of Veli Vikberg, Turenki, Finland;
HNHM	Hungarian Natural History Museum, Budapest, Hungary;
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium;
MCZ	Museum of Comparative Zoology, Cambridge, USA;
MHNG	Muséum d'Histoire Naturelle, Geneva, Switzerland;
MNHN	Muséum National d'Histoire Naturelle, Paris, France;

MZH	Finnish Museum of Natural History, Helsinki, Finland;
MZLU	Lunds universitet, Lund, Sweden;
MZUN	Museo Zoologico di Università degli Studi, Napoli, Italy;
NHRS	Naturhistoriska riksmuseet, Stockholm, Sweden;
NMW	Naturhistorisches Museum Wien, Wien, Austria;
SDEI	Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany;
SMTP	Swedish Malaise Trap Project, Station Linné, Öland, Sweden;
TROM	Tromsø University Museum, Tromsø, Norway;
TUZ	Natural History Museum, University of Tartu, Tartu, Estonia;
USNM	National Museum of Natural History, Washington D.C., USA;
ZIN	Russian Academy of Sciences, Zoological Institute, St. Petersburg, Russia;
ZSM	Zoologische Staatssammlung, München, Germany.

Names of the mentioned host plants follow The Plant List (http://www.theplantlist.org/).

Collecting data of the examined specimens is included in an excel file available at Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.tj4t0

Morphological methods

To photograph penis valves and lancets (valvula 1 or ventral part of saw), genital capsules and ovipositors were separated from the specimen and macerated in KOH (10–15%) for 6–10 hours at room temperature or treated with proteinase during DNA extraction (see below). Temporary or permanent slide preparations were made of dissected lancets and penis valves. For temporary slides, glycerine was used. After photographing, the lancets and penis valves were glued on a piece of cardboard, which was pinned with the corresponding specimen. For permanent slides, Euparal or PVA-mounting medium (mostly) was used (these specimens are labelled as ‘PR.*XXX*VV’, e.g. PR.440VV). PVA-mounting medium (Danielsson 1985) is water-soluble, is simpler to use than Euparal (no alcohol needed), and mounts remain in good quality for 30 or more years.

Photos were taken with a digital camera attached to a microscope. Composite images with an extended depth of field were created from stacks of images using the software CombineZP (Alan Hadley; http://www.hadleyweb.pwp.blueyonder.co.uk/). Most of the lancets were photographed in two overlapping parts and a single image was created using the program Image Composite Editor (Microsoft).

Morphological terminology follows Vikberg (1978; 2006) and Viitasaari (2002).

Molecular methods

DNA was extracted and purified with an EZNA Tissue DNA Kit (Omega Bio-tek) according to the manufacturer’s protocol and stored at -20 °C for later use. Typically, the middle right leg was used for DNA extraction, but for males the whole genital capsule was often additionally used to increase DNA yield and to free penis valves from muscles for photographing. One mitochondrial and one nuclear region were used in phylogenetic analyses. Primers used for amplification and sequencing are listed in Table 1. The mitochondrial region used is a large fragment (1078 bp) of cytochrome oxidase subunit I gene (COI). The first (from the 5' end) 658 bp of this fragment correspond to the standard barcode region of the animal kingdom (Hebert et al. 2003). If the amplification of the 1078 bp fragment failed, or was expected to fail because of low DNA quality, the region was amplified in two overlapping fragments, or only the barcoding (658 bp) region was obtained (Table 1). The nuclear marker used is nearly the complete gene of triose-phosphate isomerase (TPI), containing 661 bp or 676 bp (depending on the primers used for amplification) of three exons and two short introns (around 50–100 bp) in Nematinae (Table 1), altogether around 800–830 bp. New COI primers were designed based on a broad sample of sawfly COI sequences available in NCBI GenBank (http://www.ncbi.nlm.nih.gov/genbank/) or BOLD (http://www.boldsystems.org/), plus a few unpublished full COI sequences. New TPI primers were designed mainly based on four sawfly genomes and one transcriptome available in GenBank (accessions AOFN01004053, GAWW01005368, LGIB01000103, AMWH01006520, AZGP01000520) or using sequences published by Malm and Nyman (2015). Numbers in the new TPI primer names refer to the binding position of the primer's 3' end in the coding region of *Athalia rosae* mRNA (accession XM_012402337).

PCR reactions were carried out in a total volume of 15–20 µl containing 1–2 µl of extracted DNA, 0.6–0.8 µl (3–4 pmol) of primers and 7.5–10 µl of 2x Multiplex PCR Plus Master mix (QIAGEN). The PCR protocol consisted of an initial DNA polymerase (HotStar Taq) activation step at 95 °C for 5 min, followed by 38–40 cycles of 30 s at 95 °C, 90 s at 47–56 °C depending on the primer set used, and 30–70 s (depending on the amplicon size) at 72 °C; the last cycle was followed by a final 30 min extension step at 68 °C. 3 µl of PCR product was visualised on a 1.4% agarose gel and then purified with FastAP and Exonuclease I (Thermo Scientific). 1.0–1.5 U of both enzymes were added to 12–17 µl of PCR solution and incubated for 15 min at 37 °C, followed by 15 min at 85 °C. Purified PCR products were sent to Macrogen (Netherlands) for sequencing. To obtain unequivocal sequences, both sense and antisense strands were sequenced, using the primers listed in Table 1. Ambiguous positions (i.e. double peaks in chromatograms of both strands) due to heterozygosity or intragenomic variation were coded using IUPAC symbols.

Sequences reported here have been deposited in the GenBank (NCBI) database (accession numbers KX602529–KX602627).

COI sequences were aligned manually, among which only some specimens of *Pristiphora appendiculata* showed differences in length caused by deletion of six base pairs (two amino acids). The exact position of this deletion was located by translating nucleotides into amino acids (using the invertebrate mitochondrial genetic code). The TPI sequences including introns of *ruficornis* group specimens were aligned using

Table 1. Primers used for PCR and sequencing, with information provided on respective gene fragment, primer name, direction (forward, F or reverse, R) and location (internal, i or external, o) according to each gene fragment, primer sequence, standard annealing temperature, utilization (PCR/ sequencing), and reference.

Gene Region	Primer name	F/R i/o	Primer sequence 5'–3'	Annealing temperature (°)	PCR/ Sequencing	Reference
COI	SymF1	F o	TTTCAACWAATCATAAARAYATTGG	47	PCR, seq	This study
COI	SymF2	F o	TTTCAACAAATCATAAARAYATTGG	47	PCR, seq	This study
COI	sym- C1-J1718	F i/o	GGAGGATTTGGAAAYTGAYTAGTWCC	49	PCR, seq	(Nyman et al. 2006)
COI	symC1-J1751	F i/o	GGAGCNCCTGATATAGCWTTYCC	47	PCR, seq	This study
COI	C1-N1760	R i/o	GGTARAAATCARAATCTTATATTAT	47	PCR, seq	(Prous et al. 2011)
COI	SymR1	R i/o	TAAACTTCWGGRTGICCAAARAATC	47	PCR, seq	This study
COI	SymR2	R i/o	TAAACTTCTGGRTGTCCAAARAATCA	47	PCR, seq	This study
COI	A2590	R o	GCTCCTATTGATARWACATARTGRAAATG	49	PCR, seq	(Normark et al. 1999)
TPI	TPI_29Fi	F o	GYAAATTYTTYGTTGGNGGIAA	52	PCR, seq	This study
TPI	TPI 111Fb	F o	GGNAAYTGGAARATGAAYGG	56	PCR, seq	(Bertone et al. 2008)
TPI	TPI hym intF	F i	AARGGHGCNTTYACYGGNGA	56	Seq	(Malm and Nyman 2015)
TPI	TPI hym intR	R i	TCNGARTGDCCHADRATNACCCA	52	Seq	(Malm and Nyman 2015)
TPI	TPI385Fi	F o	GTRATYGCNTGYATYGGIGARA	52	PCR, seq	This study
TPI	TPI 275Ri	R o	GCCCANACNGGYTCRTAIGC	56	PCR, seq	(Malm and Nyman 2015)
TPI	TPI706R	R o	ACNATYTGTACRAARTCWGGYTT	52	PCR, seq	This study

MAFFT 7 (Katoh and Standley 2013) online version (http://mafft.cbrc.jp/alignment/server/) with the thorough iterative alignment strategy G-INS-i. Because of problems identifying homologous positions within introns between *ruficornis*-group and outgroup species, introns were excluded for all outgroup species and exons were aligned manually, which was straightforward because there were no insertions or deletions.

Sequence data were analysed using the maximum likelihood method (ML) with PhyML 3.0.1 (http://www.atgc-montpellier.fr/phyml/; Guindon and Gascuel 2003). In PhyML nearest neighbor interchanges (NNI) and subtree pruning and regrafting (SPR) were always used to estimate tree topologies (i.e. using the extensive tree search option). Robustness of reconstructed trees was estimated with 1000 bootstrap replicates and approximate likelihood-ratio test (aLRT) implemented in PhyML (Anisimova and Gascuel 2006). Prior to analyses using maximum likelihood, duplicate sequences were removed to save computation time. General Time Reversible model of nucleotide substitution under discrete Gamma model of rate heterogeneity among sites with four rate categories (GTR+G4) was used to calculate maximum likelihood trees. Estimation of proportion of invariable sites as commonly used in phylogenetic likelihood analyses was not applied, because the Gamma model already allows for sites that evolve very slowly (i.e. are effectively invariable). As described in the RAxML manual, combining Gamma model and proportion of invariable sites (G+I) is problematic for parameter estimation as they are interdependent (http://sco.h-its.org/exelixis/resource/download/NewManual.pdf). Alignment files and tree files from the PhyML analyses are available at Dryad Digital Repository (http://dx.doi.org/10.5061/dryad.tj4t0).

Some of the COI barcode sequences used here were obtained from BOLD (http://www.boldsystems.org/). In this case, DNA extraction, PCR amplification, and sequencing were conducted at the Canadian Centre for DNA Barcoding (CCDB) in Guelph, Canada using standardised high-throughput protocols (Ivanova et al. 2006; deWaard et al. 2008), available online under www.ccdb.ca/resources.php. DNA aliquots of SDEI vouchers are deposited in the DNA storage facility of the SDEI (including those that were originally extracted in CCDB).

Barcode distance calculations were based on p-distances (proportion of nucleotide differences) and were taken from the BOLD BIN (Barcode Index Number) database (http://www.boldsystems.org/).

Preparation of the keys

The electronic identification key for the species of *ruficornis*-group was prepared in Lucid 3.5 Builder (http://www.lucidcentral.org/) and a zip file containing all the Lucid data files is available at Dryad Digital Repository (http://dx.doi.org/10.5061/dryad.tj4t0). If the licence for Lucid 3.5 is lacking, the free version of Lucid 3.3 can be used to run the key. Only species of the *ruficornis* group are included in the key, but there are additional characters that do not vary within the group, but which can be used to exclude other *Pristiphora* species. In case of ambiguities or polymorphisms in character states, we conservatively coded these to multiple states. The key contains 37 morphological features with 94 character states and 43 entities (species and groups, 20 for males and 23 for females). The first choice given in the key is between female and male, one of which has to be chosen to see all other characters. After that, characters can be chosen freely or one can use 'Best' and 'Next Best' tools in Lucid that suggests the most efficient sequence of characters for identification.

A traditional dichotomous key was constructed manually to emphasise the most reliable characters (usually penis valves or lancets).

Results

Definition of the *Pristiphora ruficornis* group and its separation from other *Pristiphora* species

Phylogenetic analyses of mitochondrial COI sequences (Fig. 1) identify a strongly supported clade within *Pristiphora*, that is morphologically best characterised by male penis valves, which have a large and bent (often strongly) ventro-apical spine (Figs 77–103). When ignoring the species that are missing from our nuclear TPI dataset, the same clade is recovered with strong support also based on this gene (Fig. 2). Here, we call this clade the *Pristiphora ruficornis* group (=*melanocarpa* group). Externally there are no characters to unambiguously unite all species within this group to the exclusion of all other *Pristiphora* species. Females have a typical *Pristiphora*-type sawsheath (Figs 3–4) with large scopa, and the body is completely black (Figs 9, 11) in nearly all species (except *P. beaumonti* and some specimens of *P. subopaca*; Figs 9, 12–13). Bodies of males are also nearly always completely black (except some specimens of *P. beaumonti*). The short post-ocellar area (Fig. 5) helps to distinguish the *ruficornis* group from some completely black species [e.g. *P. geniculata* (Hartig, 1840), *P. pseudogeniculata* Lindqvist, 1969, some specimens in *rufipes* group] with long post-ocellar area (Fig. 6), although this character might not be reliable for males. Very similar to the *ruficornis* group are species in the *rufipes* group (=*thalictri* group). Generally the species in the *rufipes* group have a rather smooth mesopostnotum compared to most species in *ruficornis* group, except *P. appendiculata*, which has a completely smooth mesopostnotum (Fig. 7). However, *P. appendiculata* has simple claws, while species of the *rufipes* group have a small subapical tooth. The only reliable way to separate the *rufipes* and *ruficornis* groups is by studying lancets and penis valves. Female lancets lack ctenidia entirely in the *rufipes* group (Fig. 40), while there are weakly or well-developed ctenidia present on at least some annulets of the lancet in most species of *ruficornis*-group (e.g. Fig. 39). Unfortunately, if the ctenidia are weakly developed, they might not be visible without making a slide preparation and studying the lancet under a microscope using phase contrast. The *Betula*-feeding *Pristiphora melanocarpa* and *P. ruficornis* practically lack ctenidia, but their lancets have a distinctly shaped tangium (Figs 46–53), usually visible without dissecting the saw (Fig. 14), which separates these two species from other *Pristiphora*. *Pristiphora appendiculata* also lacks or almost lacks ctenidia (Figs 37–38), but the shape of the serrulae distinguishes it from species in the *rufipes* group (Fig. 40). Identification based on male penis valves is easier, because many distinct characteristics enable their separation from each other (usually) and from other species of *Pristiphora* that are similar in colouration to the *ruficornis* group (Figs 77–104). A separate electronic key is provided to separate species of the *ruficornis* group from each other and from other *Pristiphora* species.

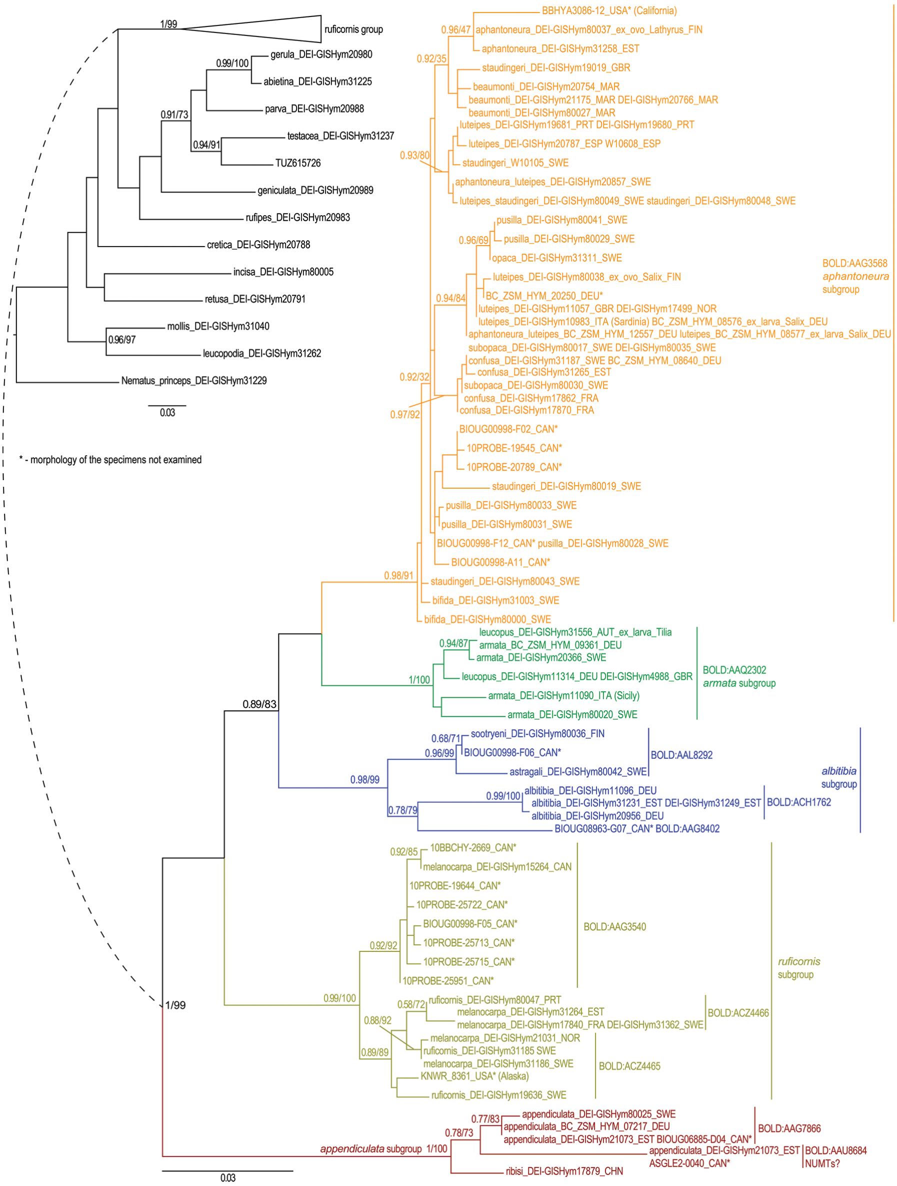


Figure 1. Maximum likelihood tree of *Pristiphora ruficornis* group based on cytochrome oxidase subunit I (COI) sequences (1078 bp). Specimens that had at least the full barcode sequence (658 bp) were included in the analysis. Branches with multiple specimen identification labels represent identical sequences, only one of which was used in the analysis. Numbers on the nodes show approximate likelihood-ratio test (aLRT) support values and bootstrap proportions (%, BP). Support values for weakly supported branches (aLRT<0.9 and/or BP<70) are not shown. The inset shows the tree with outgroup species. The scale bar shows the number of estimated substitutions per nucleotide position. An asterisk (*) indicates the specimens that we have not studied. AUT, Austria; CAN, Canada; CHN, China; DEU, Germany; ESP, Spain; EST, Estonia; FIN, Finland, FRA, France; GBR, United Kingdom; ITA, Italy; MAR, Morocco; NOR, Norway; PRT, Portugal; SWE, Sweden; USA, United States of America. NUMTs?, possible nuclear mitochondrial pseudogenes.

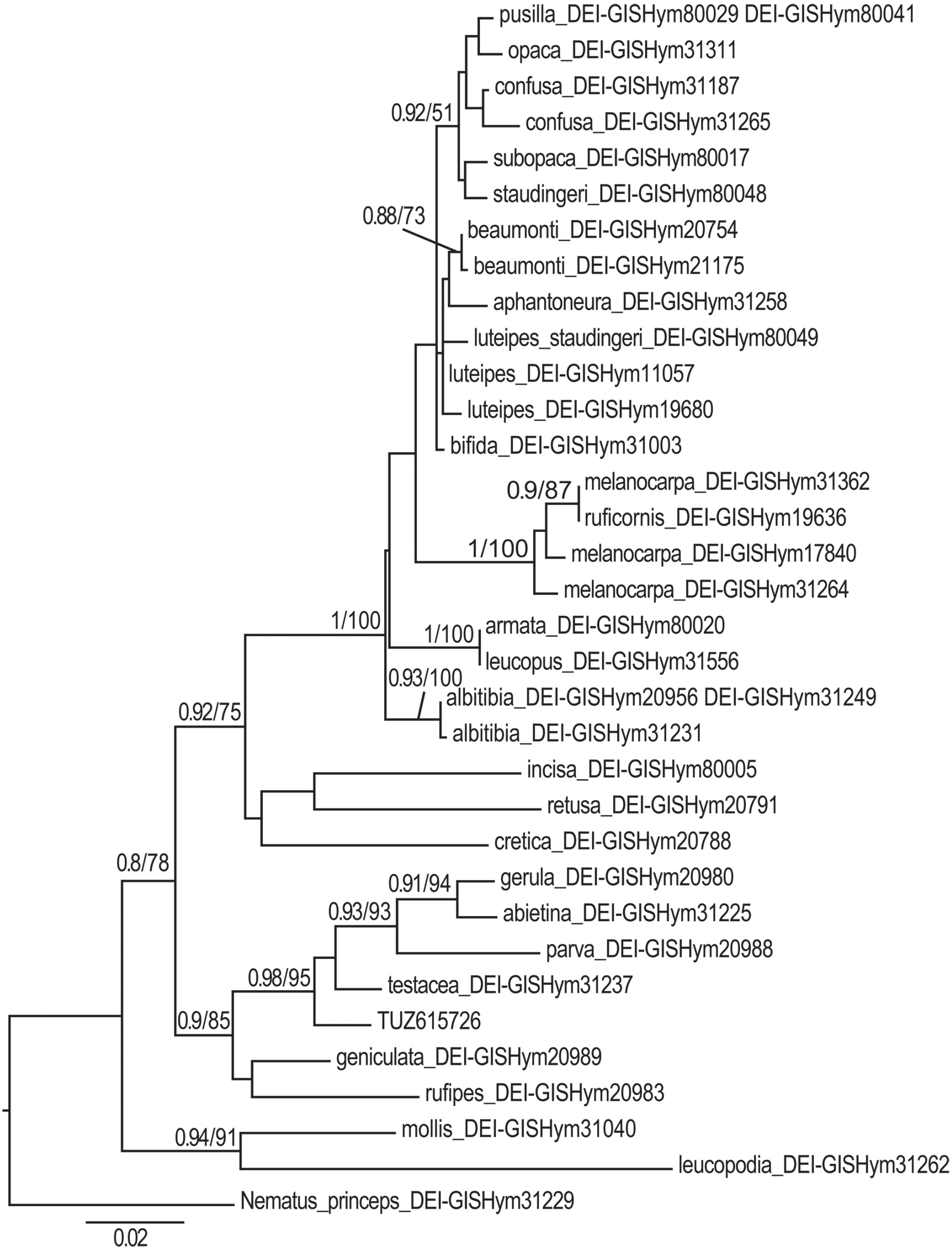


Figure 2. Maximum likelihood tree of *Pristiphora ruficornis* group based on triose-phosphate isomerase (TPI) sequences (alignment length 842 bp). Branches with multiple specimen identification labels represent identical sequences, only one of which was used in the analysis. Numbers on the nodes show approximate likelihood-ratio test (aLRT) support values and bootstrap proportions (%, BP). Support values for weakly supported branches (aLRT<0.9 and/or BP<70) are not shown. The scale bar shows the number of estimated substitutions per nucleotide position.

Phylogeny of the *Pristiphora ruficornis* group and characterisation of subgroups

Genetic data reveal five well separated subgroups within the *ruficornis* group, which correlate well with morphological and ecological data. According to phylogenetic analyses of COI sequences (Fig. 1), *Pristiphora appendiculata* together with *P. ribisi* (identified based on the description and the pictures of the saw given by Togashi 1990) form a sister group (*appendiculata* subgroup) to a clade containing all other species (we were unable to amplify TPI for any specimens of *P. appendiculata* and *P. ribisi*, possibly because of low DNA quality). This is supported by morphological data: species of the *appendiculata* subgroup are the only species in the *ruficornis* group having simple claws (Fig. 30) and a completely smooth mesopostnotum (Fig. 7). The host plants of *P. appendiculata* and *P. ribisi* (*Ribes* spp.) also differ from those of other species. The second group (*ruficornis* subgroup) includes two species (*P. ruficornis* and *P. melanocarpa*) feeding on *Betula*, females of which have a lobe at the base of tangium of the lancet that is often visible without dissection (Fig. 14) and males of which have a membranous fold near or covering the tip of the ventro-apical spine (Figs 79–82). The host plants and genetics are not known for *P. frigida*, but because of the similar membranous fold of penis valves (Fig. 88), this species might be related to *P. ruficornis* and *P. melanocarpa*. The third group (*albitibia* subgroup) includes three species feeding on Fabaceae (*P. astragali*, *P. albitibia*, and *P. sootryeni*), which have, uniquely within the *ruficornis*-group, on the inner surface of the lancet small spiny pectines (or dentes semicirculares) that reach the sclerora (Figs 41–45). The fourth group (*armata* subgroup) includes two species that feed on *Crataegus* (*P. armata*) and *Tilia* (*P. leucopus*), males of which have uniquely within *Pristiphora*, but similarly to *Euura* (as defined by Prous et al. 2014), a distinct apical projection at the posterior end of tergum 8 (Fig. 16). The last, fifth group (*aphantoneura* subgroup), includes mainly species feeding on *Salix*, but *P. aphantoneura* feeds on Fabaceae (*Lathyrus pratensis* L.) and host plants are not known for *P. opaca* and *P. pusilla*. There appear to be no morphological characters that uniquely define the *aphantoneura* subgroup.

Assessment of morphological characters of the adults

Because of the high similarity of the species in *ruficornis* group, the number of external characters that can be used for species identification is rather small. These include colour of trochanters, trochantelli, metafemur (Figs 21–23), flagellum (Figs 24–26, 35–36), and pterostigma (Figs 27–29); sculpture of mesopostnotum (Figs 7–8) and mesepisternum (Figs 18–29); size of the subapical tooth (Figs 30–34); and shape of tergum 8 in males (Figs 16, 18). Shape of frontal area as used by Lindqvist (1955) and followed by Benson (1958) was found not to be a reliable character for species identification. Most of these characters vary continuously within the group and sometimes there is a large degree of variation also within species. Nevertheless, these characters can be useful to recognise species, because usually there are different tendencies in different species. The shape of tergum 8 in males of *P. armata* and *P. leucopus* (with distinct apical projection; Fig. 16) is the clearest character to distinguish the males of these species from all other *Pristiphora* (Fig. 17). Sculpture of mesopostnotum and the presence or absence of a subapical tooth on the claws are also good characters to recognise *P. appendiculata* (smooth mesopostnotum and simple claws; Figs 7, 30) from other European species (matt mesopostnotum and claws with at least a small subapical tooth; Figs 8, 31–34) in the group. Size or the shape of the subapical tooth is also a relatively stable character. Two species (*P. bifida*, *P. frigida*) have a long subapical tooth close to the apical one (bifid; Fig. 34), while others have a large or small subapical tooth clearly separated from apical one (Figs 31–33), although this difference can be rather small when compared to large subapical tooth of *P. armata* and *P. leucopus*. Antennae vary from completely black to completely yellow, depending on the species, being either always black (Figs 24, 35), black or ventrally pale (Fig. 25, 36), or always at least ventrally pale (Figs 25–26, 36). Trochanters, trochantelli, and pterostigma show a similar pattern of variation. The metafemur is completely black in most species, but in a few species it is often or always partly or completely pale (Figs 21–23). If the metafemur is pale, it can be either whitish (as in *P. appendiculata* and *P. leucopus*; Fig. 22) or yellowish (*P. aphantoneura* and *P. luteipes*; Fig. 23), although this distinction is not particularly clear. Sculpture of mesepisternum varies from completely smooth to strongly matt, depending on the species, being either always smooth (Fig. 18), smooth or slightly matt (Fig. 19), or usually strongly matt (Fig. 20).

Characters of the lancet that can be used for species identification are the shape of the tangium and serrulae, number of ctenidia, and the presence or absence of small spiny pectines. The tangium can have a distinct lobe (Figs 14, 46–53) or a membranous fold (Fig. 64–65). Depending on the species, there are (almost) no (Figs 37–38, 43–44, 46–53), few (43–44, 46–53, 72), or many (Figs 39, 41–42, 45, 54–71, 73–76) ctenidia. Although the presence of small spiny pectines that reach the sclerora clearly distinguish three species (*P. albitibia*, *P. astragali*, and *P. sootryeni*) from others (Figs 41–45), observing this character is not possible without making slide preparations and examining them under a microscope. The shape of the serrulae has rather limited utility for distinguishing species in the *ruficornis* group. Only *P. appendiculata* has distinctly different apical and middle serrulae from other species. Serrulae of this species have an almost non-serrate (without denticles) ventro-apical surface (Figs 37–38), while in others it is clearly serrate (with numerous denticles) (Figs 39, 41–76). Structure of serrulae in the remaining species is rather similar, but shape can be sufficiently distinct to distinguish between at least some species (e.g. between *P. confusa* and *P. opaca*; Figs 62–65).

The clearest differences between species in the *ruficornis* group are found in the penis valves. Shape of the ventro-apical spine and pseudoceps usually show distinct and stable differences between most species. In *P. frigida* (Fig. 88), *P. melanocarpa* (Figs 80, 82), and *P. ruficornis* (Figs 79, 81) there is also a membranous fold near to or covering the tip of the ventro-apical spine that is missing in other species. Interestingly, we discovered that left and right penis valves differ consistently and distinctly in shape in *P. pusilla*. The left penis valve (Fig. 93) has a noticeably stronger dorsal depression in the middle of the pseudoceps and a more strongly bent ventro-apical spine than the right one (Fig. 94). Among sawflies, asymmetrical penis valves have been observed also for *Cladius compressicornis* (Fabricius, 1804) (Benson 1958; as *Priophorus pallipes*). Asymmetrical genitalia are apparently very rare in Hymenoptera, as Huber et al. (2007) did not mention any cases for this group in their review.

Dichotomous key to *Pristiphora ruficornis* group adults

1 a Mesopostnotum smooth (Fig. 7)
b Claws without subapical tooth (Fig. 30)
c Mesepisternum smooth (Fig. 18)
d Antenna *usually* ventrally paler than dorsally (Fig. 25) ... ***P. appendiculata***
– aa Mesopostnotum matt (Fig. 8)
bb Claws with subapical tooth (Figs 31–34)
cc Mesepisternum smooth or matt (Figs 18–20)
dd Antenna uniformly black or ventrally paler than dorsally (Figs 24–26, 36).. **2**
2(1) a Metafemur pale in most part (Figs 22–23).. **3**
– aa Metafemur black in most part (Fig. 21).. **4**
3(2) a Claws with large subapical tooth (Fig. 33)
b Antenna ventrally paler than dorsally (Figs 25, 36) or uniformly yellow (Fig. 26)
c Metafemur whitish (Fig. 22) .... ***P. leucopus*** in part
– aa Claws with small subapical tooth (Fig. 31)
bb Antenna uniformly black (Fig. 24)
cc Metafemur yellowish (Fig. 23)..
.... **females of *P. aphantoneura* (on *Lathyrus*) and *P. luteipes* (on *Salix*)** (see Vikberg 2006 for minor characters for separating these species)
4(2) a Claws with long subapical tooth close to apical one (bifid) (Fig. 34) **5**
– aa Claws with small or large subapical tooth clearly separated from apical one (Figs 31–33) **6**
5(4) a Hind trochanters, trochantelli, and tibia partly pale
b Antenna (usually?) ventrally at least slightly paler than dorsally (Figs 25, 36)
c In males, antennae with numerous and clearly visible stout black setae among finer paler ones (Fig. 36)
d Apical serrulae of lancet short and protruding, and tangium long and narrow (Fig. 70)
e Penis valve without membranous fold near tip of ventro-apical spine and pseudoceps with distinct dorsal depression in middle or basal part (Fig. 87)...
.... ***P. bifida***

– aa Hind trochanters, trochantelli, and tibia uniformly black or brown
bb Antenna uniformly black (Fig. 24)
cc In males, antennae with only some barely visible stout black setae among finer paler ones (Fig. 35)
dd Apical serrulae of lancet long and flat, and tangium short and broad (Fig. 71)
ee Penis valve with membranous fold near tip of ventro-apical spine and pseudoceps without dorsal depression in middle or basal part (Fig. 88) .... ***P. frigida***

6(4) a ♀ **7**
– aa ♂ **17**

7(6) a Tangium of lancet with distinct lobe (Figs 14, 46–53)
b Mesepisternum smooth (Fig. 18)
c Claws with small subapical tooth (rarely with large) (Fig. 31) **8**
– aa Tangium of lancet without distinct lobe (Figs 41–45, 54–57, 62–69, 72–76)
bb Mesepisternum smooth or matt (Figs 18–20)
cc Claws with small or large subapical tooth (Figs 31–33) **9**

8(7) a Antenna ventrally distinctly paler than dorsally (Fig. 25) ....***P. ruficornis***
– aa Antenna *usually* uniformly black (Fig. 24), but sometimes ventrally slightly paler than dorsally.................. ***P. melanocarpa***

9(7) a Inner surface of lancet with small spiny pectines (or dentes semicirculares) that reach sclerora (Figs 41–45) (visible only by examining slide preparations of the lancet with high magnification) **10**
– aa Inner surface of lancet without small spiny pectines (Figs 54–57, 62–69, 72–76).................. **12**

10(9) a Mesepisternum smooth (Fig. 18)
b Lancet with numerous ctenidia (Figs 41–42)
c Apical serrulae of lancet short (Figs 41–42)
d Pterostigma basally dark brown and apically brown (Fig. 28) .....***P. albitibia***
– aa Mesepisternum at least slightly matt (Figs 19–20)
bb Lancet with numerous or few ctenidia (Figs 43–45)
cc Apical serrulae of lancet short or long (Figs 43–45)
dd Pterostigma uniformly yellow or brown (Fig. 27) **11**

11(10) a Lancet with numerous ctenidia (Fig. 45)
b Apical serrulae of lancet long (Fig. 45) ....***P. sootryeni***
– aa Lancet with few ctenidia (Figs 43–44)
bb Apical serrulae of lancet short (Figs 43–44)......................... ***P. astragali***

12(9) a Lancet with few ctenidia (Fig. 72)
b Serrulae of lancet flat (Fig. 72)
c Antenna (usually?) ventrally slightly paler than dorsally (Fig. 25) .... ***P. pusilla***
– aa Lancet with numerous ctenidia (Figs 54–57, 62–69, 73–76)

bb Serrulae of lancet flat or protruding (Figs 54–57, 62–69, 73–76)
cc Antenna uniformly black or ventrally paler than dorsally (Figs 24–25) ... **13**
13(12) a Mesepisternum (usually?) strongly matt (Fig. 20)
b Antenna uniformly black (Fig. 24)
c Pterostigma (usually?) uniformly yellow or brown (Fig. 27)
d Arctic habitats...***P. staudingeri***
– aa Mesepisternum (usually?) smooth or slightly matt (Figs 18–19)
bb Antenna uniformly black or ventrally paler than dorsally (Figs 24–25)
cc Pterostigma uniformly yellow to dark brown, or basally dark brown and apically brown (Figs 27–29)
dd *Usually* non-arctic habitats...**14**
14(13) a Apical serrulae protruding (Figs 54–57, 62–63)
b Antenna *often* ventrally paler than dorsally (Fig. 25) **15**
– aa Apical serrulae flat (Figs 64–69)
bb Antenna uniformly black or ventrally paler than dorsally (Figs 24–25).... **16**
15(14) a Pterostigma *usually* basally dark brown and apically brown (Fig. 28)
b Ctenidia of lancet more distinct (Figs 62–63)........................ ***P. confusa***
– aa Pterostigma *usually* uniformly dark brown (Fig. 29)
bb Ctenidia of lancet less distinct (Figs 54–57) ....
..***P. armata*** **(on *Crataegus*) and *P. leucopus* (on *Tilia*)** in part (see the main text and Grearson and Liston 2012 for discussion separating these species)
16(14) a Tangium of lancet without fold (Figs 66–69)
b Antenna uniformly black (Fig. 24)
c Pterostigma uniformly yellow (Fig. 27) ....***P. subopaca***
– aa Tangium of lancet with fold (Figs 64–65)
bb Antenna ventrally slightly paler than dorsally (Fig. 25)
cc Pterostigma (usually?) basally dark brown and apically brown (Fig. 28)....
....***P. opaca***
17(6) a Tergum 8 with apical projection (Fig. 16)
b Antennae ventrally distinctly paler than dorsally or uniformly yellow (Figs 26, 36)
c Claws with large subapical tooth (Fig. 33)
d Mesepisternum smooth (Fig. 18) ....
...........***P. armata*** **(on Crataegus) and *P. leucopus* (on Tilia)** (see the main text and Grearson and Liston 2012 for discussion separating these species)
– aa Tergum 8 without apical projection (Fig. 17)
bb Antennae uniformly black to uniformly yellow (Figs 24–26, 36)
cc Claws with small or large subapical tooth (Figs 31–33)
dd Mesepisternum smooth or matt (Figs 18–20) **18**
18(17) a Penis valve with membranous fold near or covering tip of ventro-apical spine (Figs 79–82)

b Claws with small subapical tooth (Fig. 31)
c Mesepisternum smooth (Fig. 18) **19**
– aa Penis valve without membranous fold (Figs 78, 89–103)
bb Claws with small or large subapical tooth (Figs 31–33)
cc Mesepisternum smooth or matt (Figs 18–20) **20**
19(18) a Ventro-apical spine of penis valve less sharply bent (forming half circle) (Figs 79, 81) .... ***P. ruficornis***
– aa Ventro-apical spine of penis valve more sharply bent (being almost L-shaped) (Figs 80, 82) .... ***P. melanocarpa***
20(18) a Pseudoceps of penis valve short and broad (Fig. 78)
b Mesepisternum smooth (Fig. 18)
c Antennae uniformly black (Fig. 24)
d Pterostigma (usually?) basally dark brown and apically brown (Fig. 28) .... ***P. albitibia***
– aa Pseudoceps of penis valve longer and narrower (Figs 89–103)
bb Mesepisternum smooth or matt (Figs 18–20)
cc Antennae uniformly black (Fig. 24) or ventrally paler than dorsally (Fig. 36)
dd Pterostigma uniformly yellow to uniformly dark brown (Figs 27–29) ... **21**
21(20) a Penis valve with weakly bent and broad ventro-apical spine, and with narrow pseudoceps without distinct dorsal depression in middle part (Figs 89–90) .... ***P. confusa***
– aa Penis valve with different combination of characters (Figs 91–103) ... **22**
22(21) a Ventro-apical spine of penis valve narrow and with blunt tip (Figs 95–96)
b Antennae ventrally paler than dorsally (Fig. 36) .... ***P. opaca***
– aa Ventro-apical spine of penis valve broad or narrow and with sharp tip (Figs 91–94, 97–103)
bb Antennae uniformly black (Fig. 24) or ventrally paler than dorsally (Fig. 36) **23**
23(22) a Ventro-apical spine of penis valve narrow (Figs 97–103)
b Antennae uniformly black (Fig. 24) **24**
– aa Ventro-apical spine of penis valve broad (Figs 91–94)
bb Antennae uniformly black (Fig. 24) or ventrally paler than dorsally (Fig. 36) **25**
24(23) a Mesepisternum smooth to slightly matt (Figs 18–19)
b *Usually* non-arctic habitats .... ***P. luteipes***
– aa Mesepisternum *usually* strongly matt (Fig. 20)
bb Arctic habitats .... ***P. staudingeri***
25(23) a Pseudoceps of left and right penis valve without distinct dorsal depression in middle part and with weakly bent ventro-apical spine (Figs 91–92)
b Antennae uniformly black (Fig. 24) .... ***P. subopaca***
– aa Pseudoceps of left penis valve with distinct dorsal depression in middle part and with strongly bent ventro-apical spine (Fig. 93)
bb Antenna ventrally paler than dorsally (Fig. 36) .... ***P. pusilla***

Taxonomy

Pristiphora albitibia (Costa, 1859)

Nematus albitibia Costa, 1859: 21. Syntype(s) ♂ possibly in MZUN, not examined. Type locality: Sila Grande, Calabria, Italy.

Nematus puncticeps Thomson, 1863: 619. Syntypes ♀♂ in MZLU, examined. Type locality: Dalarne, Stockholm, Ostergöthland, Småland, and Skåne, Sweden.

Nematus agilis Zaddach in Brischke, 1884: 142. Primary homonym of *Nematus agilis* Cresson, 1880 [= *Euura agilis* (Cresson, 1880)]. 3 ♂♀ syntypes possibly destroyed (Blank and Taeger 1998). Type locality: not specified, but probably in former East Prussia (now Kaliningrad Oblast of Russia, or Poland).

Pristiphora aterrima Lindqvist, 1977: 92, **syn. n.** Holotype ♀ (DEI-GISHym20896) in MZH, examined. Type locality: Tolyany, Usolje, Irkutsk, Russia.

Similar species. Externally, the most similar species are *P. armata*, *P. confusa*, *P. leucopus*, *P. opaca*, and *P. subopaca*, from which it is best distinguished by the structure of the saw (Figs 41–42) and the penis valve (Fig. 78). On the inner surface of the lancet there are small spiny pectines (or dentes semicirculares) that reach the sclerora, which are absent in other similar species. The saw (Fig. 42) and external morphology of the holotype of *Pristiphora aterrima* Lindqvist, 1977 is not distinguishable from the studied *P. albitibia* specimens and therefore we synonymise *aterrima* with *albitibia*.

Genetic data. Based on COI barcode sequences, *P. albitibia* belongs to its own BIN cluster (BOLD:ACH1762) (Fig. 1). The nearest neighbour (BOLD:AAL8277, *P. astragali*?) is 2.06% different. Although there are no nuclear TPI sequences for any of the genetically closest (according to COI barcodes) species (*P. astragali* and *P. sootryeni*), the three sequenced specimens of *P. albitibia* are nearly identical to each other (one specimen differed by one nucleotide from the other two) and clearly different from the other sequenced species (Fig. 2).

Host plants. *Vicia cracca* L. (Stein 1885, as *P. puncticeps*; Vikberg 2006), *V. hirsuta* (L.) Gray, *V. tetrasperma* (L.) Schreb. (Kangas 1985, as *P. puncticeps*),*Vicia baicalensis* Turcz., *Vicia unijuga* A. Br. (Verzhutskii 1981, as *P. puncticeps*).

Distribution and material examined. Palaearctic. Specimens studied are from Estonia, Finland, Germany, Russia, and Sweden.

Pristiphora aphantoneura (Förster, 1854)

Tenthredo fulvipes Fallén, 1808: 113. Primary homonym of *Tenthredo fulvipes* Scopoli, 1763 [= *Aglaostigma* (*Astochus*) *fulvipes* (Scopoli, 1763)]. Lectotype ♀ (designated by Vikberg 2006) in MZLU, examined. Type locality: Sweden.

Nematus aphantoneurus Förster, 1854: 323–325. Lectotype ♀ (DEI-GISHym31561; designated by Vikberg 2006) in ZSM, examined. Type locality: Aachen, North Rhine-Westphalia, Germany.

Figures 3–17. 3 *Pristiphora bifida* DEI-GISHym31507, sawsheath with large scopa (arrows) in dorsal view **4** *P. appendiculata* DEI-GISHym80025, sawsheath with large scopa (arrows) in apical view **5** *P. albitibia* DEI-GISHym31514, head in dorsal view showing short postocellar area (lines and arrows) **6** *P. geniculata* DEI-GISHym20961, head in dorsal view showing long postocellar area (lines and arrows) **7** *P. appendiculata* DEI-GISHym31500, smooth mesopostnotum (arrow) **8** *P. albitibia* DEI-GISHym31516, matt mesopostnotum (arrow) **9** *P. ruficornis* DEI-GISHym31185, dorsal view **10** *P. subopaca* DEI-GISHym20899, dorsal view **11** *P. ruficornis* DEI-GISHym31185, lateral view **12** *P. subopaca* DEI-GISHym20899, lateral view **13** *P. beaumonti* DEI-GISHym20766, lateral view **14** *P. melanocarpa* DEI-GISHym21031, abdomen in lateral view **15** *P. luteipes* DEI-GISHym18872, abdomen in lateral view **16** *P. armata* DEI-GISHym11092, tergum 8 in dorsal view with apical projection (arrow) **17** *P. subopaca* DEI-GISHym31560, tergum 8 in dorsal view without apical projection.

Cryptocampus distinctus Costa, 1882: 198. Syntype(s) ♀ possibly in MZUN, not examined. Type locality: Oschiri, Sardinia, Italy. Note. Identity of the type(s) is uncertain, could be *P. luteipes*.

Pristiphora pygmaea Lindqvist, 1964: 130. Holotype ♀ in MZH, examined. Type locality: Helsinki, Finland.

Similar species. The most similar species is *P. luteipes*, from which it cannot be always distinguished morphologically. Vikberg (2006) mentions that the mesepisternum is completely smooth unlike in *P. luteipes*, which should show at least slightly coriaceous sculpture (Fig. 19 and Fig. 6a in Vikberg 2006). However, *P. luteipes* can also have a completely smooth mesepisternum, especially in southern European specimens. See Vikberg (2006) for additional minor characters for separating these species. Males are unknown.

Genetic data. Based on a COI barcode sequence of one confidently identified specimen (reared *ex ovo* from *Lathyrus pratensis*) from Finland (DEI-GISHym80037), it belongs to the same BIN cluster (BOLD:AAG3568) as *P. bifida*, *P. confusa*, *P. luteipes*, *P. opaca*, *P. pusilla*, *P. staudingeri*, and *P. subopaca* (Fig. 1). The nearest neighbour (BOLD:AAQ2302, *P. armata* and *P. leucopus*) is 2.76% different. Amplification of TPI of the specimen DEI-GISHym80037 failed, but we were able to obtain this nuclear sequence for one specimen from Estonia (DEI-GISHym31258) which had a nearly identical COI barcode (one nucleotide difference). Because the mesepisternum of this female was completely smooth, we identified it as *P. aphantoneura*. If this is correct, then TPI sequence data would be consistent in separating *P. aphantoneura* from closely related *P. luteipes* feeding on *Salix* (Fig. 2), although more specimens and some other nuclear sequences should be sampled to confirm this.

Host plants. *Lathyrus pratensis* L. (Vikberg 2006).

Distribution and material examined. Palaearctic. Specimens studied are from Estonia, Finland, and Germany.

Pristiphora appendiculata (Hartig, 1837)

Pristiphora pallipes Serville, 1823: 75. Secondary homonym of *Tenthredo pallipes* Fallén, 1808 [= *Pristiphora* (*Lygaeotus*) *carinata* (Hartig, 1837)]. Lectotype ♀ (designated by Lacourt 2000) in MNHN, not examined. Type locality: Paris, France.

Pristiphora pallipes Lepeletier, 1823: 60. Primary homonym of *Pristiphora pallipes* Serville, 1823 [= *Pristiphora* (*Pristiphora*) *appendiculata* (Hartig, 1837)]. Lectotype ♀ (designated by Lacourt 2000) in MNHN, not examined. Type locality: Paris, France.

Tenthredo (*Nematus*) *pallicornis* T.W. Harris, 1835: 583. Type(s) not available. Nomen nudum.

Tenthredo (*Nematus*) *labrata* T.W. Harris, 1835: 583. Type(s) not available. Nomen nudum.

Nematus flavipes Dahlbom, 1835a: 25–26. Nomen oblitum. Holotype ♀ in MZLU, examined. Type locality: Lund, Sweden.

Figures 18–36. 18 *P. albitibia* DEI-GISHym31514, thorax in lateral view **19** *P. luteipes* DEI-GISHym80038, thorax in lateral view **20** *P. astragali* holotype, thorax in lateral view **21** *P. leucopus* DEI-GISHym31556, lateral **22** *P. leucopus* DEI-GISHym4989, lateral **23** *P. luteipes* DEI-GISHym80038, lateral **24** *P. luteipes* DEI-GISHym80038, flagellum **25** *P. ruficornis* DEI-GISHym31185, flagellum **26** *P. armata* DEI-GISHym11092 **27** *P. subopaca* holotype, pterostigma (arrow) **28** *P. opaca* holotype, pterostigma (arrow) **29** *P. ruficornis* DEI-GISHym31185, pterostigma (arrow) **30** *P. appendiculata* DEI-GISHym31500, claw **31** *P. opaca* holotype, claw **32** *P. subopaca* holotype, claw **33** *P. armata* DEI-GISHym11554, claw **34** *P. bifida* DEI-GISHym31507, claw **35** *P. frigida* NHRS-HEVA000005006, flagellum with barely visible stout black setae (arrows) **36** *P. pusilla* DEI-GISHym80050, flagellum with clearly visible stout black setae.

Nematus appendiculatus Hartig, 1837: 202–203. Nomen protectum. See Blank et al. (2009). Lectotype ♀ (GBIF-GISHym3197; here designated) in ZSM, examined. Type locality: Germany according to the title of the publication.

Nematus fuscicornis Hartig, 1837: 225. No syntypes were found in ZSM. Type locality: Harz, Germany.

Nematus enervis Herrich-Schäffer, 1840: 176. Replacement name for *Pristiphora pallipes* Lepeletier, 1823.

Nematus cathoraticus Förster, 1854: 325–326. Lectotype ♀ (GBIF-GISHym3214; here designated) in ZSM, examined. Type locality: Aachen, North Rhine-Westphalia, Germany.

Nematus pallicornis Norton, 1861: 160. 3 ♀ syntypes in MCZ (http://140.247.119.225/mcz/Species_record.php?id=22468), although 4 specimens were mentioned in the original description, not examined. Type locality: Massachusetts, USA.

Nematus pallicornis var. *labratus* Norton, 1861: 160. Holotype ♀ possibly in ANSP or MHNG, not examined. Type locality: Massachusetts, USA. Note. *Nematus labratus* Norton, 1861 and *Nematus pallicornis* var. *labratus* Norton, 1862 (Norton 1861) were wrongly both listed as available names by Taeger et al. (2010). They refer to the same nominal taxon, described together with *N. pallicornis* in a single text section by Norton (1861). In the headline to this section, Norton mentions the manuscript names *N. pallicornis* and *N. labratus* (nomina nuda) used by Harris (1835). At the end of his description, Norton wrote "A variety named *labratus*, by Dr. Harris [...]". The name *labratus* was therefore originally published as a variety.

Pristiphora grossulariae Walsh, 1866: 123. Neotype ♀ (selected by Zinovjev and Smith 2000) in ANSP, not examined. Type locality: possibly (if the neotype belongs to syntype series) Davenport, Iowa, USA.

Nematus Peletieri [sic!] André, 1880: 111. Name for *Pristiphora pallipes* Lepeletier, 1823.

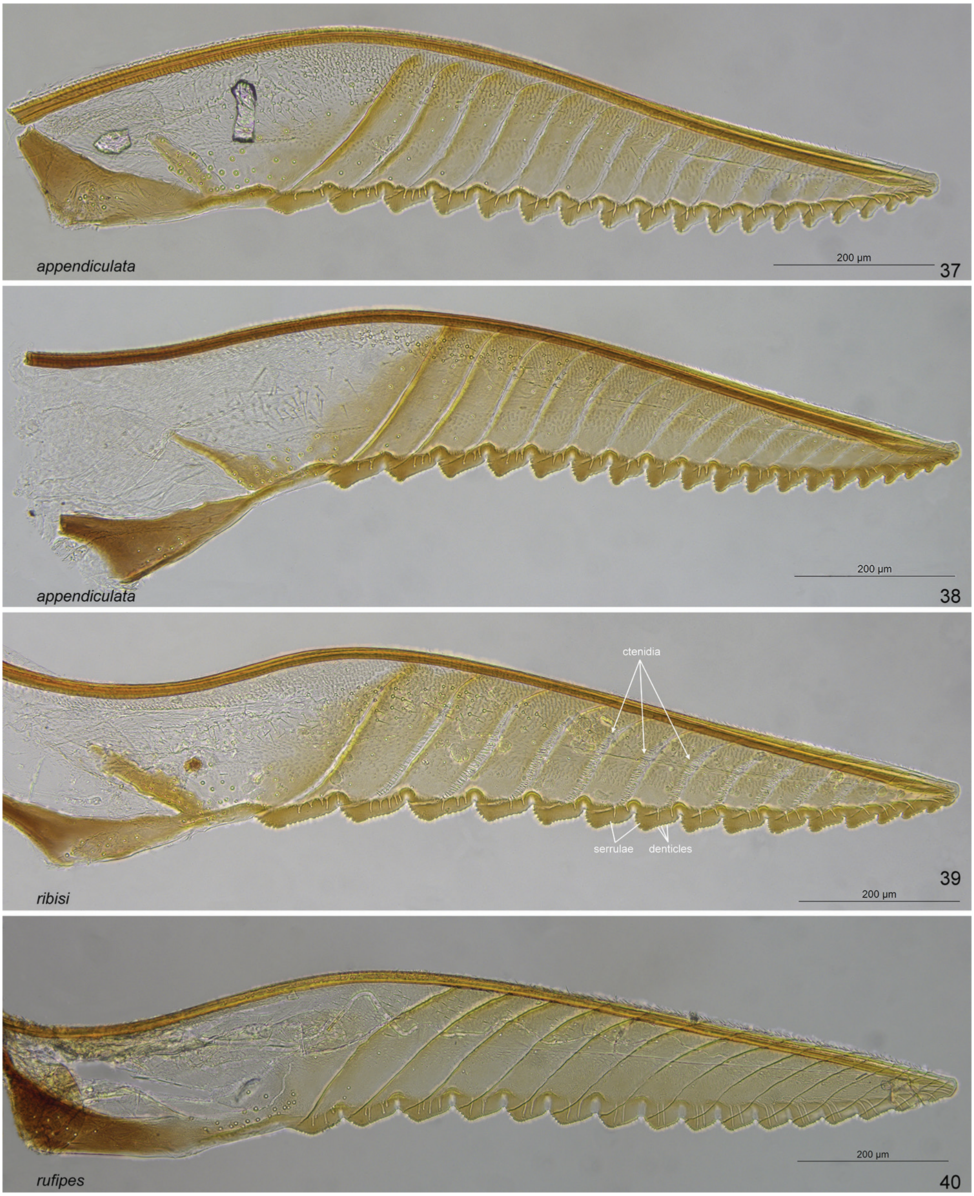
Nematus hypobalius Zaddach in Brischke, 1884: 154. Holotype ♀ possibly destroyed (Blank and Taeger 1998). Type locality: Hungary.

Nematus pumilus Zaddach in Brischke, 1884: 172. 2 ♂ syntypes possibly destroyed (Blank and Taeger 1998). Type locality: Chernyakhovsk [Insterburg], Kaliningrad Oblast, Russia.

Nematus Ghilianii [sic!] Costa, 1894: 73. Syntype(s) ♂ possibly in MZUN, not examined. Type locality: Alps [Alpi boreali], Europe.

Similar species. Smooth mesopostnotum (Fig. 7) and claws without subapical tooth (Fig. 30) allow unambiguous distinction of this species from other European species of the *ruficornis* group. A specimen from China (DEI-GISHym17879) that can be identified as *P. ribisi* Togashi, 1990 (described from Japan), is externally not distinguishable from *P. appendiculata*, but has a distinctly different saw (Fig. 39) by having well developed ctenidia and serrulae with numerous denticles on the ventro-apical surface (ctenidia are practically absent and serrulae are almost without denticles on the ventro-apical surface in *P. appendiculata*; Figs 37–38).

Genetic data. Based on COI barcode sequences, specimens of this species are divided between two BIN clusters (BOLD:AAG7866 and BOLD:AAU8684). Minimum distance between the clusters is 3.26%. However, one of the BINs might represent a cluster of nuclear mitochondrial pseudogenes (NUMTs). The COI sequence (1078 bp) we obtained from the specimen DEI-GISHym21073 was different (belonging to BOLD:AAG7866) from the one present in BOLD (BASYM3303-14, 652 bp; belonging to BOLD:AAU8684) (Fig. 1). Our use of different primers (see Material and methods) from those used by the Canadian Centre for DNA Barcoding might explain the result. Because the sequences under BOLD:AAU8684 (all 8 sequences in BOLD are identical) have an unusual 6-nucleotide deletion and this BIN forms a distinctly longer branch (which means more mutations) in the phylogenetic tree (Fig.



Figures 37–40. Lancets of *Pristiphora appendiculata* subgroup and *P. rufipes***. 37** *P. appendiculata* DEI-GISHym17852 **38** *P. appendiculata* DEI-GISHym21073 **39** *P. ribisi* DEI-GISHym17879 **40** *P. rufipes* DEI-GISHym31537.

1) than other sequences in the *appendiculata* subgroup, it might represent the NUMT cluster rather than BOLD:AAG7866. Alternatively, specimen DEI-GISHym21073 might be heteroplasmic for mitochondrial DNA (different mitochondria co-existing in the same cell or individual). Because sequences from both of these BINs can apparently

be present in the same individual, these BINs seem to form a monophyletic group (Fig. 1), and because there appear to be no morphological characters that distinguish these BIN clusters, we treat them as one species. Closest to these BIN clusters is a specimen from China that we identified as *P. ribisi* (Fig. 1). Amplification of nuclear TPI sequences was unfortunately unsuccessful.

Host plants. *Ribes* spp. *Ribes alpinum* L. (Kangas 1985, as *P. rufipes*), *R. rubrum* L. (Adam 1973, as *P. pallipes*), *R. uva-crispa* L. emend. Lam. (Adam 1973; Kangas 1985), *R. aureum* Pursh (Adam 1973), *R. sanguineum* Pursh (Adam 1973), *R. nigrum* L. (Adam 1973), *R. spicatum* Robs. (Kontuniemi 1975, as *P. pallipes*).

Distribution and material examined. Palaearctic, Nearctic. Specimens studied are from Austria, Canada, Estonia, Finland, Germany, Russia, and Sweden.

Pristiphora armata (Thomson, 1863)

Nematus crassicornis Hartig, 1837: 204–205. Primary homonym of *Nematus crassicornis* Stephens, 1829 [= *Cladius* (*Cladius*) *pectinicornis* (Geoffroy, 1785)]. 3 ♀♀ and 13 ♂♂ possible syntypes belonging to *P. armata* and *P. leucopus* in ZSM, examined. Type locality: Germany according to the title of the publication.

Nematus armatus Thomson, 1863: 619. Seven possible female syntypes belonging to *P. armata* and *P. leucopus* in MZLU, examined. Type locality: Bohus Län (Bohuslän), Stockholm, and Skåne, Sweden.

Nematus crataegi Brischke, 1883: pl. I(7), 6. Syntype(s) possibly destroyed (Blank and Taeger 1998). Type locality: not stated, but probably in former East Prussia (now Kaliningrad Oblast of Russia, or Poland).

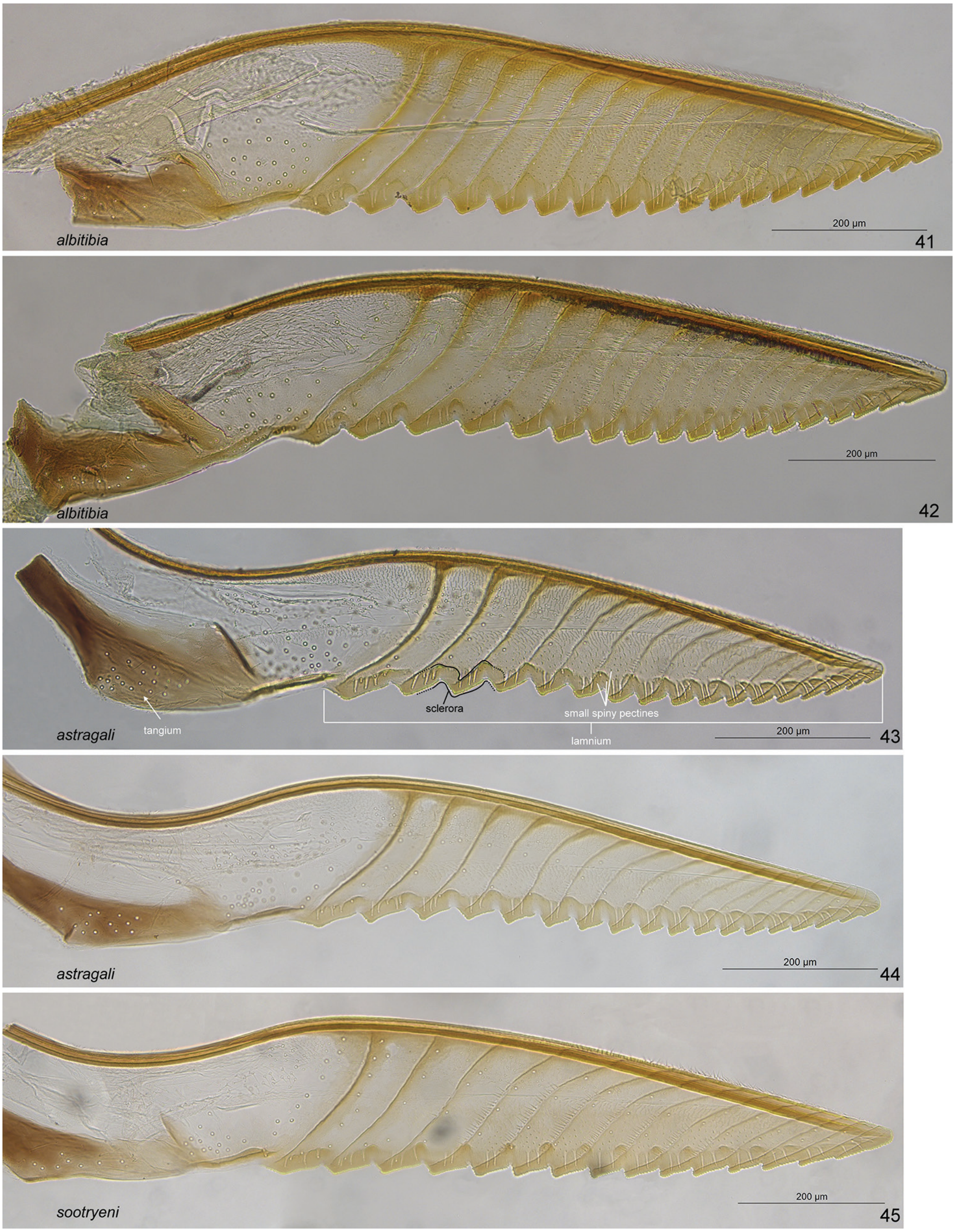
Nematus Fletcheri [sic!] Cameron, 1884: 26. Syntype(s) possibly in BMNH, not examined. Type locality: Worcester and Clydesdale, United Kingdom.

Nematus melanostomus Zaddach in Brischke, 1884: 140–141. Holotype ♀ possibly destroyed (Blank and Taeger 1998). Type locality: Bautzen, Saxony, Germany.

Nematus ensicornis Jacobs, 1884: XXIII. Syntype(s) ♀ possibly in IRSNB, not examined. Type locality: near Brussels, Belgium.

Nematus nigricollis Cameron, 1885: 66. Syntype(s) possibly in BMNH, not examined. Type locality: Worcester, United Kingdom.

Similar species. The most similar species is *P. leucopus*. Differences between these two species were extensively discussed by Grearson and Liston (2012). Briefly, specimens, both male and female, with completely or nearly completely pale metafemur (Fig. 22) belong to *P. leucopus*, but specimens with black or mostly black metafemur (Fig. 21) cannot be distinguished externally. Unfortunately, differences in lancets (Figs 54–57) and penis valves (Figs 83–86) are also small and might not always be detectable. According to Grearson and Liston (2012), the general proportions of the lamnium of *P. armata* (Figs 56–57) are wider than that of *P. leucopus* (Fig. 54), but this does not always work, because *P. leucopus* can have a distinctly wider lamnium than *P. armata*,



Figures 41–45. Lancets of *Pristiphora albitibia* subgroup. **41** *P. albitibia* DEI-GISHym20944 **42** *P. aterrima* holotype **43** *P. astragali* DEI-GISHym80042 **44** *P. astragali* PR.365VV **45** *P. sootryeni* PR.366VV.

though serrulae are in this case somewhat weaker (Fig. 55). Males can perhaps be distinguished through small differences in penis valves (Figs 85–86 and Figs 9–10 in Grearson and Liston 2012), as described by Grearson and Liston (2012): “In *P. armata*, the outer edge of the spine has a short straight section near the apex, terminated ventrally by a marked angle and below this a second section which is almost straight; there is a noticeable narrowing of the width of the spine at this point. In *P. leucopus*, the spine is almost parallel with a smoothly-curved outer edge and only a slight narrowing near the base". Unfortunately, the differences are not always evident (Figs 83–84). Females might be confused also with some specimens of *P. confusa* (if they have completely smooth mesepisternum), the only differences perhaps being the colour of pterostigma (uniformly dark brown in *P. armata*, usually basally dark brown and apically brown in *P. confusa*) and small differences in the lancet (ctenidia tend be more distinct in *P. confusa*; Figs 62–63). Differences in host plant use are the only reliable way to separate *P. armata* from *P. leucopus* that have a black metafemur (*Crataegus* in *P. armata*, *Tilia* in *P. leucopus*). Because of difficulties separating these species, we refrain from selecting lectotypes (in agreement with Grearson and Liston 2012) for *crassicornis* Hartig and *armatus* Thomson at this stage.

Genetic data. Based on COI barcode sequences, *P. armata* belongs to the same BIN cluster (BOLD:AAQ2302) as *P. leucopus* (Fig. 1). The nearest neighbour (BOLD:AAG3568) is 2.76% different. BOLD:AAG3568 includes *P. aphantoneura*, *P. bifida*, *P. confusa*, *P. luteipes*, *P. opaca*, *P. pusilla*, *P. staudingeri*, and *P. subopaca*. Although we have only one TPI sequence of *P. armata*, it also does not allow separation of *P. armata* from *P. leucopus* (Fig. 2). The single *P. armata* sequence would be identical to the single available *P. leucopus* female sequence when ambiguous positions due to heterozygosity are excluded. Examination of all the six heterozygous sites (double peaks in chromatograms) in *P. leucopus* revealed that all of them include also the nucleotide found in *P. armata*, possibly indicating haplotype sharing between these two taxa.

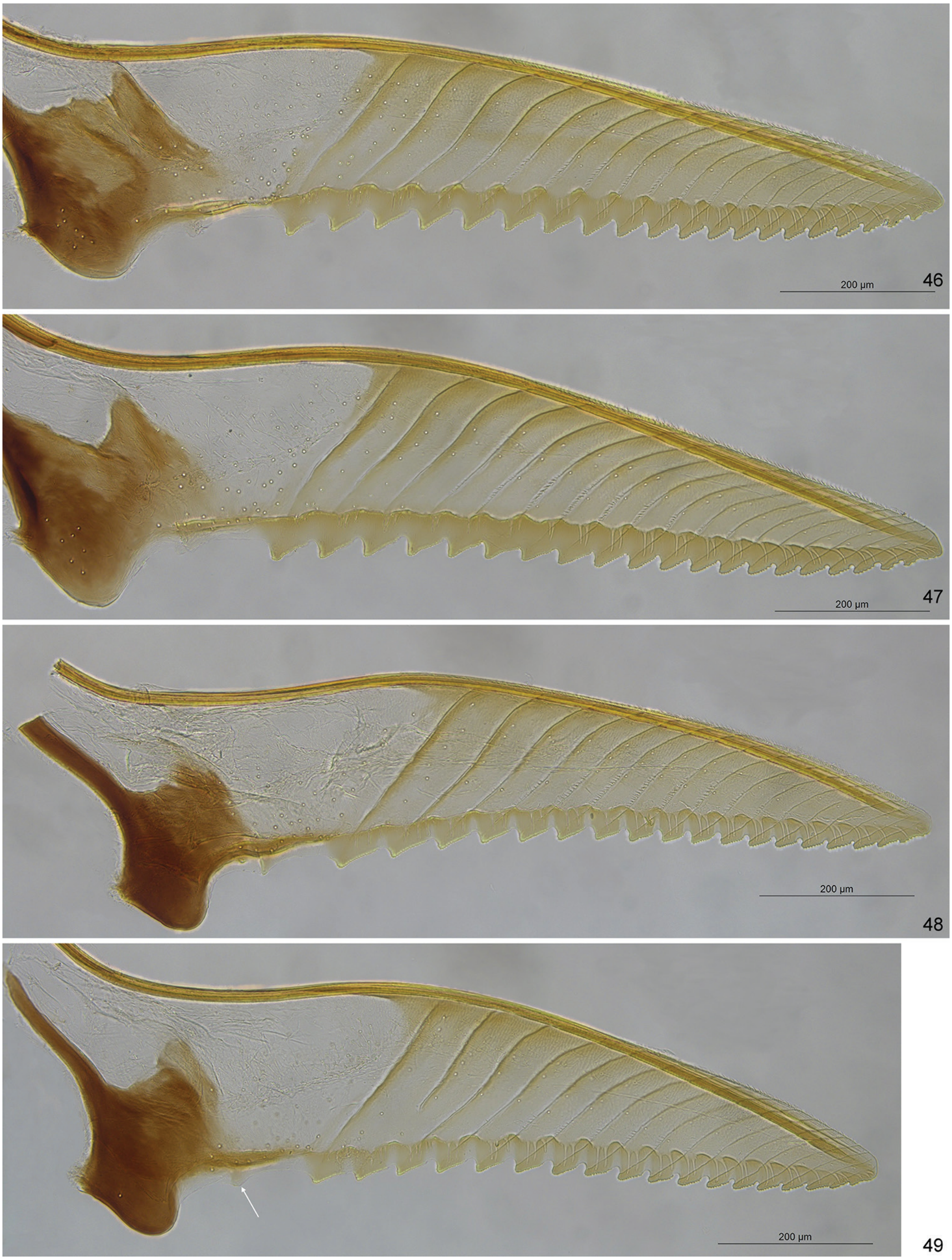
Host plants. *Crataegus* species (Brischke 1883; Grearson and Liston 2012).

Distribution and material examined. Western Palaearctic. Specimens studied are from Finland, France, Germany, Italy, and Sweden.

Pristiphora astragali Vikberg, 1978

Pristiphora astragali Vikberg, 1978: 133–137. Holotype ♀ (PR.354VV) in MZH, examined. Type locality: Kilpisjärvi, Finland.

Similar species. Based on the external morphology, the most similar species are *P. confusa*, *P. opaca*, *P. pusilla*, *P. sootryeni*, *P. staudingeri*, and *P. subopaca*, from which it is best distinguished by the structure of the lancet (Figs 43–44). The lancet has weak ctenidia (weak or well-developed in the others) and on the inner surface of the lancet there are small spiny pectines (or dentes semicirculares) that reach the sclerora (present also in *P. sootryeni*). However, differences from *P. sootryeni* (Fig. 45) are rather small. Morphologically, the subapical tooth of the claws tends be smaller, the apical serrulae of the lancet are shorter, and the number of ctenidia on the lancet is smaller than in *P. sootryeni* (Vikberg 2006). Male unknown.



Figures 46–49. Lancets of *P. melanocarpa* showing variation in the shape of the tangium. Some of the specimens have rather distinct small outgrowth between tangium and laminum (arrow in Fig. 49). **46** PR.436VV reared *ex larva* from *Betula pubescens* **47** PR.423VV reared *ex larva* from *Betula pubescens* **48** PR.434VV **49** PR.431VV, several larvae were reared *ex ovo* from this female ovipositing in the leaves of *Betula nana*.

Genetic data. Based on a COI barcode sequence of one confidently identified specimen of *P. astragali* from Abisko (Sweden; DEI-GISHym80042), it belongs to the same BIN cluster as *P. sootryeni* (BOLD:AAL8292), which in the BOLD database includes two other unidentified specimens from Manitoba, Canada (Fig. 1). The nearest neighbour (BOLD:AAL8277) is 2.40% different. BIN cluster BOLD:AAL8277 includes possibly also *P. astragali*: in the BOLD database there are two specimens from Manitoba (Canada) and one from Inari (Finland), the latter identified by Matti Viitasaari as "*Pristiphora* nr. *astragali*". Amplification of TPI failed.

Host plants. *Astragalus alpinus* L. (Vikberg 1978; 2006).

Distribution and material examined. Western Palaearctic. Specimens studied are from Finland and Sweden.

Pristiphora bifida (Hellén, 1948)

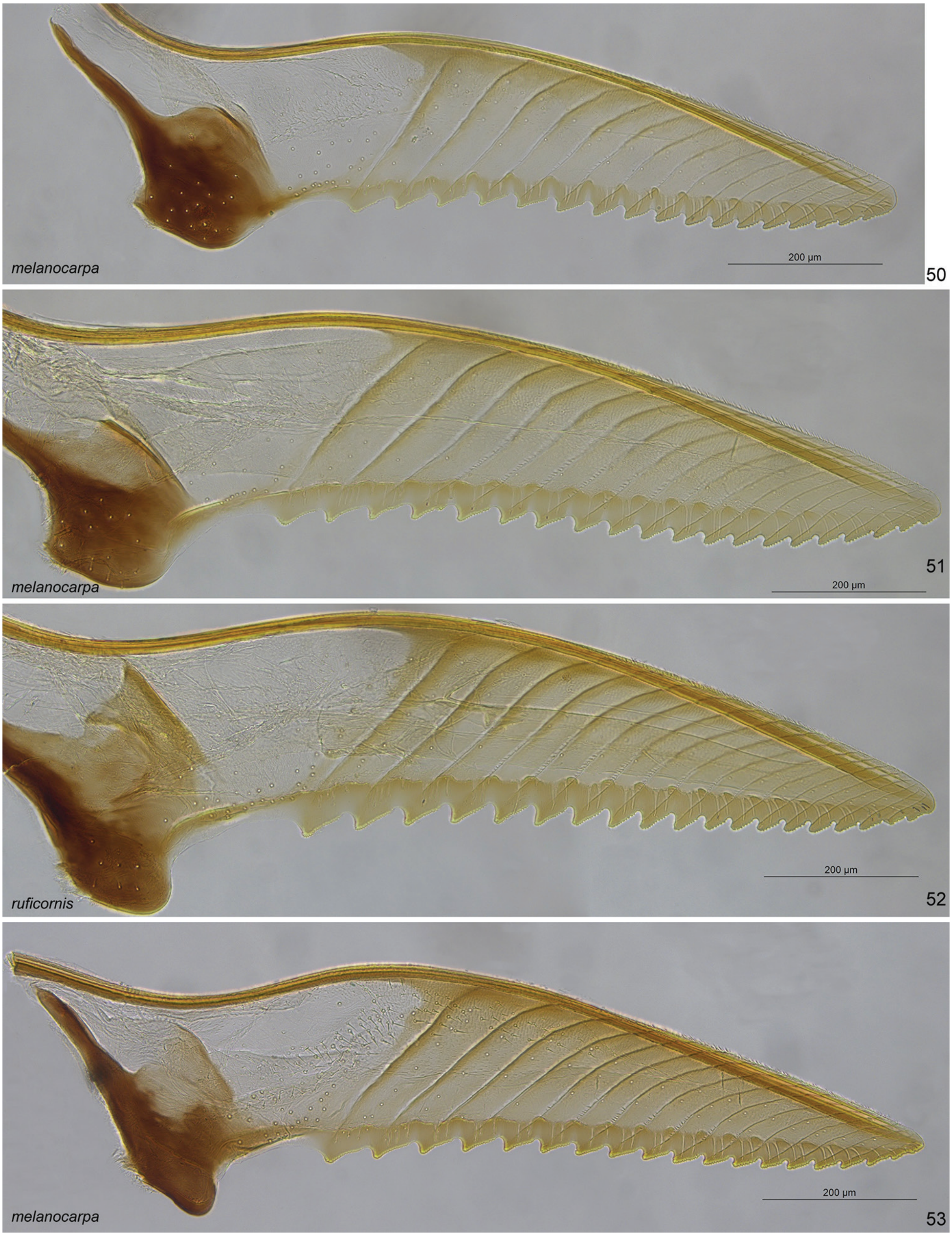
Nematus (*Pristiphora*) *bifidus* Hellén, 1948: 116–117. Lectotype ♀ (http://id.luomus.fi/GL.5214; here designated) in MZH, examined. Type locality: Malla, Kilpisjärvi, Enontekiö, Finland.

Similar species. Externally, perhaps the most similar species is *P. frigida*, from which it can be distinguished by having pale hind trochanters, trochantelli, and tibiae (black or brown in *P. frigida*). In addition, antennae of males have numerous and clearly visible stout black setae among finer paler ones (Fig. 36), while in *P. frigida* there are only a few barely visible ones (Fig. 35). The lancets (Figs 70–71) and penis valves (87–88) are also different. Apical serrulae are somewhat shorter and more protruding and the tangium of the lancet tends to be longer and narrower (Fig. 70) than in *P. frigida* (Fig. 71). The penis valve lacks (Fig. 87) a membranous fold near the tip of the ventro-apical spine (present in *P. frigida*; Fig. 88) and the pseudoceps has a distinct dorsal depression in the middle or basal part (absent in *P. frigida*).

Genetic data. Based on COI barcode sequences, *P. bifida* belongs to the same BIN cluster (BOLD:AAG3568) as *P. aphantoneura*, *P. confusa*, *P. luteipes*, *P. opaca*, *P. pusilla*, *P. staudingeri*, and *P. subopaca* (Fig. 1). The nearest neighbour (BOLD:AAQ2302, *P. armata* and *P. leucopus*) is 2.76% different. Only one partial TPI sequence (sequencing of the first exon and part of the following intron failed apparently because of intron length polymorphism) of *P. bifida* is available, which can be distinguished from other species (Fig. 2).

Host plants. *Salix viminalis* L. (Liston and Burger 2009). In Kilpisjärvi (Finland) some other species must be the host, as *S. viminalis* does not occur there.

Distribution and material examined. Western Palaearctic. Specimens studied are from Finland, Germany, Norway, and Sweden. According to the BOLD database, this species may also be present in North America. The identifications of North American specimens falling within BIN cluster BOLD:AAG3568 are however uncertain.



Figures 50–53. Lancets of *P. melanocarpa* and *P. ruficornis* showing variation in the shape of the tangium. Lancets shown here clearly lack small outgrowth between tangium and laminum, which can be seen at least in Figs 48–49 **50** *P. melanocarpa* PR.440VV **51** *P. melanocarpa* PR.407VV **52** *P. ruficornis* PR.479VV **53** *P. melanocarpa* PR.723VV reared *ex larva* from *Betula pendula*.

Pristiphora confusa **Lindqvist, 1955**

Pristiphora confusa Lindqvist, 1955: 40–41. Holotype ♀ (http://id.luomus.fi/GL.5209) in MZH, examined. Type locality: Sipoo [Sibbo], Uusimaa, Finland.

Similar species. Based on the external morphology, the most similar species are *P. albitibia*, *P. armata*, *P. leucopus*, *P. opaca*, *P. pusilla*, *P. sootryeni*, and *P. subopaca*. The species is best distinguished through the structure of male penis valve (Figs 89–90). Unfortunately, it is rather difficult to distinguish females from *P. armata*, *P. leucopus*, *P. opaca*, and *P. subopaca*, as the differences in lancets are small (Figs 54–57, 62–69). Apical serrulae are more protruding and shorter than in *P. opaca* and *P. subopaca* (Figs 62–69). *Pristiphora opaca* also has a fold at the base of tangium of the lancet (Figs 64–65) that is lacking in other species in the *ruficornis* group. *Pristiphora opaca* tends also to have a smaller subapical tooth than *P. confusa*. The pterostigma of *P. confusa* is apically brown and basally dark brown, like in *P. opaca* (Fig. 28), but unlike in *P. subopaca*, in which it is uniformly yellow (Fig. 27). In *P. armata* and *P. leucopus*, the pterostigma is usually dark brown (Fig. 29), but sometimes the pterostigma can have more or less the same colour as in *P. confusa*. In this case, small differences in the lancet can help distinguish *P. confusa* from *P. armata* and *P. leucopus*, as ctenidia tend to be more distinct in *P. confusa* (Figs 54–57, 62–63). Among the males, the most similar penis valves are of *P. subopaca*. The ventro-apical spine in *P. confusa* is barely bent and the pseudoceps is narrower compared to *P. subopaca* (Figs 89–92).

Genetic data. Based on COI barcode sequences, *P. confusa* belongs to the same BIN cluster (BOLD:AAG3568) as *P. aphantoneura*, *P. bifida*, *P. luteipes*, *P. opaca*, *P. pusilla*, *P. staudingeri*, and *P. subopaca* (Fig. 1). The nearest neighbour (BOLD:AAQ2302, *P. armata* and *P. leucopus*) is 2.76% different. Two available TPI sequences (one male and one heterozygous female) group weakly together and can be distinguished from other species (Fig. 2).

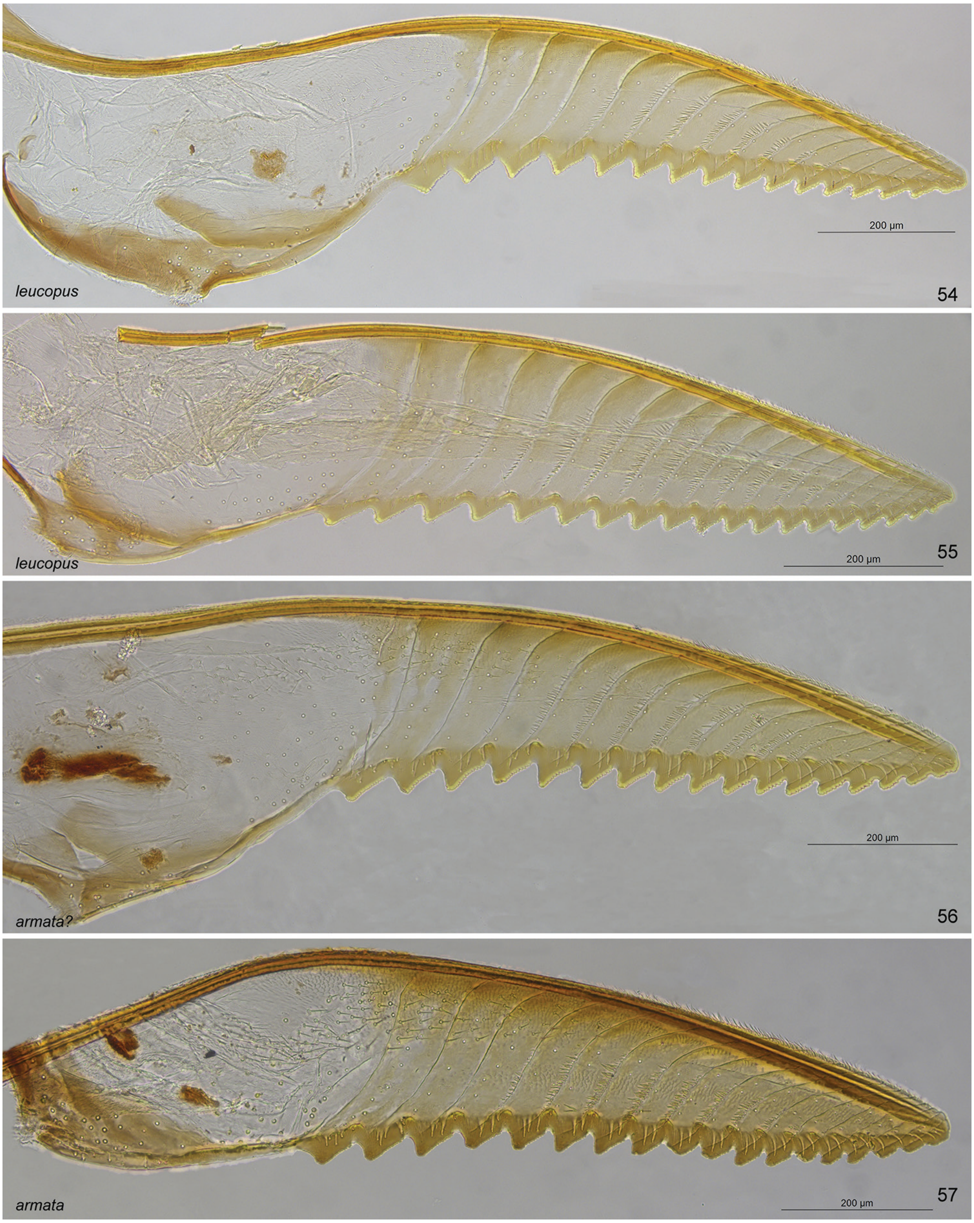
Host plants. *Salix caprea* L. (Kangas 1985), *Salix fragilis* L. (Benson 1958), *Salix phylicifolia* L. (Benson 1958).

Distribution and material examined. Western Palaearctic. Specimens studied are from Estonia, Finland, France, Germany, Sweden, and Switzerland.

Pristiphora frigida **(Boheman, 1865)**

Nematus frigidus Boheman, 1865: 568–569. Lectotype ♂ (NHRS-HEVA000005005; here designated) in NHRS, examined. Type locality: “Middel Hook in Belsund” (Spitsbergen Island), Svalbard, Norway.

Pristiphora Adelungi [sic!] Konow, 1902: 162, 167–168. Lectotype ♀ (DEI-GISHym30151; here designated) in ZIN, examined. Type locality: Hornsund (Spitsbergen Island), Svalbard, Norway. Note. Additional male specimen of *P. adelungi* labelled as “TYPE” is deposited in SDEI. Since this specimen lacks labels with detailed information given in the original description, its type status remains uncertain.



Figures 54–57. Lancets of *Pristiphora armata* subgroup. **54** *P. leucopus* PR.393VV, summer morph **55** *P. leucopus* PR.467VV reared *ex larva* from *Tilia* sp. **56** *Nematus armatus* Thomson syntype specimen 8 (X112) **57** *P. armata* DEI-GISHym20366.

Similar species. Externally, perhaps the most similar species is *P. bifida*, from which it can be distinguished by having black or brown hind trochanters, trochantelli, and tibiae (pale in *P. bifida*). In addition, antennae of males have only some barely visible stout black setae among finer paler ones (Fig. 35), while these are numerous and clearly visible in *P. bifida* (Fig. 36). On the other hand, the penis valve (Fig. 88) might indicate a closer relationship to *P. melanocarpa* and *P. ruficornis* (Figs 79–82), because of a membranous fold near the tip of the ventro-apical spine that is missing in other species of *ruficornis* group. The tangium of the lancet (Fig. 71) also resembles more closely the *Betula* feeding *P. melanocarpa* and *P. ruficornis* (Figs 46–53) rather than *P. bifida* (Fig. 70): the dark sclerotized area is rather broader than long instead of longer than broad.

Genetic data. No data.

Host plants. Unknown.

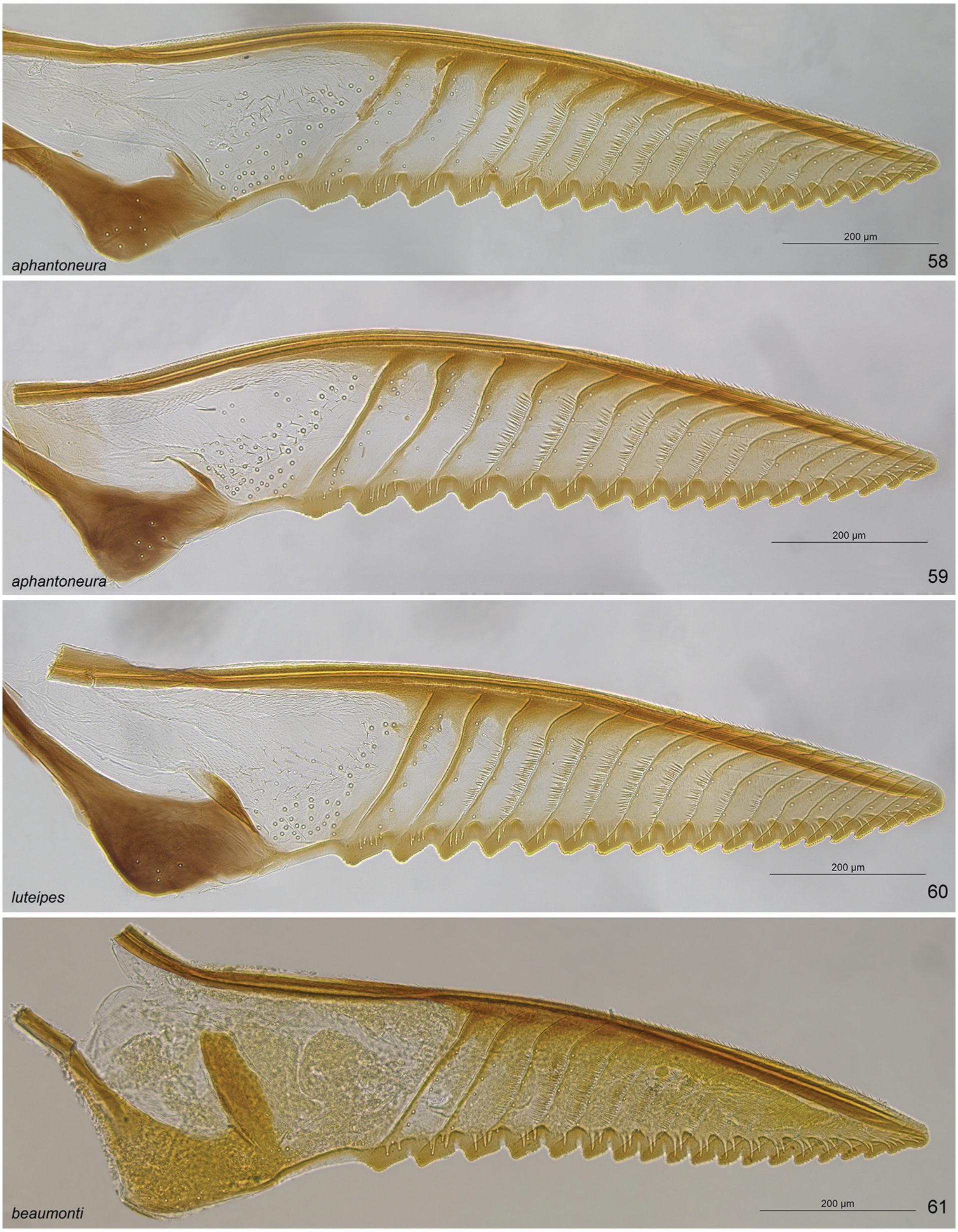
Distribution and material examined. Western Palaearctic. Specimens studied are from Norway (Svalbard).

Pristiphora leucopus (Hellén, 1948)

Nematus vitreipennis Eversmann in Kawall, 1864: 295, **syn. n. Nomen oblitum**. Note. Kawall (1864) published an unaltered manuscript from Eversmann's legacy. Lectotype ♀ (DEI-GISHym30027; here designated) in ZIN, examined. Type locality: foothills of Ural mountains [In promontor. Uralensibus], Russia.

Nematus (*Pristiphora*) *ruficornis* var. *leucopus* Hellén, 1948: 116. **Nomen protectum**. No syntypes were found in MZH. Type locality: Joutseno, South-Eastern Finland, Finland and Pionerskoye [Kuolemajärvi], Leningrad Oblast, Russia. Note. The lectotype of *Nematus vitreipennis* (which was the only specimen found under this name in Eversmann's collection in ZIN) agrees well with the summer morph (completely pale metafemur) of *P. leucopus* (Grearson and Liston 2012). The name *vitreipennis* has apparently not been used as valid since 1884 (Brischke 1884), whereas *leucopus* has been used as the valid name for this taxon more than 25 times by more than 10 different authors since 1955 (Lindqvist 1955). According to Article 23.9.1 (ICZN 1999), the prevailing usage must be maintained.

Similar species. The most similar species to *P. leucopus* is *P. armata*. Differences between these two species were extensively discussed by Grearson and Liston (2012). Whereas *P. leucopus* exhibits seasonal dimorphism of adults, involving leg colour and shape of the serrulae of the lancet, no such dimorphism has been observed in *P. armata*. Briefly, both male and female specimens which have a completely or nearly completely pale metafemur (Fig. 22) can be distinguished from *P. armata* (metafemur of which is always completely or in most part black). Other specimens, with a black or mostly black metafemur (Fig. 21), cannot be distinguished externally. Unfortunately, differences in lancets (Figs 54–57) and penis valves (Figs 83–86) are also small and might not always be detectable. According to Grearson and Liston (2012) the general proportions of the lamnium of *P. leucopus* (Fig. 54) are more slender than that of *P. armata* (Figs 56–57), but this does not always work, because *P. leucopus* can have a distinctly wider lamnium than *P. armata*, though serrulae are in this case somewhat weaker (Fig. 55). Males can perhaps be distinguished through small differences in



Figures 58–61. Lancets of *Pristiphora aphantoneura* subgroup. **58** *P. aphantoneura* holotype **59** *P. aphantoneura* PR.695VV reared from *Lathyrus pratensis* **60** *P. luteipes* PR.696VV reared from *Salix phylicifolia* **61** *P. beaumonti* DEI-GISHym20927.

penis valves (Figs 85–86 and Figs 9–10 in Grearson and Liston 2012), as described by Grearson and Liston (2012) (see also under *P. armata*). Females with a black metafemur might also be confused with some specimens of *P. confusa* (if they have a completely smooth mesepisternum). Usually, *P. leucopus* (Fig. 29) has a uniformly dark brown pterostigma (usually basally dark brown and apically brown in *P. confusa*; Fig. 28), but the specimens with pterostigma apically paler than basally might not be externally distinguishable from *P. confusa*. However, small differences in the lancets can help distinguish these species, as ctenidia in *P. confusa* tend to be more distinct (Figs 62–63).

Genetic data. Based on COI barcode sequences, *P. leucopus* belongs to the same BIN cluster (BOLD:AAQ2302) as *P. armata* (Fig. 1). The nearest neighbour (BOLD:AAG3568) is 2.76% different. BOLD:AAG3568 includes *P. aphantoneura*, *P. bifida*, *P. confusa*, *P. luteipes*, *P. opaca*, *P. pusilla*, *P. staudingeri*, and *P. subopaca*. Neither does our limited nuclear data allow separation of *P. leucopus* from *P. armata* (Fig. 2). The single heterozygous female would have a sequence identical to the single available *P. armata* sequence if heterozygous sites (double peaks in chromatograms) were excluded. All the six heterozygous sites in *P. leucopus* include also the nucleotide found in *P. armata*, possibly indicating haplotype sharing between these two taxa.

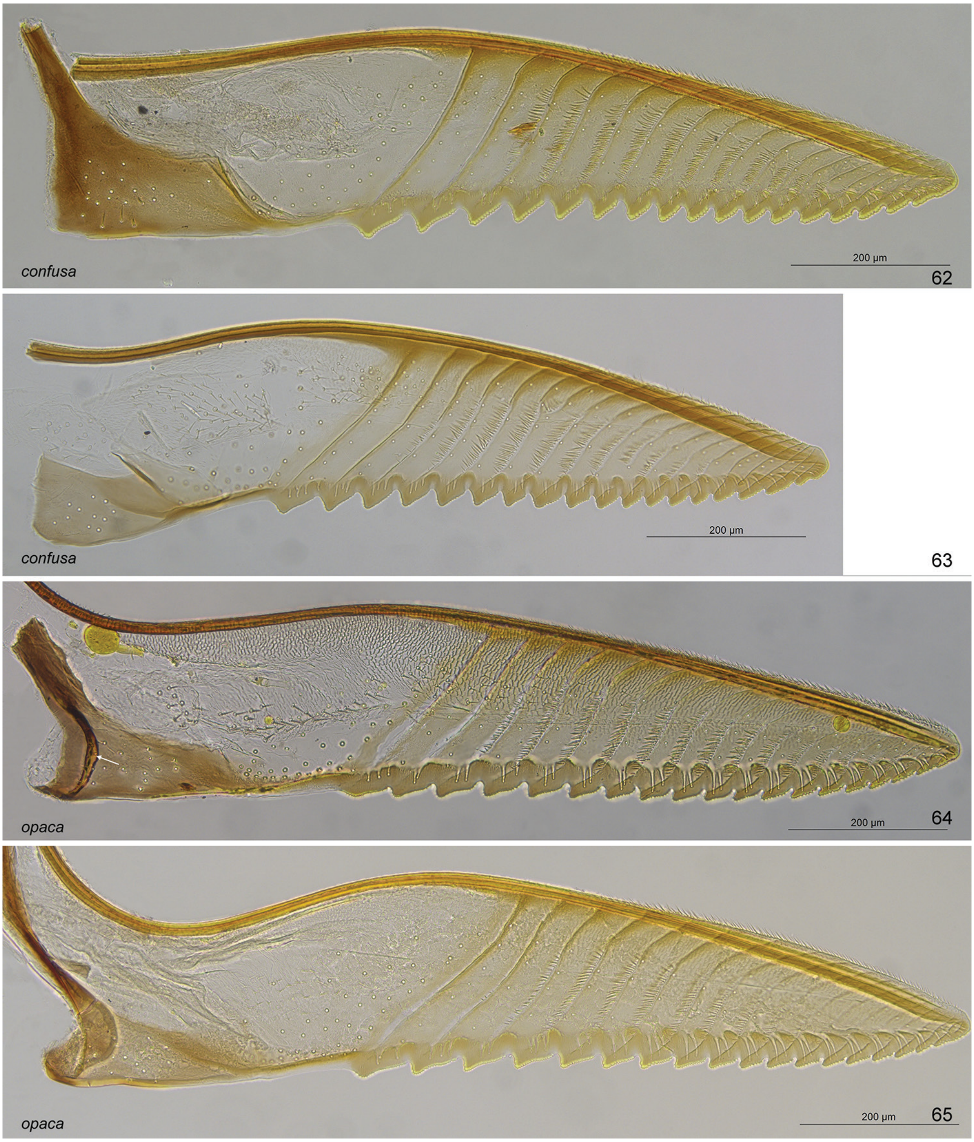
Host plants. *Tilia cordata* Mill. (Kangas 1985; Grearson 2006; Grearson and Liston 2012), *Tilia* × *vulgaris* Hayne (Grearson 2006).

Distribution and material examined. Western Palaearctic. Specimens studied are from Austria, Finland, Germany, Great Britain, Russia, and Sweden.

Pristiphora luteipes Lindqvist, 1955

Pristiphora luteipes Lindqvist, 1955: 47–48. Holotype ♀ (DEI-GISHym20897) in MZH, examined. Type locality: Degerby, Uusimaa, Finland.

Similar species. The most similar species is *P. aphantoneura*, from which it cannot be always distinguished morphologically. Vikberg (2006) mentions that the mesepisternum should show at least slightly coriaceous sculpture (fig. 19 and fig. 6a in Vikberg 2006), but should be completely smooth in *P. aphantoneura* (Fig. 18). However, the mesepisternum can also be completely smooth in *P. luteipes*, especially in southern European specimens. See Vikberg (2006) for additional minor characters for separating these species. *Pristiphora beaumonti* Zirngiebl, 1957 known from North Africa is possibly a synonym of *luteipes* Lindqvist. All the specimens of *P. beaumonti* studied from Morocco are extremely pale. Females have a completely yellow abdomen (Fig. 13) and even the thorax often has ventral and dorsal yellow markings. Males are darker: thorax and usually abdomen are black (one studied specimen had an almost completely yellow abdomen). However, all males from Morocco have a completely pale metafemur, unlike males from Portugal and Spain (with a mostly black metafemur), which we have identified as *P. luteipes* based on females that were collected at the same time from *Salix*. Females from Portugal, Spain, and Sardinia (Italy) are very similar to North European specimens of *P. luteipes*, but tend to have a completely smooth mesepisternum and dark brown pterostigma (slightly coriaceous mesepisternum and yellow pterostig-



Figures 62–65. Lancets of *Pristiphora aphantoneura* subgroup. **62** *P. confusa* holotype **63** *P. confusa* PR.544VV reared *ex larva* from *Salix caprea* **64** *P. opaca* DEI-GISHym80032 (presence of a fold is indicated by an arrow) **65** *P. opaca* PR.389VV.

ma in northern European specimens). However, the degree of coriaceous sculpture on the mesepisternum and the colour of pterostigma vary continuously and seem to correlate with latitude (specimens in the south tend to have a smoother mesepisternum and darker pterostigma). Lancets (Fig. 61) and penis valves (Fig. 101) of *P. beaumonti* are not distinguishable from *P. luteipes* (Figs 60, 103) or even from *P. staudingeri* (arctic or subarctic taxon; Figs 73–76, 97–100, 102). Males of *P. luteipes* were previously unknown (Vikberg 2006), but appear to be common in southern Europe (at least in Portugal and Spain). We have identified a possible male of *P. luteipes* (DEI-GISHym80049) also from Sweden, because according to its nuclear TPI sequence it seems to be closer to *P. luteipes* specimens than to *P. staudingeri* (Fig. 2), although COI barcode was identical to one of the *P. staudingeri* specimens (Fig. 1). The male from Sweden has distinctly coriaceous sculpture on the mesepisternum and a paler pterostigma compared to males from Spain and Portugal, which would fit the geographic pattern found in females. Because males of *P. luteipes* have a black metafemur and the penis valves are indistinguishable from those of *P. staudingeri*, identification of the Swedish male (Härjedalen at an altitude of 840 m) remains uncertain. Distinguishing females of *P. luteipes* from *P. staudingeri* might not always work either, because we have studied two specimens (*P. staudingeri*?) from Sweden (Jämtland County at an altitude 900 m) that were intermediate in morphology, having partly yellow metafemur (apically slightly yellow in the specimen W10115 and apically half yellow in W10105).

Genetic data. Based on COI barcode sequences, *P. luteipes* belongs to the same BIN cluster (BOLD:AAG3568) as *P. aphantoneura*, *P. bifida*, *P. confusa*, *P. opaca*, *P. pusilla*, *P. staudingeri*, and *P. subopaca* (Fig. 1). The nearest neighbour (BOLD:AAQ2302, *P. armata* and *P. leucopus*) is 2.76% different. It is not clear if nuclear TPI sequences allow better identification of *P. luteipes* compared to COI barcode sequences, mainly because of the uncertain identity (*P. luteipes* or *P. staudingeri*, see above) of the specimen DEI-GISHym80049 (Fig. 2), which seems to be closer to two sequenced *P. luteipes* specimens than to other species.

Host plants. *Salix alba* L., *S. aurita* L., *S. babylonica* L., *S. repens* L. *S. rosmarinifolia* L., *S. phylicifolia* L., *S. viminalis* L., *S. purpurea* L. (see Vikberg 2006); *S. cinerea* L. and *S. fragilis* L. (Loiselle 1909, as *P. fulvipes*).

Distribution and material examined. Western Palaearctic. Specimens studied are from Finland, France, Germany, Great Britain, Italy, Norway, Portugal, Spain, and Sweden.

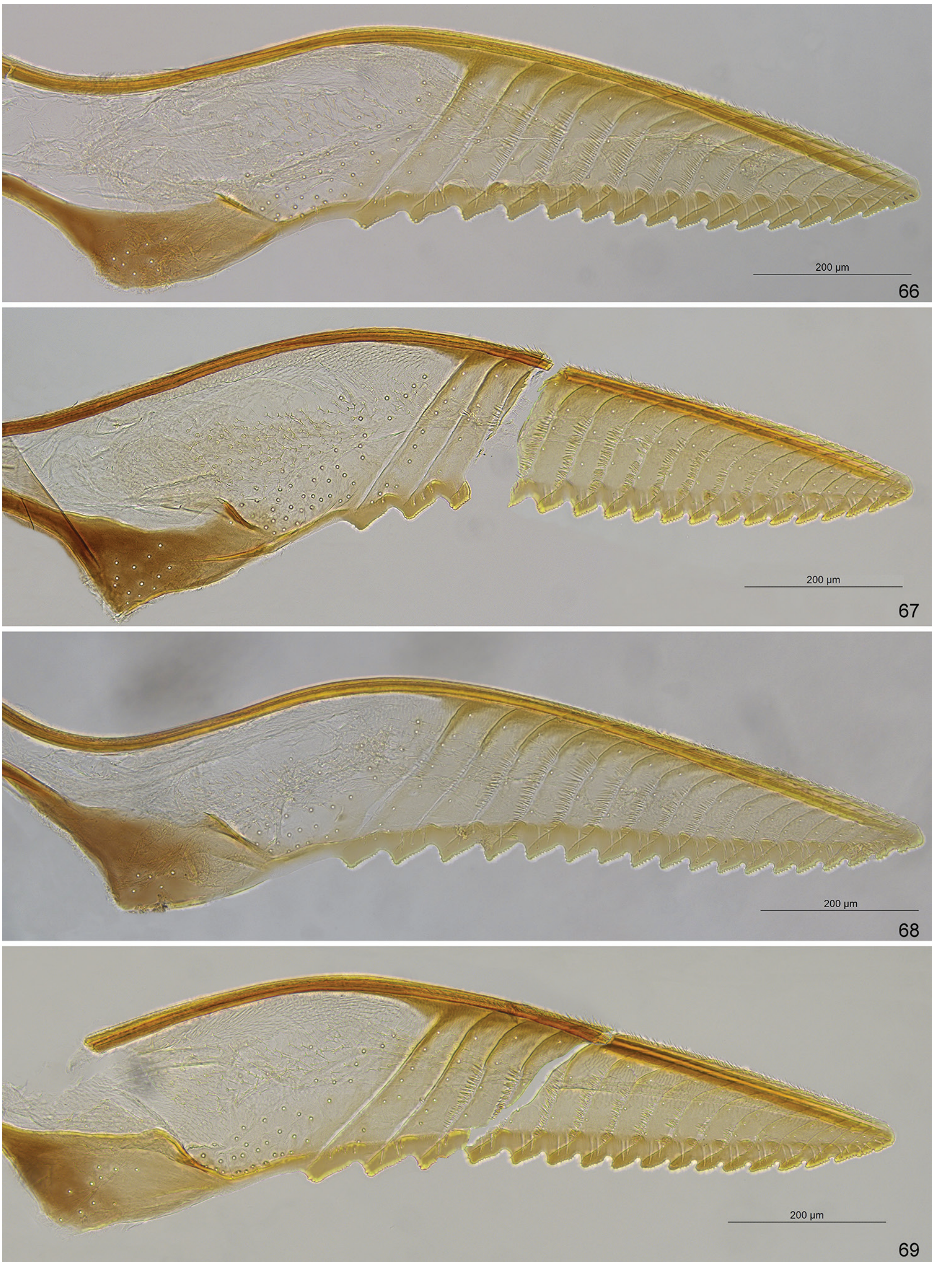
Pristiphora melanocarpa (Hartig, 1840)

Nematus melanocarpus Hartig, 1840: 27. Lectotype ♀ (GBIF-GISHym3349; here designated) in ZSM, examined. Type locality: North Germany (according to introduction).

Nematus funerulus Costa, 1859: 20–21. Syntypes ♂♀ possibly in MZUN, not examined. Type locality: vicinity of Naples, Campania, Italy.

Nematus wuestneii Stein, 1885 [mandatory correction of incorrect original spelling *N. Wüstneii*]: 304. Lectotype ♀ (here designated) in BMNH, examined. Type locality: Chodov [Chodau], Czech Republic.

Pristiphora ortinga Kincaid, 1900: 349–350. Holotype ♀ (USNMENT00778199) in USNM, not examined. Type locality: Kukak Bay, Alaska, USA. Note. Synonymised by Smith (1979: 63).



Figures 66–69. Lancets of *Pristiphora subopaca*. **66** PR.403VV **67** *P. subopaca* holotype **68** *P. coniceps* holotype **69** *P. brunniapex* holotype.

Similar species. The most similar species is *P. ruficornis*, which has paler antennae compared to *P. melanocarpa*. Females have the ventral side of antennae uniformly black (Fig. 24) or only slightly paler, while *P. ruficornis* has a distinctly paler ventral side (Fig.

25). Males of *P. melanocarpa* also tend to have darker antennae than in *P. ruficornis*, but penis valves should be studied in specimens that have conspicuously pale antennae. The ventro-apical spine of the penis valve bends distinctly more sharply (being almost L-shaped) and is usually narrower (Figs 80, 82) than in *P. ruficornis* (Figs 79, 81).

Genetic data. Based on COI barcode sequences, specimens are divided between three BIN clusters (BOLD:AAG3540, BOLD:ACZ4465, BOLD:ACZ4466), two of them (BOLD:ACZ4465 and BOLD:ACZ4466) including also *P. ruficornis* (Fig. 1). These BIN clusters form a monophyletic group (Fig. 1) and minimum distances between them are only 1.13–1.50%. Neither do nuclear TPI sequences support separation of *P. melanocarpa* and *P. ruficornis* (Fig. 2).

Host plants. *Betula pendula* Roth (Kangas 1985), *B. pubescens* Ehrh. ssp. *czerepanovii* (N. I. Orlova) Hämet-Ahti (rearings by VV), *B. nana* L. (rearings and *ex ovo* rearing experiments by VV). The records from *Salix* (e.g. Lorenz and Kraus 1957) are probably based on misidentifications. A male paratype of *P. coniceps* Lindqvist (http://id.luomus.fi/GL.5208) that belongs to *P. melanocarpa*, was reared from larvae found on *Salix* (Lindqvist 1955), but this should not be taken as a clear evidence for host association as no *ex ovo* rearings were involved.

Distribution and material examined. Holarctic. Specimens studied are from Canada, Estonia, Finland, France, Germany, Norway, and Sweden.

Pristiphora opaca Lindqvist, 1955

Pristiphora opaca Lindqvist, 1955: 42–43. Holotype ♀ (http://id.luomus.fi/GL.5204) in MZH, examined. Type locality: Pihtipudas, Central Finland.

Similar species. Based on the external morphology, the most similar species are *P. albitibia*, *P. confusa*, *P. pusilla*, *P. sootryeni*, and *P. subopaca*. The species is best distinguished through the structure of male penis valve (Figs 95–96). Unfortunately, it is rather difficult to distinguish females from *P. subopaca* as the differences in the lancets are small (Figs 64–69). The best character might be the structure of the tangium: on its basal part, *P. opaca* appears to have a fold (Figs 64–65) that is absent in other species of the *ruficornis* group, although this observation is based only on two specimens that had saws intact enough to see this (basal part of both lancets was damaged in the third female available for study, the holotype). There are also slight differences in external morphology between *P. opaca* and *P. subopaca*. In *P. opaca* (Fig. 28), the pterostigma is apically brown and basally dark brown (uniformly yellow in *P. subopaca*; Fig. 27), antennae are slightly paler ventrally (uniformly black in *P. subopaca*), and claws seem to have a somewhat smaller subapical tooth (Fig. 31) than in *P. subopaca* (Fig. 32).

Genetic data. Based on COI barcode sequences, *P. opaca* belongs to the same BIN cluster (BOLD:AAG3568) as *P. aphantoneura*, *P. bifida*, *P. confusa*, *P. pusilla*, *P. staudingeri*, and *P. subopaca* (Fig. 1). The nearest neighbour (BOLD:AAQ2302,

Figures 70–72. Lancets of *Pristiphora aphantoneura* subgroup and *P. frigida*. **70** *P. bifida* PR.408VV **71** *P. frigida* NHRS-HEVA000003873 **72** *P. pusilla* PR.369VV.

P. armata and *P. leucopus*) is 2.76% different. Only one TPI sequence is available, which can be distinguished from other species (Fig. 2).

Host plants. Unknown.

Distribution and material examined. Western Palaearctic. Specimens studied are from Finland and Sweden.

Pristiphora pusilla Malaise, 1921

Pristiphora pusilla Malaise, 1921: 11–12. Lectotype ♂ (NHRS-HEVA000004942; here designated) in NHRS, examined. Type locality: Torne Träsk, Torne Lappmark, Sweden. Note. In the original description, Malaise (1921) mentioned one female and three males collected from Torne Träsk, but only three specimens (a female and two males) probably belonging to the syntype series were found in NHRS. Among these three specimens, only the female carries the labels "Typus" and "Pristiphora pusilla n. sp." in addition to a locality label "Torne Tr. *Malaise*", the two males having originally only the identical locality label "Torne Tr. *Malaise*" (both males have in addition the label "Pristiphora pusilla Mal. Det: A. Haris 2003" and one of them also apparently relatively recent hand written label "Prist. pusilla"). According to Hege Vårdal (NHRS) there were no other males from Torne Träsk among *P. pusilla* in the collection and therefore we consider these males as part of the syntype series. Because the female specimen turned out to belong to *P. staudingeri* (Ruthe, 1859) and in order to preserve the concept of *P. pusilla* as established by Lindqvist (1953) (who also examined one of the male syntypes), and because separation of males from similar species is more reliable thanks to distinct penis valves, we decided to select one of the males as the lectotype.

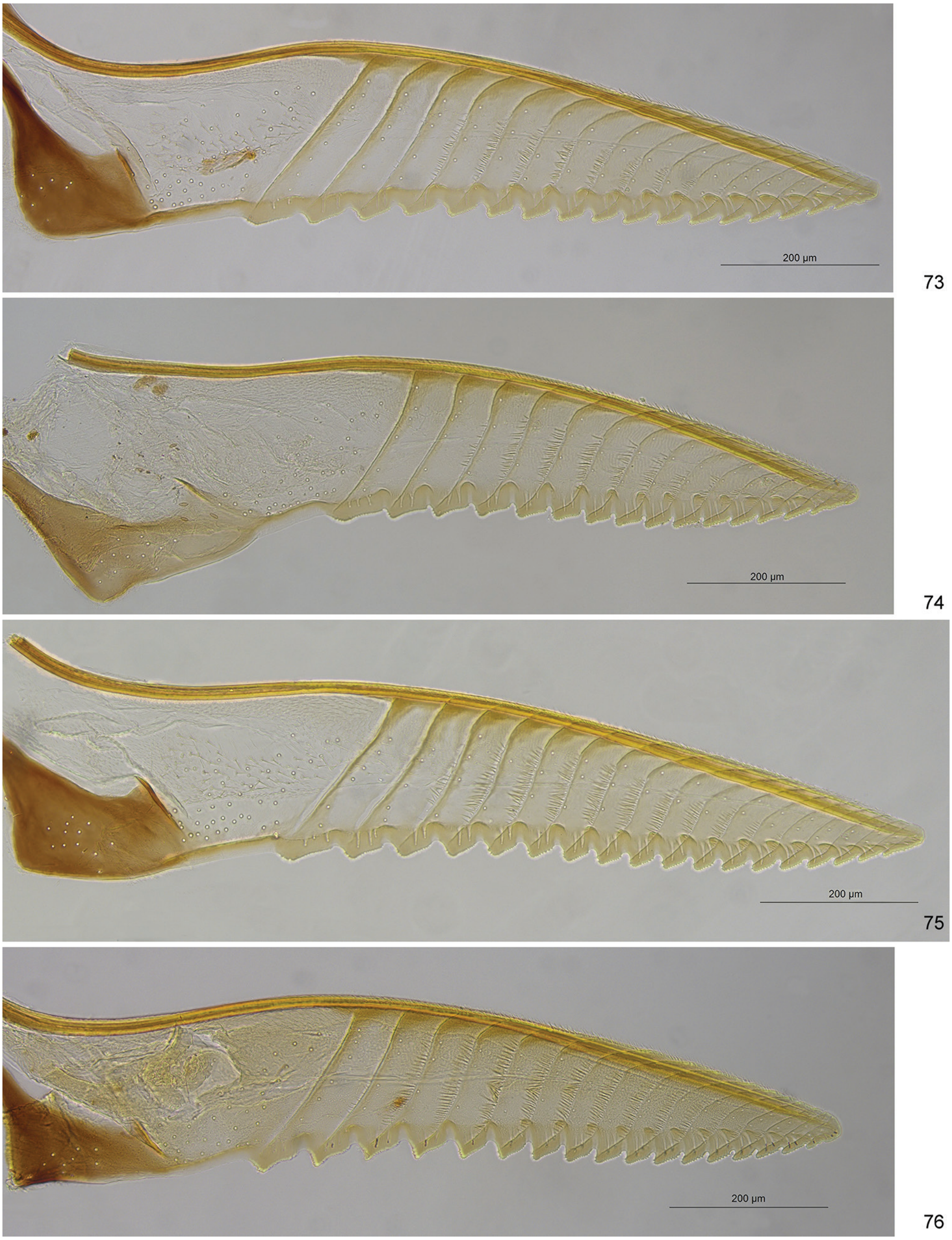
Pristiphora amaura Lindqvist, 1955: 43–45. Holotype ♀ (http://id.luomus.fi/GL.5205) in MZH, examined. Type locality: Kangasala, Pirkanmaa, Finland. Note. The male paratype of *P. amaura* (http://id.luomus.fi/GL.5206) (Fig. 96) was misidentified and belongs to *P. opaca* Lindqvist, 1955 instead.

Similar species. Based on the external morphology, the most similar species are *P. albitibia*, *P. astragali*, *P. confusa*, *P. opaca*, *P. sootryeni*, *P. staudingeri*, and *P. subopaca*. The species is best distinguished through the structure of male penis valve (Figs 93–94) and female lancet (Fig. 72). In females, the lack of small spiny pectines (or dentes semicirculares) on the inner surface of the lancet and weakly developed ctenidia, distinguish it from other similar species. Male penis valves are asymmetric (confirmed for six specimens), the left one (Fig. 93) having a noticeably stronger dorsal depression in the middle of pseudoceps and a more strongly bent ventro-apical spine than the right one (Fig. 94). The most similar penis valves are those of *P. subopaca* (Figs 91–92), which have a less distinct dorsal depression in the middle of pseudoceps and a less strongly bent ventro-apical spine, but this difference is clear only when compared to the left penis valve of *P. pusilla*. Externally, *P. pusilla* might be distinguished from *P. subopaca* by having ventrally paler antennae (uniformly black in *P. subopaca*; Fig. 24), which is more evident in males (Fig. 36).

Genetic data. Based on COI barcode sequences, *P. pusilla* belongs to the same BIN cluster (BOLD:AAG3568) as *P. aphantoneura*, *P. bifida*, *P. confusa*, *P. opaca*, *P. staudingeri*, and *P. subopaca* (Fig. 1). The nearest neighbour (BOLD:AAQ2302, *P. armata* and *P. leucopus*) is 2.76% different. Two available nuclear TPI sequences are identical and distinguishable from other species (Fig. 2).

Host plants. Unknown.

Distribution and material examined. Western Palaearctic. Specimens studied are from Finland, Norway, and Sweden.



Figures 73–76. Lancets of *Pristiphora staudingeri* showing variation in the number of ctenidia. **73** PR.441VV with ctenidia on annulets (3)4–12(13) **74** PR.402VV with ctenidia on annulets 3–13 **75** PR.373VV with ctenidia on annulets 3–14 **76** PR.457VV with ctenidia on annulets (2)3–15.

Pristiphora ruficornis **(Olivier, 1811)**

Nematus ruficornis Olivier in Olivier and Manuel 1811: 167. Syntype(s) possibly in MNHN, not examined. Type locality: near Paris, France.

Pristiphora testaceicornis Serville, 1823: 75. Syntype(s) ♂ not found in MNHN (Lacourt 2000). Type locality: Paris, France.

Pristiphora testaceicornis Lepeletier, 1823: 60. Primary homonym of *Pristiphora testaceicornis* Serville, 1823 [= *Pristiphora* (*Pristiphora*) *ruficornis* (Olivier, 1811)]. Syntype(s) ♂ not found in MNHN (Lacourt 2000). Type locality: Paris, France.

Nematus (*Nematus*) *robustellus* Dahlbom, 1835b: 9. Type(s) not available. Nomen nudum.

Nematus fraxini Hartig, 1837: 204. Lectotype ♀ (GBIF-GISHym3285; here designated) in ZSM, examined. Type locality: Harz, Germany.

Nematus testaceicornis Jacobs, 1884: XXIII-XXIV. Syntype(s) ♀ possibly in IRSNB, not examined. Type locality: near Brussels, Belgium.

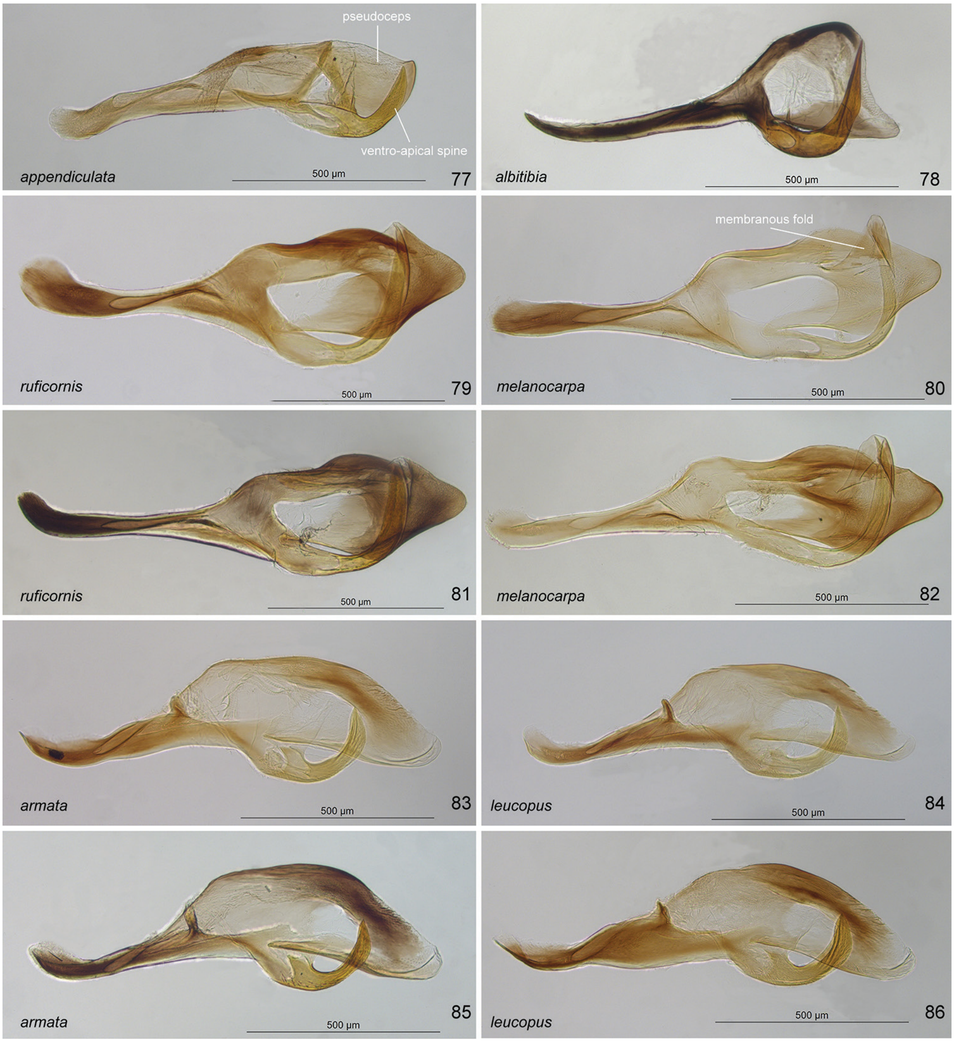
Nematus (*Pristiphora*) *ruficornis* var. *integer* Hellén, 1948: 116, **syn. n.** Primary homonym of *Nematus integer* Say, 1836. Holotype ♀ (http://id.luomus.fi/GL.5212) in MZH, examined. Type locality: Hammaslahti, North Karelia, Finland.

Similar species. The most similar species is *P. melanocarpa*, which has darker antennae compared to *P. ruficornis*. Females have a distinctly paler ventral side of antennae (Fig. 25), while antennae in *P. melanocarpa* are uniformly black (Fig. 24) or have only a slightly paler ventral side. Males of *P. ruficornis* also have generally paler antennae than in *P. melanocarpa* (Fig. 26), but penis valves should be studied to distinguish them from *P. melanocarpa* specimens having conspicuously pale antennae. Ventro-apical spine of penis valve (Figs 79, 81) bends more gradually (forming a half circle) and is usually broader than in *P. melanocarpa* (Figs 80, 82).

Genetic data. Based on COI barcode sequences, specimens of *P. ruficornis* are divided between two BIN clusters (BOLD:ACZ4465 and BOLD:ACZ4466) that also include *P. melanocarpa* (Fig. 1). Minimal distance between these two clusters is only 1.13%. Nuclear TPI sequences do not support separation of *P. ruficornis* from *P. melanocarpa* either (Fig. 2). The single sequenced male would be identical to one of the heterozygous *P. melanocarpa* females when ambiguous positions due heterozygosity are excluded. Examination of all the 14 heterozygous sites (double peaks in chromatograms) in this *P. melanocarpa* specimen revealed that all of them include also the nucleotide found in *P. ruficornis*, possibly indicating haplotype sharing between these two taxa.

Host plants. *Betula pubescens* Ehrh. ssp. *czerepanovii* (N. I. Orlova) Hämet-Ahti (rearings and *ex ovo* rearing experiments by VV).

Distribution and material examined. Western Palaearctic. Specimens studied are from Finland, Germany, Portugal, and Sweden.



Figures 77–86. Penis valves of *Pristiphora ruficornis* group. **77** *P. appendiculata* DEI-GISHym31555 **78** *P. albitibia* DEI-GISHym20956 **79** *P. ruficornis* PR.462VV **80** *P. melanocarpa* PR.425VV **81** *P. ruficornis* DEI-GISHym19636 **82** *P. melanocarpa* PR.409VV **83** *P. armata* PR.465VV **84** *P. leucopus* PR.466VV reared *ex ovo* from *Tilia* sp. **85** *P. armata* DEI-GISHym80020 **86** *P. leucopus* GBIF-GISHym3246 (syntype of *Nematus crassicornis* Hartig).

Pristiphora sootryeni Lindqvist, 1955

Pristiphora sootryeni Lindqvist, 1955: 46. Holotype ♀ in TROM, not examined. Type locality: Småströmmen, Finnmark, Norway.

Similar species. Based on the external morphology, the most similar species are *P. astragali*, *P. confusa*, *P. opaca*, *P. pusilla*, *P. staudingeri*, and *P. subopaca*, from which it is best distinguished by the structure of the lancet (Fig. 45). The lancet has weak ctenidia (weak or well-developed in the others) and on the inner surface of the lancet there are small spiny pectines (or dentes semicirculares) that reach the sclerora (present also in *P. astragali*). However, differences from *P. astragali* are rather small. Morphologically, the subapical tooth of the claws tends to be larger, the apical serrulae of the lancet are longer, and the number of ctenidia on the lancet is larger than in *P. astragali* (Figs 43–44; Vikberg 2006). Male unknown.

Genetic data. Based on a COI barcode sequence of one confidently identified specimen from Kuusamo (Finland; DEI-GISHym80036), it belongs to the same BIN cluster as *P. astragali* (BOLD:AAL8292), which in the BOLD database includes two other unidentified specimens from Manitoba, Canada (Fig. 1). The nearest neighbour (BOLD:AAL8277) is 2.40% different. BIN cluster BOLD:AAL8277 might include *P. astragali*, as one of the included specimens in BOLD database was identified by Matti Viitasaari as "*Pristiphora* nr. *astragali*". Amplification of TPI failed.

Host plants. *Oxytropis campestris* (L.) DC. (Lindqvist 1973; Vikberg 2006).

Distribution and material examined. Western Palaearctic. Specimens studied are from Finland.

Pristiphora staudingeri (Ruthe, 1859)

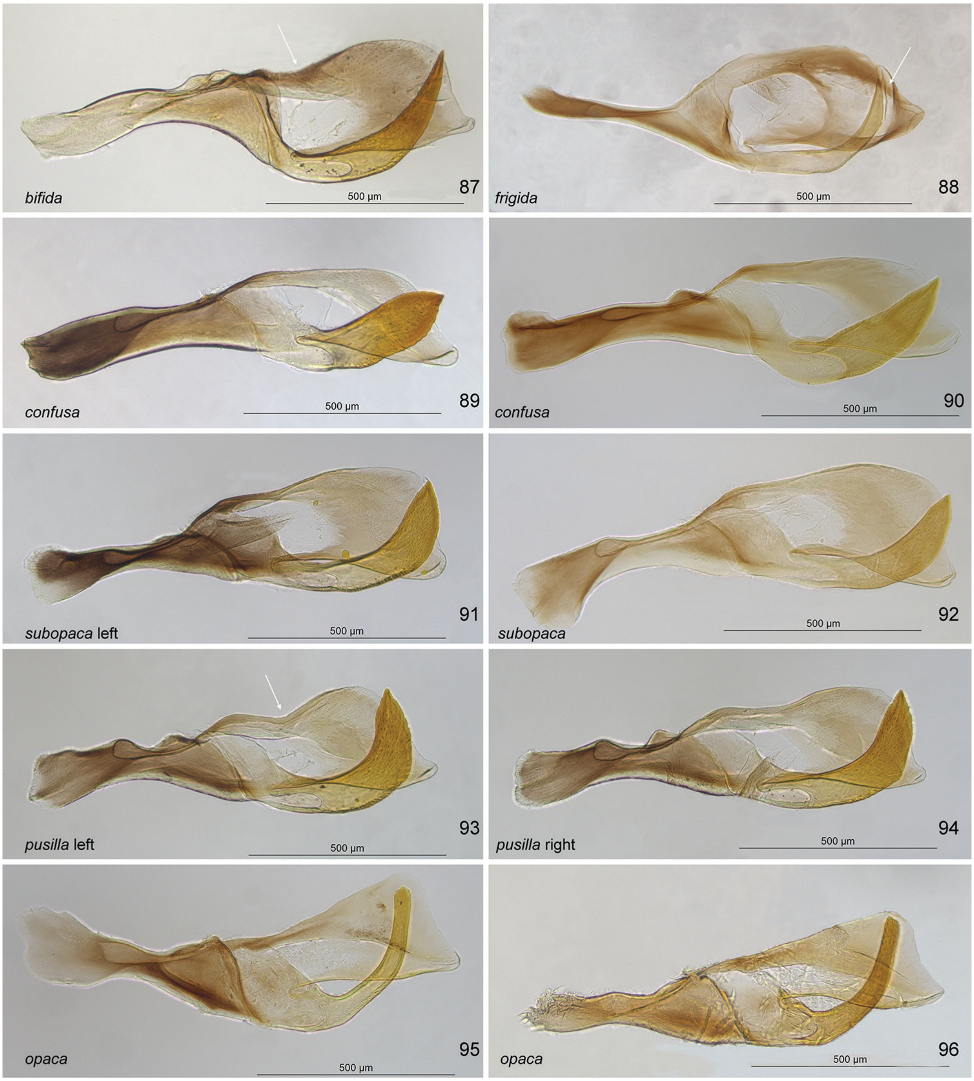
Nematus Staudingeri [sic!] Ruthe, 1859: 306–307. Lectotype ♀ (designated by Vikberg 1978) in NMW, examined. Type locality: Iceland.

Pristiphora circularis Kincaid, 1900: 350. Holotype ♀ (USNMENT00778165) in USNM, not examined. Type locality: Popof Island, Alaska, USA.

Pristiphora hyperborea Malaise, 1921: 11. Lectotype ♀ (NHRS-HEVA000003650; designated by Vikberg 1978) in NHRS, examined. Type locality: Torne Träsk, Torne Lappmark, Sweden.

Pristiphora asperlatus Benson, 1935: 35–38. Holotype ♀ in BMNH, not examined. Type locality: Mount Braeriach, Inverness, Scotland, United Kingdom.

Similar species. Based on the external morphology, the most similar species are *P. astragali*, *P. confusa*, *P. luteipes*, *P. opaca*, *P. pusilla*, *P. sootryeni*, and *P. subopaca*. The combination of usually strongly coriaceous sculpture on the mesepisternum (Fig. 20), the habitat (arctic or subarctic), and the structure of the lancet (absence of small spiny pectines or dentes semicirculares and well developed ctenidia; Figs 73–76) or penis valves (Figs 97–100, 102) should usually enable distinction of the species from other similar species. Vikberg (1978) treated *P. hyperborea* Malaise tentatively as a separate species, but no characters distinguish it unambiguously from *P. staudingeri*. The small differences in lancets (Figs 73–76), penis valves (Figs 97–100, 102) and the sculpture of the mesepisternum most likely represent within species variation and therefore we treat *P. hyperborea* as a synonym of *P. staudingeri* as suggested by Lindqvist (1953). In addition, penis valves and lancets cannot be distinguished from *P. luteipes* and *P.*



Figures 87–96. Penis valves of *Pristiphora ruficornis* group. **87** *P. bifida* DEI-GISHym80000 (arrow indicates a dorsal depression of the pseudoceps) **88** *P. frigida* NHRS-HEVA000003861 (arrow indicates a membranous fold near the tip of the ventro-apical spine) **89** *P. confusa* DEI-GISHym31265 **90** *P. confusa* PR.460VV **91** *P. subopaca* DEI-GISHym80030, left penis valve **92** *P. subopaca* paratype http://id.luomus.fi/GL.5203 **93** *P. pusilla* DEI-GISHym80029, left penis valve with strong dorsal depression of the pseudoceps (arrow) **94** *P. pusilla* DEI-GISHym80029, right penis valve with weak dorsal depression of the pseudoceps **95** *P. opaca* PR.459VV **96** *P. opaca* http://id.luomus.fi/GL.5206, paratype of *P. amaura* Lindqvist.

beaumonti (see under *P. luteipes*) (Figs 60–61, 101, 103), which can have a completely smooth mesepisternum (Fig. 19) and can be extremely pale (Fig. 13). Because of the black metafemur, females of *P. staudingeri* can easily be distinguished from *P. luteipes* (completely yellow metafemur; Fig. 23), but two studied Swedish specimens (Jämtland County at an altitude 900 m) had an apically slightly yellow (W10115) or even apically half yellow metafemur (W10105), weakening the distinction between these taxa.

Genetic data. Based on COI barcode sequences, belongs to the same BIN cluster (BOLD:AAG3568) as *P. aphantoneura*, *P. bifida*, *P. confusa*, *P. opaca*, *P. pusilla*, and *P. subopaca* (Fig. 1). The nearest neighbour (BOLD:AAQ2302, *P. armata* and *P. leucopus*) is 2.76% different. It is not clear if nuclear TPI sequences allow better identification of *P. staudingeri* compared to COI barcode sequences, mainly because the identity of the male specimen DEI-GISHym80049 (Fig. 2) is uncertain. According to TPI sequence, this male from Sweden is closer to *P. luteipes* (males of which are not known from northern Europe for certain) than to *P. staudingeri* (Fig. 2), but morphological characters and collecting locality (Härjedalen at an altitude of 840 m) does not allow for certain identification. In addition, COI barcode of DEI-GISHym80049 is identical to one of the *P. staudingeri* specimens (Fig. 1).

Host plants. *Salix herbacea* L. and *S. phylicifolia* L. (Vikberg 1978).

Distribution and material examined. Western Palaearctic, Nearctic. Specimens studied are from Finland, France, Great Britain, Iceland, Norway, Sweden, and Switzerland. The species should be removed from the fauna of Denmark. Publications (e.g. Taeger et al. 2006) mentioning this species from Denmark are based on misinterpretation of Nielsen and Henriksen (1915), who actually recorded *P. albitibia* under the name *P. staudingeri*, as evidenced by the mentioned hostplant, *Vicia cracca*.

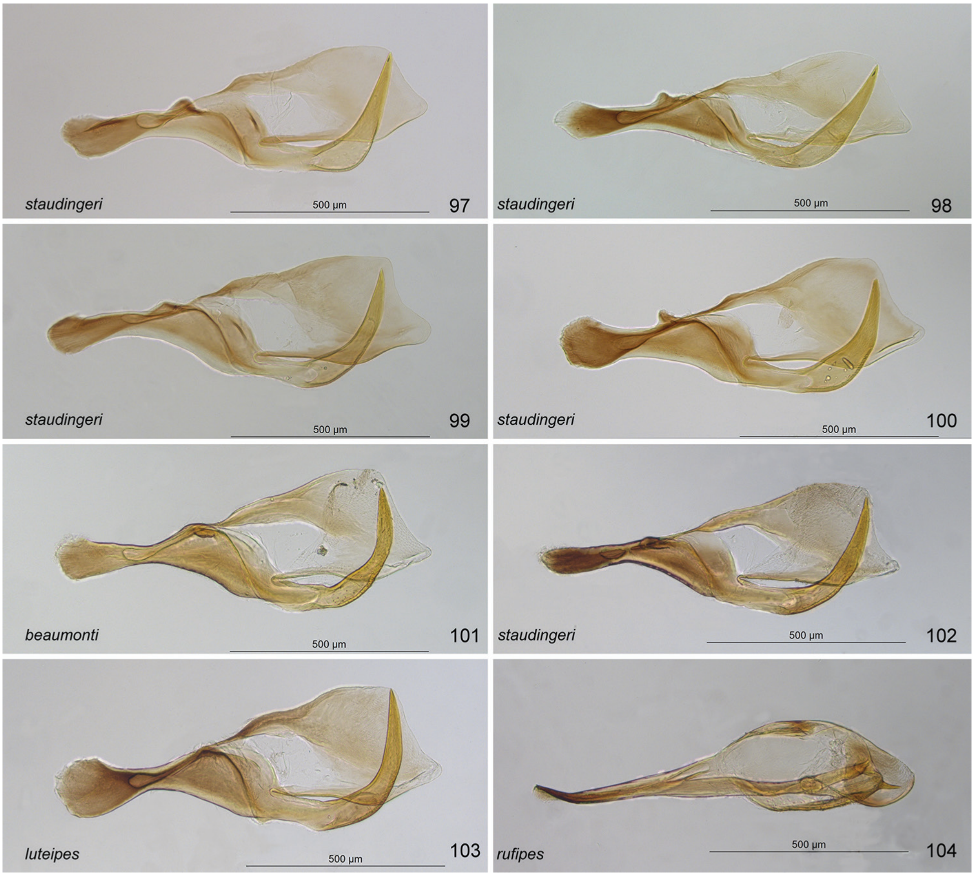
Pristiphora subopaca Lindqvist, 1955

Pristiphora subopaca Lindqvist, 1955: 41–42. Holotype ♀ (http://id.luomus.fi/GL.5202) in MZH, examined. Type locality: Munksnäs, Uusimaa, Finland.

Pristiphora coniceps Lindqvist, 1955: 39–40, **syn. n.** Holotype ♀ (http://id.luomus.fi/GL.5207) in MZH, examined. Type locality: Pihtipudas, Central Finland, Finland. Note. The male paratype (http://id.luomus.fi/GL.5208) is not conspecific with the holotype female and belongs to *P. melanocarpa*; therefore most records of *P. coniceps* in the literature based on the penis valve belong to that species.

Pristiphora brunniapex Lindqvist, 1960: 37–38, **syn. n.** Holotype ♀ in MZH, examined. Type locality: Pisa, Rovaniemi, Finland.

Similar species. Based on the external morphology, the most similar species are *P. albitibia*, *P. confusa*, *P. opaca*, *P. pusilla*, and *P. sootryeni*. The species is best distinguished through the structure of male penis valve (Figs. 91–92). Unfortunately, it is rather difficult to separate females from *P. confusa* and *P. opaca* as the differences in the lancets are small (Figs 62–69). Apical serrulae are perhaps less protruding and longer (Figs 66–69) than in *P. confusa* (Figs 62–63) and the basal part of the tangium lacks a fold that is present in *P. opaca* (Figs 64–65). Externally, the pterostigma is uniformly yellow (Fig. 27) unlike in *P. confusa* and *P. opaca*, in which the pterostigma is basally



Figures 97–104. Penis valves of *Pristiphora ruficornis* group and *P. rufipes*. **97** *P. staudingeri* PR.361VV **98** *P. staudingeri* PR.447VV **99** *P. staudingeri* PR.352VV **100** *P. staudingeri* PR.453VV **101** *P. beaumonti* DEI-GISHym21176 **102** *P. staudingeri* DEI-GISHym21228 **103** *P. luteipes* DEI-GISHym19681 **104** *P. rufipes* DEI-GISHym15263.

dark brown and apically brown (Fig. 28). In addition, the claws of *P. subopaca* tend to have a larger subapical tooth (Fig. 32) than in *P. opaca* (Fig. 31). Among the males, the most similar penis valves are of *P. confusa* and *P. pusilla*. The ventro-apical spine is bent more strongly and the pseudoceps is broader (Figs 91–92) than in *P. confusa* (Figs 89–90). Compared to *P. pusilla* (Figs 93–94), the ventro-apical spine is bent less strongly and the dorsal depression in the middle of pseudoceps is less distinct, which is clear only when compared to the left penis valve of *P. pusilla* (Fig. 93). The holotype of *coniceps* Lindqvist does not differ in any significant way from the holotype of *subopaca* Lindqvist. The characters mentioned in the structure of the head and thorax for *coniceps* in the original description (Lindqvist 1955), that are supposed to differentiate this species from others in the *ruficornis* group, are minute and unreliable. The characters that help in species identifications in closely related species (colour of pterostigma and antennae, degree of coriaceous sculpture of mesepisternum, size of subapical tooth of claws, and the structure of the lancet) are not different between the holotypes of *coniceps* and *subopaca*. The host (*Salix*) mentioned for *coniceps* in the original description (Lindqvist 1955) and by Kangas (1985) (as *Salix caprea* L.) also fits with the data recorded for *P. subopaca* (Lindqvist 1965; Kangas 1985). Consequently we treat *coniceps* as a synonym of *subopaca*. We also treat *brunniapex* Lindqvist as a rare colour form (only the holotype and one additional female are known to us) of *subopaca* Lindqvist, because the only difference is that *brunniapex* has a pale tip of the abdomen (terga 7–10 or 8–10; Figs 10, 12). Based on the second known specimen (DEI-GISHym20899, deposited in MZH) reared by J. Perkiömäki from *Salix* sp. (near Helsinki, Finland), we can say that the host is not different from *subopaca* either. Although the lancet of *brunniapex* cannot be distinguished from *P. aphantoneura*, *P. luteipes* and *P. staudingeri*, these species can be separated from *subopaca-brunniapex* by having different host (*Lathyrus pratensis* for *P. aphantoneura*), yellow metafemur (*P. aphantoneura* and *P. luteipes*), or as in *P. staudingeri* usually strongly coriaceous sculpture of mesepisternum and different habitat (arctic or subarctic).

Genetic data. Based on COI barcode sequences, *P. subopaca* belongs to the same BIN cluster (BOLD:AAG3568) as *P. aphantoneura*, *P. bifida*, *P. confusa*, *P. opaca*, *P. pusilla*, and *P. staudingeri* (Fig. 1). The nearest neighbour (BOLD:AAQ2302, *P. armata* and *P. leucopus*) is 2.76% different. Only one TPI sequence is available, which can be distinguished from other species (Fig. 2).

Host plants. *Salix caprea* L. (Lindqvist 1965; Kangas 1985) and *S. phylicifolia* L. (Lindqvist 1965).

Distribution and material examined. Western Palaearctic. Specimens studied are from Finland and Sweden.

Discussion

Taxonomy of the species belonging to the *ruficornis* group as defined here (Fig. 1) has hitherto been rather complicated, and there has not been a review of all the species involved. The main questions have been, how many species there are, how to identify them, and association of males and females. For northern Europe, we identified which species are well supported (most) and should be recognised and which ones require more detailed studies (e.g. host plant choice experiments and sequencing of more nuclear DNA data) to decide their validity. The species pairs that are not well supported are *P. aphantoneura-P. luteipes*, *P. armata-P. leucopus*, and *P. melanocarpa-P.ruficornis*, identification of which is difficult or not always possible. Although our limited genetic data is consistent with separation of *P. luteipes* from *P. aphantoneura* (Fig. 2), the limited sampling of specimens does not allow us to make any definite conclusions. There is no clear genetic support for separating *P. leucopus* from *P. armata*, nor *P. melanocarpa* from *P. ruficornis*. The separation of *P. leucopus* from *P. armata* is currently supported mainly by two biological differences: their different hosts, and the existence of seasonal morphs in the former, but not in the latter. Furthermore, the coloration of the larvae may be different (see above, under Introduction). However, the larval morphology of both species needs more detailed study. *P. melanocarpa* is separated from *P. ruficornis* only on minor morphological differences in the adults. Here too, the larvae require further study. Another issue not entirely solved involves *P. luteipes*, *P. staudingeri*, and *P. beaumonti* (North African taxon not treated here), because morphological characters used to distinguish them (colouration and sculpture of the mesepisternum) might be influenced by environmental factors rather than genetic ones, though our limited nuclear data indicates several separate lineages (Fig. 2). The other taxa treated here can be considered to be distinct species, although the evidence for treating *P. astragali* and *P. sootryeni* as separate species is currently relatively weak (basically based only on the differences in the structure of the lancet), as the males are unknown and nuclear DNA data are lacking.

Even if most of the species treated here can be considered distinct, their identification unfortunately remains relatively difficult. For reliable results, lancets and penis valves should be studied. Nevertheless, we hope that the current revision removes most of the previous confusion about species identities, their names and the association of females and males, as well as enabling more reliable and confident identification of the species. One further issue that is worth following up is the identity of the species in North America, as barcoding has revealed close connections to Northern Europe (there are many identical or nearly identical barcodes between the continents; Fig. 1), presumably via northern Eurasia. The only species that definitely belongs to the *ruficornis* group in the East Palaearctic or Oriental Regions, and which is not known in the West Palaearctic, is *P. ribisi*. However, the *Pristiphora* of these regions have not been intensively investigated.

Examination of most of the barcoded specimens from Europe revealed that most of the species within the *Pristiphora ruficornis* group cannot be unambiguously identified based on mitochondrial COI barcodes. Nevertheless, barcoding showed the presence of five well separated clusters within the *ruficornis* group, each containing a unique set of species (Fig. 1). This enables detection of at least some misidentifications. For example, specimens in BOLD identified as *P. melanocarpa* or *P. ruficornis* within the *armata* subgroup are almost certainly wrong and should be re-examined to check if they belong to *P. armata*, *P. leucopus*, or both. Another benefit of barcoding is placing unidentified specimens, which can reveal important specimens worthy of a closer look (for example new distributional records or new phylogenetic lineages). The inability of mitochondrial DNA to identify closely related species, even when there is enough variation (barcode differences around 2–3%), has been shown to be the case in several other sawfly groups (Linnen and Farrel 2007; Prous et al. 2011). This is perhaps not so surprising in the light of recent theoretical population genetic studies (Patten et al. 2015) that found biased introgression patterns of mitochondrial DNA in comparison to nuclear DNA in haplodiploid species (as is the case for Hymenoptera). This suggests that nuclear DNA might be more successful in identifying closely related species in these cases, as was found to be the case in *Empria* and *Neodiprion* (Linnen and Farrel 2007; Prous et al. 2011). Although our results for the *ruficornis* group based on one single-copy nuclear protein coding gene (TPI) are consistent with this observation

(Fig. 2), the small number of specimens sequenced (due to poor quality DNA of most of the available samples, i.e. air-dried pinned specimens) does not at the moment allow us to propose that this particular nuclear gene is definitely better for species identification than COI barcodes. Additional studies based on more nuclear genes and more specimens from different sawfly groups are needed to decide which nuclear region might be useful for species identification of most sawflies.

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RESEARCH ARTICLE

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Sawflies (Hymenoptera: Argidae, Pergidae, Tenthredinidae) from southern Ecuador, with a new record for the country and some ecological data

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Abstract

An illustrated list of species of sawflies collected during 2014 and 2015 in southern Ecuador is given. One genus and species, *Pristiphora fernandezi* Smith (Tenthredinidae), is new for the country. Ecological data are provided for *Lagideus podocarpus* Smith, **sp. n.** (Pergidae) that was observed feeding on *Fuchsia vulcanica* L. (Onagraceae). Three new combinations are proposed: *Bolivius notabilis* (Konow, 1899), *Plaumanniana biclinea* (Konow, 1899), and *Proselandria alvina* (Konow, 1899) (Tenthredinidae: Selandriinae).

Keywords

Species list, páramo, host plant, *Fuchsia*, *Lagideus*, larva, defence behaviour

Introduction

Most sawflies described from South America belong to the Tenthredinidae (Smith 2003a, 2003b), Argidae (Smith 1992), and Pergidae (Smith 1990). Worldwide, the most species-rich family is the Tenthredinidae with over 5700 species (Taeger et al. 2010). The Argidae include ca. 900 species distributed throughout the world but with a greatest number and diversity occurring in the Neotropical Region (Smith 1992). They are mainly associated with angiosperms. The Pergidae include ca. 440 species, occurring in the Australasian, Nearctic, and Neotropical regions (Smith 1990; Schmidt and Smith 2006). They are the most diverse in Australia and the Neotropics.

Related to its size, Ecuador is among the countries with highest biodiversity, which is mainly due to its tropical location as well as the presence of the Andes, Amazon Basin and two major ocean streams. These combined factors lead to a high variety of distinct environments. One typical biotope for tropical highlands is called the 'páramo' which occurs in southern Ecuador.

Here, we list the sawflies which were collected mainly in the Podocarpus National Park (NP) that is characterized by the páramo. The collections were performed in the frame of a Global Taxonomy Initiative (GTI) project.

Methods

Sawflies were collected in southern Ecuador, mainly around Loja (e.g., Fig. 1) and during October 2014. Most sawflies were collected as adults using a net, a few being collected in yellow pan traps, while larvae were found only at one location. The specimens were stored in ethanol, but some of the larvae were reared to obtain the adults.

Most pictures were taken by J.-L. Boevé with the following cameras: Pentax Optio W10, Nikon Coolpix P300, and Nikon D7000. Since adult specimens are kept in ethanol, they were slightly dried to take the pictures, which were mainly intended to illustrate the habitus. Pictures were also taken by D. R. Smith (Fig. 10) and Thibaut Delsinne (Fig. 21b, e, f, g).

The sawfly specimens collected as part of the GTI project are stored in the Royal Belgian Institute of Natural Sciences, Brussels, Belgium (RBINS; J.-L. Boevé collection, with specimen reference codes starting with 'P'), with duplicates located in the National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (USNM), and Museo de Colecciones Biológicas, Universidad Técnica Particular de Loja, Ecuador (MUTPL). Sawfly specimens from the RBINS, Senckenberg Deutsche Entomologisches Institut, Müncheberg, Germany (SDEI), and USNM were examined. Dates are given by dd.mm.year.

Taxonomic changes presented here are by D.R. Smith. Identifications of Argidae, Pergidae, and Tenthredinidae (Nematinae) are based on Smith (1990, 1992, 2003b). Identifications of Blennocampinae and Selandriinae (Tenthredinidae) are based on Smith (2007) and unpublished manuscripts by D.R. Smith.

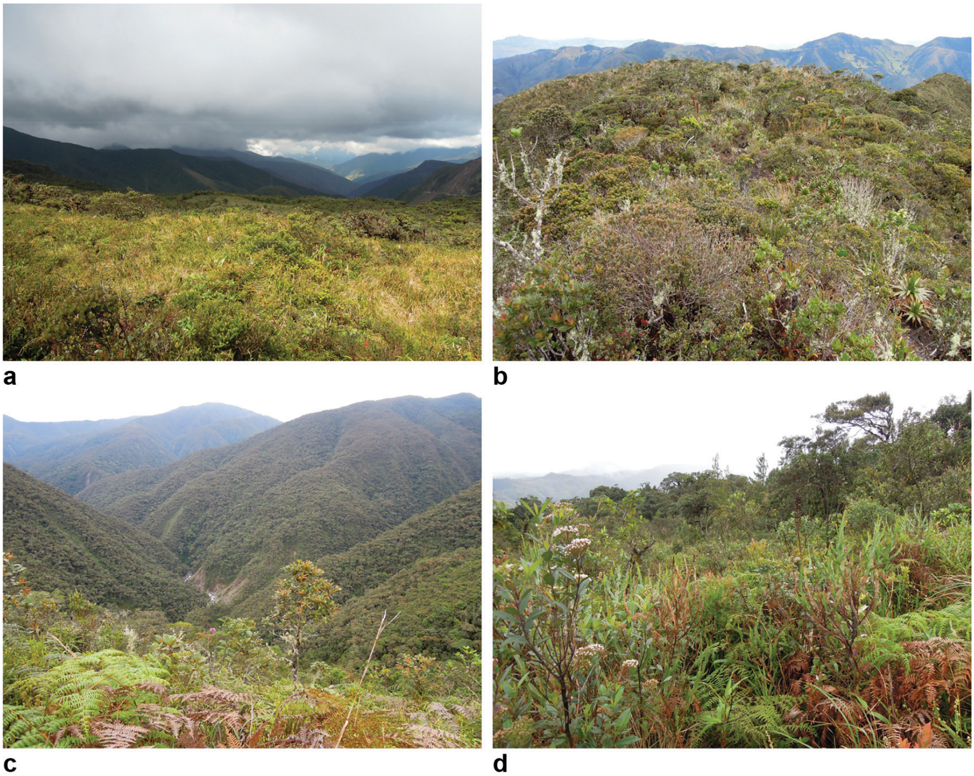

Figure 1. Examples of biotopes in southern Ecuador and where sawflies were collected. **a** El Tiro (altitude 2815 m) **b** Cajanuma "Mirador" (3000 m) **c** Colibrí Station (2170 m) **d** Yangana (ca. 2500 m).

Results

Family Argidae

Scobina bolivari (Konow, 1899)

Fig. 2

Distribution. This species is known from Colombia, Ecuador, Peru, Bolivia, and northern Argentina (Jujuy) (Smith 1992).

Material. Los Geraneos, 04°09'S, 078°38'W, 855m, 18.10.2014, P3944.B (1 ♀), leg. A. Pauly, J.-L. Boevé.

Scobina inculta (Konow, 1906)

Fig. 3

Distribution. Known from Venezuela, Ecuador, Peru, Bolivia, and northern Argentina (Jujuy) (Smith 1992).

Figure 2. *Scobina bolivari*, female (P3944.B), body length 8.0 mm. **a** Dorsal view **b** ventral view.

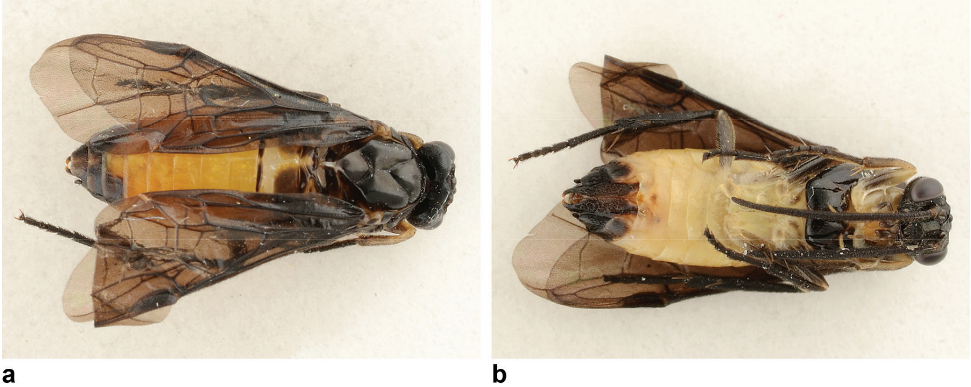

Figure 3. *Scobina inculta*, female (P4120.A), body length 9.5 mm. **a** Dorsal view **b** ventral view.

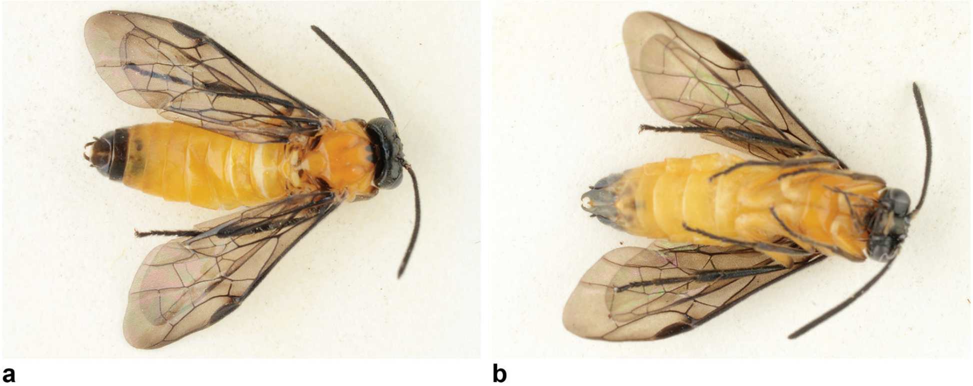

Figure 4. *Scobina notaticollis*, female (P3891), body length 8.5 mm. **a** Dorsal view **b** ventral view.

Material. Bombuscaro, 04°05'S, 078°57'W, 930m, 22.03.2015, P4120.A (1 ♀), leg. T. Delsinne.

Scobina notaticollis (Konow, 1899)

Fig. 4

Distribution. Known from Costa Rica, Panama, Venezuela, Colombia, Ecuador, Peru, and Bolivia (Smith 1992).

Material. Vilcabamba, 04°16'S, 079°13'W, 1570m, 11.10.2014, P3891, P3892 (2 ♀), leg. A. Pauly, J.-L. Boevé.

Scobina spp.

Fig. 5

Material. S. of Yangana, 04°22'S, 079°10'W, 1940m, 09.10.2014, flying, P3890 (1 ♀), leg. A. Pauly, J.-L. Boevé; nr Loja, Reserva El Madrigal, 04°02'S, 079°11'W, 2275m, 21.10.2014, on *Rumex crispus* (Polygonaceae), P3953.B (1 ♂), leg. J.-L. Boevé.

Sericoceros gibbus (Klug, 1834)

Fig. 6

Distribution. A widespread species known from Mexico south to Guyana, Brazil, and Peru.

Material. Bombuscaro, Podocarpus NP, 04°06'S, 078°58'W, 995m, 17.10.2014, flying while crossing footpath, P3937 (1 ♀), leg. A. Pauly, J.-L. Boevé.

Remarks. Larvae have been recorded from *Coccoloba manzinellensis* Beurl. and *C. caracasana* Meisn. in Panama, and *C. guanacastensis* W. C. Biurger (Polygonaceae) in Costa Rica. Notes on the biology were given by Smith and Janzen (2003).

Family Pergidae

Acordulecera spp.

Remarks. Probably four species were found in this study. It is a large genus of perhaps 200 or more species that occurs from Canada to Chile. Smith (1990) listed 45 described species from the Neotropics.

Material. Valle de Quinara, 04°18'S, 079°16'W, 1550m, 09.10.2014, P3888.A, P3888.B (2 ♂), leg. A. Pauly, J.-L. Boevé; Station Colibrí, Podocarpus NP, 03°59'S,

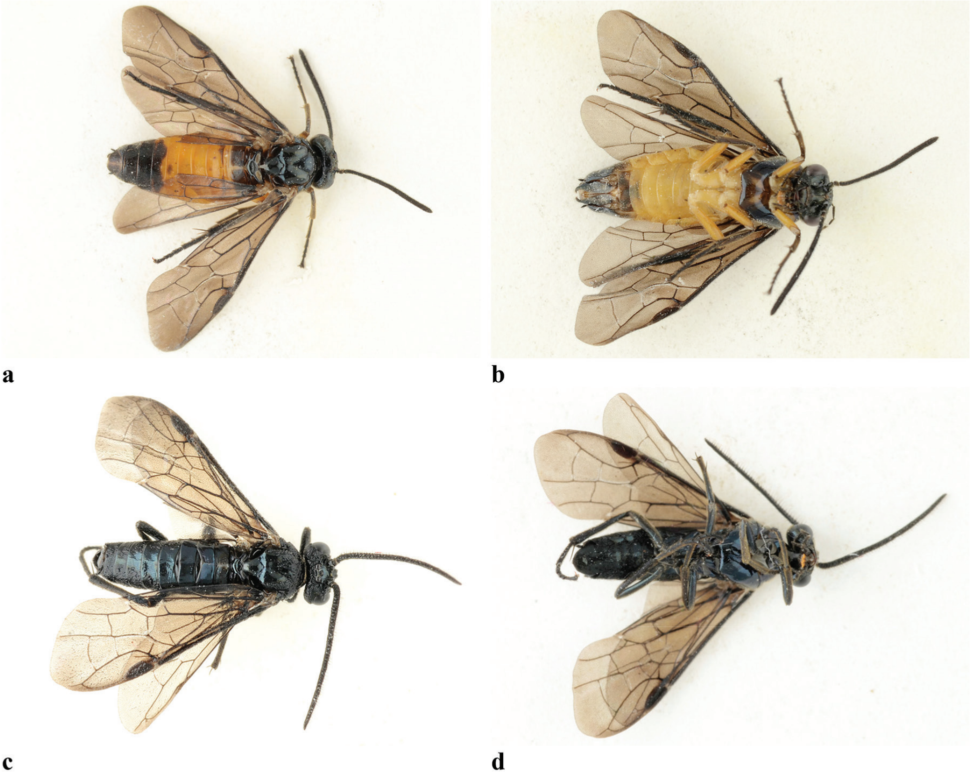

Figure 5. Scobina sp. **a, b** Female (P3890), body length 8.0 mm **c, d** male (P3953.B), body length 7.5 mm **a, c** Dorsal views **b, d** ventral views.

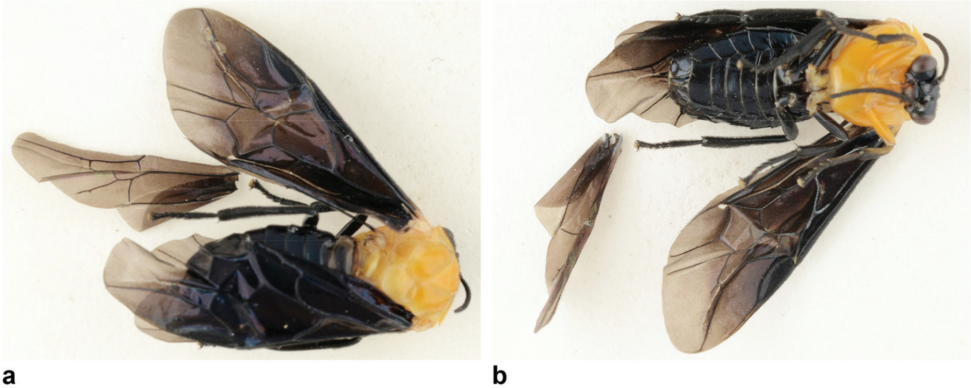

Figure 6. *Sericoceros gibbus*, female (P3937), body length 9.5 mm. **a** Dorsal view **b** ventral view.

079°06'W, 2170m, 13.10.2014, by sweeping, P3902 (1 ♂), leg. A. Pauly, J.-L. Boevé; Bombuscaro, Podocarpus NP, 04°07'S, 078°58'W, 995m, 16.10.2014, P3934 (1 ♀), leg. A. Pauly, J.-L. Boevé; nr Loja, Reserva El Madrigal, 04°02'S, 079°11'W, 2275m,

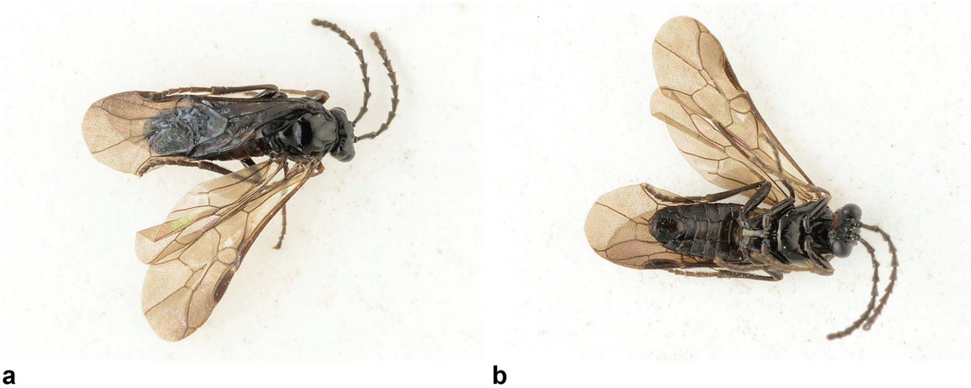

Figure 7. *Decameria varipes*, male (P3956.B), body length 4.0 mm. **a** Dorsal view **b** ventral view.

21.10.2014, near rivulet, P3956.G (1 ♀), P3956.H, P3956.I, P3956.J (3 ♂), leg. T. Delsinne, J.-L. Boevé; Cajanuma, Podocarpus NP, 04°07'S, 079°10'W, 2810m, 23.10.2014, on leaf, P3971 (1 ♀), leg. T. Delsinne, J.-L. Boevé.

Decameria varipes Cameron, 1883

Fig. 7

Distribution. This species occurs from Guatemala south to Ecuador (Smith 1990).

Material. nr Loja, Reserva El Madrigal, 04°02'S, 079°11'W, 2275m, 21.10.2014, near rivulet, P3956.A, P3956.B, P3956.C, P3956.D, P3956.E, P3956.F (6 ♂), leg. T. Delsinne, J.-L. Boevé, on leaf of *Rubus* sp. (Rosaceae), P3950 (1 ♂), leg. J.-L. Boevé.

Remarks. The thorax is typically partly red in most specimens; however melanic forms are occasionally found. The specimens collected here are entirely black but agree in all structural features with the red form. Colour variation is common in some Perreyiinae.

Decameria sp.

Fig. 8

Material. Loja, Reinaldo Espinosa Botanical Garden, 04°02'S, 079°12'W, 2145m, 14.10.2014, P3915 (1 ♂), leg. J.-L. Boevé.

Lagideus podocarpus Smith, sp. n.

http://zoobank.org/A9FD9A79-348D-42A2-8176-AAF8A2C0DA07

Figs 9–11

Description. Female. Unknown.

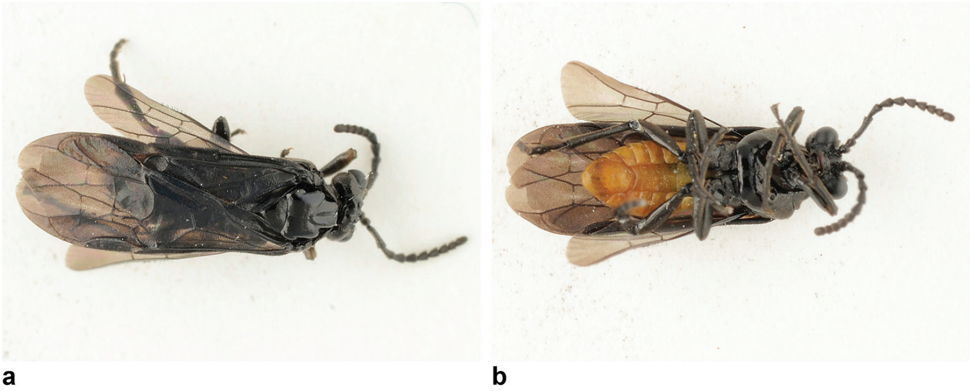

Figure 8. *Decameria* sp., male (P3915), body length 5.5 mm. **a** Dorsal view **b** ventral view.

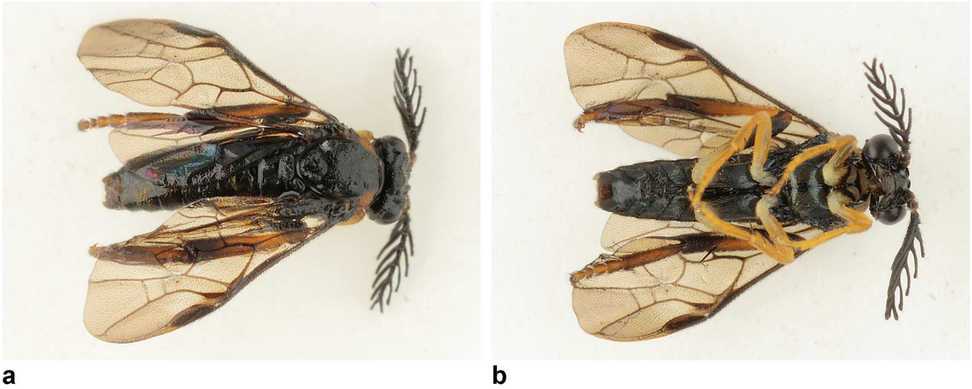

Figure 9. *Lagideus podocarpus*, male (P3898.etc>13), body length 6.0 mm. **a** Dorsal view **b** ventral view.

Figure 10. Male genitalia of *Lagideus podocarpus*. At left, genital capsule, ventral view; at right, penis valve, lateral view with dorsal margin to right.

Male. Length 7.0 mm. Antenna and head black; labrum and mouthparts white; mandible dark red brown. Thorax black with posterior corners of pronotum orange. Fore and midlegs light orange; fore coxa black with white stripe on outer surface and extreme apex white; mid coxa black with extreme apex white. Hind legs black with extreme apex of coxa, trochanters, and extreme base of femur white and about basal half of tibia light orange. Wings hyaline; veins and stigma black.

Head with vertex and frons shiny, very few widely scattered punctures; area adjacent to inner orbits slightly dull, micropunctured; with long golden hairs, as long as or longer than second antennomere. Antenna 1.5× head width; antennomeres 4-8 bipectinate, antennomere 3 unipectinate with inner ramus absent to very slightly indicated (Smith 2012: fig. 25); apical antennomere with rami less than half length of stem. Malar space linear. Thorax shiny; mesonotum with distinct punctures, separated by flat shiny interspaces more than puncture diameters; with long golden hair on dorsum and grey to white hair on pleurae and sterna. Hindbasitarsomere slightly longer than length of remaining tarsomeres combined; inner hind tibial spur about 0.6× length of basitarsomere. Genitalia in Fig. 10; parapenis uniformly broad, not distinctly indented on posterior margin; valviceps of penis valve with dorsal margin concave.

Type material. Holotype labelled "Ad.M, ex-larva," "ECUADOR: Cajanuma, Podocarpus NP, 04°07'S, 079°10'W, 2810 m, X.2014, on Fuchsia vulcanica, JLBoevé leg. RBINS, EtOH100%, P3898.etc>10" (RBINS). Paratypes: Same data as for holotype except P3898.etc>01 (1 ♂), P3898.etc>02 (1 ♂), P3898.etc>03 (1 ♂), P3898.etc>04 (1 ♂), P3898.etc>05 (1 ♂), P3898.etc>06 (1 ♂), P3898.etc>07 (1 ♂), P3898.etc>08 (1 ♂), P3898.etc>09 (1 ♂), P3898.etc>11 (1 ♂), P3898.etc>12 (1 ♂), P3898.etc>14 (1 ♂); these specimens are in RBINS, USNM and MUTPL.

Other material. Cajanuma, Podocarpus NP, 04°07'S, 079°10'W, 2810m, 11.10.2014, on *Fuchsia vulcanica* (Onagraceae), P3898 (6 larvae), 14.10.2014, on *F. vulcanica*, P3917 (4 larvae), P3919 (20–30 larvae), 23.10.2014, on *F. vulcanica*, P3968 (>30 larvae), P3969 (6 larvae), P3970 (6 larvae), P3976 (4 larvae), leg. J.-L. Boevé.

Etymology. Named for Podocarpus National Park, Ecuador, where the collections were made; a noun in apposition.

Comments. Although only the male is known, it differs from described species, and we prefer to have a name since it was reared and the life history and host plant are known. Only females are known for most species of *Lagideus*, and this could be the opposite sex of one of those. However, this won't be known until the sexes are associated.

The bipectinate antennomeres 4-8 and unipectinate antennomere 3 will take this species to couplet 17c in Smith (2012) which includes *L. longicus* Smith and *L. tapanti* Smith, both known from Costa Rica. The black antenna and similarity of genitalia will put it closest to *L. longicus*.

Lagideus tapanti has white hairs on the head and body, antennomeres 1-3 or 4 yellowish, thorax black, and legs black with the base of the femora white; the antenna (Smith 2012: fig. 25) has the rami of the apical antennomere much longer than the stem;

Figure 11. Life history traits of *Lagideus podocarpus*. **a** A patch of the host plant *Fuchsia vulcanica* **b** a plant with feeding damage, seen from above **c–e** larvae attached to the underside of leaves, seen from below **f** a larva that just moulted with exuvia visible.

and the parapenis of the male genitalia are lobed posteriorly with a central, shallow posterior emargination (Smith 2012: fig. 28). *Lagideus longicus* is entirely black and the apical antennomere has long rami as in *L. tapanti*; the parapenis of the genitalia is distinctly indented posteriorly for at least a third of its medial length (Smith 2012: fig. 29); and the valviceps of the penis valve have a straight dorsal margin (Smith 2012: fig. 33).

Lagideus podocarpus can be distinguished from both these species by light orange posterior corners of the pronotum; the light orange fore and mid legs (except the partly black coxae); basal half of the hind tibia light orange; the antennae, similar to *L. longicus* (Smith 2012: fig. 25) except the rami of the apical antennomere are short, less than half the length of the stem; and the male genitalia (Fig. 10) which has the parapenis nearly uniformly broad, without a central posterior emargination and the valviceps of the penis valve distinctly concave dorsally.

The length varies slightly 6.0–7.5 mm. The tegulae may be black to brown or partly light orange as are posterior corners of the pronotum.

Life history. The population of *L. podocarpus* at Cajanuma (Fig. 11) consisted of larvae found within a circumference of ca. 100 m, on several patches of the host plant, *F. vulcanica* L. (Onagraceae). The larvae were attached to the underside of a leaf and they were generally aggregated in that one or a few individuals occurred per leaf. Younger larvae skeletonised the leaves and made holes in the leaf, whereas larvae of later instars attacked the leaf up to its edge. Larvae fed on both younger and older leaves. One large patch of flowering plants clearly harboured fewer larvae than the smaller and more numerous spots of non-flowering plants. The larvae being kept in rearing still appeared as healthy, despite the fact that the offered leaves (during November 2014) were less fresh and rather decaying. A couple of plant species and varieties were also offered to them to roughly establish their diet breadth. *Fuchsia* 'Koralle' was rather accepted, whereas only very few small holes were made on leaves of *Fuchsia* 'Gartenmeister Bonstedt'. These two varieties are cultivars of *Fuchsia triphylla* that is related to *F. vulcanica* (Marc Reynders, personal communication). A leaf of *Oenothera* sp. (Onagraceae) was also tested, but not accepted.

Larvae of nearly all instars were found in the field, but no adults were collected by sweeping. Among the larvae kept in rearing, several individuals reached the eonymph stage (Fig. 11g–h), during the first ten days of October 2014. They formed a cocoon between fresh or rather decaying leaves (Fig.11i), or in an offered layer of moistened sand. At the end of October, prepupae and cocoons occurred in the rearing. A total of 14 adults, all males, emerged from 20.11 to 12.12.2014.

Once disturbed, a larva of *L. podocarpus* reacted immediately by raising its abdomen (Fig. 11j), then slowly lowering it. This reaction could be repeated several times, under successive disturbances. After several such behaviours, the larva tended to slightly walk backwards. The prepupa reacted under disturbance by curling its body and making some slow movements. To further investigate the larval defensive behaviour, a dozen workers of the ant species *Eciton burchellii* Westwood (Formicidae) were collected in the field (Pueblo Viela, 15.10.2016), held without feeding, and used ca. 36 h later. The bioassay consisted of placing seven ant workers and one larva settled on a host plant leaf in an open box, the interactions being then filmed. As far as no ant contacted the larva, the latter remained merely immobile. But once contacted, the larva instantly raised its abdomen and directed the apical filaments towards the aggressor (Fig. 11k–l). Thus, these filaments seem to play a major role in defence. Their size is impressive, with a length of 13 mm for a remaining body size of 16 mm. The

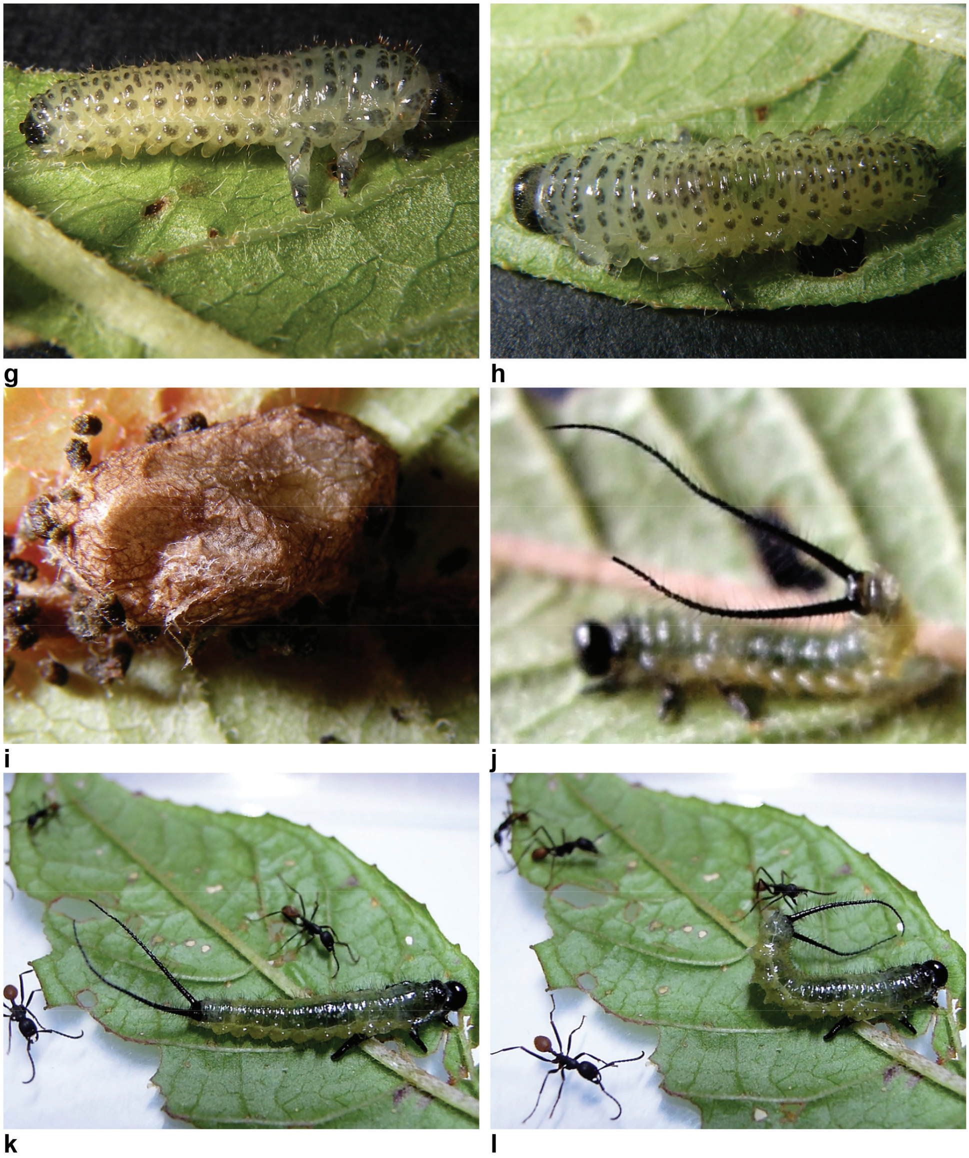

Figure 11. Continue. **g, h** prepupal stage **i** cocoon **j** screenshot of a video clip, the thorax of the larva was touched with flexible forceps a second before **k, l** two screenshots of a video clip performed during a bioassay, both being spaced by 1 sec: an ant is approaching the larva (first screenshot), then touching it, which immediately provokes the defensive behaviour of the larva that directs its caudal filaments towards its aggressor (second screenshot).

filaments resemble those of the larvae of *Philomastix*; the two genera are sister-groups (Schmidt and Walter 2014). However, the filaments protrude from the apical segment in *Lagideus* and the ninth one in *Philomastix* (Smith and Bado 2004). Moreover, it seems that they are clearly covered with spines in *Lagideus* only (Fig. 11; Smith and Bado 2004). It is unclear whether the defence is only physical, or includes chemical compounds. Larvae of Pergidae contain toxic peptides which are active against vertebrates and invertebrates (Boevé et al. 2014), but whether *Lagideus* sp. contains such compounds remains unknown.

Note that another sawfly species (Tenthredinidae) was found among the collected leaves (and stems) of *F. vulcanica*, but in much lower numbers (2 individuals: 11.10.2014, P3899, and 14.10.2014, P3919.C1) than *Lagideus* sp. (>90 in total). This plant constitutes a host plant, since a larva of the tenthredinid was placed on an intact leaf and the larva ingested significant parts of it.

Perreyia picea **(Westwood, 1874)**

Fig. 12

Distribution. This species is known from Colombia, Ecuador, Peru, and Brazil (Smith 1990).

Material. nr Loja, Reserva El Madrigal, 04°02'S, 079°11'W, 2270m, 21.10.2014, P3957.E (1 ♂), leg. A. Pauly, J.-L. Boevé.

Family Tenthredinidae

Subfamily Blennocampinae

Metapedias **sp.**

Fig. 13

Distribution. This Neotropical genus occurs from Mexico to Argentina and includes about 25 species.

Material. Bombuscaro, Podocarpus NP, 04°07'S, 078°58'W, 995m, 16.10.2014, flying just above the ground, P3935 (1 ♀), leg. J.-L. Boevé; N. of Pachicutza, 04°04'S, 078°38'W, 900m, 18.10.2014, P3942.C (1 ♂), leg. A. Pauly, J.-L. Boevé; Loja, Estación Científica San Francisco, 03°58'S, 079°05'W, 1820m, 24.03.2015, P4121.B (1 ♀), leg. T. Delsinne.

Waldheimia atripennis **(Fabricius, 1804)**

Fig. 14

Distribution. This is a relatively common species occurring from Costa Rica to Brazil and Argentina.

Material. Bombuscaro, road to Podocarpus NP, 04°06'S, 078°58'W, 975m, 08.10.2014, P3883 (1 ♂), leg. A. Pauly, J.-L. Boevé; Bombuscaro, Podocarpus NP,

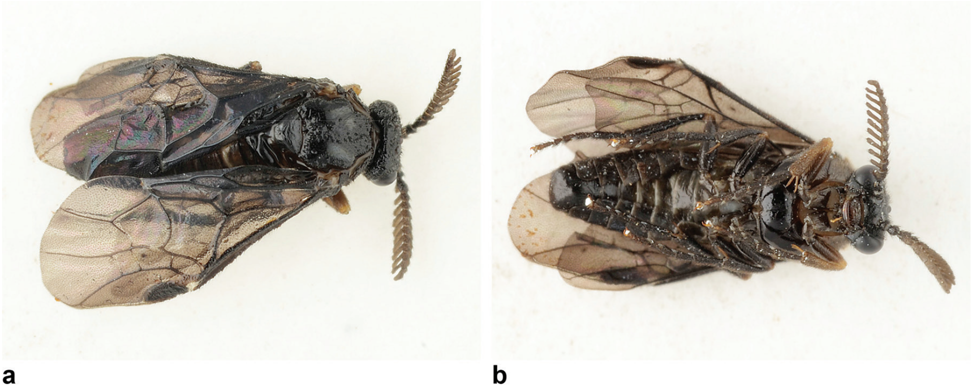

Figure 12. *Perreyia picea*, male (P3957.E), body length 6.5 mm. **a** Dorsal view **b** ventral view.

Figure 13. *Metapedias* sp. **a, b** Female (P4121.B), body length 6.0 mm **c, d** male (P3942.C), body length 6.5 mm. **a, c** Dorsal views **b, d** ventral views.

04°06'S, 078°58'W, 995m, 16.10.2014, P3936.D (1 ♂), leg. A. Pauly, J.-L. Boevé; Los Geraneos, 04°09'S, 078°38'W, 855m, 18.10.2014, P3944.A (1 ♀), leg. A. Pauly, J.-L. Boevé, P3941 (1 ♂), leg. J.-L. Boevé; Miasi, 04°15'S, 078°20'W, 875m, 19.10.2014,

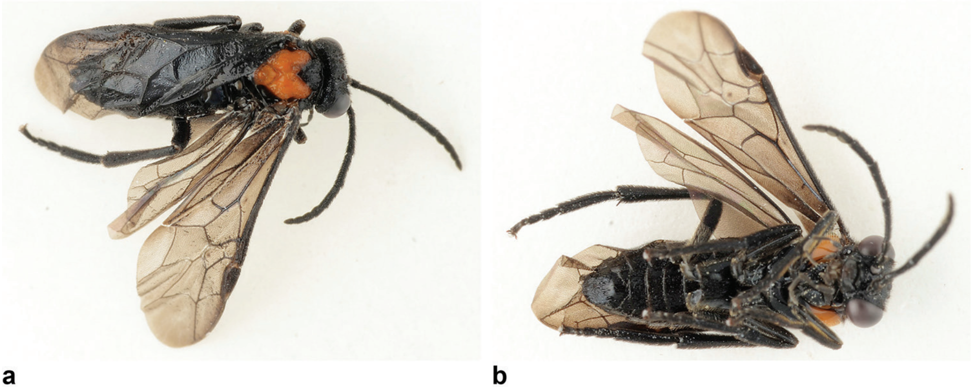

Figure 14. *Waldheimia atripennis*, male (P3967.U), body length 7.0 mm. **a** Dorsal view **b** ventral view.

P3945 (1 ♂), leg. A. Pauly, J.-L. Boevé, on/around leaf of *Anthurium* sp. (Araceae), P3946.A, P3946.B, P3946.C (3 ♂), leg. J.-L. Boevé; Romerillos, nr Podocarpus NP, 04°09'S, 078°56'W, 1100m, 22.10.2014, P3967.O (1 ♀), P3967.U, P3967.W (2 ♂), leg. A. Pauly, J.-L. Boevé.

Waldheimia erebus **(W.F. Kirby, 1882)**

Fig. 15

Distribution. This species is known from Guyana, Brazil, Colombia, Ecuador, and Peru.

Material. Bombuscaro, road to Podocarpus NP, 04°06'S, 078°58'W, 955–975m, 08.10.2014, flying around plants of *Sticherus* sp. (Gleicheniaceae), P3866, P3867, P3868, P3869 (4 ♂), leg. J.-L. Boevé, P3880, P3881, P3882, (3 ♂), leg. A. Pauly, J.-L. Boevé; Pueblo Viela, 04°38'S, 079°08'W, 1060m, 15.10.2014, on leaf of *Anthurium* sp., P3926.B (1 ♀), P3926.A, P3926.C, P3926.D, P3926.E, P3926.F, P3926.H (6 ♂), leg. A. Pauly, J.-L. Boevé; Bombuscaro, Podocarpus NP, 04°06'S, 078°58'W, 995m, 16.10.2014, P3936.B, P3936.C, P3936.E (3 ♂), leg. A. Pauly, J.-L. Boevé; Romerillos, nr Podocarpus NP, 04°09'S, 078°56'W, 1100m, 22.10.2014, P3967.V (1 ♀), leg. A. Pauly, J.-L. Boevé, P3962.B, P3962.C, P3962.D, P3962.E (4 ♂), leg. J.-L. Boevé, P3967.Q, P3967.R, P3967.S, P3967.T, P3967.X, P3967.Y (6 ♂), leg. A. Pauly, J.-L. Boevé, flying, P3959, P3961, P3963.I, P3963.J, P3963.K, P3963.L, P3963.M, P3963.N, P3963.O (9 ♂), on leaf of *Hedychium coronarium* (Zingiberaceae), P3960.C, P3960.D (2 ♂), on leaf of *Anthurium* sp., P3958.F, P3958.G (2 ♂), leg. J.-L. Boevé; Bombuscaro, 04°05'S, 078°57'W, 930m, 22.03.2015, P4120.D, P4120.E, P4120.G (3 ♂), leg. T. Delsinne; Zamora, Copalinga, 04°05'S, 078°57'W, 1000m, 21.07.2015, P4125 (1 ♂), leg. T. Delsinne.

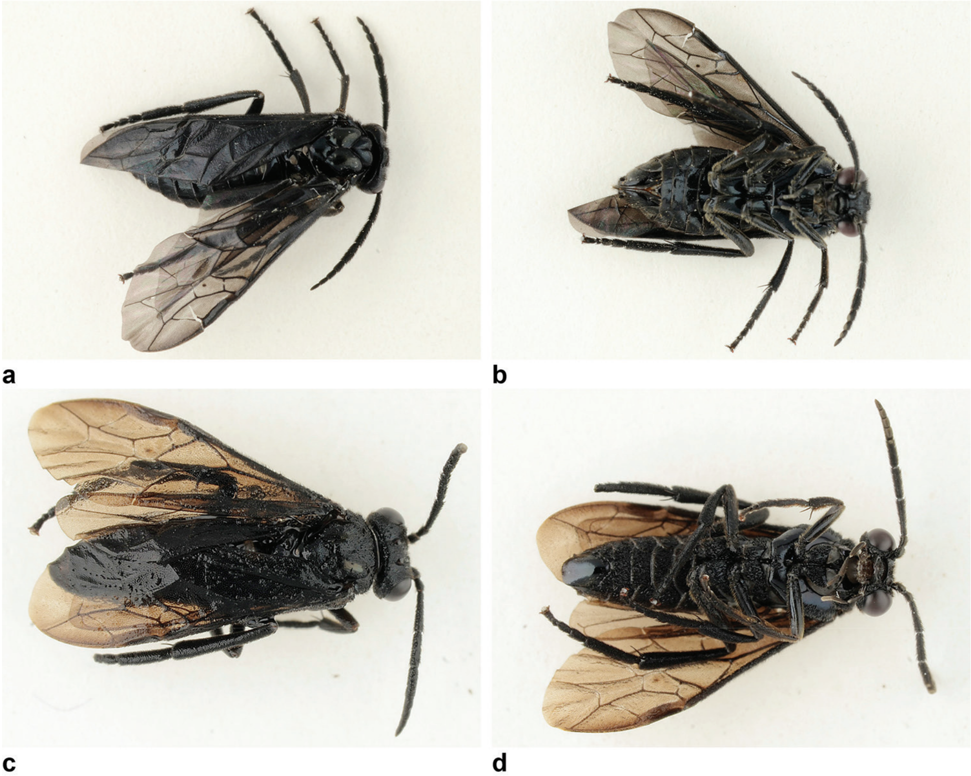

Figure 15. *Waldheimia erebus*. **a, b** Female (P3926.B), body length 7.5 mm **c, d** male (P3967.R), body length 8.0 mm. **a, c** Dorsal views **b, d** ventral views.

Figure 16. *Waldheimia pellucida*, male (P3958.D), body length 6.5 mm. **a** Dorsal view **b** ventral view.

Waldheimia pellucida Konow, 1904

Fig. 16

Distribution. Known from Colombia, Ecuador, Peru, and Bolivia.

Material. Bombuscaro, road to Podocarpus NP, 04°06'S, 078°58'W, 955m, 08.10.2014, flying, P3865 (1 ♂), leg. J.-L. Boevé, P3875, P3876, P3877 (3 ♂), leg. A. Pauly, J.-L. Boevé; Pueblo Viela, 04°38'S, 079°08'W, 1060m, 15.10.2014, on leaf of *Anthurium* sp., P3928.A (1 ♀), leg. A. Pauly, J.-L. Boevé; N. of Pachicutza, 04°04'S, 078°38'W, 900m, 18.10.2014, P3942.B (1 ♂), leg. A. Pauly, J.-L. Boevé; Miasi, 04°15'S, 078°20'W, 875m, 19.10.2014, on/around leaf of *Anthurium* sp., P3946.E, P3946.F, P3946.G (3 ♂), leg. J.-L. Boevé; Romerillos, nr Podocarpus NP, 04°06'S, 078°57'W, 995m, 22.10.2014, on leaf of *Anthurium* sp., P3958.D (1 ♂), leg. J.-L. Boevé.

***Waldheimia* sp.**

Fig. 17

Material. nr Loja, Reserva El Madrigal, 04°02'S, 079°11'W, 2270m, 21.10.2014, P3957.A (1 ♂), leg. A. Pauly, J.-L. Boevé.

Subfamily Nematinae

***Pristiphora fernandezi* D.R. Smith, 2003**

Fig. 18

Distribution. *Pristiphora* is the only native genus of Nematinae in the Neotropics. Nine species were recorded by Smith (2003), from Mexico to Brazil. *Pristiphora fernandezi* was described from Colombia, and the specimen from the Podocarpus NP is the first record of both the species and genus from Ecuador.

Material. Station Colibrí, Podocarpus NP, 03°59'S, 079°06'W, 2170m, 17–20.10.2014, with yellow pan trap, P3948 (1 ♀), leg. A. Pauly, J.-L. Boevé.

Subfamily Selandriinae

Neotropical Selandriinae are poorly studied. Identifications below are based on a key to genera in Smith (2007). Correct combinations of many of the described species have not been published, including three species collected in this study. To apply the correct name to them, the new combinations are presented here.

***Adiaclema* sp.**

Fig. 19

Remarks. A large genus of about 30 species which occur from Mexico to Argentina.

Material. Romerillos, nr Podocarpus NP, 04°09'S, 078°57'W, 1135m, 22.10.2014, flying near rivulet, P3964.B (1 ♀), leg. J.-L. Boevé.

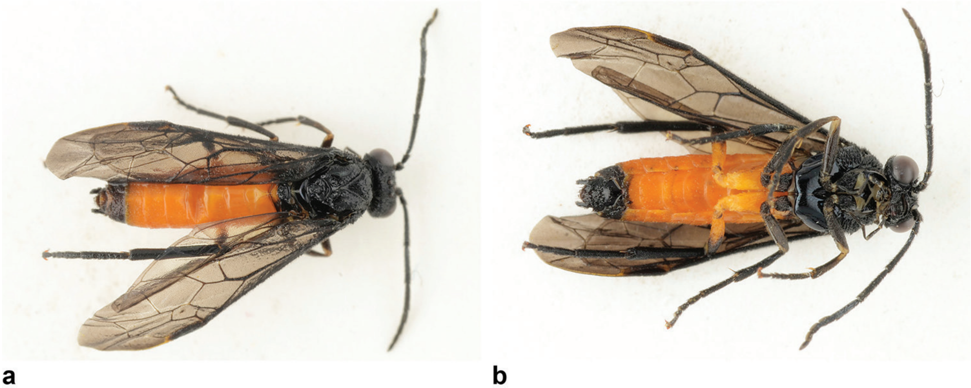

Figure 17. *Waldheimia* sp., male (P3957.A), 9.5 mm. **a** Dorsal view **b** ventral view.

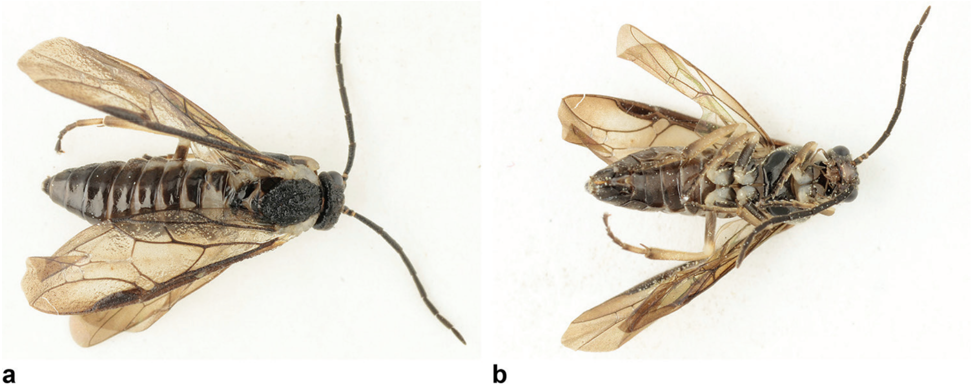

Figure 18. *Pristiphora fernandezi*, female (P3948), body length 8.0 mm. **a** Dorsal view **b** ventral view.

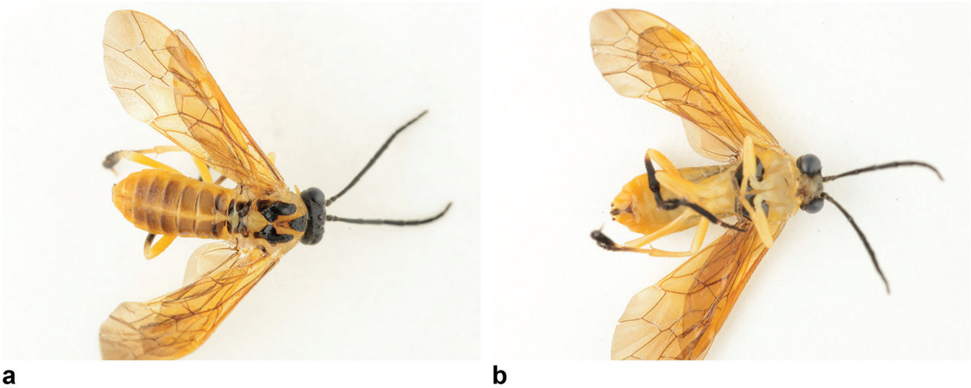

Figure 19. *Adiaclema* sp., female (P3964.B), body length 9.0 mm. **a** Dorsal view **b** ventral view.

Andeana farcta (Konow, 1900)

Figs 20, 21a–c

Distribution. This species is known from Venezuela, Colombia, Ecuador, and Peru.

Material. Yangana, 04°25'S, 079°09'W, 2450m, 09.10.2014, P3889 (1 ♂), leg. D. Domínguez, J.-L. Boevé; Cajanuma, Podocarpus NP, 04°07'S, 079°11'W, 2700m, 11.10.2014, by sweeping herbs, P3893, P3894, P3895, P3896 (4 ♂), leg. J.-L. Boevé, P3897 (1 ♂), leg. Carlos R. Carreira, J.-L. Boevé; N. of Santiago, 03°48'S, 079°16'W, 2550m, 12.10.2014, under a leaf, P3900.A (1 ♂), leg. J.-L. Boevé, P3900.B (1 ♂), leg. A. Pauly, J.-L. Boevé; Cajanuma, Podocarpus NP, 04°07'S, 079°10'W, 2750m, 14.10.2014, P3921 (1 ♂), leg. A. Pauly, J.-L. Boevé; Loja, Reinaldo Espinosa Botanical Garden, 04°02'S, 079°12'W, 2145m, 14.10.2014, by sweeping grass, P3911 (1 ♂), leg. J.-L. Boevé; S. of Yangana, 04°25'S, 079°09'W, 2515m, 15.10.2014, P3932 (1 ♂), leg. A. Pauly, J.-L. Boevé; Valladolid, along river, 04°33'S, 079°08'S, 1605m, by sweeping grass, P3929 (1 ♀), leg. J.-L. Boevé; Vilcabamba (in the car), P3933 (1 ♂), leg. J.-L. Boevé; nr Loja, Reserva El Madrigal,

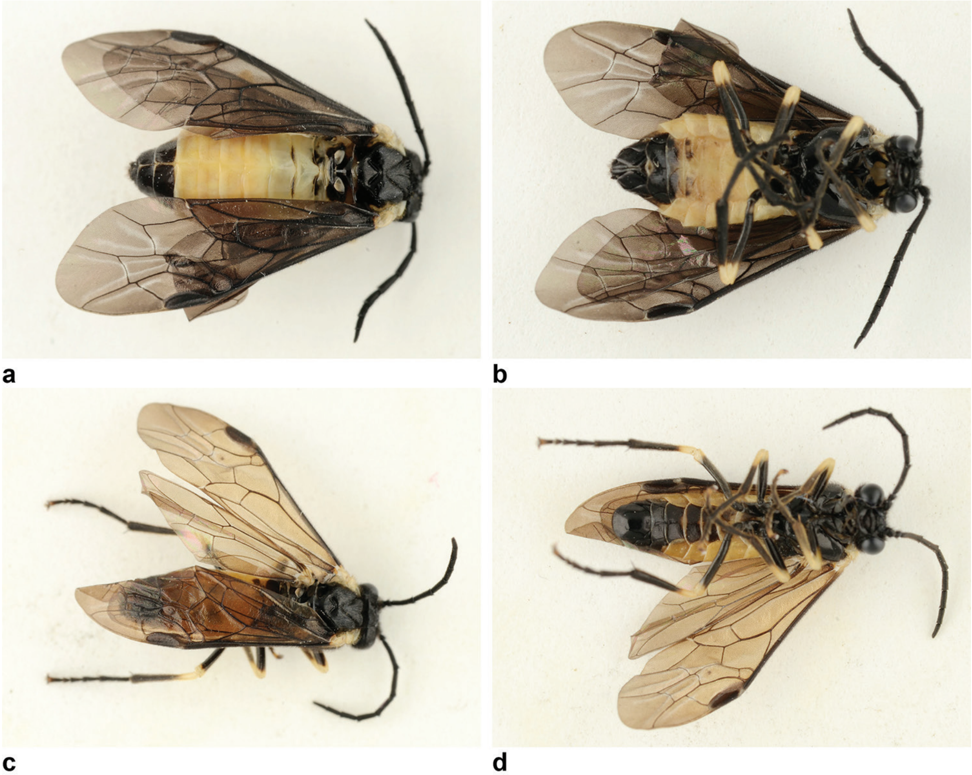

Figure 20. *Andeana farcta*. **a, b** Female (P3929), body length 10.0 mm **c, d** male (P3894), body length 8.5 mm. **a, c** Dorsal views **b, d** ventral views.

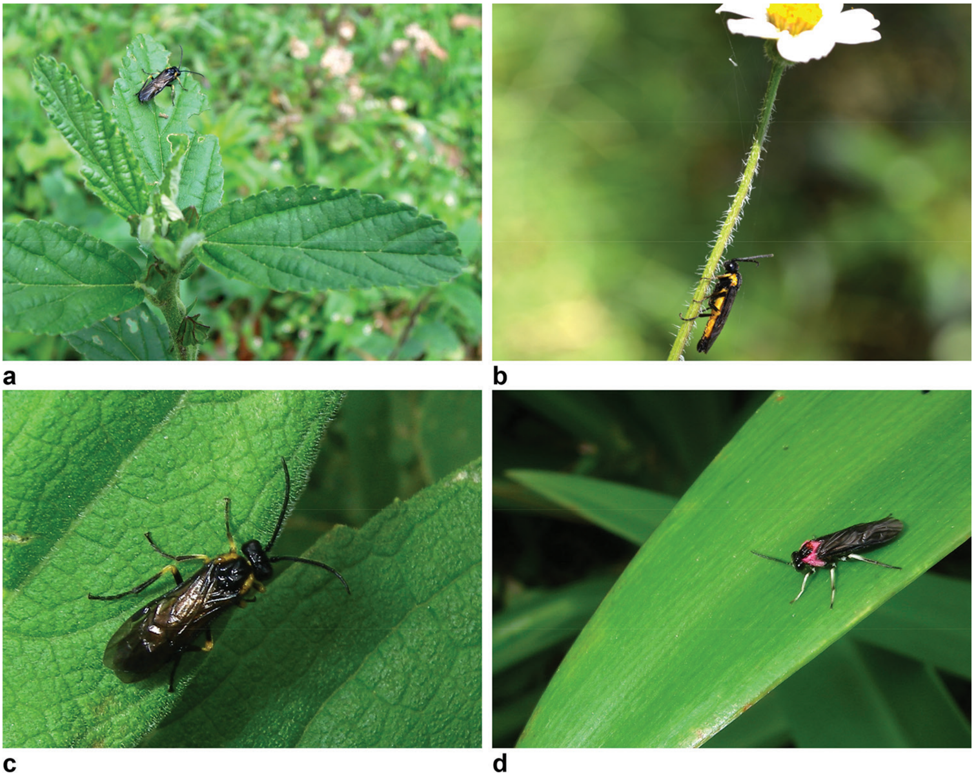

Figure 21. Pictures of sawfly adults taken in the field. **a, c** *Andeana farcta* (P3952 or P3954) **b** *A. farcta* (Reserva El Madrigal, 27.03.2015) **d** *Proselandria* sp. (P3905).

04°02'S, 079°11'W, 2270m, 21.10.2014, P3955.A (1 ♂), leg. T. Delsinne, J.-L. Boevé, P3957.B, P3957.C (2 ♂), leg. A. Pauly, J.-L. Boevé, P3954.A, P3954.B, P3954.C (3 ♂), leg. J.-L. Boevé, on *Sida* sp. (Malvaceae), P3952.A, P3952.B, P3952.C (3 ♂), leg. J.-L. Boevé; Loja, La Argelia, 04°01'S, 079°12'W, 2130m, 25.10.2014, landing on the ground, P3977 (1 ♀), leg. A. Pauly, J.-L. Boevé; nr Loja, Reserva El Madrigal, 04°02'S, 079°11'W, 2270m, 27.03.2015, one specimen on *Bidens pilosa* (Asteraceae), P4123.A, P4123.B (2 ♂), leg. T. Delsinne.

Andeana sp.

Fig. 22

Remarks. A genus of about 15 species in the Neotropics.

Material. N. of Pachicutza, 04°04'S, 078°38'W, 900m, 18.10.2014, P3940.D (1 ♀), leg. J.-L. Boevé; Loja, Estación Científica San Francisco, 03°58'S, 079°05'W, 1820m, 26.03.2015, P4122 (1 ♀), leg. T. Delsinne.

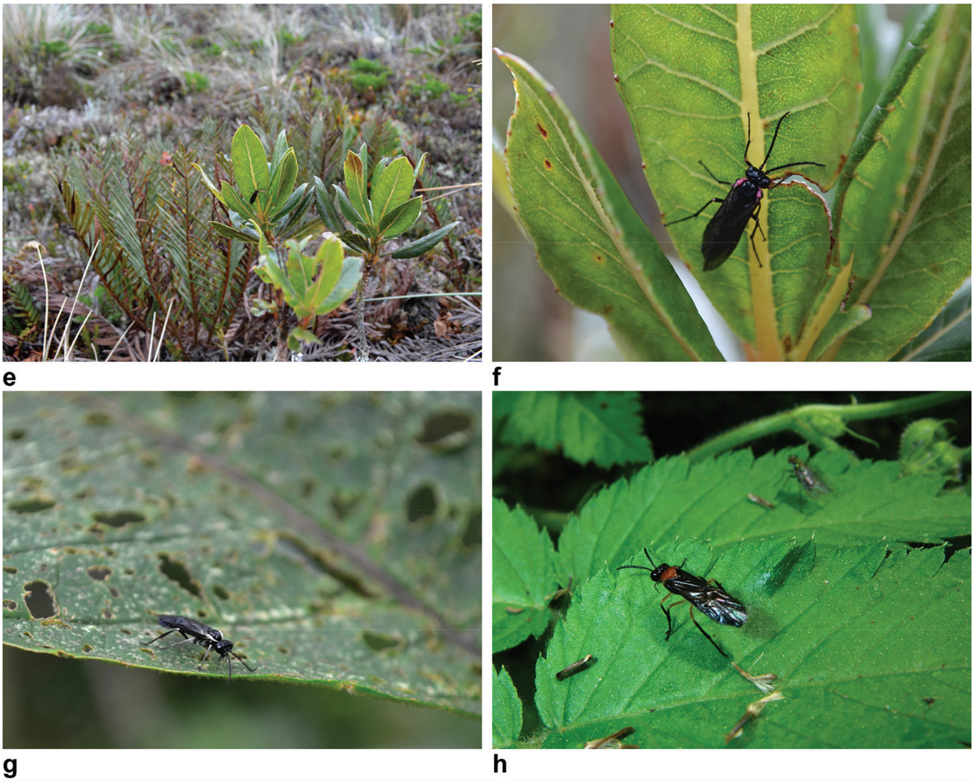

Figure 21. Continue. Pictures of sawfly adults taken in the field. **e, f** *Neonapeptamena* sp. (P3973.B) **g** *Stromboceridea albilabris* (Reserva El Madrigal, 27.03.2015) **h** *Bolivius notabilis* (P3966).

Aneugmenus sp.

Fig. 23

Remarks. Smith (2005) recorded two species in northern South America, Venezuela, Colombia, and Ecuador, the southern extent of this Holarctic genus. One species, *A. merida* Smith, was reared from bracken fern, *Pteridium aquilinum* (L.) in Venezuela. The specimen collected here is a male and could be either of the two species; the male is not known for *A. colombia* Smith.

Material. nr Loja, Reserva El Madrigal, 04°02'S, 079°11'W, 2280m, 21.10.2014, by sweeping on *Pteridium* sp. (Dennstaedtiaceae), P3949 (1 ♂), leg. J.-L. Boevé.

Bolivius notabilis (Konow, 1899), comb. n.

Figs 21h, 24

Stromboceros notabilis Konow 1899: 294; Konow 1903: 148 (female); Konow 1905: 98; Oehlke and Wudowenz 1984: 399; Taeger et al. 2010: 534.

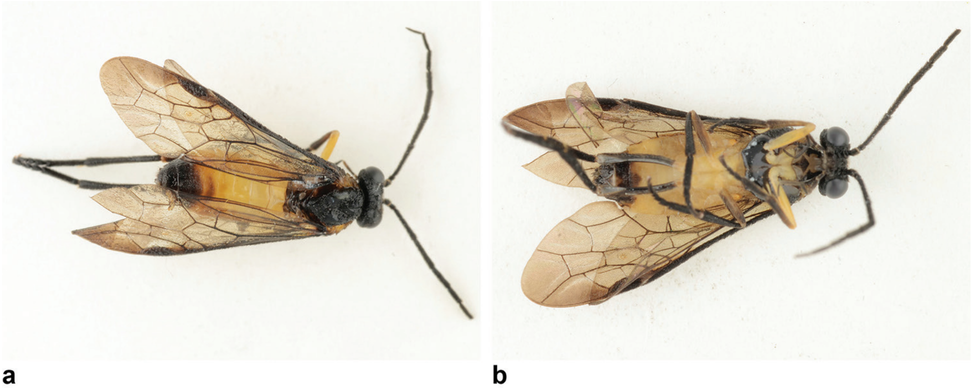

Figure 22. *Andeana* sp., female (P3940.D), body length 8.5 mm. **a** Dorsal view **b** ventral view.

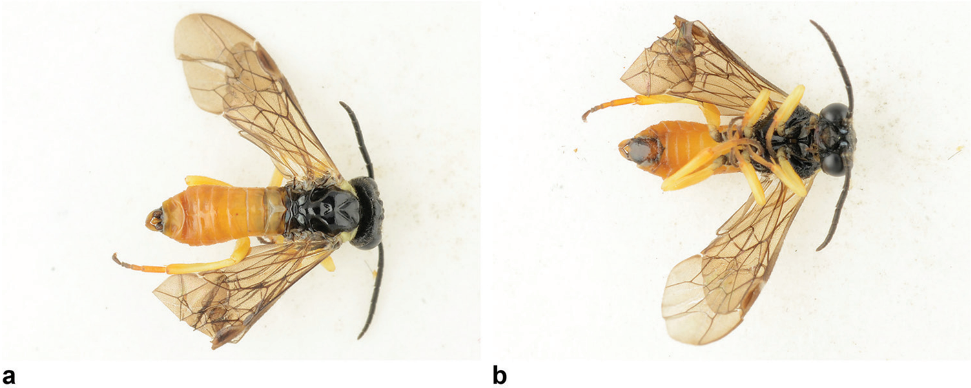

Figure 23. *Aneugmenus* sp., male (P3949), body length 6.0 mm. **a** Dorsal view **b** ventral view.

Remarks. The male holotype cited by Oehlke and Wudowenz (1984) at SDEI is here considered a lectotype designation. Konow did not give the number of specimens available, but it was the only one found at SDEI. It is labelled "Callanga, Cuczo, Peru,", "Coll. Konow," "TYPE", "*Stromboeros notabilis* Knw., Peru.".

Distribution. This species is now known from Ecuador, Peru, and Bolivia.

Material. Bombuscaro, road to Podocarpus NP, 04°06'S, 078°58'W, 975m, 08.10.2014, P3873, P3874, P3878 (3 ♂), leg. A. Pauly, J.-L. Boevé; Bombuscaro, Podocarpus NP, 04°06'S, 078°58'W, 995m, 16.10.2014, P3936.A (1 ♂), leg. A. Pauly, J.-L. Boevé; N. of Pachicutza, 04°04'S, 078°38'W, 900m, 18.10.2014, P3940.C (1 ♀), leg. J.-L. Boevé, P3940.B (1 ♂), leg. J.-L. Boevé, P3942.A (1 ♂), leg. A. Pauly, J.-L. Boevé; Romerillos, nr Podocarpus NP, 04°09'S, 078°56'W, 1100m, 22.10.2014, P3962.A (1 ♂), leg. J.-L. Boevé, P3967.B, P3967.C, P3967.D, P3967.E, P3967.F, P3967.G, P3967.H, P3967.K, P3967.L, P3967.P (10 ♂), leg. A. Pauly, J.-L. Boevé, flying, P3963.A (1 ♀), P3963.B, P3963.C, P3963.D, P3963.E, P3963.F, P3963.G, P3963.H (7 ♂), flying near rivulet, P3964.A (1 ♀), P3965,

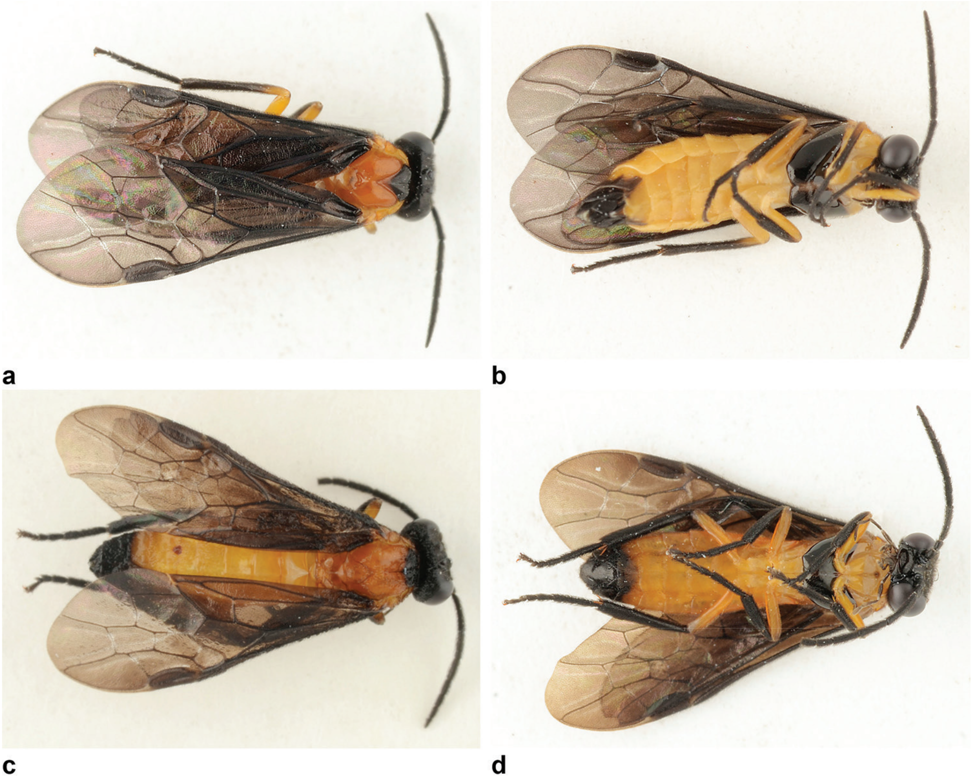

Figure 24. *Bolivius notabilis*. **a, b** Female (P3940.C), body length 6.5 mm **c, d** male (P3940.B), body length 7.0 mm. **a, c** Dorsal views **b, d** ventral views.

P3966 (2 ♂), leg. J.-L. Boevé; Bombuscaro, 04°05'S, 078°57'W, 930m, 22.03.2015, P4120.C (1 ♀), leg. T. Delsinne.

Dochmioglene sp.

Fig. 25

Remarks. A genus of about 10 species in Central and South America.

Material. Loja, Estación Científica San Francisco, 03°58'S, 079°05'W, 1820m, 24.03.2015, P4121.A (1 ♀), leg. T. Delsinne.

Inea sp.

Fig. 26

Remarks. A genus of about 20 species in Mexico, Central America, and northern South America.

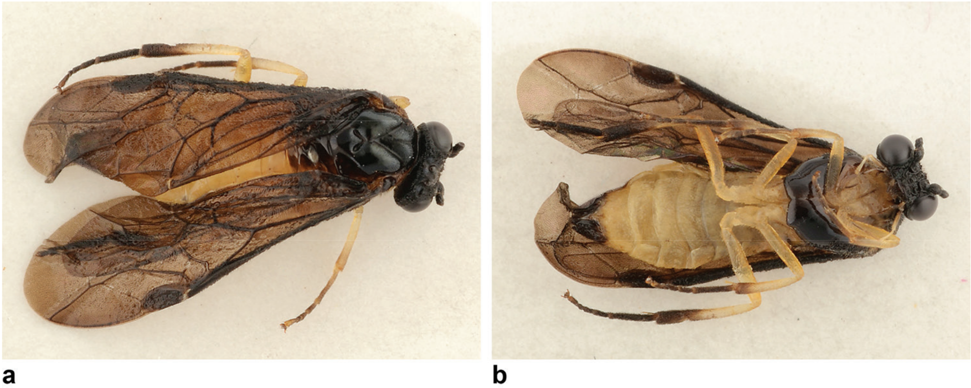

Figure 25. *Dochmioglene* sp., female (P4121.A), body length 8.0 mm. **a** Dorsal view **b** ventral view.

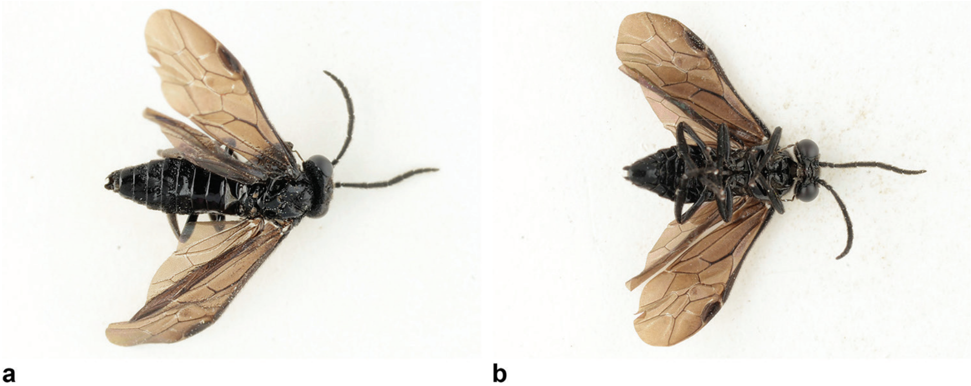

Figure 26. *Inea* sp., male (P3943.A), body length 5.5 mm. **a** Dorsal view **b** ventral view.

Material. Bombuscaro, Podocarpus NP, 04°06'S, 078°58'W, 955m, 08.10.2014, flying, P3870, P3871, P3872 (3 ♂), leg. J.-L. Boevé; Pueblo Viela, 04°38'S, 079°08'W, 1060m, 15.10.2014, on leaf of *Anthurium* sp., P3926.G (1 ♂), leg. A. Pauly, J.-L. Boevé; Bombuscaro, Podocarpus NP, 04°06'S, 078°58'W, 995m, 16.10.2014, P3936.F (1 ♂), leg. A. Pauly, J.-L. Boevé; Los Geraneos, 04°09'S, 078°38'W, 855m, 18.10.2014, P3944.C (1 ♀), leg. A. Pauly, J.-L. Boevé, P3943.A, P3943.B (2 ♂), leg. J.-L. Boevé; Bombuscaro, 04°05'S, 078°57'W, 930m, 22.03.2015, P4120.F (1 ♂), leg. T. Delsinne; Romerillos, nr Podocarpus NP, 04°06'S, 078°57'W, 995m, 22.10.2014, on leaf of *Anthurium* sp., P3958.E (1 ♀), leg. J.-L. Boevé.

Neoanapeptamena sp.

Figs 21e–f, 27

Remarks. This genus includes about three species and occurs only in Colombia, Ecuador, and Peru.

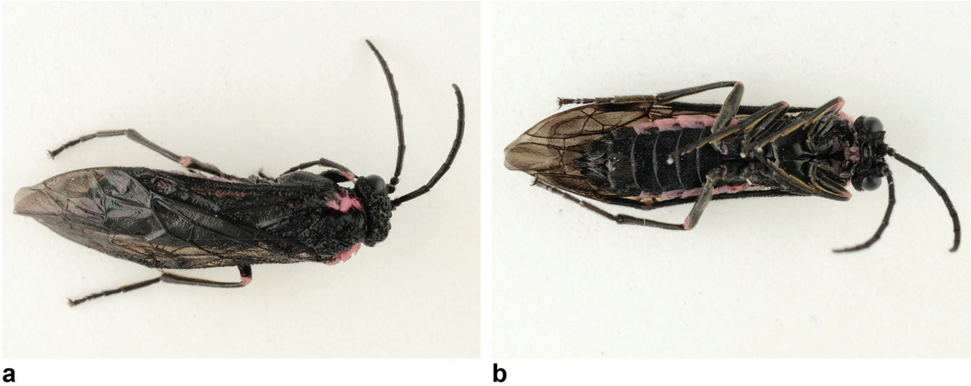

Figure 27. *Neoanapeptamena* sp., female (P3973.B), body length 9.0 mm. **a** Dorsal view **b** ventral view.

Material. Cajanuma "Mirador", Podocarpus NP, 04°07'S, 079°11'W, 3000m, 14.10.2014, on leaf of *Macrocarpaea arborescens* (Gentianaceae), P3918 (1 ♂), leg. J.-L. Boevé, 23.10.2014, P3973.A, P3973.B (2 ♀), leg. T. Delsinne, J.-L. Boevé; Cajanuma, Podocarpus NP, 04°07'S, 079°10'W, 2750m, 14.10.2014, P3920 (1 ♀), leg. A. Pauly, J.-L. Boevé, 2810m, 23.10.2014, P3972.A, P3972.B (2 ♀), leg. T. Delsinne, J.-L. Boevé.

Plaumanniana biclinea (Konow, 1899), comb. n.

Fig. 28

Stromboceros biclinius Konow 1899: 293; Konow 1905: 97; Oehlke and Wudowenz 1984: 369; Taeger et al. 2010: 532.
Strongylogaster biclinius: Enderlein 1920: 361.

Remarks. Two males and four females at SDEI are labelled "Callanga, Cuczo, Peru," "Coll. Konow," "TYPUS", and one male has the label "Stromboceros biclinius Konow, Peru." The male with Konow's, determination label is hereby designated lectotype. The other specimens are paralectotypes.

This species is now known from Colombia, Ecuador, and Peru.

Material. Pueblo Viela, 04°38'S, 079°08'W, 1060m, 15.10.2014, on leaf of *Anthurium* sp., P3927.A, P3927.B, P3927.C, P3927.D, P3927.E, P3927.F, P3927.G, P3927.H (8 ♂), leg. A. Pauly, J.-L. Boevé; Romerillos, nr Podocarpus NP, 04°06'S, 078°57'W, 995m, 22.10.2014, on leaf of *Anthurium* sp., P3958.C (1 ♀), leg. J.-L. Boevé.

Plaumanniana sp.

Fig. 29

Remarks. About 20 species are included in this genus which occurs form Central America to Argentina.

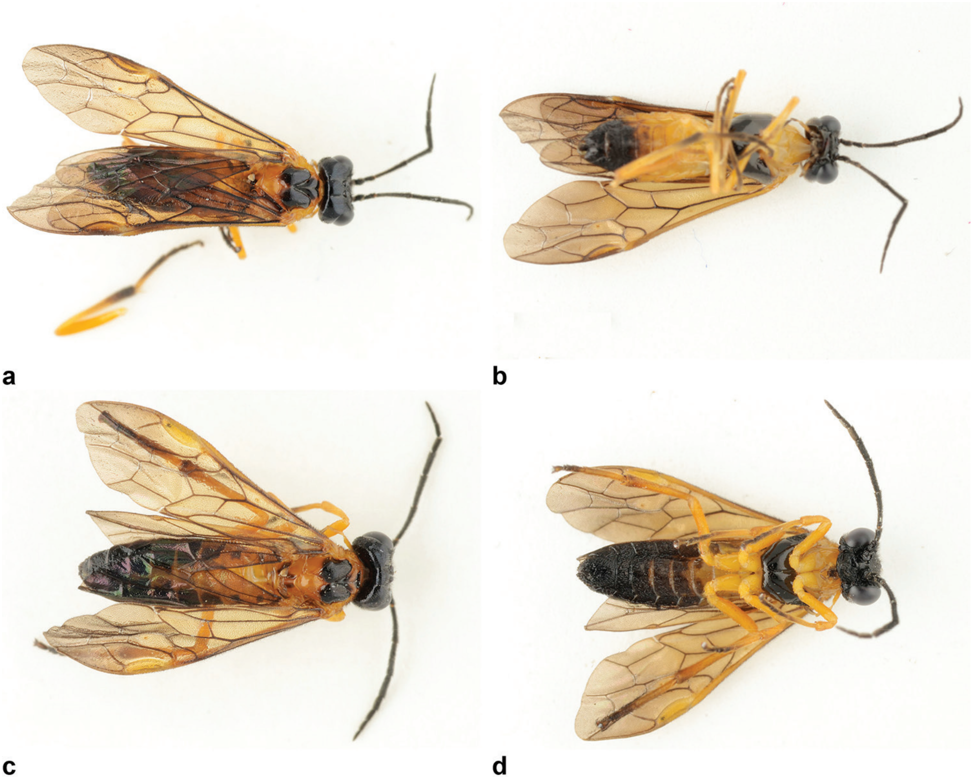

Figure 28. *Plaumanniana biclinea*. **a, b** Female (P3958.C), body length 9.0 mm **c, d** male (P3927.B), body length 8.5 mm. **a, c** Dorsal views **b, d** ventral views.

Material. Miasi, 04°15'S, 078°20'W, 875m, 19.10.2014, flying under leaf of *Anthurium* sp., P3946.H (1 ♀), leg. T. Delsinne, J.-L. Boevé; Bombuscaro, 04°05'S, 078°57'W, 930m, 22.03.2015, P4120.B (1 ♀), leg. T. Delsinne; Romerillos, nr Podocarpus NP, 04°09'S, 078°56'W, 1100m, 22.10.2014, P3967.A (1 ♀), leg. A. Pauly, J.-L. Boevé, P3967.I, P3967.J, P3967.M, P3967.N (4 ♂), leg. A. Pauly, J.-L. Boevé, on leaf of *Hedychium coronarium*, P3960.A, P3960.B (2 ♂), leg. J.-L. Boevé, on leaf of *Anthurium* sp., P3958.A, P3958.B (2 ♂), leg. J.-L. Boevé.

Proselandria alvina (Konow, 1899), comb. n.

Fig. 30

Stromboceros alvinus Konow, 1899: 292; Oehlke and Wudowenz 1984: 366; Taeger et al. 2010: 532.

Remarks. Konow described both sexes of this species from "Peru (Callanga, Cuczo)". Two males and one female labelled as types are at SDEI. The lectotype, here designated, is a male labelled "Callanga, Cuczo, Peru," "coll. Konow," "TYPE", "Strom-

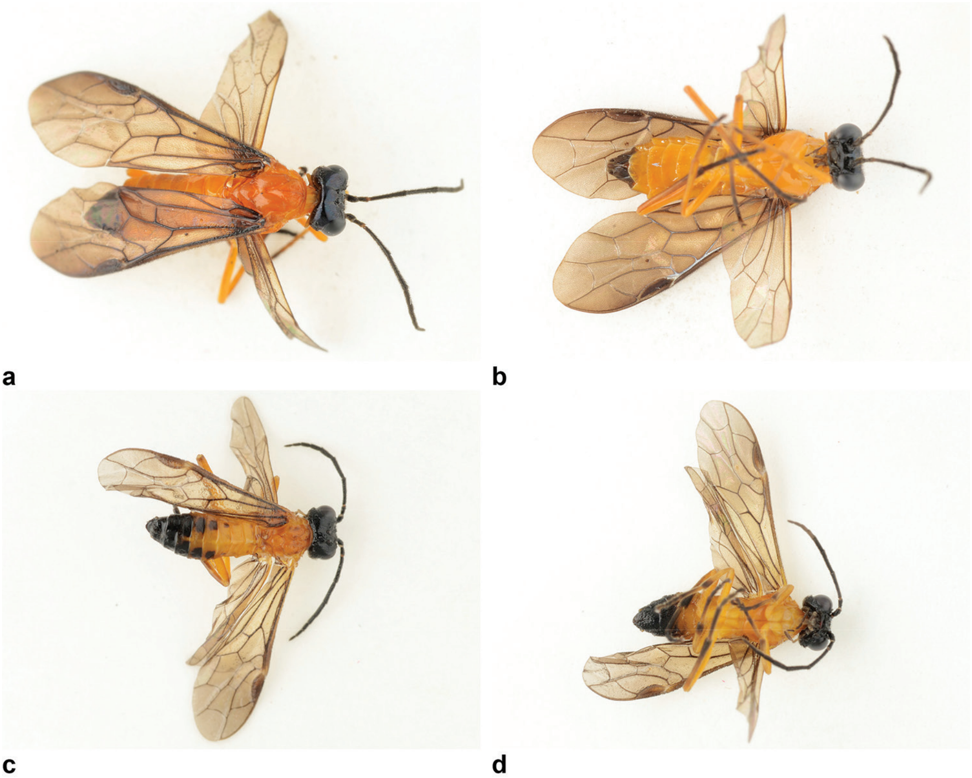

Figure 29. *Plaumanniana* sp. **a, b** Female (P3946.H), body length 9.0 mm **c, d** male (P3960.A), body length 7.5 mm. **a, c** Dorsal views **b, d** ventral views.

boceros alvinus Knw, Peru." The female and other male have the same data but lack a determination label. The female is a paralectotype, but the male belongs to the genus *Bolivius*. D. R. Smith did not designate a lectotype prior to Oehlke and Wudowenz (1984) who stated one was designated by D. R. Smith in 1976.

Distribution. This species is now known from Colombia, Ecuador, and Peru.

Material. Pueblo Viela, 04°38'S, 079°08'W, 1060m, 15.10.2014, on leaf of *Anthurium* sp., P3928.C (1 ♂), leg. A. Pauly, J.-L. Boevé; Bombuscaro, Podocarpus NP, 04°06'S, 078°58'W, 995m, 17.10.2014, P3938 (1 ♀), leg. A. Pauly, J.-L. Boevé; N. of Pachicutza, 04°04'S, 078°38'W, 900m, 18.10.2014, P3940.A (1 ♂), leg. J.-L. Boevé.

Proselandria carminea (Jörgensen, 1913)

Fig. 31

Remarks. This species occurs only in western South America from Colombia to northern Argentina.

Material. nr Loja, Reserva El Madrigal, 04°02'S, 079°11'W, 2270m, 27.03.2015, P4123.O, P4123.P (2 ♂), leg. T. Delsinne.

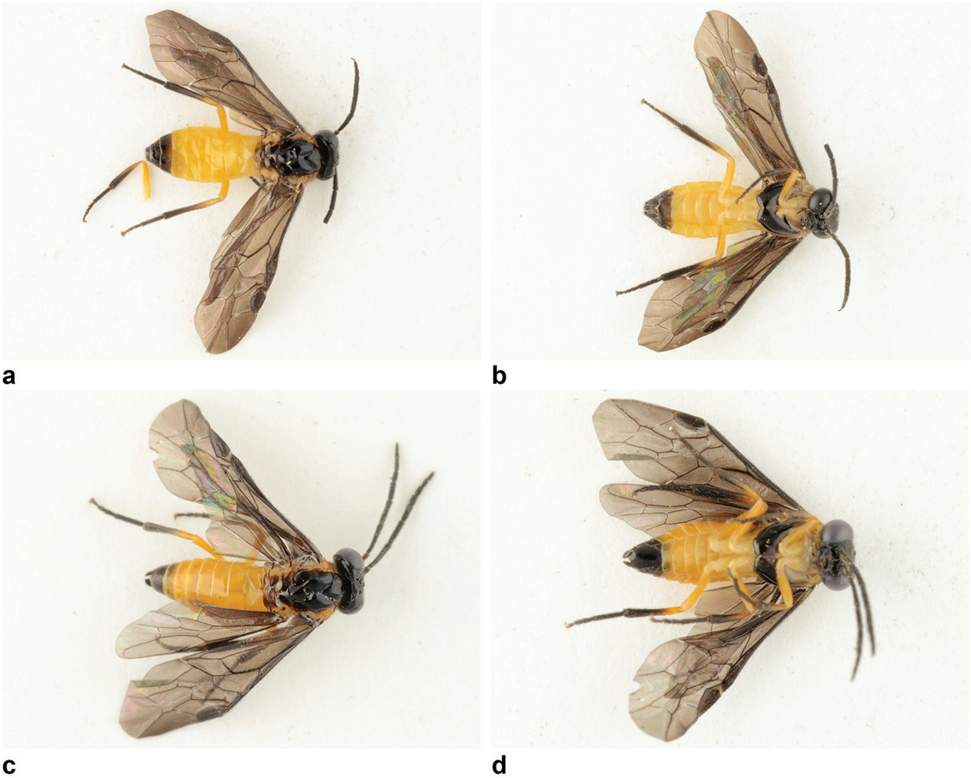

Figure 30. *Proselandria alvina*. **a, b** Female (P3938), body length 5.5 mm **c, d** male (P3928.C), body length 5.5 mm. **a, c** Dorsal views **b, d** ventral views.

Figure 31. *Proselandria carminea*, male (P4123.O), body length 5.5 mm, lateral view.

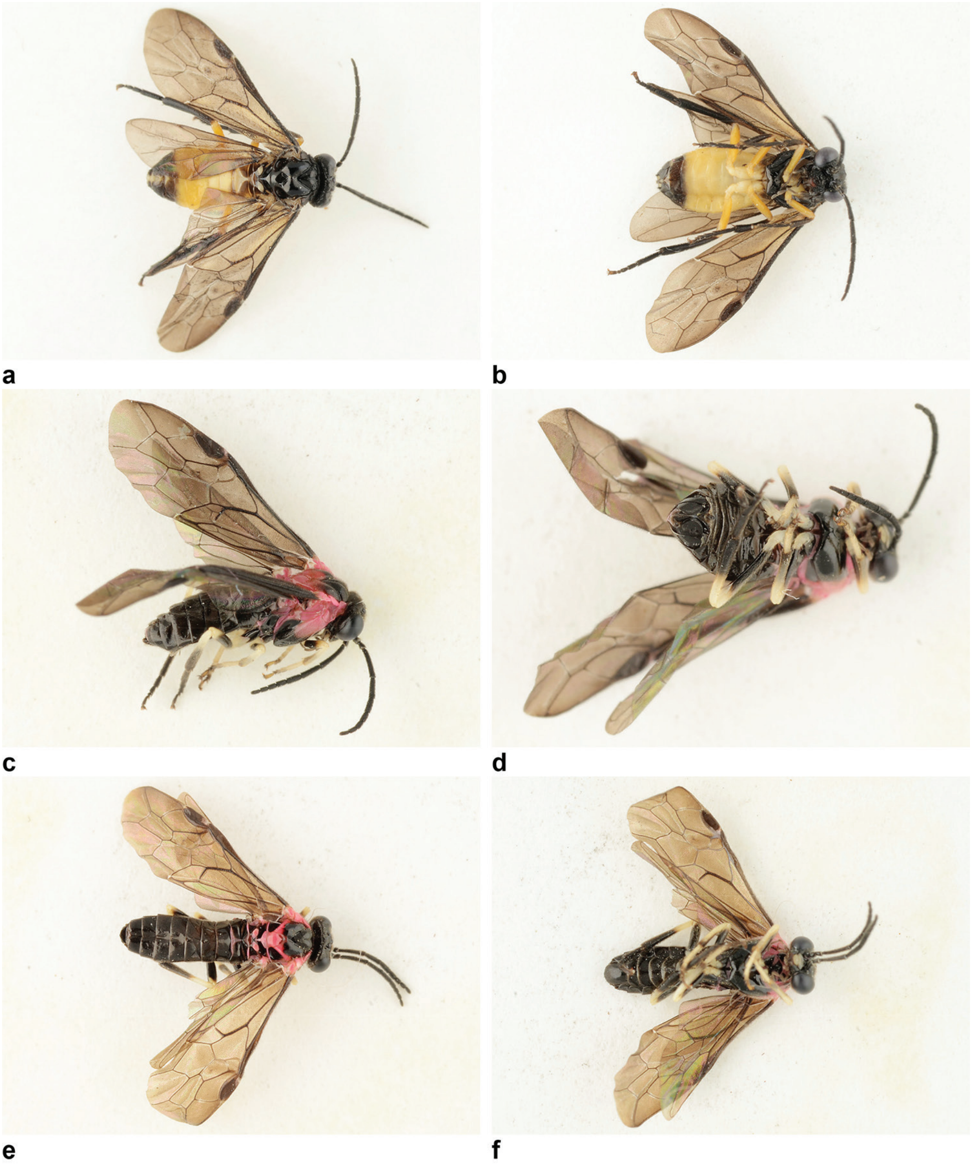

Figure 32. *Proselandria* sp. **a, b** Female (P3928.B), body length 6.0 mm **c, d** female (P3903), body length 6.0 mm **e, f** male (P3904), body length 6.0 mm. **a, e** Dorsal views **b, d, f** ventral views, **c** lateral view.

Proselandria spp.

Figs 21d, 32

Remarks. About 20 species are known, from Mexico to Argentina.

Material. Loja, Reinaldo Espinosa Botanical Garden, 04°02'S, 079°12'W, 2145m, 14.10.2014, P3903 (1 ♀), leg. J.-L. Boevé, P3904, P3909, P3910 (3 ♂), leg. J.-L. Boevé, P3916 (1 ♂), leg. A. Pauly, J.-L. Boevé, flying, P3908 (1 ♂), by sweeping grass, P3912 (1 ♀), on leaf of *Ismene longipetala* (Amaryllidaceae), P3905, P3907 (2 ♀), P3906 (1 ♂), leg. J.-L. Boevé; Pueblo Viela, 04°38'S, 079°08'W, 1060m, 15.10.2014, on leaf of *Anthurium* sp., P3928.B (1 ♀), leg. A. Pauly, J.-L. Boevé; Miasi, 04°15'S, 078°20'W, 875m, 19.10.2014, on/around leaf of *Anthurium* sp., P3946.D (1 ♀), leg. J.-L. Boevé.

Stromboceridea albilabris (Konow, 1885)

Figs 21g, 33

Distribution. *Stromboceridea* occurs from southwestern United States through western South America to northern Argentina. This species is known from Colombia, Ecuador, Peru and Bolivia.

Material. Bosque "El Sayo", 03°49'S, 079°17'W, 2760m, 12.10.2014, under leaf of bamboo (Poaceae), P3901 (1 ♂), leg. J.-L. Boevé; Cajanuma, Podocarpus NP, 04°07'S, 079°10'W, 2750m, 14.10.2014, P3922, P3923, P3924 (3 ♂), 2810m, 23.10.2014,

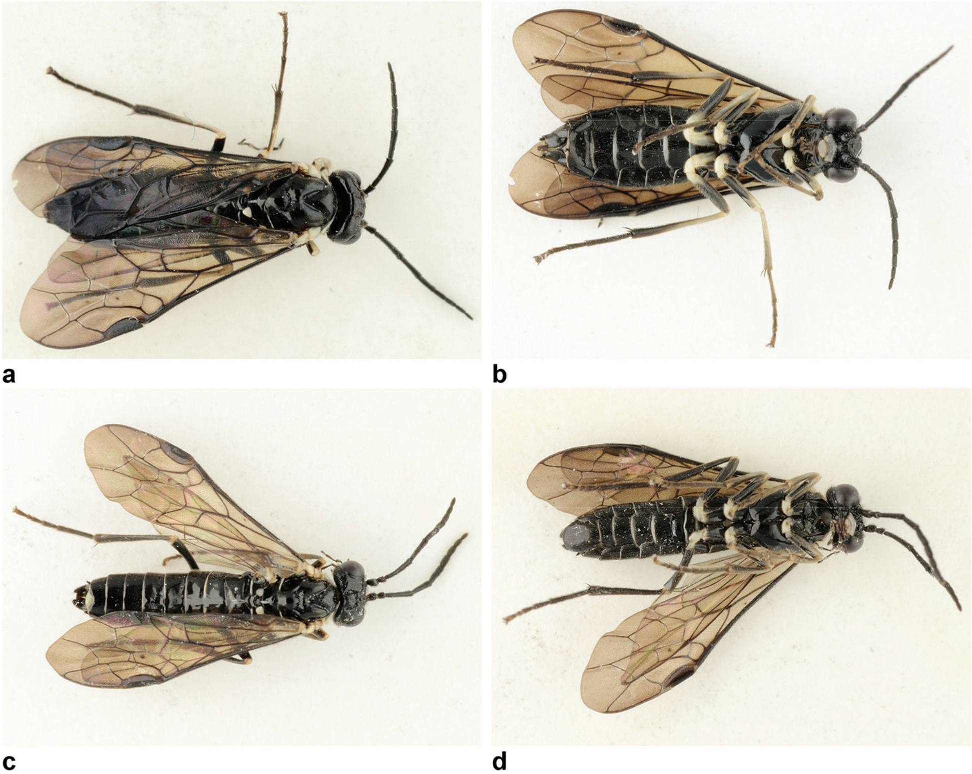

Figure 33. *Stromboceridea albilabris*. **a, b** Female (P3957.D), body length 9.5 mm **c, d** male (P3922), body length 7.5 mm. **a, c** Dorsal views **b, d** ventral views.

P3975.A, P3975.B, P3975.C, P3975.D, P3975.E, P3975.F (6 ♂), leg. A. Pauly, J.-L. Boevé; Loja, Reinaldo Espinosa Botanical Garden, 04°02'S, 079°12'W, 2145m, 14.10.2014, by sweeping grass, P3914 (1 ♀), leg. J.-L. Boevé; S. of Yangana, 04°32'S, 079°08'W, 1880m, 15.10.2014, on leaf of *Anthurium* sp., P3930.A, P3930.B, P3930.C, P3930.D, P3930.E (5 ♂), leg. J.-L. Boevé, P3931.A, P3931.B, P3931.C, P3931.D (4 ♂), leg. A. Pauly, J.-L. Boevé; nr Loja, Reserva El Madrigal, 04°02'S, 079°11'W, 2270m, 21.10.2014, P3957.D (1 ♀), leg. A. Pauly, J.-L. Boevé, P3955.B (1 ♂), leg. T. Delsinne, J.-L. Boevé, on *Rumex crispus*, P3953.A (1 ♂), leg. J.-L. Boevé; Cajanuma "Mirador", Podocarpus NP, 04°07'S, 079°10'W, 2810m, 23.10.2014, P3974 (1 ♂), leg. T. Delsinne, J.-L. Boevé; nr Loja, Reserva El Madrigal, 04°02'S, 079°11'W, 2270m, 27.03.2015, P4123.E (1 ♀), leg. T. Delsinne, P4123.C, P4123.D, P4123.I, P4123.J, P4123.K, P4123.L, P4123.M, P4123.N (8 ♂), leg. T. Delsinne.

Stromboceridea sp.

Fig. 34

Remarks. About 20 species are known.

Material. Loja, Reinaldo Espinosa Botanical Garden, 04°02'S, 079°12'W, 2145m, 14.10.2014, by sweeping grass, P3913 (1 ♀), leg. J.-L. Boevé; nr Loja, Reserva El Madrigal, 04°02'S, 079°11'W, 2280m, 21.10.2014, near rivulet, P3951 (1 ♂), leg. J.-L. Boevé; nr Loja, Reserva El Madrigal, 04°02'S, 079°11'W, 2270m, 27.03.2015, P4123.F, P4123.G, P4123.H (3 ♀), leg. T. Delsinne, P4123.Q, P4123.R (2 ♂), leg. T. Delsinne.

Tioloma nigrita Strand, 1911

Fig. 35

Distribution. Known only from Ecuador.

Figure 34. *Stromboceridea* sp., male (P3951), body length 5.5 mm. **a** Dorsal view **b** ventral view.

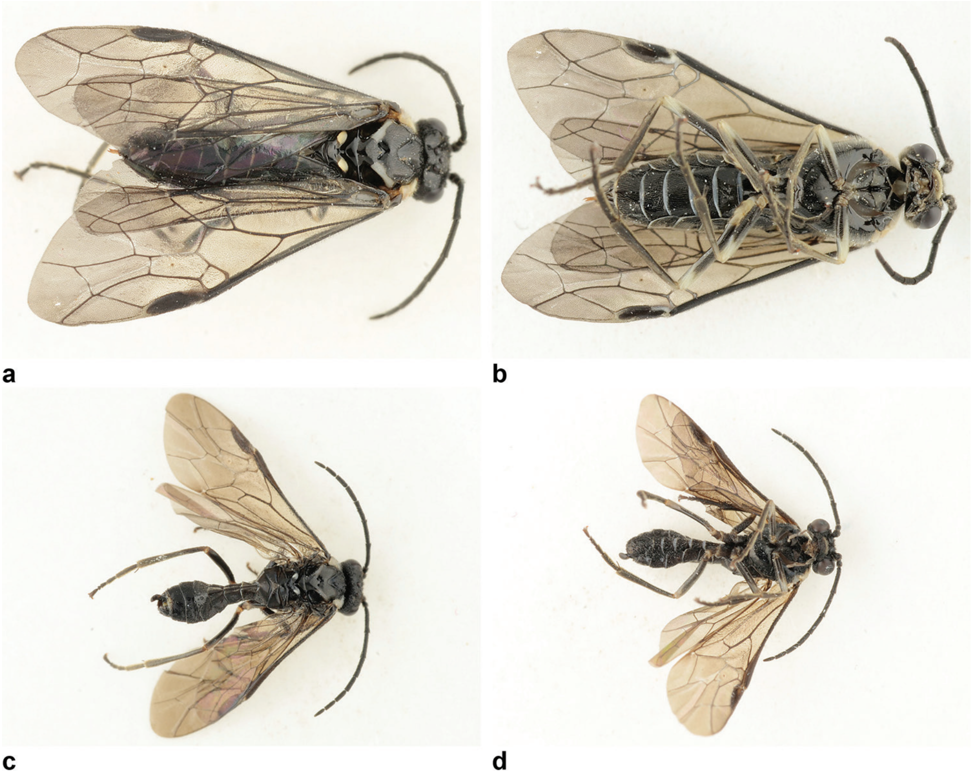

Figure 35. *Tioloma nigrita*. **a, b** Female (P3939), body length 8.5 mm **c, d** male (P3947), body length 7.0 mm. **a, c** Dorsal views **b, d** ventral views.

Material. El Tiro, road Loja - Zamora, 03°59'S, 079°09'W, 2815m, 08.10.2014, P3884 (1 ♀), leg. J.-L. Boevé, P3886 (1 ♀), leg. A. Pauly, J.-L. Boevé, P3885, P3887 (2 ♂), leg. A. Pauly, J.-L. Boevé; El Tiro, road Loja - Zamora, 03°59'S, 079°09'W, 2815m, 17.10.2014, with yellow pan trap, P3939 (1 ♀), 17–20.10.2014, with yellow pan trap, P3947 (1 ♂), leg. A. Pauly, J.-L. Boevé.

Altitudinal distribution

Sawflies were collected in the field at altitudes ranging from ca. 900 to 3000 m (Fig. 36). Some trends can be deduced from this figure, although with caution because, first, for several species only one or a couple of specimens could be collected, and, second, no systematic (e.g., trapping) methodology was used. At all collection sites, however, no specimens were discarded a priori. Thus, conclusions drawn from this figure may become pertinent by considering relatively common species, and/or when these were collected at several sites far from each other.

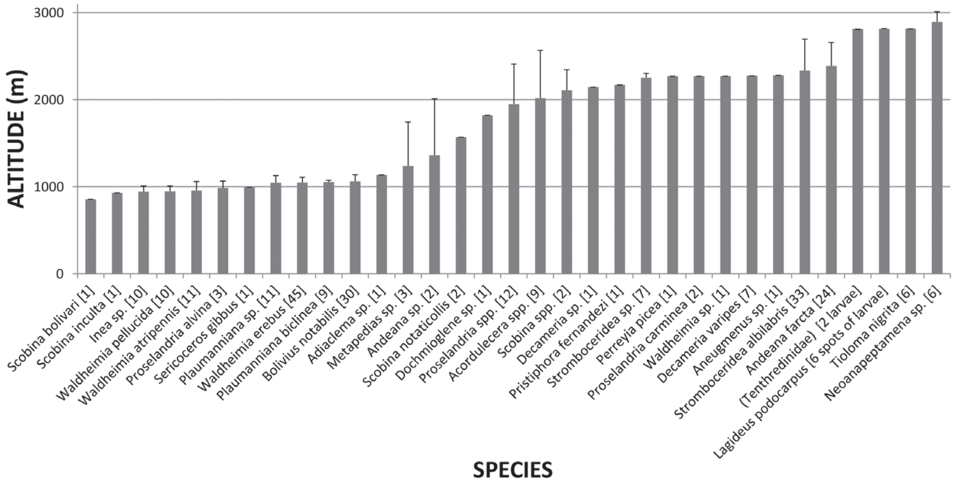

Figure 36. Distribution of collected sawfly species in function of the altitude. The histogram shows mean values with standard deviations; numbers of individuals are given between square brackets.

Among species with more than eight exemplars, *Inea* sp., the three identified *Waldheimia* species, the two *Plaumanniana* species, and *Bolivius notabilis* occurred at an altitude of ca. 1000 m. In contrast, *Stromboceridea albilabris* and *Andeana farcta* were collected above 2000 m. The variation in specific altitudes is rather low (Fig. 36) and most of these nine species were collected at different sites, which suggests that each species is indeed restricted to a given altitude. Three other species, *Lagideus podocarpus*, *Tioloma nigrita*, and *Neoanapeptamena* sp., were collected at an altitude of 2500–3000 m, the two latter taxa being known to occur at high altitudes (Malaise 1963, Strand 1913).

The 'altitudinal slots' of the sawfly species are probably linked to those of their host plants and/or to abiotic factors. However, such ecological data are still missing for most South American sawflies, and the present identification and description of *L. podocarpus* is just one example of a species that has remained unknown, and which are living at a high altitude. It emphasizes the importance of preserving a diversity of biotopes. In the case of a country such as Ecuador, the páramo clearly belongs to such valuable natural environments characterized by both a high altitude and very high biological value.

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Thibaut Delsinne is warmly thanked for the identification of ants, and for providing a significant amount of specimens and several pictures. We thank Alain Pauly (RBINS, Brussels) who also provided us with specimens, Hugo Omar Cabrera (Herbario UTPL) for the identification of plants, Ximena Cueva and Carlos Ruiz Carreira (MUTPL) for attending some field trips, and M. Reynders (Botanical Garden Meise, Belgium) for providing *Fuchsia* plants, as well as the subject editor Marko Prous, and the reviewers Stefan Schmidt and Andrew Liston for comments on the manuscript. D. R. Smith thanks A. Taeger (SDEI) for allowing study of Konow's type material. The GTI project was managed in collaboration with C. R. Carreira and David Donoso (MUTPL) and funded by the Belgian Directorate-General for Development Cooperation. Permits were obtained from the Ministerio del Ambiente Loja, Ecuador.

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RESEARCH ARTICLE

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Venifurca, a new genus of neotropical Doryctinae (Hymenoptera: Braconidae), and its phylogenetic placement

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Abstract

A new genus belonging to the braconid wasp subfamily Doryctinae, *Venifurca* **gen. n.**, is described containing one species, *Venifurca leiosoma* **sp. n.** The new genus is morphologically similar to *Johnsonius* Marsh and *Semirhytus* Szépligeti. A phylogenetic analysis based on one nuclear (28S) and one mitochondrial (COI) gene marker supported the close affinity of these three genera + *Bolivar* Zaldívar-Riverón & Rodríguez-Jiménez and *Parallorhogas* Marsh. All these genera are mainly characterized by having vein m-cu of the hind wing slightly curved distally.

Keywords

Ichneumonoidea, cyclostome braconids, taxonomy, parasitoid wasps, phylogeny

Introduction

With about 201 genera and 1700 described species (Yu et al. 2012, Braet 2016, Gadelha et al. 2016, Martínez et al. 2016) Doryctinae is one of most diverse subfamilies of Braconidae. This subfamily was erected over 150 years ago (Forster 1862); however, it is far from being fully known even at the supraspecific level. Proof of this is the considerable number of new doryctine genera that have been described over the last few years (Nunes et al. 2012, Marsh et al. 2013, Zaldívar-Riverón et al. 2013, 2014, Belokobylskij et al. 2015, Gadelha et al. 2016, Martínez et al. 2016). This emphasizes the necessity of conducting more studies in the New World tropics, where most of its species-richness occurs (Hanson and Gauld 1995, Wharton et al. 1997, Marsh 2002, Braet et al. 2003).

Most members of the Doryctinae are distinguished by the following external morphological features (Zaldívar-Riverón et al. 2008): 1) presence of a row of spines on the fore tibia, 2) separate insertion of two secondary venom ducts into the primary duct, 3) a heavily sclerotized ovipositor apex, 4) double nodus on the upper valve, 5) and modified serration on the lower valves of the ovipositor, usually as isolated tooth-like processes or as well-developed distal grooves along the dorsolateral edge of the valve (Quicke et al. 1992).

Morphological and molecular phylogenetic studies that have been conducted for the Doryctinae have demonstrated high levels of morphological homoplasy at different taxonomic levels (Belokobylskij et al. 2004, Zaldívar-Riverón et al. 2007, 2008). The use of coupled molecular and morphological data in taxonomic studies within this subfamily is therefore necessary to establish with more confidence its higher-level classification. In this work, we describe a new genus, and reconstruct its phylogenetic relationships with respect to other members of the Doryctinae.

Methods

Specimens and terminology

The specimens examined in this study are deposited in the Coleção de Invertebrados do Instituto Nacional de Pesquisas da Amazônia (INPA) and Colección Nacional de Insectos, Instituto de Biología, Universidad Nacional Autónoma de México (CNIN IB-UNAM). Morphological comparisons were performed using the relevant literature (Marsh 1997, 2002) and by direct comparison with material deposited in the above collections. We followed the terminology proposed by Sharkey and Wharton (1997), except for surface sculpture, which follows Harris (1979).

Digital photographs were taken with a Leica® stereomicroscope M165C coupled with a Leica® DFC420 camera and the Leica Application Suite program version 3.4.1.

Phylogenetic affinities of the new genus

We generated sequences of one nuclear and one mitochondrial (mt) marker for one specimen of the new genus to reconstruct its phylogenetic affinities within the Doryctinae. These markers correspond to 546 bp of the cytochrome oxidase I (COI) mtDNA and about 600 bp of the second and third domain regions of the nuclear ribosomal 28S genes. The laboratory procedures to extract, amplify and sequence the above sample are described in Ceccarelli et al. (2012) and Ceccarelli and Zaldívar-Riverón (2013). These sequences were included in previously published 28S + COI datasets (Zaldívar-Riverón et al. 2008, Belokobylskij et al. 2015) that included 107 doryctine species and 21 members of other Braconidae subfamilies (see Suppl. material 1).

A partitioned Bayesian analysis was performed for the 28S + COI matrix with the program MrBayes version 3.2.2 (Ronquist et al. 2012). The analysis had two simultaneous runs of 20 million generations each, saving trees every 1,000 generations, using four chains and default priors. Three partitions were considered for COI according to their codon position, and one partition was established for 28S. The evolutionary models selected for each partition were selected as in Zaldívar-Riverón et al. (2008). Burn-in was established after the first 10 million generations, and the remaining trees were used to reconstruct a phylogram with posterior probability of clades, considering values ≥ 0.95 as significantly supported (Huelsenbeck and Ronquist 2001).

Results

Phylogeny

The reconstructed Bayesian phylogram showing the phylogenetic placement of the new genus within the Doryctinae is shown in Figure 1. The new genus was recovered within the "South American major doryctine clade" previously proposed by Zaldívar-Riverón et al. (2008), nested with significant support in a clade with the following four genera: *Parallorhogas* Marsh, *Bolivar* Zaldívar-Riverón & Rodríguez-Jiménez, *Semirhytus* Szépligeti and *Johnsonius* Marsh.

Taxonomy

***Venifurca* Gadelha, Nunes & Zaldívar-Riverón, gen. n.**
http://zoobank.org/74CE1EC7-F570-48A0-8E0F-E87FF088ABBD

Type species. *Venifurca leiosoma* Gadelha, Nunes & Zaldívar-Riverón, sp. n.

Diagnosis. *Venifurca* gen. n. differs from the remaining doryctine genera by having hind wing vein m-cu bifurcate, with its two sides curving towards the base and apex (Fig. 2E). It is morphologically similar to *Semirhytus* and *Johnsonius*; however, it

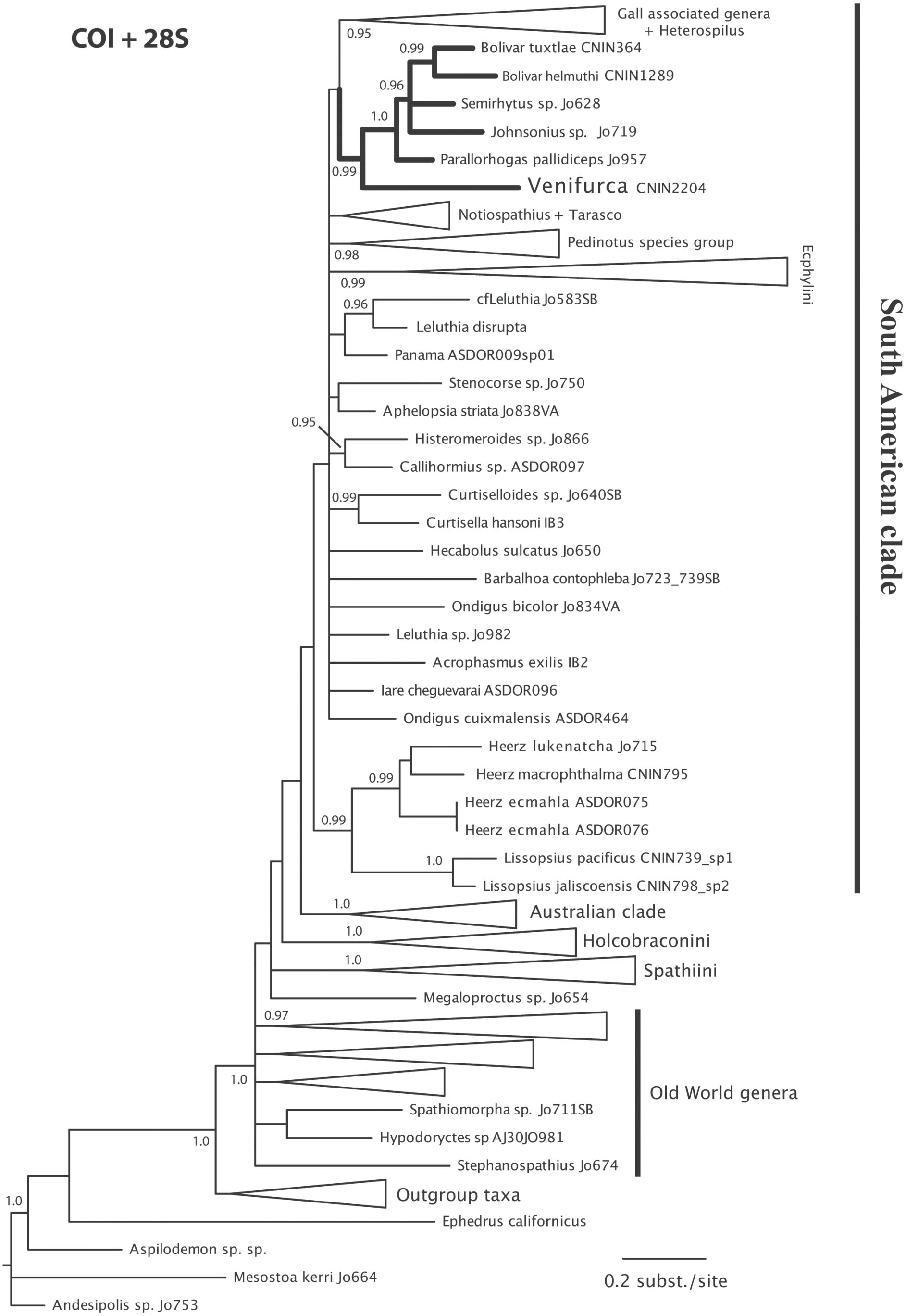

Figure 1. Bayesian phylogram derived from a 28S + COI matrix. The phylogram shows the phylogenetic affinity of the genus *Venifurca* gen. n. within the Doryctinae. Posterior probabilities ≥ 0.95 are indicate near branches.

mainly differs from them by having the propodeal areola poorly defined or absent (always present and defined in *Johnsonius* and *Semirhytus*). It also differs from *Semirhytus* by having a smaller oral cavity, less than four times the malar space length (equal to or greater than four times the malar space length in *Semirhytus*).

Description. Body length 6.6–7.9 mm; body mostly smooth and polished, with few carinae (Fig. 2A–B); clypeus margined dorsally by a distinct carina; occipital carina not meeting hypostomal carina; mesoscutum declivous anteriorly; notauli narrow and smooth, not meeting, present only on anterior part of mesoscutum; propodeum smooth and polished, sometimes with weak lateral and median carinae, areola absent or poorly defined; fore wing vein r-m present; first subdiscal cell open at apex, vein 2cu-a absent; hind wing vein M+CU 0.5 times length of 1M; vein m-cu bifurcate at apex (Fig. 2E); hind coxa with anteroventral basal tubercle; first metasomal tergite with two parallel longitudinal carinae, extending to half length of tergite, area between longitudinal carinae higher than tergite edges; basal sternal plate of first metasomal segment 0.2 times length of tergum; remaining tergites smooth and polished; ovipositor length equal to metasoma.

Distribution. French Guiana and Brazil.

Biology. Unknown

Etymology. This genus refers to the Latin words *vena* and *furca* in reference to its main feature, hind wing vein m-cu bifurcate at the apex.

Key to *Venifurca* Gadelha, Nunes & Zaldívar-Riverón, gen. n.

Venifurca gen. n. runs to couplet 71 of the key to New World doryctine genera (Marsh 1997) as follows:

71 Cyclostome opening wide and oval, nearly as wide as eye height; clypeus long and thin .... ***Semirhytus* Szépligeti, 1902**
– Cyclostome opening circular, at most as wide as half height of eye; clypeus wide **71a**
71a Hind wing vein m-cu bifurcate at apex, next to the posterior margin of wing (Fig. 2E) .... ***Venifurca* Gadelha, Nunes & Zaldívar-Riverón, gen. n.**
– Hind wing vein m-cu curved distally toward apical margin of wing or extending straight to posterior margin of wing, but never bifurcate..................... **72**

Venifurca leiosoma Gadelha, Nunes & Zaldívar-Riverón, sp. n.

http://zoobank.org/8FE53E4F-A380-4CFF-A119-1E03F824AD16
Figures 2A–F

Description. Female. Body length: 6.6 mm (Fig. 2A). *Body colour*: head dark brown, including scape and pedicel; clypeus honey yellow; mandible honey yellow at base, turning dark brown at apex; palpi light yellow; mesosoma honey yellow, except for pro-

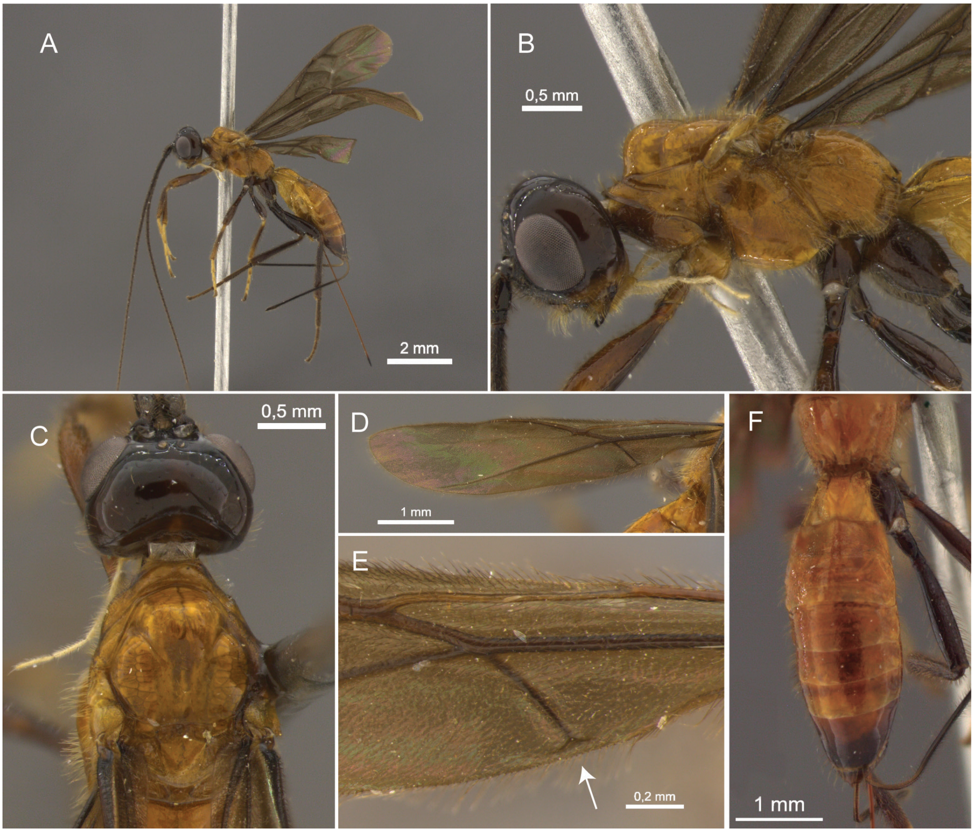

Figure 2. *Venifurca leiosoma* sp. n. (Holotype). Lateral habitus (**A**), lateral head and mesosoma (**B**), dorsal head and mesonotum (**C**), hind wing (**D**), hind wing with emphasis on the bifurcate m-cu (**E**), dorsal propodeum and metasoma (**F**).

pleuron, which is slightly darker; fore coxa yellow, trochanter, trochantellus, femur and tibia brown, tarsi yellow; mid and hind legs brown, except mid tarsus, which is yellow; first to sixth metasomal tergites honey yellow, seventh tergite honey yellow anteriorly, turning dark brown distally; eight tergite dark brown; ovipositor sheath dark brown only in basal third, remaining area black; ovipositor dark brown, strongly sclerotized at apex; wings light brown, veins and pterostigma brown; tegula yellow.

Head: clypeus smooth, with a row of setae on its ventral margin and dorsally delimited by carina; face covered with setae inserted into punctations; remainder of head smooth, polished and covered with more widely spaced setae (Fig. 2B–C); scape and pedicel covered with setae inserted into punctations; antenna with 44 flagellomeres; oral cavity oval, width 1.5 times length of malar space; ocellar–ocular distance three times diameter of lateral ocellus; occipital carina present, poorly marked in dorsal region and not meeting hypostomal carina.

Mesosoma: smooth and polished, almost with no clearly defined carinae (Fig. 2B-C); pronotum densely setose posterolaterally, pronotal groove smooth and narrow; propleuron with setae over entire surface; mesoscutum covered with setae, notauli smooth and narrow, not converging, finishing before middle of mesoscutum (Fig. 2C); scutellar disk smooth anteriorly, with setae posteriorly; mesopleuron with a smooth, polished and shallow precoxal sulcus, extending along half of mesopleuron; posteroventral area more setose than remaining part of mesopleuron; venter of mesosoma smooth, polished and with few setae; propodeum and metapleuron setose, propodeal lateral carinae poorly defined (Fig. 2F).

Wings: fore wing vein r equal to 3RSa; m-cu in line with 2RS; 1cu-a slightly distal to 1M; first subdiscal cell open, 2cu-a absent; hind wing vein M+CU equal to 0.52 length of vein 1M (Fig. 2D); m-cu vein clearly bifurcate at apex (Fig. 2E).

Legs: smooth, polished and covered with setae; ventral and lateral areas of coxae more setose than dorsal area; hind coxa with a well defined anteroventral basal tubercle; tibiae and tarsi more setose than femora.

Metasoma: first metasomal tergite with two parallel longitudinal carinae, extending half length of tergite, area between two longitudinal carinae higher than tergite edges; dorsope distinct and deep; basal sternal plate 0.20 length of first tergum; suture between second and third tergites indistinct (Fig. 2F); remaining part of metasoma smooth and polished; ovipositor length equal to metasoma.

Male. Unknown.

Variation. Propleuron yellow to dark brown; fore coxa yellow to brown; clypeus and face smooth to slightly striate; occipital carina even throughout or slightly sinuous laterally; propodeal areola poorly defined to absent.

Distribution. French Guiana and Brazil (Amazonas and Pará states).

Etymology. The specific name comes from the Greek *leio* (= smooth) and *soma* (= body), in reference to the smooth body of this species.

Material examined. *Holotype*: female, BRAZIL, Amazonas, Manaus, Reserva Ducke, Igarapé Bolívia, 28.ii.2003, Arm. Malaise, J. M. F. Ribeiro, (INPA). *Paratypes*: three specimens. One female, FRENCH GUIANA, Regina Road Roura – Kaw Km 37.5, Kaw Mountain, 04°33'20"N 52°08'19"W, 217m, i.2005, J. A. Cerda leg, CNIN 2204, (CNIN IB-UNAM); One female, BRAZIL, Amazonas, Manaus, Reserva Ducke – INPA, 09-16.x.2005, Arm. Malaise, A. P. Aguiar, (INPA); One female, BRAZIL, Pará, Repartimento, Vicinal 08, 04°26'42"S / 49°54'25"W, 28.xi.2001, Malaise, J. A. Rafael & J. Vidal, (INPA).

Discussion

The four genera that were recovered in the same clade with *Venifurca* gen. n. (*Parallorhogas*, *Bolivar*, *Semirhytus* and *Johnsonius*) (Fig. 1) are mainly characterised by having hind wing vein m-cu distinctly curved towards the apex and the propodeal areola present and well defined. However, in *Venifurca* gen. n. m-cu is clearly bifurcate, with its two sides curving towards the base and apex of the wing, and the propodeal areola is poorly defined or absent. The only described species of this genus, *Venifurca leiosoma* sp. n., is morphologically similar to those of *Semirhytus* and *Johnsonius* in various external morphological features, including the smooth and polished body, the declivous mesoscutum, a distinct dorsope and the length of hind wing vein M+CU, which is 0.5 or less of the length of vein 1M. Further morphological examination and molecular phylogenetic studies will clarify whether the above genera form a monophyletic group and thus deserve to be recognized as a separate tribe.

Acknowledgments

We thank Michael Sharkey for providing the paratype specimen from French Guiana; and Cristina Mayorga and Guillermina Ortega for helping SDSG during his stay at the IB UNAM. This work was supported by grants given by the Consejo Nacional de Ciencia y Tecnología (CONACyT; Red Temática del Código de Barras de la Vida; Proyecto Ciencia Básica 2014 No. 220454) and PAPIIT-UNAM (No. IN207016) to AZR; and by a scholarship given by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) to SDSG.

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Supplementary material 1

28S + COI matrix

Authors: Sian de Souza Gadelha, Juliano Fiorelini Nunes, Alejandro Zaldívar-Riverón, Marcio Luiz de Oliveira

Data type: Nexus file

Explanation note: 28S + COI data set including 107 doryctine species and 21 members of other Braconidae subfamilies, used in the Bayesian analysis.

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RESEARCH ARTICLE

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Insect species described by Karl-Johan Hedqvist

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Abstract

The Swedish entomologist, Karl-Johan Hedqvist (1917–2009) described 261 species of insects, 260 species of Hymenoptera and one of Coleoptera, plus 72 genera and a small number of family-level taxa. These taxa are catalogued and the current depositories of the types are listed, as well as some brief notes on the history of the Hedqvist collection. We also discuss some issues that can arise when type-rich specimen collections are put on the commercial market.

Keywords

Chalcidoidea, Pteromalidae, Braconidae, Type catalogue

Introduction

Karl-Johan Hedqvist (1917–2009) was a well-known Swedish hymenopterist who published a large body of work in applied entomology, faunistics and systematics, with a special focus on Chalcidoidea (particularly Pteromalidae), but also dealing with all major groups of parasitoid Hymenoptera. In 2011 his collection of more than 50 000 specimens of Hymenoptera from around the world (Figure 1) was purchased from his relatives by the Natural History Museum (London) (henceforth abbreviated to BMNH) (Figure 2). Since Hedqvist spent a significant part of his career as a taxonomist at the Stockholm Museum of Natural History (NHRS), voices were raised arguing that his collection at least in part belonged there. We have investigated the

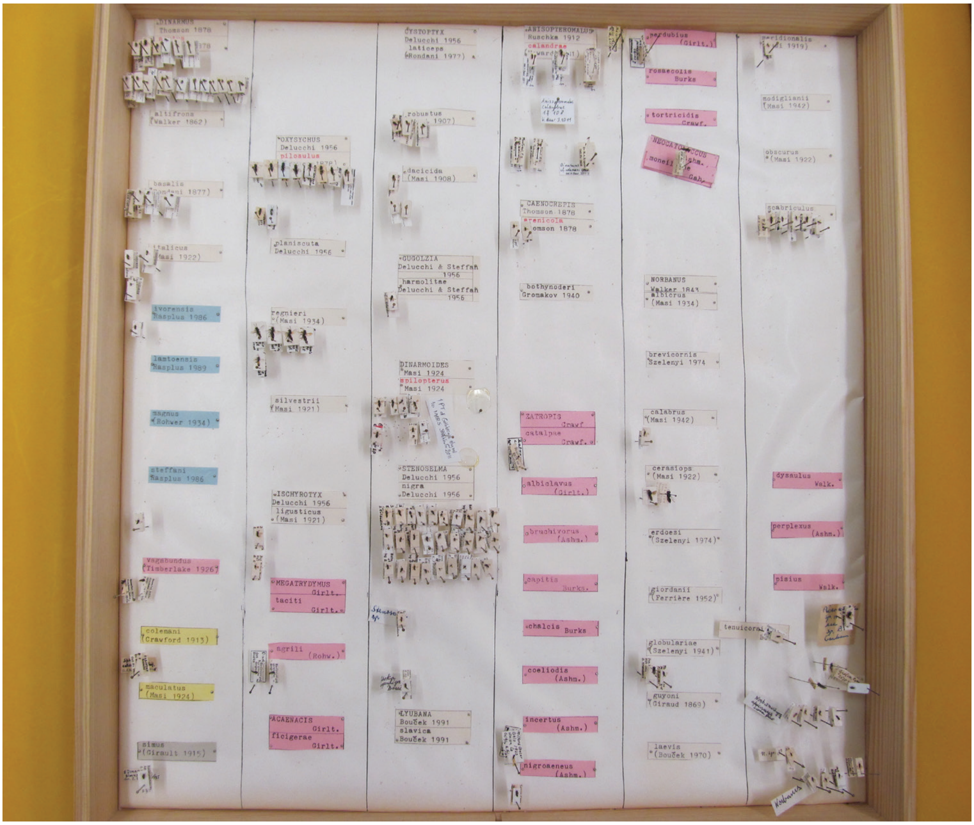

Figure 1. A representative original drawer from coll. Hedqvist.

different provenances of material in the collection and together established criteria to be used in determining in which institution the type specimens belong. On the basis of these criteria and on expectations relating to specimen deposition on the behalf of employers and various collectors, the material was divided between BMNH and NHRS. We have also commenced specimen exchanges as part of a wider exchange program of Hymenoptera specimens between the two museums.

As well as the obvious utility of an annotated catalogue of type material to Hymenoptera researchers, as many species were originally described as being deposited in Hedqvist's personal collection, we think that hymenopterists may be interested in the details of the BMNH acquisition and the agreements between BMNH and NHRS. Specimens purchased by BMNH have been registered under the registration number BMNH(E) 2011-27, with the parts of the collection subsequently transferred to NHRS under number 2012-NHRS-005 (Figure 3). This catalogue only deals with the type specimens of taxa described by Hedqvist; the collection he bequeathed is obviously much larger than these taxa and includes large numbers of both named and unnamed specimens of many Hymenoptera families.

Figure 2. Coll. Hedqvist arrived at BMNH.

Brief biographic sketch

Hedqvist was born on July 18, 1917 in Bodarna of Västerbotten County in northern Sweden. In the summer of 1939, at the age of 22, he took his first insect-related job as a field assistant looking at forest pest insects. Retaining a focus on forest entomology, he moved to Stockholm for further studies and an assistant position at the Swedish Forest Research Institute from 1949. In this capacity, he travelled extensively around Sweden, working on forest pest management. At the same time he was building up a large personal insect collection and started publishing widely (from 1945) on faunistics and applied entomology, on a wide range of subject taxa across the major insect orders Coleoptera, Lepidoptera, Hymenoptera and Hemiptera. In 1951 he married and settled down in Vallentuna, north of Stockholm. He and his wife Margit eventually had two children.

In the mid-50s, Hedqvist embarked upon his career as a taxonomist, describing first a new bark beetle and then what would become a very large number of Hymenoptera species and genera. In 1959 he got a position as an amanuensis (a kind of research assistant position) at the Swedish Museum of Natural History in Stockholm (NHRS), where he had the opportunity to focus more on taxonomy. Nevertheless he left the position in favour of employment as a field entomologist back at the Swedish Forest Research Institute in 1963. Later, in 1971, he moved back to NHRS, holding a newly established position as a taxonomist with special focus on parasitoid wasps, funded by

Figure 3. A drawer of Hedqvist types in NHRS.

the Swedish Research Council. Hedqvist received an honorary doctorate from the Uppsala University in 1977 for his work on the taxonomy of parasitoid wasps. During his time at NHRS he supervised two successful PhD students in the systematics of parasitoid wasps, Lars-Åke Janzon and Göran Nordlander. Hedqvist stayed at the Stockholm museum until his retirement in 1984. After retirement, he kept up his taxonomic and faunistic work from home, as well as his active involvement in the Stockholm Entomological Society (adding a stint as president to his previous period as secretary) but published only a few more taxonomic contributions, until he passed away in 2009.

Based on his initial route into the parasitoid wasps, much of Hedqvist's work concerns parasitoids of insects that are considered forest pests, and especially parasitoids of the bark beetles (Curculionidae: Scolytinae). The most significant focus of his taxonomic work was the huge and complicated chalcidoid family, Pteromalidae, but he also worked with several other groups of parasitoid wasps. In 2003 he published a Swedish checklist of the Chalcidoidea with province records for the entire superfamily based almost exclusively on specimens in his own collection. This was followed in 2007 by a similar checklist of Proctotrupoidea, and he was preparing a volume on Braconidae at the time of his death.

For a somewhat more detailed biography (in Swedish), including a complete bibliography, we direct the interested reader to Hansson (2010).

Criteria for type deposition

Specimens that were in Hedqvist's collection at the time of its purchase have been deposited in collections according to the following criteria.

* Holotypes of taxa described when Hedqvist was employed in NHRS from 1971–1984) have been deposited in NHRS. Those from the 1959–1963 period however are in the BMNH, for the reason that this stint was unknown to us at the time of the initial agreement (omitted from Hansson's biography (2010) as well as the official records from the central secretariat of NHRS, and obvious mainly from the museum's very detailed annual reports (KVA 1961–1965)).

* Holotypes of species described on the basis of Swedish specimens have mostly been deposited in NHRS; other holotypes (described outside the period 1971–1984) have been retained by BMNH.

* Paratypes, where there are multiple paratypes, have been divided between BMNH and NHRS.

* Some specimens that were present in Hedqvist's collection resulted from expeditions or inventories carried out by institutes (primarily NHRS and ZMLU). Some had loan labels or belonged to older collections of various institutes. Many apparently came from donations to NHRS, or were handed to Hedqvist by colleagues at the NHRS or by private collectors for identification. In many cases we have received confirmation from the collectors (B. Gustafsson, L.-Å. Janzon, et al., pers. comm.) that they intended and expected the specimens to be added or returned to the NHRS collection, or in some cases returned to them personally, rather than being gifts to Hedqvist's personal collection. It has proved impractical to establish the exact status and ownership of each specimen; only some which are clear loans have been returned to NHRS and elsewhere.

* For a large number of Chalcidoidea taxa – some 820 species – Hedqvist's records in the 2003 catalogue (or elsewhere in his writings) represent the only Swedish records. Thus, his collection holds many specimens that are important as vouchers for the national occurence of these taxa, and are nationally important especially in the light of the ongoing Swedish Taxonomy Initiative. Wherever numbers allowed, such taxa have been shared between NHRS and BMNH. In exchange, material is being donated from the Swedish Malaise Trap Project to BMNH.

* Hedqvist's handwritten folders of notes on specimens, including many faunistic records, are in the BMNH, but digitised versions are shared with NHRS.

Material and methods

Type catalogue

We have listed all taxa described by Hedqvist in alphabetical order. The issue number of journals is given only in cases where pagination is separate for each issue. For each taxon there is then a page reference.

The current status of names is according to the best knowledge available to the authors, and mostly based on standard taxonomic databases such as Taxapad (Yu et al. 2012), the Universal Chalcidoidea Database (Noyes 2016) and specific web searches. Family and subfamily placements also follow these and other (e.g. Shaw 1990; Johnson 1992; Broad et al. 2016) publications.

Type repository is given in abbreviated format. Sex and geographical origin (country level or similar) is given for holotypes. The numbers of paratypes present in different repositories is listed without separating sexes or citing label data. Detailed specimen data are available in the original publications. Obvious mistakes are corrected. Paratypes are frequently exchanged with or donated to other collections, and sometimes there have been errors in publications, or specimens have not been returned; for these and other reasons, there are very frequently discrepancies between the published paratype repositories and the current situation. In cases where there are more specimens labelled as paratypes than mentioned in the original publication, we must remember that "all the specimens included by the author in the new taxon" (§72.4.1, ICZN 1999) unless "expressly excluded" by being listed with some other status are part of the type series. All specimens available to the author at the time of description are thus considered to belong to the type series, unless published or unpublished evidence suggests they were not considered for establishing the author's concept of the species. In this case, paratypes not mentioned in the original description can often be regarded as part of the type series, unless they are different in some sense that would have been mentioned, or the species described as monotypic with a unique holotype, in which case the extra specimens must be considered to be deliberately excluded from the type series - or unless there is some particular reason to believe that they came to the author's attention after publication.

Unfortunately, we have been unable to find the holotypes (or in some cases any type material) of 28 species. Very few of these taxa were published as being in Hedqvist's collection so it is possible that many of them will be found, unregistered, in institutional collections. The missing holotypes are listed in Table 1. Notably, most of the types of Hedqvist's species of Microgastrinae, Cheloninae and Opiinae are missing, and a substantial number of Mymaridae, but only few of other groups.

Recognition of Hedqvist specimens

In order to facilitate recognition of Hedqvist specimens, in general and for future location of currently missing types, we give a short description of typical characteristics.

Table 1. Missing types. Taxa described by Hedqvist where holotypes have not been located, listed in chronological order, in their original combinations.

Taxon
Anagrus tullgreni Heqvist, 1954
Camptoptera lapponica Heqvist, 1954
Pachyceras janssoni Heqvist, 1955
Camptoptera strobilicola Heqvist, 1956 (?)
Chelonus caboverdensis Hedqvist, 1965
Phanerotoma caboverdensis Hedqvist, 1965
Rhogas caboverdensis Hedqvist, 1965
Microgaster insularis Hedqvist, 1965
Apanteles brevimetacarpus Hedqvist, 1965
Apanteles rufithorax Hedqvist, 1965
Apanteles compressithorax Hedqvist, 1965
Apanteles robustus Hedqvist, 1965
Apanteles proagynus Hedqvist, 1965
Apanteles hyalinis Hedqvist, 1965
Apanteles procoxalis Hedqvist, 1965
Apanteles lindbergi Hedqvist, 1965
Apanteles salensis Hedqvist, 1965
Apanteles danaisae Hedqvist, 1965
Apanteles progahinga Hedqvist, 1965
Opius caboverdensis Hedqvist, 1965
Opius insularis Hedqvist, 1965
Opius lindbergi Hedqvist, 1965
Eurytoma tilicola Hedqvist, 1966
Plutothrix cisae Hedqvist, 1966
Eurytoma annilai Hedqvist, 1974
Legolasia dinotiscoides Hedqvist, 1974
Brimeria clavata Hedqvist, 1977
Kvaseria flavipes Hedqvist, 1978

Hymenoptera specimens mounted by Hedqvist are typically glued onto rectangular or more or less quadratic pieces of cardboard. In the early years, specimens are typically glued with the ventral side to the board (Figure 4A, cf also Figure 6D), probably revealing his background as a coleopterist. This often makes it difficult to observe characters in the face and on sides, particularly when both pairs of wings are stretched out and glued to the board. However from his later years, specimens are usually glued on their right-hand side, head usually facing left or up, and with the right pair of wings spread and glued to the board (Figures 4B, C, 5). This often allows inspection of larger parts of the body, even when no great effort has been made to homogenise posture, spread out body parts or clean the specimen.

Hedqvist's own locality labels are mostly printed, with details added by hand (Figure 6A–C). Most specimens are collected in Sweden, and label data starts with an abbreviation of the Swedish province, most commonly Sk., Upl. and Vb. (for Skåne,

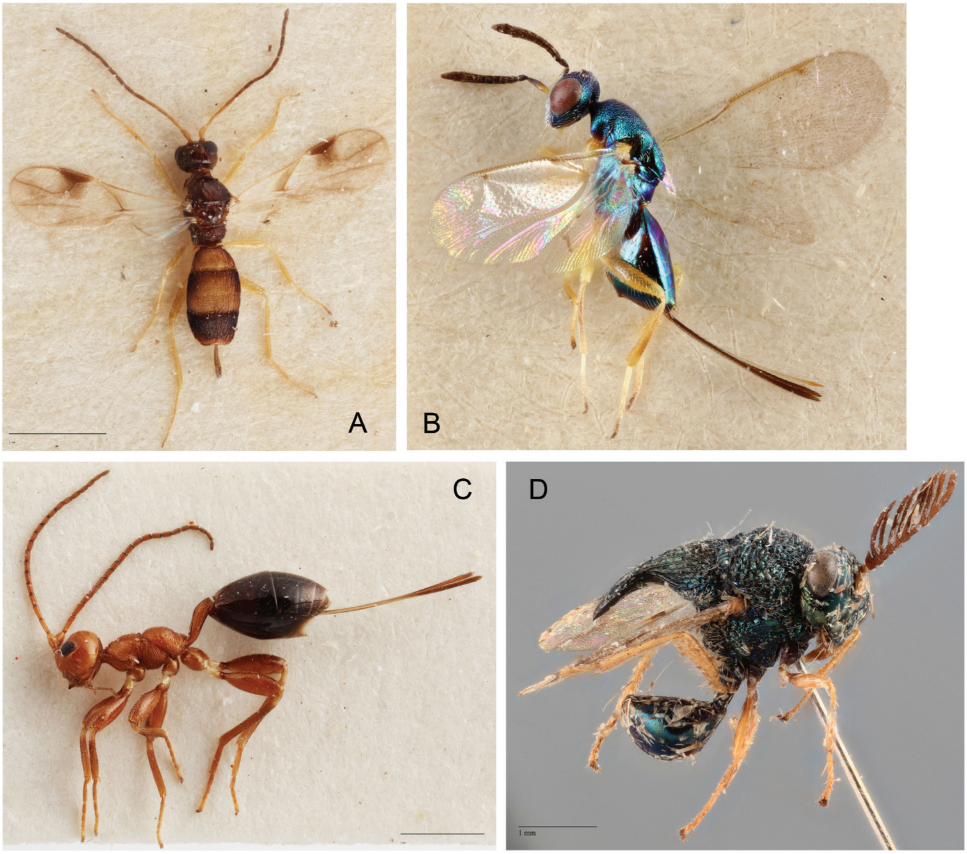

Figure 4. Examples of type specimens of Hedqvist. **A** Holotype of *Paracedria suecica* Heqvist, 1956 in NHRS **B** Holotype of *Torymus canariensis* Hedqvist, 1977 in BMNH **C** Holotype of *Spathius canariensis* Hedqvist, 1976 in NHRS **D** A paratype of *Schizaspidia tawiensis* Hedqvist, 1978 in NHRS.

Uppland and Västerbotten respectively) and a locality name; then a second row date (day/month year, all in arabic numerals). The name is typically given on a third row as "K.-J. Hedqvist", but many small variations occur. The abbreviated version "KJH" or "K.-J.H." is common if little space is available, and on entirely hand-written labels. Entirely handwritten labels are more common from later years, especially after Hedqvist's retirement. The handwriting is small and rather uneven but perfectly legible, usually even in his last years when it was getting notably shaky. Sometimes a separate label for the host plant or host insect is added (as in Figures 6A and 6D).

Of course, a lot of the material he worked on was collected or mounted by himself, so the mounts vary (Figure 4D shows a very different example), and in many cases identification labels provide the only way to connect a specimen with Hedqvist. Identification labels and type labels are usually similar in structure as locality labels, with a preprinted part and details added in handwriting. A number of identification labels however are entirely in his handwriting and without his name or signature (Figure 6C). Red type labels typically have "HOLOTYPUS" or "PARATYPUS", and "K-J

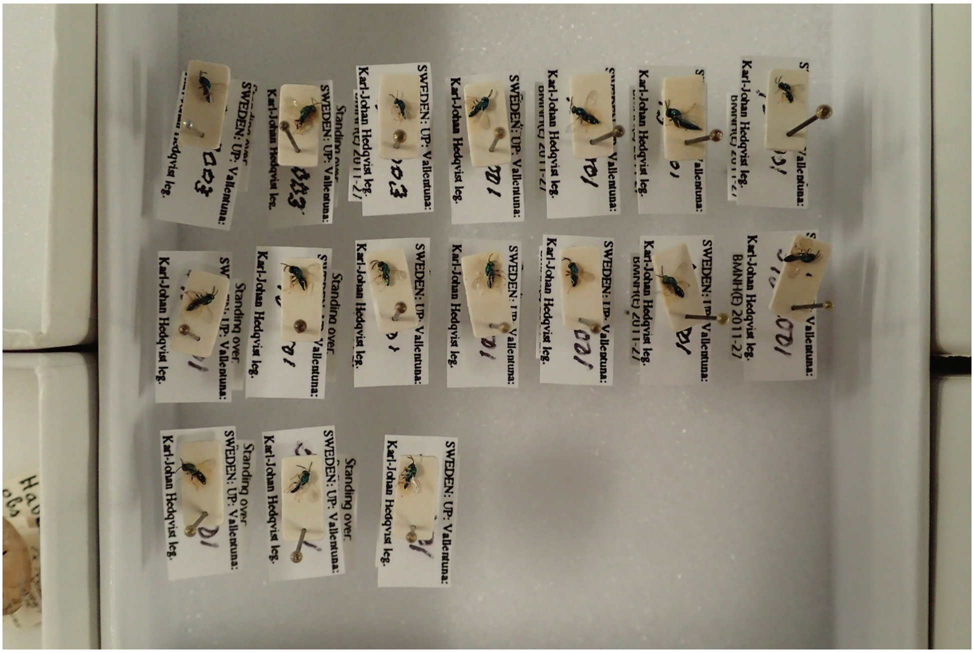

Figure 5. A unit tray with a series of specimens showing the characteristic variation of Hedqvist's mounts.

Hedqvist det. 19" printed (Figures 6A and 6B). More rarely, in early taxa, there is a small red label saying "Holotyp" without the name, combined with a regular identification label (Figure 6D). However, as our difficulties in finding many types have shown, there are several cases where type labels have been omitted or mixed up.

Collection abbreviations

AEIC	American Entomological Institute, Gainesville, USA
BMNH	Natural History Museum, London, UK
CFUA	Universidad Austral de Chile, Valdivia, Chile
CNC	Canadian National collection of Insects, Ottawa, Canada
EEZA	Estación Experimental de Zonas Aridas, Almeria, Spain
KUEC	Kyushu University, Fukuoka, Japan
MDLA	Museo do Dundo, Dundo, Angola
MHNG	Muséum d'Histoire Naturelle de Genève, Geneva, Switzerland
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MZH	Finnish Museum of Natural History, Helsinki, Finland
NHRS	Naturhistoriska Riksmuseet, Stockholm, Sweden
OUMNH	Oxford University Museum of Natural History, Oxford, UK
RMCA	Musée Royal de l'Afrique Central, Tervuren, Belgium
SLUU	Swedish University of Agricultural Sciences, Ultuna, Uppsala, Sweden

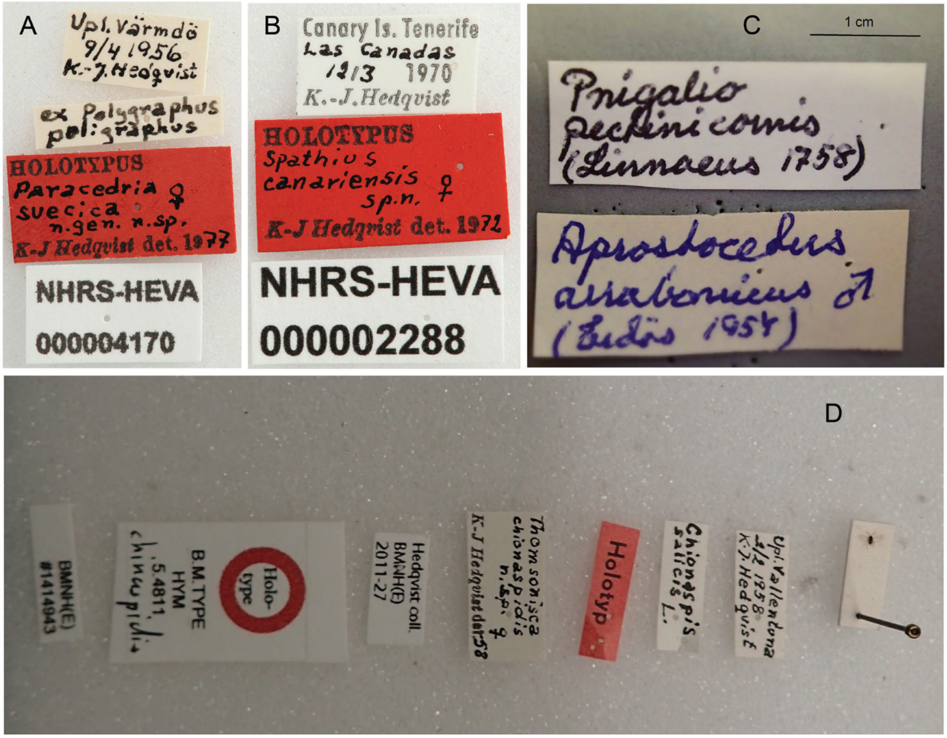

Figure 6. Examples of labels of Hedqvist. **A** Labels from holotype of *Paracedra suecica* Heqvist, 1956 in NHRS **B** Labels from holotype of *Spathius canariensis* Hedqvist, 1976 in NHRS **C** Two identification labels of non-type specimens without Hedqvist's name or signature **D** Holotype with labels of *Thomsonisca chinaspidis* Heqvist, 1958 in BMNH.

SSFRI	Swedish State Forest Research Institute, Stockholm, Sweden (now assimilated into the Swedish Agricultural University SLU at Uppsala, Sweden)
ULCI	Universidad de la Laguna, Tenerife, Spain
USNM	National Museum of Natural History, Washington DC, USA
ZMBN	Zoological Museum, University of Bergen, Norway
ZMHB	Museum für Naturkunde der Humboldt Universität, Berlin, Germany
ZMLU	Zoological Museum, Lund University, Lund, Sweden
ZMUC	Zoologisk Museum, Københavns Universitet, Copenhagen, Denmark
ZMUN	Zoologisk Museum, Oslo Universitet, Oslo, Norway

coll. T.-E. Leiler, now at NHRS
coll. H. Lindberg, now at MZH
coll. J. Mateu, now at EEZA
coll. Institute of Agricultural and Forest Zoology, University of Helsinki, Finland, now at MZH

Table 2. New names published by Hedqvist. Number of new names and their current status, assigned according to current classification (in a few cases different from Hedqvist's view).

	species group names	(of which valid)	fraction valid	genus group names	(of which valid)	fraction valid	family group names	(of which valid)	fraction valid
HYMENOPTERA	260	207	0.80	72	36	0.50	8	3	0.38
Chalcidoidea	182	153	0.84	59	30	0.51	5	3	0.60
Pteromalidae	97	89	0.92	47	27	0.57	4	2	0.50
Eupelmidae	24	18	0.75	0	0	n a	0	0	n a
Eulophidae	22	21	0.95	8	2	0.25	1	1	1.00
Eurytomidae	12	6	0.50	1	0	0.00	0	0	n a
Eucharitidae	8	7	0.88	1	1	1.00	0	0	n a
Mymaridae	8	3	0.38	2	0	0.00	0	0	n a
Encyrtidae	3	1	0.33	0	0	n a	0	0	n a
Perilampidae	3	3	1.00	0	0	n a	0	0	n a
Torymidae	2	2	1.00	0	0	n a	0	0	n a
Leucospidae	1	1	1.00	0	0	n a	0	0	n a
Ormyridae	1	1	1.00	0	0	n a	0	0	n a
Chalcididae	1	1	1.00	0	0	n a	0	0	n a
Ichneumonoidea	66	44	0.67	10	5	0.50	1	0	0.00
Braconidae	65	44	0.68	10	5	0.50	1	0	0.00
Ichneumonidae	1	0	0.00	0	0	n a	0	0	n a
Megalyroidea	6	6	1.00	1	1	1.00	2	0	0.00
Megalyridae	6	6	1.00	1	1	1.00	2	0	0.00
Proctotrupoidea	2	2	1.00	1	0	0.00	0	0	n a
Diapriidae	0	0	n a	1	0	0.00	0	0	n a
Roproniidae	1	1	1.00	0	0	n a	0	0	n a
Vanhorniidae	1	1	1.00	0	0	n a	0	0	n a
Chrysidoidea	1	1	1.00	1	0	0.00	0	0	n a
Bethylidae	1	1	1.00	1	0	0.00	0	0	n a
Tenthredinoidea	1	0	0.00	0	0	n a	0	0	n a
Diprionidae	1	0	0.00	0	0	n a	0	0	n a
Platygastroidea	1	1	1.00	0	0	n a	0	0	n a
Scelionidae	1	1	1.00	0	0	n a	0	0	n a
Stephanoidea	1	0	0.00	0	0	n a	0	0	n a
Stephanidae	1	0	0.00	0	0	n a	0	0	n a
COLEOPTERA	1	1	1.00	0	0	n a	0	0	n a
Curculionidae	1	1	1.00	0	0	n a	0	0	n a
Σ	261	208	0.80	72	36	0.50	8	3	0.38

Hedqvist's taxonomic publications

Hedqvist described 261 insect species in 88 papers published between 1954 and 2004 (all but one 1954–1985) in various journals, often the Scandinavian ones, Entomologisk Tidskrift, Opuscula Entomologica and Entomologica Scandinavica, but very often also in local journals connected with the countries or museums where the specimens were from. For the active period 1954–1985, he published on an average 2.7 papers a year (0–7, but zeros are very rare and only in the last years), with 2.9 new species per paper or 7.9 new species per year (0–28). These are mainly taxonomic papers, often with little other content than descriptions, but in several cases with some biological observations and attempts to synthesise available knowledge (particularly concerning parasitoids of saproxylic Coleoptera). The largest part of these papers are of ”notes” type: descriptions of a few new taxa, but several are taxonomic revisions of small groups, and a few are revisions of larger scope or treatment of larger materials (mainly 1959–1970). The bulk of the new taxa are made up of new species, but there are also a few family-group taxa, and 72 new genera (Table 2) (the new genera almost always with simultaneously described new species as type species, only 4 cases have type species that were described earlier by someone else). Very few papers, and none before 1979, were written together with co-authors. (Please note the shift in spelling of the name from Heqvist to Hedqvist between 1961 and 1962. Hedquist, as frequently seen in taxonomic literature, is a misspelling).

Results

Taxa described by Hedqvist

Names are listed in strictly alphabetical order as originally given. In order to find names pertaining to a particular family of interest, consult Table 3.

Ablaxia robusta Hedqvist, 1978c, p. 315f, valid species (Pteromalidae: Pteromalinae)

Female holotype and one paratype now in NHRS (NHRS-HEVA000002194-NHRS-HEVA000002195), one paratype in BMNH; one paratype missing.

Afrolelaps Hedqvist, 1963a, p. 47, type species *Afrolelaps maculata* Hedqvist, 1963, junior synonym of *Dipara* Walker, 1833 (Pteromalidae: Diparinae)

Afrolelaps albomaculata Hedqvist, 1963a, p. 49f plus fig. 1b on p. 48, valid as *Dipara albomaculata* (Hedqvist, 1963) (Pteromalidae: Diparinae)

Female holotype and 1 paratype from Angola deposited in MDLA, 2 paratypes now in BMNH and 1 paratype in NHRS (in original publication stated to be deposited in Angola), 2 paratypes supposedly in NHRS missing.

Table 3. Genus and family-group level names under which to look for information about different families in the alphabetical taxa list.

Family-group	Genus
COLEOPTERA	
Curculionidae	*Hylocorus*
HYMENOPTERA	
Chalcidoidea	
Chalcididae	*Tanycoryphus*
Encyrtidae	*Coelopencyrtus*, *Parablastothrix*, *Thomsonisca*
Eucharitidae	*Gollumiella*, *Losbanus*, *Rhipiphallus*, *Schizaspidia*, *Stilbula*
Eulophidae	*Aprostocetus*, *Astichus*, *Balinia*, *Beornia*, *Durinia*, *Entia*, Entiidae, *Gimlia*, *Necremnus*, *Oinia*, *Sarasvatia*, *Visnuella*
Eupelmidae	*Anastatus*, *Calosota*, *Chirolophus*, *Eupelmella*, *Eupelmus*, *Polymoria*
Eurytomidae	*Eudecatoma*, *Eurytoma*, *Pseudrileya*
Leucospidae	*Leucospis*
Mymaridae	*Anagrus*, *Baburia*, *Camptoptera*, *Herulia*, *Litus*
Ormyridae	*Ormyrus*
Perilampidae	*Chrysolampus*, *Perilampus*
Pteromalidae	passim
Torymidae	*Torymus*
Chrysidoidea	
Bethylidae	*Snappania*
Diaprioidea	
Diapriidae	*Sundholmiella*
Ichneumonoidea	
Braconidae	passim
Ichneumonidae	*Itoplectis*
Megalyroidea	
Megalyridae	Dinapsini, *Dinapsis*, Iseurini, *Megalyridia*, Megalyrini
Platygastroidea	
Scelionidae	*Telenomus*
Proctotrupoidea	
Roproniidae	*Ropronia*
Vanhorniidae	*Vanhornia*
Stephanoidea	
Stephanidae	*Foenatopus*
Tenthredinoidea	
Diprionidae	*Diprion*

Afrolelaps maculata Hedqvist, 1963a, pp. 47–49, valid as *Dipara maculata* (Hedqvist, 1963) (Pteromalidae: Diparinae), and type species of *Afrolelaps* Hedqvist, 1963

Female holotype from Angola, deposited in MDLA.

Amazonisca Heqvist, 1959c, p. 196 and key p. 178f, type species *Amazonisca batesi* Heqvist, 1959, valid genus (Pteromalidae: Cleonyminae)

Amazonisca batesi Heqvist, 1959c, p. 198 and fig. 7 on p. 197, valid species (Pteromalidae: Cleonyminae), and type species of *Amazonisca* Heqvist, 1959
Female holotype from Brazil in OUMNH.

Anagrus capensis Heqvist, 1960c, p. 426f, valid species (Mymaridae)
Female holotype from South Africa in ZMLU.

Anagrus tullgreni Heqvist, 1954b, p. 272f, junior synonym of *Anagrus atomus* (Linnaeus, 1767) (Mymaridae)
Female holotype and 45 paratypes, all from Sweden, according to original description deposited in SSFRI; 12 paratypes now in BMNH, holotype and 33 paratypes currently missing.

Anastatus capensis Hedqvist, 1970, p. 406f, valid species (Eupelmidae: Eupelminae)
Female holotype from South Africa now in BMNH.

Apanteles brevimetacarpus Hedqvist, 1965, p. 12f, valid species (Braconidae: Microgastrinae)
Female holotype and 1 paratypes from Cape Verde apparently deposited in coll. Lindberg, now missing (not in MZH), 1 male paratype now in BMNH.

Apanteles caboverdensis Hedqvist, 1965, p. 17f, junior synonym of *Apanteles hemara* Nixon, 1965 (Braconidae): Microgastrinae
Female holotype and 20 paratypes from Cape Verde originally deposited in coll. Lindberg, now missing (not in MZH), 2 paratypes now in BMNH.

Apanteles compressithorax Hedqvist, 1965, p. 14f, junior synonym of *Cotesia pistrinariae* (Wilkinson, 1929: Microgastrinae)
Female holotype and 10 paratypes from Cape Verde apparently deposited in coll. Lindberg, now missing (not in MZH), 2 paratypes now in BMNH.

Apanteles danaisae Hedqvist, 1965, p. 23 plus fig. 22 on p. 22, valid as *Cotesia danaisae* (Hedqvist, 1965) (Braconidae: Microgastrinae)
Fifty-six paratypes from Cape Verde apparently deposited in coll. Lindberg, now missing (not in MZH), holotype and 5 paratypes now in BMNH, 2 paratypes in NHRS (NHRS-HEVA000003782-NHRS-HEVA000003783).

Apanteles hyalinis Hedqvist, 1965, p. 18f, valid species (Braconidae: Microgastrinae)
Male holotype from Cape Verde apparently deposited in coll. Lindberg, now missing (not in MZH).

Apanteles jubmeli Hedqvist, 1972, p. 63f, valid species (Braconidae: Microgastrinae)
Female holotype and one paratype from Sweden now in NHRS (NHRS-HEVA000002275-NHRS-HEVA000002276), two paratypes now in BMNH.

Apanteles lindbergi Hedqvist, 1965, p. 21f, junior synonym of *Apanteles sodalis* (Haliday, 1834) (Braconidae: Microgastrinae)

Female holotype and 4 paratypes from Cape Verde apparently deposited in coll. Lindberg, now missing (not in MZH), 2 paratypes now in BMNH.

Apanteles proagynus Hedqvist, 1965, p. 17, valid species (Braconidae: Microgastrinae)

Male holotype and 1 paratype from Cape Verde apparently deposited in coll. Lindberg, now missing (not in MZH).

Apanteles proalastor Hedqvist, 1965, p. 20f, junior synonym of *Apanteles hemara* Nixon, 1965 (Braconidae: Microgastrinae)

Female holotype and 1 paratype from Cape Verde originally deposited in coll. Lindberg, now missing (not in MZH), 1 paratype now in BMNH.

Apanteles procoxalis Hedqvist, 1965, p. 19f, valid species (Braconidae: Microgastrinae)

Female holotype and 23 paratypes from Cape Verde apparently deposited in coll. Lindberg, now missing (not in MZH), 2 paratypes now in BMNH.

Apanteles progahinga Hedqvist, 1965, p. 23f, valid as *Cotesia progahinga* (Hedqvist, 1965) (Braconidae: Microgastrinae)

Female holotype and 5 paratypes from Cape Verde apparently deposited in coll. Lindberg, now missing (not in MZH), 2 paratypes now in BMNH.

Apanteles robustus Hedqvist, 1965, p. 15 plus fig. 13 on p. 16, valid species (Braconidae: Microgastrinae)

Female holotype from Cape Verde apparently deposited in coll. Lindberg, now missing (not in MZH).

Apanteles rufithorax Hedqvist, 1965, p. 13f, valid species (Braconidae: Microgastrinae)

Female holotype and 1 paratype from Cape Verde apparently deposited in coll. Lindberg, now missing (not in MZH).

Apanteles salensis Hedqvist, 1965, p. 22, junior synonym of *Glyptapanteles eucosmae* (Wilkinson, 1929) (listed as *Protapanteles eucosmae* in Yu *et al.*, 2012) (Braconidae: Microgastrinae)

Female holotype from Cape Verde apparently deposited in coll. Lindberg, now missing (not in MZH).

Apanteles salverdensis Hedqvist, 1965, p. 14 plus fig. 11 on p. 15, junior synonym of *Apanteles appellator* Telenga 1949 (Braconidae: Microgastrinae)

Female holotype and 1 paratype from Cape Verde originally deposited in coll. Lindberg, now missing (not in MZH).

Apanteles striatopleurus Hedqvist, 1965, p. 16, valid species (Braconidae: Microgastrinae)
Female holotype from Cape Verde originally deposited in coll. Lindberg, now in MZH.

Aspilota kempei Hedqvist, 1973f, p. 91 plus figs 1, 2c-d, 3a on p. 92, valid as *Dinotrema kempei* (Hedqvist, 1973) (Braconidae: Alysiinae)
Female holotype from Sweden now in NHRS (NHRS-HEVA000002277).

Aspilota necrophila Hedqvist, 1973b (1972 in Yu *et al.*, 2012), pp. 217–219, valid as *Dinotrema necrophilum* (Hedqvist, 1973) (Braconidae: Alysiinae)
Female holotype from Sweden now in NHRS (NHRS-HEVA000002278), one paratype now in BMNH.

Aspilota nidicola Hedqvist, 1973b (1972 in Yu et al., 2012), p. 216f, valid species (Braconidae: Alysiinae)
Female holotype from Sweden now in NHRS (NHRS-HEVA000002279), one paratype now in BMNH.

Aprostocetus dryocoetae Hedqvist, 1963c, pp. 147f, valid as *Baryscapus dryocoetae* (Hedqvist, 1963) (Eulophidae: Tetrastichinae)
Female holotype and 1 paratype from Sweden now in BMNH.

Astichus intermedius Hedqvist, 1969b, pp. 167–169 plus fig. 4b on p. 171, valid species (Eulophidae: Entiinae)
Female holotype and 2 paratypes from Sweden now in BMNH, 2 paratypes in NHRS, 4 paratypes in CNC.

Astichus maculatus Hedqvist, 1969b, p. 170f, valid species (Eulophidae: Entiinae)
Female holotype and 2 paratypes from Sweden now in BMNH.

Astichus polyporicola Hedqvist, 1969b, p. 172 plus fig. 2a on p. 169 and fig. 4c on p. 171, valid species (Eulophidae: Entiinae)
Female holotype and 25 paratypes from Canada in CNC, 8 paratypes now in BMNH.

Aulosaphes capensis Hedqvist 1963b, p. 43f, valid as *Afrotritermus capensis* (Hedqvist, 1963) (Braconidae: Lysiterminae)
Male holotype from South Africa in ZMLU.

Baburia Hedqvist, 2004, p. 235, type species *Baburia narendrani* Hedqvist, 2004, preoccupied name (nec *Baburia* Koçak, 1981 in Lepidoptera), junior synonym of *Acmopolynema* Oglobin, 1946 (Mymaridae)

Baburia fasciata Hedqvist, 2004, p. 236 plus fig. 7 on p. 239, junior synonym of *Acmopolynema tachikawai* Taguchi, 1971 (Mymaridae)
Female holotype from Sri Lanka now in BMNH.

Baburia narendrani Hedqvist, 2004, p. 235f plus fig. 5 on p. 238, fig. 6 on p. 239, valid as *Acmopolynema narendrani* (Hedqvist, 2004) (Mymaridae), type species of *Baburia* Hedqvist, 2004

Female holotype and 1 paratype from Sri Lanka now in BMNH.

Balinia Hedqvist, 1978a, p. 63, type species *Balinia stylata* Hedqvist, 1978, junior synonym of *Acrias* Walker, 1847 (Eulophidae: Entiinae)

Balinia stylata Hedqvist, 1978a, p. 63f, valid as *Acrias stylata* (Hedqvist, 1978) (Eulophidae: Entiinae), and type species of *Balinia* Hedqvist, 1978

Female holotype and 5 paratypes from Brazil now in BMNH, 5 paratypes in NHRS (NHRS-HEVA000002151-NHRS-HEVA000002155).

Balrogia Hedqvist, 1977a, p. 79f, type species *Balrogia striata* Hedqvist, 1977, valid genus (Pteromalidae: Erotolepsiinae)

Balrogia striata Hedqvist, 1977a, p. 80 plus fig. 2 on p. 79, valid species (Pteromalidae: Erotolepsiinae)

Female holotype from Brazil now in BMNH.

Beornia Hedqvist, 1975d, p. 133f, type species *Beornia femorata* Hedqvist, 1975, valid genus (described in Pteromalidae: Chrysolampinae, but now in Eulophidae: Entiinae)

Beornia femorata Hedqvist, 1975d, p. 134 plus fig. 1 on p. 135, valid species, and type species of *Beornia* Hedqvist, 1975 (Eulophidae: Entiinae nec Pteromalidae or Perilampidae)

Female holotype and 1 paratype from Sweden now in NHRS (NHRS-HEVA000002156-NHRS-HEVA000002157), 1 paratype in BMNH. 1 paratype currently missing.

Blacus nidicola Hedqvist, 1974h, p. 184 plus fig. 1 on p. 185, currently valid as a subspecies of *Blacus maryi* Hellén, 1958 (Braconidae: Brachistinae)

Female holotype and 1 paratype from Sweden now in NHRS (NHRS-HEVA000002280-NHRS-HEVA000002281), 1 paratype now in BMNH.

Boeria Hedqvist, 1969c, p. 185 and key pp. 174–176, type species *Boeria saetosa* Hedqvist, 1975, preoccupied (nec *Boeria* Kirkaldy, 1908 in Hemiptera), replaced with *Hedqvistina* Koçak, Hüseyinoglu & Kemal, 2008 (Pteromalidae: Diparinae)

Boeria saetosa Hedqvist, 1969c, p. 185 plus fig. 8 on p. 186, valid as *Hedqvistina saetosa* (Hedqvist, 1969) (Pteromalidae: Diparinae), and type species of *Boeria* Hedqvist, 1969 and its replacement name *Hedqvistina* Koçak, Hüseyinoglu & Kemal, 2008

Female holotype and 4 paratypes from South Africa in BMNH (1 paratype ex coll. Hedqvist).

Bofuria Hedqvist, 1978b, p. 137 and key p. 135, type species *Bofuria maculata* Hedqvist, 1978, valid genus (Pteromalidae; Colotrechninae)

Bofuria maculata Hedqvist, 1978b, p. 137, valid species (Pteromalidae: Colotrechninae), and type species of *Bofuria* Hedqvist, 1978

Female holotype from Brazil now in BMNH.

Bomburia Hedqvist, 1978b, p. 135f, type species *Bomburia femorata* Hedqvist, 1978, valid genus (Pteromalidae: Colotrechninae)

Bomburia femorata Hedqvist, 1978b, p. 136f, valid species (Pteromalidae: Colotrechninae), and type species of *Bomburia* Hedqvist, 1978

Female holotype from Brazil now in NHRS (NHRS-HEVA000003596), one paratype now in BMNH.

Bracon caboverdensis Hedqvist, 1965, p. 4, junior synonym of *Bracon unimaculatus* Szépligeti, 1913 (Braconidae: Braconinae)

Female holotype and 6 paratypes from Cape Verde apparently deposited in coll. Lindberg, now missing (not in MZH).

Bracon xyletini Hedqvist, 1973e, p. 89 plus fig. 1 on p. 90, junior synonym of *Bracon mirus* Szépligeti, 1901 (Braconidae: Braconinae)

Female holotype from Sweden now in NHRS (NHRS-HEVA000002282).

Brimeria Hedqvist, 1977b, p. 153, type species *Brimeria clavata* Hedqvist, 1977, junior synonym of *Sceptrothelys* Graham, 1956 (Pteromalidae; Pteromalinae)

Brimeria clavata Hedqvist, 1977b, p. 153 plus fig. 1 on p. 154, junior synonym of *Sceptrothelys grandiclava* (Walker, 1835) (Pteromalidae: Pteromalinae), and type species of *Brimeria* Hedqvist, 1977

Female holotype from Sweden deposited in coll. Hedqvist according to original description, but missing; will be deposited in NHRS if retained.

Brokkia Hedqvist, 1977b, p. 154, type species *Brokkia paradoxa* Hedqvist, 1977, junior synonym of *Rakosina* Bouček, 1956 (Pteromalidae: Pteromalinae)

Brokkia paradoxa Hedqvist, 1977b, p. 154f, junior synonym of *Rakosina deplanata* Bouček, 1956 (Pteromalidae: Pteromalinae), and type species of *Brokkia* Hedqvist, 1977

Female holotype from Sweden now in NHRS (NHRS-HEVA000003595).

Bruesisca Heqvist, 1961, p. 93, type species *Cleonymus submersus* Brues, 1910, valid genus (Pteromalidae: Cleonyminae)

Calosota affinis Hedqvist, 1970, p. 416 plus fig. 10d-f on p. 415 and fig. 11b on p. 417, valid species (Eupelmidae: Calosotinae)

Female holotype and 1 paratype from South Africa in BMNH (paratype ex coll. Hedqvist).

Calosota capensis Hedqvist, 1970, p. 410f plus fig. 5g-i on p. 408 and fig. 6c on p. 409, valid species (Eupelmidae: Calosotinae)

Female holotype from South Africa now in BMNH. 3 paratypes apparently missing.

Calosota cyanea Hedqvist, 1970, pp. 414–416 plus fig. 7g-i on p. 411 and fig. 8c on p. 412, valid species (Eupelmidae: Calosotinae)

Female holotype plus 2 paratypes from South Africa in BMNH.

Calosota ferrierei Hedqvist, 1970, p. 414 plus fig. 9a on p. 413, fig. 10a-c on p. 415 and fig. 11a on p. 417, valid species (Eupelmidae: Calosotinae)

Female holotype from Uganda and 2 paratypes in BMNH, 2 paratypes missing.

Calosota flavostylus Hedqvist, 1970, p. 413f plus fig. 7d-f on p. 411 and fig. 8b on p. 412, valid species (Eupelmidae: Calosotinae)

Female holotype from South Africa in BMNH; two specimens labelled as paratypes, although not mentioned in original description, in BMNH.

Calosota punctata Hedqvist, 1970, p. 418 plus fig. 12a-c on p. 419, valid species (Eupelmidae: Calosotinae)

Female holotype from South Africa in BMNH.

Calosota purpurata Hedqvist, 1970, p. 416f plus fig. 10g-i on p. 415, valid species (Eupelmidae: Calosotinae)

Female holotype from South Africa in BMNH.

Calosota robusta Hedqvist, 1970, p. 410 plus fig. 5d-e on p. 408 and fig. 6b on p. 409, valid species (Eupelmidae: Calosotinae)

Female holotype plus 1 paratype from South Africa in BMNH; 1 paratype deposited in coll. Hedqvist according to original description but missing.

Calosota rugosopunctata Hedqvist, 1970, p. 417f plus fig. 12d-e on p. 419, junior synonym of *Balcha cylindrica* Walker, 1862 (Eupelmidae: Calosotinae)

Female holotype from South Africa in BMNH.

Calosota septentrionalis Heqvist, 1956c, p. 96f, junior synonym of *Calosota aestivalis* Curtis, 1836 (Eupelmidae: Calosotinae)

Female holotype and 1 paratype from Sweden now in BMNH.

Calosota testaceipes Hedqvist, 1970, p. 412f plus fig. 7a-c on p. 411, valid species (Eupelmidae: Calosotinae)

Female holotype and 2 paratypes from South Africa in BMNH (one paratype ex coll. Hedqvist).

Calosota turneri Hedqvist, 1970, p. 408f, valid species (Eupelmidae: Calosotinae) Female holotype plus 4 paratypes from South Africa in BMNH (1 paratype ex coll. Hedqvist).

Camptoptera lapponica Heqvist, 1954b, pp. 273–275, junior synonym of *Camptoptera cardui* (Förster, 1856) (Mymaridae)

Female holotype and 1 paratype, all from Sweden, according to original description deposited in SSFRI; currently missing.

Camptoptera strobilicola Heqvist, 1956a, pp. 37–39, junior synonym of *Camptoptera magna* Soyka, 1946 (Mymaridae)

Female holotype and 1 paratype from Norway deposited in ZMUN, where 2 females and 1 male with matching collecting data not labelled as types were found and not considered types (probably erroneously) by Trjapitsyn (2014); according to original description, 42 paratypes deposited in SSFRI, also currently missing.

Cantharoctonus brunneus Hedqvist, 1963b, p. 38f, valid species (Braconidae: Rhysipolinae)

Female holotype from USA in USNM.

Cerocephala petiolata Hedqvist, 1969a, p. 459, valid species (Pteromalidae: Cerocephalinae)

Female holotype from Democratic Republic of Congo in RMCA.

Chalcedectoides Hedqvist, 1967a, p. 182, type species *Chalcedectoides saharensis* Hedqvist, 1967, junior synonym of *Agrilocida* Steffan, 1964 (Pteromalidae: Cleonymidae)

Chalcedectoides saharensis Hedqvist, 1967a, pp. 182–184, junior synonym of *Agrilocida ferrierei* Steffan, 1964 (Pteromalidae: Cleonyminae), and type species of *Chalcedectoides* Hedqvist, 1967

Female holotype from Algeria in MHNG, 2 paratypes now in BMNH, 5 paratypes missing (paratypes published as divided between coll. Hedqvist and coll. Mateu, though none are in EEZA where most of coll. Mateu is deposited).

Chalcedectes niger Hedqvist, 1967a, pp. 180–182, junior synonym of *Chalcedectus sinaiticus* (Masi, 1936) (Pteromalidae: Cleonyminae)

Female holotype from Algeria in MHNG, one paratype now in BMNH, one missing (not in EEZA, where most of coll. Mateu is deposited).

Chelonus caboverdensis Hedqvist, 1965, p. 9 plus fig. 5 on p. 10, valid species (Braconidae: Cheloninae)

Female holotype and 1 paratype from Cape Verde apparently deposited in coll. Lindberg, now missing (not in MZH), 1 paratype now in BMNH.

Chirolophus hyalinus Hedqvist, 1970, p. 430 plus fig. 19 on p. 431, valid as *Calosota hyalina* (Hedqvist, 1970) (Eupelmidae: Calosotinae)

Female holotype from South Africa in BMNH.

Choetospilisca Hedqvist, 1969a, p. 452 and key p. 450f, type species *Choetospilisca tabidoides* Hedqvist, 1969, valid genus (Pteromalidae: Cerocephalinae)

Choetospilisca tabidoides Hedqvist, 1969a, p. 452 plus fig. 1a on p. 543 (*tabiloides* is a later misspelling), valid species (Pteromalidae: Cerocephalinae), and type species of *Choetospilisca* Hedqvist, 1969

Female holotype plus 6 paratypes from Brazil now in BMNH.

Chrysolampus niger Hedqvist, 1968b, p. 156f, valid species (Perilampidae: Chrysolampinae)

Female holotype from the Philippines in ZMUC.

Cirdania Hedqvist, 1974a, p. 145, type species *Cirdania styliclava* Hedqvist, 1974, junior synonym of *Toxeuma* Walker, 1833 (Pteromalidae: Pteromalinae)

Cirdania styliclava Hedqvist, 1974a, p. 145f plus fig. 6–7 on p. 147, valid as *Toxeuma styliclava* (Hedqvist, 1974) (Pteromalidae: Pteromalinae), and type species of *Cirdania* Hedqvist, 1974

Female holotype and 2 paratypes from Sweden now in NHRS (NHRS-HEVA000002196- NHRS-HEVA000002198), 5 paratypes now in BMNH. According to original description 8 paratypes were deposited in coll. Hedqvist and 2 in ZMLU, thus 1 paratype appears to be missing.

Cleonymus albomaculatus Heqvist, 1960a, p. 415 plus fig. 1 on p. 416, valid species (Pteromalidae: Cleonyminae)

Female holotype from South Africa in ZMLU.

Cleonymus canariensis Hedqvist, 1983a, p. 129f plus figs 1a-c, 2a on p. 131, valid species (Pteromalidae: Cleonyminae)

Female holotype from the Canary Islands now in BMNH, one paratype now in NHRS (NHRS-HEVA000002201).

Coelopencyrtus cephalotus Hedqvist, 1973d, p. 94f, junior synonym of *Coelopencyrtus callidii* (Jansson, 1957) (Encyrtidae: Encyrtinae)

Female holotype from Sweden now in NHRS (NHRS-HEVA000002147).

Conodipara Hedqvist, 1971b, p. 58, replacement name for *Turneria* Hedqvist, 1969, type species *Turneria scutellata* Hedqvist, 1969, valid genus (Pteromalidae: Diparinae)

Conophorisca Hedqvist, 1969c, p. 199f and key pp. 174–176, type species *Conophorisca annulata* Hedqvist, 1969, valid genus (Pteromalidae: Diparinae)

Conophorisca annulata Hedqvist, 1969c, p. 201 plus fig. 19 on p. 200, valid species (Pteromalidae: Diparinae), and type species of *Conophorisca* Hedqvist, 1969

Female holotype from South Africa in BMNH, 1 paratype deposited in coll. Hedqvist according to original description but missing.

Cosmophoridia Heqvist, 1955b, p. 93, type species *Cosmophorus flaviceps* Marshall, 1898, downgraded and valid as a subgenus of *Streblocera* Westwood, 1833 (Braconidae: Euphorinae)

Cosmophorus lapponicus Heqvist, 1955b, p. 97f, junior synonym of *Cosmophorus klugi* Ratzeburg, 1848 (Braconidae: Euphorinae)

Female holotype from Sweden now in BMNH.

Cosmophorus narendrani Hedqvist, 2004, p. 233 plus fig. 1 on p. 236, valid species (Braconidae: Euphorinae)

Female holotype from Sri Lanka now in BMNH.

Dasyneurophaga Heqvist, 1957, p. 26f, type genus *Dasyneurophaga japonica* Heqvist, 1964, valid genus (Pteromalidae: Pteromalinae)

Dasyneurophaga japonica Heqvist, 1957, p. 27 plus fig. 2 on p. 25, valid species (Pteromalidae: Pteromalinae), and type species of *Dasyneurophaga* Heqvist, 1957

Female holotype plus 6 paratypes (3 of which were not labelled as types) from Japan now in BMNH, 1 paratype missing.

Dinapsini Hedqvist, 1967b, p. 139f, type genus *Dinapsis* Waterston, 1922, cited as ”Dinapsini Hedqv.” from 1959, where it was launched as as ”tribus nov.” (Hedqvist, 1959a, p. 486) but lacking a description and thus unavailable from that date according to §13.1 of the code, made available here through diagnosis in key, in any case invalid as a junior objective synonym and junior homonym of Dinapsinae Waterston, 1922 (Megalyridae).

Dinapsis albicoxa Hedqvist, 1967b, p. 244f, valid species (Megalyridae)

Female holotype from Madagascar in MNHN.

Dinapsis hirtipes Hedqvist, 1967b, p. 245 plus fig. 2a-b on p. 243, valid species (Megalyridae)

Female holotype in MNHN according to original description; one paratype now in BMNH.

Dinapsis oculohirta Hedqvist, 1967b, p. 242 plus fig. 2c on p. 243, valid species (Megalyridae)
Female holotype from Madagascar in MNHN; of 12 paratypes mentioned in original description (without repository specified), 2 now in BMNH.

Dinapsis nubilus Hedqvist, 1967b, p. 243f, valid species (Megalyridae)
Female holotype from Madagascar in MNHN.

Dinapsis seyrigi Hedqvist, 1967b, p. 241 plus fig. 1a on p. 242 and fig. 2d on p. 243, valid species (Megalyridae)
Female holotype from Madagascar in MNHN.

Dipara canadensis Hedqvist, 1969c, p. 193 plus fig. 13g on p. 192, valid species (Pteromalidae: Diparinae)
Female holotype from Canada now in BMNH.

Dipara nigrita Hedqvist, 1969c, p. 195 plus fig. 16 on p. 196, valid species (Pteromalidae: Diparinae)
Female holotype from Democratic Republic of Congo in RMCA.

Dipara nigrofasciata Hedqvist, 1969c, p. 194f, valid species (Pteromalidae: Diparinae)
Female holotype from Madagascar in RMCA.

Dipara turneri Hedqvist, 1969c, p. 193f, valid species (Pteromalidae: Diparinae)
Female holotype and 2 paratypes from South Africa in BMNH, 2 paratypes in RMCA.

Diparisca Hedqvist, 1964, p. 54f, type species *Diparisca ferrieri* Hedqvist, 1964, junior synonym of *Spalangiopelta* Masi, 1922 (Pteromalidae, described in Diparinae, currently in Ceinae)

Diparisca ferrierei Hedqvist, 1964, p. 55f, valid as *Spalangiopelta ferrierei* (Hedqvist, 1964) (Pteromalidae: Ceinae), type species of *Diparisca* Hedvist, 1964
Female holotype and 1 paratype from Brazil now in BMNH.

Diparomorpha Hedqvist, 1971b, pp. 57–59, type species *Diparomorpha machadoi* Hedqvist, 1971, junior synonym of *Dipara* Walker, 1833 (Pteromalidae: Diparinae)

Diparomorpha machadoi Hedqvist, 1971b, p. 57f, valid as *Dipara machadoi* (Hedqvist, 1971) (Pteromalidae: Diparinae), and type species of *Diparomorpha* Hedqvist, 1971
Female holotype from Angola deposited in MDLA according to original description.

Diprion butovitschi Hedqvist, 1967c, pp. 72–75, junior synonym of *Diprion pini* (Linnaeus, 1758) (Diprionidae)

Female holotype from Sweden deposited (according to original description) at SSFRI; 59 plus "hundreds" of paratypes mentioned in publication; holotype and 10 paratypes now in BMNH; other paratypes missing.

Dolichodipara Hedqvist, 1969c, p. 180f and key pp. 174–176, type species *Dolichodipara scutellata* Hedqvist, 1969, simultaneous synonym of *Myrmicolelaps* Hedqvist, 1969, the latter deemed junior by first revisor (Desjardins, 2007) (Pteromalidae: Diparinae)

Dolichodipara scutellata Hedqvist, 1969c, p. 181f plus fig. 4 on p. 180, valid as *Myrmicolelaps scutellata* (Hedqvist, 1969) (Pteromalidae: Diparinae), and type species of *Dolichodipara* Hedqvist, 1969

Female holotype from Namibia in BMNH, one paratype deposited in coll. Hedqvist according to original description but missing.

Durinia Hedqvist, 1978a, p. 64, type species *Durinia elegans* Hedqvist, 1978, junior synonym of *Acrias* Walker, 1847 (Eulophidae: Entiinae)

Durinia elegans Hedqvist, 1978a, p. 65 plus fig. 2 on p. 64, valid as *Acrias elegans* (Hedqvist, 1978) (Eulophidae: Entiinae), and type species of *Durinia* Hedqvist, 1978, junior synonym of *Acrias* Walker, 1847

Female holotype and 3 paratypes from Brazil now in NHRS (NHRS-HEVA000002158-NHRS-HEVA000002161), 4 paratypes now in BMNH; paratype numbers unclear in description (perhaps as many as 60; in that case, most are currently unaccounted for).

Dvalinia Hedqvist, 1977a, p. 78, type species *Dvalinia axillaris* Hedqvist, 1977, valid genus (Pteromalidae: Colotrechninae)

Dvalinia axillaris Hedqvist, 1977a, p. 78f, valid species (Pteromalidae: Colotrechninae), and type species of *Dvalinia* Hedqvist, 1977

Female holotype from Brazil now in BMNH, 1 paratype in NHRS (NHRS-HEVA000002205); original description does not specify number of paratypes so additional ones might possibly be present in other collections.

Dvaliniinae Hedqvist, 1978b, p. 135, type genus *Dvalinia* Hedqvist, 1977 (currently not recognised and thus a junior synonym of Pteromalidae: Colotrechninae)

Ecphylus carinatus Hedqvist, 1967d, p. 68f plus fig. 2b on p. 67, junior synonym of *Ecphylus silesiacus* (Ratzeburg, 1848) (Braconidae: Doryctinae)

Female holotype and 9 paratypes from Iran in MHNG, 1 paratype in BMNH.

Ecphylus pinicola Hedqvist, 1967d, p. 70, valid species (Broad et al., 2016) although often regarded as a junior synonym of *Ecphylus silesiacus* (Ratzeburg, 1848) (Braconidae: Doryctinae)

Female holotype and 23 paratypes from Sweden now in BMNH; in original description 26 paratypes are mentioned, thus 3 paratypes missing.

Elachertus lasiodermae Hedqvist, 1977c, p. 236f, valid species (Eulophidae: Eulophinae)

Female holotype and 10 paratypes from the Canary Islands now in BMNH, 12 paratypes in NHRS (NHRS-HEVA000002162-NHRS-HEVA000002173); 3 paratypes currently missing.

Elasmus capensis Heqvist, 1960b, p. 419f plus fig. 1f-h on p. 421, valid species (Eulophidae: Eulophinae)

Female holotype and 1 paratype from South Africa in ZMLU, 1 paratype now in BMNH (although the original description gives ZMLU as the depository).

Elasmus circulus Hedqvist, 2004, p. 234f plus fig. 3 on p. 237, valid species (Eulophidae: Eulophinae)

Female holotype from Sri Lanka now in BMNH.

Elasmus ferrieri Heqvist, 1960b (*ferrierei* is a later, unjustified emendation), pp. 420–422, valid species (Eulophidae: Eulophinae)

Female holotype from South Africa in ZMLU.

Elasmus nagombiensis Hedqvist, 2004, p. 235 plus fig. 4 on p. 238, valid species (Eulophidae: Eulophinae)

Female holotype and 3 paratypes from Sri Lanka now in BMNH.

Elasmus narendrani Hedqvist, 2004, p. 234 plus fig. 2 on p. 237, valid species (Eulophidae: Eulophinae)

Female holotype and 7 putative paratypes from Sri Lanka now in BMNH, although only 6 paratypes are mentioned in the original description.

Elasmus homonaeoides Heqvist, 1960b, p. 420 plus fig. 1d-e on p. 421, valid species (Eulophidae: Eulophinae)

Female holotype from South Africa in ZMLU.

Elderia Hedqvist, 1977b, p. 155, type species *Elderia suecica* Hedqvist, 1977, valid genus (Pteromalidae: Pteromalinae)

Elderia suecica Hedqvist, 1977b, p. 155f, valid species (Pteromalidae: Pteromalinae), and type species of *Elderia* Hedqvist, 1977

Female holotype and 2 paratypes from Sweden now in NHRS (NHRS-HEVA000002206- NHRS-HEVA000002208), 2 paratypes in BMNH.

Entedon stephanopachi Heqvist, 1959e, p. 140 plus figs 1–2 on pp. 141–142, valid species (Eulophidae: Entedoninae)

Female holotype missing and 3 paratypes from Sweden now in BMNH.

Entia Hedqvist, 1974e, p. 253f, type species *Entia leileri* Hedqvist, 1977, junior synonym of *Boucekastichus* Andriescu, 1971 (Eulophidae: Entiinae)

Entia leileri Hedqvist, 1974e, pp. 254–256, valid as *Boucekastichus leileri* (Hedqvist, 1974) (Eulophidae), type species of *Entia* Hedqvist, 1974

Female holotype from Romania now in NHRS (NHRS-HEVA000002174).

Entiidae Hedqvist, 1974e, p. 253, type genus *Entia* Hedqvist, 1974, junior synonym of Euderinae Erdös, 1956, but since that turned out to be a junior homonym (of Euderinae Lacordaire, 1866 in Coleoptera), Hedqvist's name became the oldest potentially valid family-group name and is currently valid as Entiinae (Pteromalidae) (cf Hansson and Straka 2009)

Epistenia burksi Hedqvist, 1968a, p. 3f plus fig. 6c on p. 6, fig. 4c on p. 8 and fig. 5c on p. 9, valid species (Pteromalidae: Cleonyminae)

Female holotype from USA in USNM, 1 paratype now in BMNH, 1 paratype in USNM.

Epistenia media Hedqvist, 1968a, pp. 5–7 plus fig. 4d on p. 8, valid species (Pteromalidae: Cleonyminae)

Female holotype plus 10 paratypes from USA in USNM.

Eubadizon synchitae Heqvist, 1956b, p. 91 plus figs 1–2 on pp. 92–93, junior synonym of *Eubazus macrocephalus* Nees, 1812 (Braconidae: Brachistinae)

Female holotype from Sweden now in BMNH; 8 paratypes in NHRS (should be 2 according to original description), 2 paratypes in ZMLU, 14 paratypes now in BMNH, 7 paratypes deposited in SSFRI according to the original description but currently missing; 55 paratypes should have been in the Hedqvist collection; as there were 6 more paratypes than expected at NHRS, 35 paratype are currently missing or not labelled as paratypes (and were not standing under the name *synchitae*).

Eudecatoma mallorcae Hedqvist, 1962c, p. 212 plus fig. 1 on p. 213, junior synonym of *Sycophila pistacina* (Rondani, 1872) (Eurytomidae: Eurytominae)

Female holotype and 4 paratypes from Spain in NHRS.

Eupelmella albohirta Hedqvist, 1970, p. 402f, valid as *Eupelmus albohirtus* (Hedqvist, 1970) (Eupelmidae: Eupelminae)

Female holotype from South Africa in MZLU.

Eupelmella brincki Hedqvist, 1970, p. 403f, valid as *Eupelmus brincki* (Hedqvist, 1970) (Eupelmidae: Eupelminae)

Female holotype from South Africa in MZLU, one paratype now in BMNH.

Eupelmella pedatorioides Hedqvist, 1970, p. 404f, valid as *Eupelmus pedatorioides* (Hedqvist, 1970) (Eupelmidae: Eupelminae)

Female holotype from South Africa in MZLU, two paratypes now in BMNH, only one of which mentioned in original publication.

Eupelmus suecicus Hedqvist, 1963c, p. 137f, junior synonym of *Eupelmus pini* Taylor, 1927 (Eupelmidae: Eupelminae)

Female holotype from Sweden now in BMNH.

Eurytoma acaciacola Hedqvist, 1967f, pp. 137–139, valid as *Aximopsis acaciacola* (Hedqvist, 1967) (Eurytomidae: Eurytominae)

Female holotype and 2 paratypes from Chad in MNHN, 2 paratypes now in BMNH.

Eurytoma annilai Hedqvist, 1974f, p. 28f, valid species (Eurytomidae)

Female holotype and 9? paratypes from Finland in coll. Finnish Forest Institute (now missing, not currently present in HZM), 1 paratype now in BMNH and 1 paratype in NHRS (NHRS-HEVA000002187).

Eurytoma asphodeli Hedqvist, 1976a, p. 67f, valid species (Eurytomidae: Eurytominae)

Female holotype and 1 paratype from Spain now in NHRS (NHRS-HEVA000002188-NHRS-HEVA000002189), 3 paratypes in BMNH; 1 paratype currently missing.

Eurytoma blastophagi Hedqvist, 1963c, pp. 38–41 plus fig. 19a on p. 42 and fig. 20b on p. 43, junior synonym of *Eurytoma arctica* Thomson, 1876 (Eurytomidae: Eurytominae)

Female holotype and 13 paratypes from Sweden now in BMNH, 3 paratypes missing (depository not stated in publication).

Eurytoma fraxinicola Hedqvist, 1963c (*fraxincola* is a subsequent misspelling), p. 35f plus fig. 18a on p. 40 and fig. 19d on p. 42, junior synonym of *Eurytoma morio* Boheman, 1836 (Eurytomidae: Eurytominae)

Male holotype and 1 paratype from Sweden now in BMNH, 2 paratypes missing (depository not stated in publication).

Eurytoma kangasi Hedqvist, 1966, pp. 194–196, valid species (Eurytomidae: Eurytominae)

Female holotype and one paratype originally deposited in the Institute of Agricultural and Forest Zoology, University of Helsinki, Finland now in HZM. One specimen labelled paratype, not mentioned in the original publication, now in BMNH.

Eurytoma mateui Hedqvist, 1967f, pp. 139–141, valid as *Aximopsis mateui* (Hedqvist, 1967) (Eurytomidae: Eurytominae)

Female holotype and one paratype in MNHN, 1 paratype now in BMNH.

Eurytoma oliphantis Hedqvist, 1976a, p. 66f, valid species (Eurytomidae: Eurytominae)

Female holotype and 2 paratypes from Sudan now in BMNH, 4 paratypes in NHRS (NHRS-HEVA000002190-NHRS-HEVA000002193); 3 paratypes currently missing.

Eurytoma saharensis Hedqvist, 1967f, p. 141f, valid as *Aximopsis saharensis* (Hedqvist, 1967) (Eurytomidae: Eurytominae)

Female holotype and two possible paratypes from Algeria in MNHN, 1 paratype now in BMNH.

Eurytoma tilicola Hedqvist, 1966, p. 196f, valid species (Eurytomidae: Eurytominae)

According to the original description, female holotype from Finland deposited in the coll. Institute of Agricultural and Forest Zoology, University of Helsinki, Finland (now missing, not found in HZM). One paratype now in BMNH.

Eutelisca Hedqvist, 1968c, p. 39f, type species *Eutelisca chilensis* Hedqvist, 1968, valid genus (Pteromalidae: Pteromalinae)

Eutelisca chilensis Hedqvist, 1968c, p. 40 plus fig. 3 on p. 41, valid species (Pteromalidae: Pteromalinae), and type species of *Eutelisca* Hedqvist, 1968

Female holotype from Chile now in BMNH.

Foenatopus hoggarensis Hedqvist, 1967a, p. 188f, junior synonym of *Foenatopus mirei* Benoit, 1953 (Stephanidae)

Female holotype and 1 paratype from Algeria in MHNG, 2 paratypes now in BMNH and 6 in EEZA; one more paratype is mentioned in original description but not found.

Gahanisca Hedqvist, 1969a, p. 466 and key p. 450f, type species *Gahanisca gnathocerus* Hedqvist, 1969, valid genus (Pteromalidae: Cerocephalinae)

Gahanisca gnathocerus Hedqvist, 1969a, p. 466 plus fig. 5 on p. 465, valid species (Pteromalidae: Cerocephalinae), and type species of *Gahanisca* Hedqvist, 1969

Female holotype from Brazil now in BMNH.

Gildoria Hedqvist, 1974d, p. 29f, type species *Gildoria elegans* Hedqvist, 1974, valid genus (Braconidae: Doryctinae)

Gildoria elegans Hedqvist, 1974d, p. 30 plus fig. 1 on p. 32, valid species (Braconidae: Doryctinae), and type species of *Gildoria* Hedqvist, 1974

Female holotype and 1 paratype from the Canary Islands now in BMNH, 4 paratypes now in NHRS (NHRS-HEVA000002283-NHRS-HEVA000002286).

Gimlia Hedqvist, 1978a, p. 66, type species *Gimlia fasciata* Hedqvist, 1978, junior synonym of *Allocerastichus* Masi, 1924 (Eulophidae: Entiinae)

Gimlia fasciata Hedqvist, 1978a, p. 66f, valid as *Allocerastichus fasciatus* (Hedqvist, 1978) (Eulophidae: Entiinae), and type species of *Gimlia* Hedqvist, 1978

Female holotype and 4 paratypes from Brazil now in BMNH, 4 paratypes in NHRS (NHRS-HEVA000002175-NHRS-HEVA000002178).

Glyptosticha burmanica Hedqvist, 1968c, p. 50 plus fig. 8a-d on p. 51, valid as *Miscogasteriella burmanica* (Hedqvist, 1968) (Pteromalidae: Pteromalinae)

Female holotype from Burma in NHRS, 1 paratype in coll. Hedqvist according to original description but currently missing.

Glyptosticha perakensis Hedqvist, 1968c, p. 49 plus fig. 8e-f on p. 51, valid as *Miscogasteriella perakensis* (Hedqvist, 1968) (Pteromalidae: Pteromalinae)

Female holotype and 1 paratype from Malaysia in BMNH.

Gnathophorisca Hedqvist, 1969a, p. 463 and key p. 450f, type species *Gnathophorisca monstrosus* Hedqvist, 1969, valid genus (Pteromalidae: Cerocephalinae)

Gnathophorisca monstrosus Hedqvist, 1969a, pp. 463–465, valid species (Pteromalidae: Cerocephalinae), and type species of *Gnathophorisca* Hedqvist, 1969

Male holotype from Brazil now in BMNH.

Gollumiella Hedqvist, 1978e, p. 230, type species *Gollumiella longipetiolata* Hedqvist, 1978, valid genus (Eucharitidae)

Gollumiella longipetiolata Hedqvist, 1978e, p. 230f, figs 8–10 on p. 231, valid species (Eucharitidae: Gollumiellinae), and type species of *Gollumiella* Hedqvist, 1978

Female holotype and 1 paratype from the Philippines in ZMUC, 1 paratype now in BMNH, 1 paratype in NHRS (NHRS-HEVA000002149).

Gothbergia Heqvist, 1957, p. 24, type species *Gothbergia elymi* Heqvist, 1957, junior synonym of *Dinarmoides* Masi, 1924 (Pteromalidae: Pteromalinae)

Gothbergia elymi Heqvist, 1957, pp. 23–36, junior synonym of *Dinarmoides spilopterus* Masi, 1924 (Pteromalidae: Pteromalinae), and type species of *Gothbergia* Heqvist, 1957

Male holotype plus 1 paratype from Sweden now in BMNH, 1 paratype in NHRS.

Grahamisia straminea Hedqvist, 1969c, p. 187f plus fig. 10c on p. 189 and fig. 11e & g on p. 190, valid as *Dipara straminea* (Hedqvist, 1969) (Pteromalidae: Diparinae)

Female holotype from Democratic Republic of Congo in RMCA.

Grahamisia striata Hedqvist, 1969c, p. 188 plus fig. 12 on p. 191, valid as *Dipara striata* (Hedqvist, 1969) (Pteromalidae: Diparinae)

Female holotype from South Africa in BMNH.

Guancheria Hedqvist, 1978d, p. 319, type species *Guancheria compressithorax* Hedqvist, 1978, valid genus (Pteromalidae: Pteromalinae)

Guancheria compressithorax Hedqvist, 1978d, p. 319f, valid species (Pteromalidae: Pteromalinae), and type species of *Guancheria* Hedqvist, 1978

Female holotype and 3 paratypes from the Canary Islands now in BMNH, 4 paratypes now in NHRS (NHRS-HEVA000002209-NHRS-HEVA000002212), 2 paratypes deposited in coll. Leiler according to original description, but currently missing (not found in NHRS where coll Leiler currently is).

Habrocytus actinopterae Hedqvist, 1977d, p. 237 plus figs 1–2 on p. 238, valid as *Pteromalus actinopterae* (Hedqvist, 1977) (Pteromalidae: Pteromalinae)

Female holotype and 12 paratypes from Sweden now in NHRS (NHRS-HEVA000002213- NHRS-HEVA000002224), 13 paratypes in BMNH; 1 paratype appear to be missing.

Halticoptera longipetiolus Hedqvist, 1975a, p. 167f plus fig. 3l on p. 170, fig. 6c on p. 173 and fig. 8e on p. 177, valid species (Pteromalidae: Miscogasterinae)

Female holotype from Sweden now in NHRS (NHRS-HEVA000002225), 1 paratype now in BMNH.

Halticoptera scaptomyzae Hedqvist, 1977e, p. 238f, valid species (Pteromalidae: Miscogasterinae)

Female holotype and 3 paratypes from Chile deposited in CFUA and 3 paratypes in coll. Hedqvist according to original description, but holotype and 4 paratypes present in coll. Hedqvist and 2 in NHRS. Holotype and one paratype will be returned to CFUA, 1 paratype retained in BMNH and 3 in NHRS (NHRS-HEVA000002227, NHRS-HEVA000004930, NHRS-HEVA000004931); 1 paratype currently unaccounted for.

Helcon heinrichi Hedqvist, 1967e, pp. 141–143 plus fig. 6c-d on p. 140, valid species (Braconidae: Helconinae)

Male holotype and 3 paratypes from Sweden in NHRS, one paratype now in BMNH.

Herulia Hedqvist, 1962b, p. 103, type species *Herulia sundholmi* Hedqvist, 1962, junior synonym of *Macrocamptoptera* Girault, 1910 (Mymaridae)

Herulia sundholmi Hedqvist, 1962b, p. 103f, junior synonym of *Macrocamptoptera metotarsa* (Girault, 1905) (Mymaridae), and type species of *Herulia* Hedqvist, 1962

Female holotype from Sweden now in BMNH.

Heydenini Hedqvist, 1961, p. 94 and key p. 92 (valid as Heydeniini with spelling emended), type genus *Heydenia* Förster, 1856 (currently valid tribe in Pteromalidae: Cleonyminae)

†*Heydeniopsis* Heqvist, 1961, p. 94, type species *Heydeniopsis cleonymoides* Heqvist, 1961, valid genus (fossil) (Pteromalidae: Cleonyminae)

†*Heydeniopsis cleonymoides* Heqvist, 1961, p. 95f, valid fossil species (Pteromalidae: Cleonyminae), and type species of *Heydeniopsis* Heqvist, 1961

Female holotype in Baltic amber from Russia in NHRS (paleontology collections, not entomology).

Heydenisca Hedqvist, 1967f, p. 142f, type species *Heydenisca mateui* Hedqvist, 1967, junior synonym of *Heydenia* Förster, 1856 (Pteromalidae: Cleonyminae)

Heydenisca mateui Hedqvist, 1967f, p. 144f plus fig. 5 on p. 143, valid as *Heydenia mateui* (Hedqvist, 1967) (Pteromalidae: Cleonyminae), and type species of *Heydenisca* Hedqvist, 1967

Female holotype plus 1 paratype from Chad supposedly in MNHN, but missing, 3 specimens labelled as paratypes now in BMNH (one of them a female, which does not appear to be the missing holotype).

Hormius caboverdensis Hedqvist, 1965, p. 6f plus fig. 2 on p. 4, valid species (Braconidae: Hormiinae)

Female holotype and 8 paratypes from Cape Verde probably originally deposited in coll. Lindberg, now in MZH, 2 paratypes now in BMNH.

Hormius capensis Hedqvist, 1963b, p. 51f plus fig. 10a, b, g on p. 56, valid species (Braconidae: Hormiinae)

Female holotype from South Africa in ZMLU Lund, 2 paratypes now in BMNH (one of which was deposited in ZMLU according to the original description).

Hormius insularis Hedqvist, 1965, p. 7 plus fig. 3a on p. 8, junior synonym of *Hormius moniliatus* (Nees, 1811) (Braconidae: Hormiinae)

Female holotype from Cape Verde originally deposited in coll. Lindberg, now in MZH, 1 paratype now in BMNH.

Hormius micropterus Hedqvist, 1963b, p. 51 plus fig. 8 on p. 50, junior synonym of *Hormius dispar* (Brues, 1907) (Braconidae: Hormiinae)

Female holotype from USA in NHRS.

Hylocurus beckeri Heqvist, 1954a, p. 8f, valid species (Coleoptera: Curculionidae: Scolytinae) Male holotype and 2 paratypes from Guatemala deposited in BMNH.

Iseurini nomen nudum, based on *Iseura* Spinola, 1853, launched as ”tribus nov.” of Megalyridae in Heqvist 1959a, p. 486, but lacking a description and thus unavailable from that date according to §13.1 of the code, but if made available by someone else at a later date in any case a junior synonym of the braconid subfamily Cenocoeliinae Szépligeti, 1901 (cf van Achterberg 1994)

Itoplectis lapponicus Hedqvist, 1972, p. 62f, junior synonym of *Itoplectis insignis* Perkins, 1957 (Ichneumonidae: Pimplinae)

Female holotype and five paratypes from Sweden originally deposited in coll. Hedqvist according to original description, holotype and 1 paratype (NHRS-HEVA000004026-NHRS-HEVA000004027) now in NHRS, 2 paratypes in BMNH. In contrast to the original description, in which 2 female and 3 male specimens are designated as paratypes, 6 specimens were labelled as paratypes in coll. Hedqvist, 1 as a female, 5 as males; 1 female and 2 males are indeed *Itoplectis insignis* and are presumably paratypes but the remaining specimens represent 3 females and 1 male of a *Tycherus* sp. (Ichneumonidae: Ichneumoninae). We suspect that two species were mixed when labelling the type series, as *Tycherus suspicax* (Wesmael) was recorded as a parasitoid of *Epinotia nanana* in the same publication. Unfortunately we have not been able to find any more specimens of *I. lapponicus* in coll. Hedqvist. There are no other *Tycherus* specimens reared from *Epinotia nanana* in coll. Hedqvist so the record of *Tycherus suspicax* as a parasitoid of *Epinotia nanana* should be considered doubtful as these specimens are not *T. suspicax*, although GRB was unable to identify them.

Janssoniella intermedia Hedqvist, 1968c, p. 58, valid species (Pteromalidae: Pteromalinae)

Female holotype from Finland now in BMNH, 1 paratype in CNC, 3 paratypes missing.

Karpinskiella townesi Hedqvist, 1983b, p. 213 plus fig. 1 on p. 215, 2c on p. 216, 3b, f on p. 217, valid as *Tomicobia townesi* (Hedqvist, 1983) (Pteromalidae: Eunotinae)

Female holotype and one paratype from Brazil now in BMNH, 2 paratypes now in NHRS NHRS-HEVA000002228-NHRS-HEVA000002229).

Kvaseria Hedqvist, 1978c, p. 313, type species *Kvaseria flavipes* Hedqvist, 1978, junior synonym of *Tritneptis* Girault, 1908 (Pteromalidae: Pteromalinae)

Kvaseria flavipes Hedqvist, 1978c, p. 313f, valid as *Tritneptis flavipes* (Hedqvist, 1978) (Pteromalidae: Pteromalinae), and type species of *Kvaseria* Hedqvist, 1978

Female holotype and 5 paratypes from Sweden deposited in coll. Hedqvist according to original description. Holotype is missing, but will be deposited in NHRS if found. Of the 5 paratypes, 3 are now in NHRS (NHRS-HEVA000002230-NHRS-HEVA000002232) and 2 in BMNH.

Labania Hedqvist, 1963b, p. 36 and key p. 33f, type species *Labania straminea* Hedqvist, 1963, valid genus (Braconidae: Doryctinae)

Labania straminea Hedqvist, 1963b, p. 36 plus fig. 1 on p. 35, valid species (Braconidae: Doryctinae), and type species of *Labania* Hedqvist, 1963
Female holotype from Honduras in USNM.

Lariophagus rufipes Hedqvist, 1978c, p. 314, valid species (Pteromalidae: Pteromalinae)
Female holotype from Sweden now in NHRS (NHRS-HEVA000002233), one paratype now in BMNH.

Legolasia Hedqvist, 1974g, p. 177, type species *Legolasia dinotiscoides* Hedqvist, 1974, junior synonym of *Chlorocytus* Graham, 1956 (Pteromalidae: Pteromalinae)

Legolasia dinotiscoides Hedqvist, 1974g, p. 117f plus fig. 2a-f on p. 119, valid as *Chlorocytus dinotiscoides* (Hedqvist, 1974) (Pteromalidae: Pteromalinae), and type species of *Legolasia* Hedqvist, 1974
Female holotype from Sweden deposited in coll. Hedqvist according to original description but missing; will be deposited in NHRS if found; 1 paratype now in NHRS (NHRS-HEVA000002234) and 2 paratypes in BMNH.

Lelaps albofasciatus Hedqvist, 1964, p. 57f, valid species (Pteromalidae: Diparinae)
Female holotype from Puerto Rico in ZMHB.

Lelaps ferrierei Hedqvist, 1964, p. 56–57, valid species (Pteromalidae: Diparinae)
Female holotype and 1 paratype from Brazil now in BMNH (no mention of paratype in original description).

Leucospis buchi Hedqvist, 1968b, pp. 153–156, valid species (Leucospidae)
Female holotype and 3 paratypes from the Bismarck Islands in ZMUC, 2 paratypes now in BMNH.

Litus brincki Heqvist, 1960c, pp. 424–426, valid species (Mymaridae)
Female holotype and 9 paratypes from South Africa in ZMLU, 4 paratypes now in BMNH (depository given as ZMLU in original description).

Lodbrokia Hedqvist, 1962a, p. 99, type species *Lodbrokia hirta* Hedqvist, 1962, valid genus (Braconidae: Alysiinae)

Lodbrokia hirta Hedqvist, 1962a, pp. 99–101, valid species (Braconidae: Alysiinae), and type species of *Lodbrokia* Hedqvist, 1962
Female holotype from Sweden now in BMNH.

Losbanus peterseni Hedqvist, 1978e, p. 229, fig. 3 on p. 228, junior synonym of *Neolosbanus palgravei* (Girault, 1922) (Eucharitidae: Eucharitinae)
Female holotype and 2 paratypes from the Philippines in ZMUC, 1 paratype missing.

Louricini Hedqvist, 1961, p. 108 and key p. 92, type genus *Louricia* Ferrière, 1936, currently valid as subfamily Louriicinae with spelling emended (Pteromalidae)

Lycisca ogloblina Heqvist, 1961, p. 100f, valid species (Pteromalidae: Cleonyminae)
Female holotype and 1 paratype from Argentina now in BMNH, 2 paratypes will be deposited in NHRS.

Macromesus americanus Heqvist, 1960d, p. 140f plus fig. 2b, d, e on p. 142, valid species (Pteromalidae: Macromesinae)
Female holotype and 15 paratypes from USA in USNM, 2 paratypes now in BMNH, 2 paratypes in NHRS, 4 paratypes missing.

Macromesus javensis Hedqvist, 1968a, p. 9f, valid species (Pteromalidae: Macromesinae)
Female holotype from Indonesia in USNM; according to original description, the series of 7 paratypes is split between USNM and coll. Hedqvist but there are none in USNM and 8 specimens labelled as paratypes in BMNH.

Mediella Hedqvist, 1963b, p. 52 and key p. 33f, type species *Mediella romani* Hedqvist, 1863, junior synonym of *Hormius* Nees, 1819 (Braconidae: Hormiinae)

Mediella affinis Hedqvist, 1963b, p. 55 plus fig. 12d on p. 59, valid as *Hormius affinis* (Hedqvist, 1963) (Braconidae: Hormiinae)
Holotype and 3 specimens labelled as paratypes in NHRS, 1 additional specimen labelled as paratype now in BMNH, making a total of 4 alleged paratypes though the original desription mentions only 2.

Mediella elongata Hedqvist, 1963b, p. 55 plus fig. 12l-m on p. 59, valid as *Hormius elongatus* (Hedqvist, 1963) (Braconidae: Hormiinae)
Female holotype from Brazil in NHRS.

Mediella ferruginea Hedqvist, 1963b, p. 53, valid as *Hormius ferrugineus* (Hedqvist, 1963) (Braconidae: Hormiinae)
Female holotype plus 3 paratypes from Brazil in NHRS, 1 additional specimen labelled as paratype now in BMNH.

Mediella intermedia Hedqvist, 1963b, p. 53 plus fig. 12k on p. 59, valid as *Hormius intermedius* (Hedqvist, 1963) (Braconidae: Hormiinae)
Female holotype and 1 paratype from Brazil in NHRS, 1 additional specimen labelled as paratype now in BMNH.

Mediella romani Hedqvist, 1963b, p. 52 plus fig. 10c-f on p. 56 and fig. 12g-h on p. 59, valid as *Hormius romani* (Hedqvist, 1963) (Braconidae: Hormiinae), and type species of *Mediella* Hedqvist, 1963

Female holotype plus 1 paratype from Brazil in NHRS, 1 additional specimen labelled as paratype now in BMNH.

Mediella rugosa Hedqvist, 1963b, p. 53f plus fig. 12c on p. 59, valid as *Hormius rugosus* (Hedqvist, 1963) (Braconidae: Hormiinae)

Female holotype and 1 paratype from Brazil in NHRS, 1 additional specimen labelled as paratype now in BMNH.

Mediella teutoniae Hedqvist, 1963b, p. 57 plus fig. 12e-f on p. 59, valid as *Hormius teutoniae* (Hedqvist, 1963) (Braconidae: Hormiinae)

Female holotype from Brazil in NHRS.

Megalyridia Heqvist, 1959a, p. 487a, type species *Megalyridia capensis* Heqvist, 1959, valid genus (Megalyridae)

Megalyridia capensis Heqvist, 1959a, p. 489f plus fig. 1 on p. 488, valid species (Megalyridae), and type species of *Megalyridia* Heqvist, 1959

Female holotype from South Africa in ZMLU.

Megalyrini Hedqvist, 1967b, p. 239 & 241, type genus *Megalyra*, cited as ”Megalyrini Hedqv.” from 1959, where it was launched as ”tribus nov.” (Hedqvist, 1959a p 486) but lacking a description and thus unavailable from that date according to §13.1 of the code, made available here through diagnosis in key, in any case invalid as a junior objective synonym and junior homonym of Megalyrinae Schletterer, 1889

Microgaster insularis Hedqvist, 1965, p. 12 plus fig. 8 on p. 11, valid species (Braconidae: Microgastrinae)

Female holotype and one paratype from Cape Verde apparently deposited in coll. Lindberg, now missing (not in MZH).

Mithotynia Hedqvist, 1976c, p. 314, type species *Mithotynia aptera* Hedqvist, 1976, junior synonym of *Histeromerus* Wesmael, 1838 (described in Ichneumonidae, currently in Braconidae: Rhyssalinae)

Mithotynia aptera Hedqvist, 1976c, p. 315 plus fig. 1 on p. 314, junior synonym of *Histeromerus mystacinus* Wesmael, 1838 (Braconidae: Rhyssalinae nec Ichneumonidae: Metopiinae), and type species of *Mithotynia* Hedqvist, 1976

Female holotype from Sweden now in NHRS (NHRS-HEVA000002287).

Monitoriella Hedqvist, 1963b, p. 44–46 and key p. 33f, type species *Monitoriella elongata* Hedqvist, 1963, valid genus (Braconidae: Rhyssalinae)

Monitoriella compressithorax Hedqvist, 1963b, p. 48 plus fig. 7c-d on p. 47, valid species (Braconidae: Rhyssalinae)

Female holotype from Peru in USNM.

Monitoriella elongata Hedqvist, 1963b, p. 46 plus fig. 6 on p. 45, valid species (Braconidae: Rhyssalinae), and type species of *Monitoriella* Hedqvist, 1963

Female holotype plus 3 paratypes from USA in USNM, 2 apparent paratypes now in BMNH (only 4 paratypes mentioned in original publication, all as deposited in USNM).

Monitoriella rufithorax Hedqvist, 1963b, pp. 46–48, valid species (Braconidae: Rhyssalinae)

Female holotype plus 2 paratypes from Mexico in USNM, 2 apparent paratypes now in BMNH (only 3 paratypes mentioned in original publication, all as deposited in USNM).

Monodontomerus canariensis Hedqvist, 1979b, p. 78, fig. 1 on p. 80, valid species (Torymidae: Toryminae)

Female holotype and 28 paratypes from the Canary Islands split between ULCI and coll Hedqvist according to original description but all were present in coll. Hedqvist. Holotype and 10 paratypes returned to ULCI, 9 paratypes each now in NHRS (NHRS-HEVA000002251- NHRS-HEVA000002259) and BMNH.

Muesebeckisia Hedqvist, 1969a, p. 461f and key p. 450f, type species *Muesebeckisia mandibularis* Hedqvist, 1969, valid genus (Pteromalidae: Cerocephalinae)

Muesebeckisia mandibularis Hedqvist, 1969a, p. 463 plus fig. 3 on p. 462, valid species (Pteromalidae: Cerocephalinae), and type species of *Muesebeckisia* Hedqvist, 1969

Female holotype and 22 paratypes from Brazil now in BMNH, 3 paratypes in CNC.

Myrmicolelaps Hedqvist, 1969c, p. 182 and key pp. 174–176, type species *Myrmicolelaps paradoxus* Hedqvist, 1969, valid genus (Pteromalidae: Diparinae)

Myrmicolelaps paradoxus Hedqvist, 1969c, p. 182f, valid species (Pteromalidae: Diparinae), and type species of *Myrmicolelaps* Hedqvist, 1969

Female holotype and one paratype from South Africa in BMNH, one paratype not mentioned in original publication in NHRS.

Nazgulia Hedqvist, 1973c, pp. 238–240, type species *Nazgulia petiolata* Hedqvist, 1973, valid genus (Pteromalidae: Pteromalinae)

Nazgulia petiolata Hedqvist, 1973c, p. 240 plus fig. 2 on p. 239, valid species (Pteromalidae: Pteromalinae), and type species of *Nazgulia* Hedqvist, 1973

Female holotype from Sweden now in NHRS (NHRS-HEVA000002235), one paratype now in BMNH.

Necremnus norvegicus Hedqvist, 1982, p. 13f plus fig. 3 on p. 13, valid species (Eulophidae: Eulophinae)

Female holotype from Norway deposited in ZMBN.

Neodipara hispanica Hedqvist, 1971a, p. 119 plus fig. 1 on p. 120, valid species (Pteromalidae: Neodiparinae)

Female holotype from Spain and 1 paratype now in NHRS (NHRS-HEVA000002237- NHRS-HEVA000002238), 2 paratypes now in BMNH.

Neoepistenia Heqvist, 1959c, p. 194–196 and key p. 178f, type species *Neoepistenia flavoscapus* Heqvist, 1959, valid genus (Pteromalidae: Cleonyminae)

Neoepistenia flavoscapus Heqvist, 1959c, p. 196 and fig. 6o-p on p. 195, valid species (Pteromalidae: Cleonyminae), and type species of *Neoepistenia* Heqvist, 1959

Female holotype from Brazil in NHRS.

Neolycisca Heqvist, 1959c, p. 198f and key p. 178f, type species *Neolycisca maculata* Heqvist, 1959, junior synonym of *Proglochin* Philippi, 1871 (Pteromalidae: Cleonyminae)

Neolycisca maculata Heqvist, 1959c, p. 199f, valid as *Proglochin maculata* (Hedqvist, 1958) (Pteromalidae: Cleonyminae), and type species of *Neolycisca* Heqvist, 1959

Male holotype from Argentina in USNM.

Netomocera africana Hedqvist, 1971c, pp. 238–241, valid species (Pteromalidae: Diparinae)

Female holotype plus 2 paratypes from South Africa in BMNH, 2 paratypes now in NHRS.

Netomocera alboscapus Hedqvist, 1971c, p. 238 plus fig. 1e on p. 239 and fig. 2c on p. 240, valid species (Pteromalidae: Diparinae)

Male holotype (labelled as a female) from Congo (no further data) now in NHRS (NHRS-HEVA000002236).

Netomocera rufa Hedqvist, 1971c, p. 241 plus fig. 1f on p. 239 and fig. 2b on p. 240, valid species (Pteromalidae: Diparinae)

Female holotype from South Africa in BMNH.

Netomocerini Hedqvist, 1971c, p. 237, type genus *Netomocera* Boucek, 1955, (currently not recognised and thus a junior synonym of Pteromalidae: Diparinae)

Ogloblinisca Hedqvist, 1968c, p. 50–52, type species *Oglobinisca maculata* Hedqvist, 1968, valid genus (Pteromalidae: Pteromalinae)

Ogloblinisca americana Hedqvist, 1968c, pp. 54–56 plus fig. 9e on p. 53, valid species (Pteromalidae: Pteromalinae)

Female holotype plus 1 paratype from USA in USNM, 4 paratypes in CNC, 2 paratypes now in BMNH.

Ogloblinisca flavipes Hedqvist, 1968c, p. 54 plus fig. 9g on p. 53 and fig. 10c on p. 55, valid species (Pteromalidae: Pteromalinae)

Female holotype and 4 paratypes from Brazil now in BMNH.

Ogloblinisca maculata Hedqvist, 1968c, pp. 52–54 plus fig. 10a-b on p. 55, valid species (Pteromalidae: Pteromalinae), and type species of *Oglobinisca* Hedqvist, 1968

Female holotype from Argentina now in BMNH, 5 paratypes now in BMNH.

Oinia Hedqvist, 1978a, p. 65, type species *Oinia cyanea* Hedqvist, 1978, junior synonym of *Acrias* Walker, 1847 (Eulophidae: Entiinae)

Oinia cyanea Hedqvist, 1978a, p. 65, valid as *Acrias cyanea* (Hedqvist, 1978) (Eulophidae: Entiinae), and type species of *Oinia* Hedqvist, 1978

Female holotype from Brazil now in NHRS (NHRS-HEVA000002179), 2 paratypes in BMNH.

Oodera hoggarensis Hedqvist, 1967a, p. 186f, valid species (Pteromalidae: Cleonyminae)

Female holotype from Algeria in MHNG, 1 paratype now in BMNH and 2 deposited in coll. Mateu (EEZA); the paratypes of *Chalcedectoides saharensis* (above) were misplaced under this name in coll Hedqvist.

Opius caboverdensis Hedqvist, 1965, p. 26 plus fig. 24 on p. 24, valid species (Braconidae: Opiinae)

Female holotype and one paratype from Cape Verde apparently deposited in coll. Lindberg, now missing (not in MZH).

Opius insularis Hedqvist, 1965, p. 26, junior primary homonym (nec *Opius insularis* Ashmead, 1894), replacement name *Opius hedqvisti* Fischer, 1971 (Braconidae: Opiinae)

Female holotype and one paratype from Cape Verde apparently deposited in coll. Lindberg, now missing (not in MZH).

Opius lindbergi Hedqvist, 1965, p. 27, junior primary homonym (nec *Opius lindbergi* Fischer, 1963), replacement name *Psyttalia lindbergiana* (Fischer, 1971) (Braconidae: Opiinae)

Female holotype from Cape Verde possibly apparently deposited in coll. Lindberg, now missing (not in MZH).

Ormyrus philippinensis Hedqvist, 1968b, pp. 162–164, valid species (Ormyridae)

Female holotype from the Philippines in ZMUC.

Orthostigma lokei Hedqvist, 1973f, pp. 91–93, valid species (Braconidae: Alysiinae)

Female holotype from Sweden now in NHRS (NHRS-HEVA000002200).

Ottaria Hedqvist, 1974b, p. 54f, type species *Ottaria perplexa* Hedqvist, 1974, valid genus (Pteromalidae: Pteromalinae)

Ottaria perplexa Hedqvist, 1974b, p. 55f plus fig. 1e on p. 54, valid species (Pteromalidae: Pteromalinae), and type species of *Ottaria* Hedqvist, 1974

Female holotype from Sweden in coll. Hedqvist according to original description but missing; will be deposited in NHRS if found.

Pachyceras janssoni Heqvist, 1955a, p. 84f, junior synonym of *Roptrocerus mirus* (Walker, 1834) (Pteromalidae: Pteromalinae)

Female holotype and 5 paratypes, all from Sweden; according to original description deposited in coll. Hedqvist but currently missing.

Parablastothrix nepticulae Hedqvist, 1976b, p. 50 plus fig. 1 p. 51, valid species (Encyrtidae: Encyrtinae)

Female holotype from Sri Lanka now in NHRS (NHRS-HEVA000002148).

Paracedria Heqvist, 1956d, p. 219, type species *Paracedria suecica* Heqvist, 1956, junior synonym of *Lysitermus* Förster, 1862 (Braconidae: Lysiterminae)

Paracedria suecica Heqvist, 1956d, p. 219f, valid as *Lysitermus suecicus* (Heqvist, 1956) (Braconidae: Lysiterminae), and type species of *Paracedria* Heqvist, 1956

Female holotype from Sweden now in NHRS (NHRS-HEVA000004170) (Figures 4A and 6A), 1 male paratype from Sweden now in BMNH, 1 paratype missing (depository not stated in publication).

Paracerocephala Hedqvist, 1969a, p. 458 and key p. 450f, type species *Paracerocephala hirta* Hedqvist, 1969, valid genus (Pteromalidae: Cerocephalinae)

Paracerocephala hirta Hedqvist, 1969a, p. 458 plus fig. 1b on p. 453 (*Paracephala hirta* in original description is obviously a misprint, since both identification key p. 451 and genus description p. 458 gives genus as *Paracerocephala*), valid species (Pteromalidae: Cerocephalinae), and type species of *Paracerocephala* Hedqvist, 1969

Female holotype from Democratic Republic of Congo in RMCA.

Paraheydenia madagascariensis Heqvist, 1961, p. 96 plus fig. 1 on p. 97, valid as *Heydenia madagascariensis* (Hedqvist, 1961) (Pteromalidae: Cleonyminae)

Female holotype from Madagascar in BMNH.

Parahormius areolaris Hedqvist, 1965, p. 5f, valid species (Braconidae: Hormiinae)

Male holotype form Cape Verde deposited in MZH.

Paralycisca Heqvist, 1959c, p. 192 and key p. 178f, type species *Paralycisca cristata* Heqvist, 1959, valid genus (Pteromalidae: Cleonyminae)

Paralycisca cristata Heqvist, 1959c, p. 192f and fig. 6t on p. 195, valid species (Pteromalidae: Cleonyminae), and type species of *Paralycisca* Heqvist, 1959

Female holotype and 2 paratypes from Brazil in NHRS according to original description, but holotype is missing.

Pentatermus Hedqvist, 1963b, p. 40 and key p. 33f, type species *Pentatermus carinatus* Hedqvist, 1963, valid genus (Braconidae: Lysiterminae)

Pentatermus carinatus Hedqvist, 1963b, pp. 40–42, junior synonym of *Pentatermus striatus* (Szépligeti, 1908) (Braconidae: Lysiterminae), type species of *Pentatermus* Hedqvist, 1963

Female holotype from Nigeria in USNM.

Perilampus dalawanensis Hedqvist, 1968b, p. 161f plus figs 17–18 on p. 163, valid species (Perilampidae: Perilampinae)

Female holotype from the Philippines in ZMUC.

Perilampus peterseni Hedqvist, 1968b, p. 160f, valid species (Perilampidae: Perilampinae)

Female holotype from the Philippines in ZMUC.

Perilitus areolaris Gerdin & Hedqvist, 1985, pp. 363–365 plus fig. 3b on p. 366, valid species (Braconidae: Euphorinae)

Female holotype and 494 paratypes from Sweden not accounted for in detail, but holotype and at least 56 paratypes are in UUZM; 7 paratypes now in BMNH.

Phanerotoma caboverdensis Hedqvist, 1965, p. 9f, junior synonym of *Phanerotoma leucobasis* Kriechbaumer, 1894 (Braconidae: Cheloninae)

Female holotype and 49 paratypes from Cape Verde apparently deposited in coll. Lindberg, now missing (not in MZH), 4 paratypes now in BMNH.

Platygerrhus americanus Hedqvist, 1968c, p. 38, valid species (Pteromalidae: Pteromalinae)

Female holotype plus 1 paratype from USA in USNM, 2 paratypes published as deposited in USNM currently missing.

Plutothrix canariensis Hedqvist, 1974c, p. 26f plus fig. 1 on p. 28, valid species (Pteromalidae: Pteromalinae)

Female holotype from the Canary Islands now in BMNH.

Plutothrix cisae Hedqvist, 1966, p. 197f, junior synonym of *Plutothrix acuminata* (Thomson, 1878) (Pteromalidae: Pteromalinae)

According to the original description, female holotype and 37 paratypes from Sweden deposited in coll. Hedqvist and two paratypes in the coll. Institute of Agricultural and Forest Zoology, University of Helsinki, Finland (now missing, not found in HZM); 33 paratypes now in BMNH, holotype and four paratypes missing.

Polymoria affinis Hedqvist, 1970, p. 426 plus fig. 17a-b on p. 427, valid as *Eusandalum affine* (Hedqvist, 1970) (Eupelmidae: Calosotinae)

Female holotype and 1 paratype from South Africa in BMNH, 2 paratypes missing.

Polymoria cyanea Hedqvist, 1970, p. 425f, a junior secondary homonym in *Eusandalum*, replaced by *Eusandalum africanum* Özdikmen, 2011 (Eupelmidae: Calosotinae)

Female holotype from South Africa in BMNH.

Polymoria elongata Hedqvist, 1970, p. 427f, a junior secondary homonym in *Eusandalum*, replaced by *Eusandalum hedqvisti* Bouček, 1976 (Eupelmidae: Calosotinae)

Female holotype and 7 paratypes from South Africa in BMNH (2 paratypes ex coll. Hedqvist).

Polymoria excavata Hedqvist, 1970, p. 426f, valid as *Eusandalum excavatum* (Hedqvist, 1970) (Eupelmidae: Calosotinae)

Female holotype from South Africa in BMNH.

Polymoria latifrons Hedqvist, 1970, p. 423f, valid as *Eusandalum latifrons* (Hedqvist, 1970) (Eupelmidae: Calosotinae)

Female holotype from South Africa in BMNH.

Polymoria stylata Hedqvist, 1970, p. 424f, a junior secondary homonym in *Eusandalum*, replaced by *Eusandalum namibiaense* Özdikmen, 2011 (Eupelmidae: Calosotinae)
Female holotype and 1 paratype from South Africa in BMNH (paratype ex coll. Hedqvist).

Pondia Hedqvist, 1969c, p. 197 and key pp 174–176, type species *Pondia punctulata* Hedqvist, 1969, preoccupied name (nec *Pondia* Oder, 1932 in Mollusca), replaced with *Africesa* Koçak, Hüseyinoglu & Kemal 2008, junior synonym of *Dipara* Walker, 1833 (Pteromalidae: Diparinae)

Pondia pallida Hedqvist, 1969c, p. 198f, valid as *Dipara pallida* (Hedqvist, 1969) (Pteromalidae: Diparinae)
Female holotype and 12 paratypes from South Africa in BMNH.

Pondia punctulata Hedqvist, 1969c, p. 197f plus fig. 18e on p. 199, valid as *Dipara punctulata* (Hedqvist, 1969) (Pteromalidae: Diparinae), and type species of *Pondia* Hedqvist, 1969
Female holotype and 4 paratypes from South Africa in BMNH.

Pseudocleonymus Hedqvist, 1967a, p. 184, type species *Pseudocleonymus spinifer* Hedqvist, 1967, junior synonym of *Zolotarewskya* Risbec, 1955 (Pteromalidae: Cleonyminae)

Pseudocleonymus spinifer Hedqvist, 1967a, pp. 184–186, valid as *Zolotarewskya spinifera* (Hedqvist, 1967) (Pteromalidae: Cleonyminae), and type species of *Pseudocleonymus* Hedqvist, 1967
Female holotype from Algeria in MHNG, 1 paratype in coll. Mateu (EEZA).

Pseudrileya Hedqvist, 1980, p. 160f, type species *Pseudrileya brasiliensis* Hedqvist, 1980, junior synonym of *Rileya* Ashmead, 1888 (Eurytomidae: Rileyinae)

Pseudrileya brasiliensis Hedqvist, 1980, p. 160 plus fig. 1 on p. 159, junior synonym of *Rileya haumani* (Brèthes, 1918) (Eurytomidae: Rileyinae), and type species of *Pseudrileya* Hedqvist, 1980
Female holotype from Brazil currently missing (will be deposited in NHRS if found), one paratype now in BMNH.

Pteromalus osmiae Hedqvist, 1979a, p. 157 plus fig. 1c-e on p. 155 and fig. 2a on p. 156, valid species (Pteromalidae: Pteromalinae)
Female holotype and 9 paratypes from Sweden now in NHRS, 10 paratypes now in BMNH. According to original description there were 28 female and 13 male paratypes, thus 22 paratypes are missing.

Pteromalus sylveni Hedqvist, 1979a, p. 155f, valid species (Pteromalidae: Pteromalinae)
Female holotype and 4 paratypes from Sweden now in NHRS (NHRS-HEVA000002239- NHRS-HEVA000002243), 6 paratypes now in BMNH.

Pyramidophoriella Hedqvist, 1969c, p. 178f and key pp. 174–176, type species *Pyramidophoriella albiclava* Hedqvist, 1969, valid genus (Pteromalidae: Diparinae)

Pyramidophoriella albiclava Hedqvist, 1969c, p. 179 plus fig. 2c on p. 176 and fig. 3e-g on p. 178, valid species (Pteromalidae: Diparinae), and type species of *Pyramidophoriella* Hedqvist, 1969
Female holotype and 18 paratypes from South Africa in BMNH.

Pyramidophoriella brunnea Hedqvist, 1969c, p. 179f plus fig. 3c-d on p. 178, valid species (Pteromalidae: Diparinae)
Female holotype from South Africa in BMNH.

Rhaconotinus Hedqvist, 1965, p. 8, type species *Rhaconotinus caboverdensis* Hedqvist, 1965, junior synonym of *Rhaconotus* Ruthe, 1854 (Braconidae: Doryctinae)

Rhaconotinus caboverdensis Hedqvist, 1965, p. 8f, junior synonym of *Rhaconotus concinnus* (Enderlein, 1912) (Braconidae: Doryctinae), and type species of *Rhaconotinus* Hedqvist, 1965
Female holotype from Cape Verde originally deposited in coll. Lindberg, now in MZH.

Rhipipallus peterseni Hedqvist, 1978e, p. 244, figs 53–55 on p. 245, valid as *Chalcura peterseni* (Hedqvist, 1978) (Eucharitidae: Eucharitinae)
Female holotype and 1 paratype from the Bismarck Islands in ZMUC.

Rhogas caboverdensis Hedqvist, 1965, p. 11f, valid as *Aleiodes caboverdensis* (Hedqvist, 1965) (Braconidae: Rogadinae)
Female holotype and 36 paratypes from Cape Verde apparently deposited in coll. Lindberg, now missing (not in MZH), 1 paratype now in BMNH.

Risbecisca Heqvist, 1960a, p. 418, type species *Lycisca burgeoni* Risbec, 1955, junior synonym of *Heydenia* Förster, 1856 (Pteromalidae: Cleonyminae)

Romanisca Heqvist, 1959c, p. 194 and key p. 178f, type species *Romanisca annulicornis* Heqvist, 1959, valid genus (Pteromalidae: Cleonyminae)

Romanisca annulicornis Heqvist, 1959c, p. 194 and fig. 6r and 6v on p. 195, valid species (Pteromalidae: Cleonyminae), and type species of *Romanisca* Heqvist, 1959
Female holotype from Brazil in USNM.

Ropronia malaisei Heqvist, 1959d, p. 137f, plus fig. 3 on p. 139, valid species (Roproniidae) Male holotype from Burma in NHRS. There was one specimen with the same collection data ("same locality") as the holotype in the Hedqvist collection, but this is not a paratype because the species is monotypic according to the original description (ICZN (1999) §73.1.2). This specimen may have come to Hedqvist's attention after the original description, or it may have been implicitly excluded from the type series.

Sarasvatia Hedqvist, 1976b, p. 50f, type species *Sarasvatia srilankiensis* Hedqvist, 1976, valid genus (Eulophidae: Entedoninae)

Sarasvatia srilankiensis Hedqvist, 1976b (*srilankensis* is a later, unjustified emendment), p. 51 plus fig. 2 on p. 52, valid species (Eulophidae: Entedoninae), and type species of *Sarasvatia* Hedqvist, 1976

Female holotype and 1 paratype from Sri Lanka now in NHRS (NHRS-HEVA000002180-NHRS-HEVA000002181), 2 paratypes now in BMNH.

Schizaspidia batuensis Hedqvist, 1978e, p. 232, fig. 19 on p. 233, valid species (Eucharitidae: Eucharitinae)

Male holotype from the Philippines in ZMUC.

Schizaspidia palawanensis Hedqvist, 1978e, p. 233f, fig. 26 on p. 233, valid species (Eucharitidae: Eucharitinae)

Male holotype from the Philippines in ZMUC.

Schizaspidia peterseni Hedqvist, 1978e, p. 234, fig. 30 on p. 234, valid species (Eucharitidae: Eucharitinae)

Male holotype from the Philippines in ZMUC.

Schizaspidia tawiensis Hedqvist, 1978e, p. 235, fig. 36 on p. 235, valid species (Eucharitidae: Eucharitinae)

Female holotype and 16 paratypes from the Philippines in ZMUC, 2 paratypes in BMNH, 1 paratype in NHRS (NHRS-HEVA000002150) (Figure 4D).

Sigynia Hedqvist, 1974b, p. 53, type species *Sigynia ernobii* Hedqvist, 1974, valid genus (Pteromalidae: Pteromalinae)

Sigynia ernobii Hedqvist, 1974b, p. 53f plus fig. 2a on p. 55 and fig. 3b on p. 56, valid species (Pteromalidae: Pteromalinae), and type species of *Sigynia* Hedqvist, 1974

Female holotype from Sweden now in NHRS (NHRS-HEVA000002244).

Smeagolia Hedqvist, 1973c, p. 237, type species *Smeagolia perplexa* Hedqvist, 1973, junior synonym of *Muscidifurax* Girault & Sanders, 1910 (Pteromalidae: Pteromalinae)

Smeagolia perplexa Hedqvist, 1973c, p. 237f, junior synonym of *Muscidifurax raptor* Girault & Sanders, 1910 (Pteromalidae: Pteromalinae), and type species of *Smeagolia* Hedqvist, 1973

Female holotype from Sweden now in NHRS, one paratype now in BMNH.

Snappania Hedqvist, 1975c, p. 130 and key p. 128, type species *Snappania ahusiensis* Hedqvist, 1975, junior synonym of *Plastanoxus* Kieffer, 1905 (Bethylidae)

Snappania ahusiensis Hedqvist, 1975c (*ahuiensis* is a subsequent misspelling), p. 130 plus fig. 6d on p. 126, valid as *Plastanoxus ahusiensis* (Hedqvist, 1975) (Bethylidae: Epyrinae), and type species of *Snappania* Hedqvist, 1975

Male holotype from Sweden now in NHRS (NHRS-HEVA000002274), 1 paratype in BMNH.

Spathius canariensis Hedqvist, 1976d, p. 51f plus fig. 1b on p. 53, valid species (Braconidae: Doryctinae)

Female holotype (Figures 4C and 6B) and 3 paratypes from the Canary Islands now in NHRS (NHRS-HEVA000002288-NHRS-HEVA000002291), 4 paratypes in BMNH.

Spathius depressus Hedqvist, 1976d, pp. 52–54 plus fig. 2a on p. 55, fig. 3f on p. 58 and fig. 5c on p. 61, junior synonym of *Spathius rubidus* (Rossi, 1794) (Braconidae: Doryctinae)

Female holotype from Sweden now in NHRS (NHRS-HEVA000002292), one paratype now in BMNH.

Spathius hirtus Hedqvist, 1976d, p. 52 plus fig. 1c on p. 53, junior synonym of *Spathius maderi* Fahringer, 1930 (Braconidae: Doryctinae)

Female holotype from Spain now in NHRS (NHRS-HEVA000002293).

Stilbula palawanensis Hedqvist, 1978e, p. 246, figs 56, 58 on p. 245, valid species (Eucharitidae: Eucharitinae)

Male holotype from the Philippines in ZMUC.

Sundholmiella Hedqvist, 1975b, p. 51, type species *Prosynacra giraudi* Kieffer, 1910, junior synonym of *Synacra* Förster, 1856 (Diapriidae)

Syntomopus agromyzae Hedqvist, 1973a, p. 215 plus fig. 4 on p. 214, valid species (Pteromalidae: Pteromalinae)

Female holotype and 3 paratypes from Sweden now in NHRS (NHRS-HEVA000002245- NHRS-HEVA000002248), 3 paratypes now in BMNH.

Tanycoryphus saharensis Hedqvist, 1967f, pp. 135–137, valid species (Chalcididae: Haltichellinae)

Female holotype from Chad deposited in MNHN according to original description, but currently missing.

Telenomus guancheri Hedqvist, 1979b (in several subsequent sources mistakenly ascribed to Huggert, 1979) (Scelionidae: Telenominae)

Holotype (presumably female but sex not stated in description) from the Canary Islands deposited in ULCI according to original description but missing. The series of 13 paratypes mentioned in the original description as split between ULCI and coll. Hedqvist was found present in its entirety but unlabelled in coll. Hedqvist. Eight paratypes now in NHRS (NHRS-HEVA000003597-NHRS-HEVA000003604) and 5 in BMNH.

Telepsogina Heqvist, 1958b, p. 58f, type species *Telepsogina adelognathi* Heqvist, 1958, valid genus (Pteromalidae: Miscogasterinae)

Telepsogina adelognathi Heqvist, 1958b, p. 59f, valid species (Pteromalidae: Miscogastrinae), and type species of *Telepsogina* Heqvist, 1958

Female holotype from Sweden now in BMNH.

Tetrastichus galerucivorus Heqvist, 1959e, p. 141f plus figs 3–4 on pp. 143–14, valid as *Oomyzus galerucivorus* (Heqvist, 1959) (Eulophidae: Tetrastichinae)

Female holotype and 2 paratypes from Sweden now in BMNH, 2 paratypes will be deposited in NHRS, 46 paratypes missing.

Theocolaxia bifasciata Hedqvist, 1969a, p. 454f, valid as *Neocalosoter bifasciatus* (Hedqvist, 1969) (Pteromalidae: Cerocephalinae)

Female holotype plus 10 paratypes from Brazil in BMNH.

Theocolaxia ferrugineus Hedvist, 1969a, p. 456, valid as *Neocalosoter ferrugineus* (Hedqvist, 1969) (Pteromalidae: Cerocephalinae)

Female holotype from South Africa plus 1 paratype in BMNH, one paratype in RMCA.

Theocolaxia muesebecki Hedqvist, 1969a, p. 456, valid as *Neocalosoter muesebecki* (Hedqvist, 1969) (Pteromalidae: Cerocephalinae)

Female holotype from the Philippines now in BMNH.

Theocolaxia turneri Hedqvist, 1969a, p. 457, valid as *Neocalosoter turneri* (Hedqvist, 1969) (Pteromalidae: Cerocephalinae)

Female holotype and 1 paratype from South Africa in BMNH.

Thomsonisca chinaspidis Heqvist, 1958a (*chionaspidis* is a later, unjustified emendation), p. 55f, junior synonym of *Thomsonisca amathus* (Walker, 1838) (Encyrtidae: Encyrtinae)

Female holotype and 1 paratype from Sweden now in BMNH; according to the original descripton, 6 more paratypes were deposited in the author's collection but are now missing from coll. Hedqvist in BMNH.

Tomicobia acuminati Heqvist, 1959b, p. 179f plus fig. 1 on p. 178, valid species (Pteromalidae: Pteromalinae)

Female holotype and 9 paratypes from Sweden now in BMNH, 9 paratypes in NHRS (NHRS-HEVA000002199 and further), 5 paratypes missing.

Tomicobia ferrierei Heqvist, 1959b, p. 178f, valid as *Dirhicnus ferrierei* (Heqvist, 1959) (Pteromalidae: Pteromalinae)

Female holotype and one paratype from France in BMNH, one paratype will be deposited in NHRS.

Torymus canariensis Hedqvist, 1977c, p. 235f, valid species (Torymidae: Toryminae)

Female holotype (Figure 4B) and 12 paratypes from the Canary Islands now in BMNH, 12 paratypes in NHRS (NHRS-HEVA000002260- NHRS-HEVA000002271).

Trichomalus norvegicus Hedqvist, 1982, p. 10f plus fig. 2 on p. 10, valid species (Pteromalidae: Pteromalinae)

Female holotype from Norway deposited in ZMBN.

Trigonoderus malaisei Hedqvist, 1968c, p. 46 plus fig. 6b & f on p. 47, valid species (Pteromalidae: Pteromalinae)

Female holotype from Burma in NHRS, 1 paratype now in BMNH.

Trychnosoma ernobii Hedqvist, 1974g, p. 118 plus fig. 4b on p. 121, valid species (Pteromalidae: Pteromalinae)

Female holotype from Sweden now in NHRS (NHRS-HEVA000002250).

Turneria Hedqvist, 1969c, p. 177 and key pp. 174–176, type species *Turneria scutellata* Hedqvist, 1969, preoccupied (nec *Turneria* Forel, 1895 in Formicidae), now *Conodipara* Hedqvist, 1971 (Pteromalidae: Diparinae)

Turneria scutellata Hedqvist, 1969c, p. 177f plus fig. 2b on p. 176, valid as *Conodipara scutellata* (Hedqvist, 1969) (Pteromalidae: Diparinae), and type species of *Turneria* Hedqvist, 1969 and *Conodipara* Hedqvist, 1971

Female holotype and 45 paratypes from South Africa in BMNH.

Vanhornia leileri Hedqvist, 1976e, p. 315f, valid species (Vanhorniidae)
Female holotype from Sweden now in NHRS (NHRS-HEVA000002533), 1 paratype (published as a male, but actually a female lacking the ovipositor) in BMNH.

Visnuella Hedqvist, 1976b, p. 51f, type species *Visnuella nepticulae* Hedqvist, 1976, junior synonym of *Zaommomentedon* Girault, 1915 (Eulophidae: Entedoninae)

Visnuella nepticulae Hedqvist, 1976b, pp. 52–54, valid as *Zaommomentedon nepticulae* (Hedqvist, 1976) (Eulophidae: Entedoninae), and type species of *Visnuella* Hedqvist, 1976, junior synonym of *Zaommomentedon* Girault, 1915
Female holotype and 1 paratype from Sri Lanka now in NHRS (NHRS-HEVA000002185-NHRS-HEVA000002186), 2 paratypes in BMNH.

Wroughtonia mikagei Hedqvist & Togashi, 1979c, p. 95f, figs 1–11 on p. 97, valid species (Braconidae: Helconinae)
Holotype female from Japan in KUEC, 2 paratypes were deposited in NHRS, 9 paratypes in Laboratory of Science, Ishikawa Prefecture College of Agriculture; one paratype now in BMNH.

Discussion

The decision by Hedqvist to sell his collection to a major museum outside Sweden came as a surprise to many Swedish entomologists. When the sale was finalised after his death, this attracted much criticism, including articles in the popular press. We would not want this sort of event to recur so we are using this opportunity to (a) explore some of the differences in opinion regarding the legal depository of the Hedqvist collection; (b) document our rationale behind the process of specimen restitution; and (c) propose some basic recommendations to institutions with large collections of natural history specimens, that would go some way to prevent conflicts of interest arising between employees with personal collections and the institutions they are employed by.

a) Some perspectives on the legal depositories of the Hedqvist collection

Hedqvist deposited many of his type specimens in his personal collection (indicated as 'coll. mea' in his publications). For this reason, the Hedqvist collection is very rich in name-bearing types, unusually so for a private collection. This made it obviously desirable that it be housed in a major international museum, which was the clear intention of Hedqvist.

The perspective from BMNH was that they had bought the collection legitimately, and through the major part of the process were not aware of any objections. NHRS, on the other hand, considered that Hedqvist had been employed by the state of Sweden, at the Swedish Forest Research Institute and the NHRS, for most of his career as a taxonomist. Thus it was considered that the collection belonged in a larger museum in Sweden, and that claims could be made by the NHRS on material that Hedqvist worked on and published under the museum address. We have no intention to give a full resumé of the numerous arguments that were raised on the two sides of the disagreement. More importantly, we were happy to reach an agreement between the two museums, where BMNH did agree to the restitution of some of the material to NHRS (see list in type catalogue section). For BMNH there were at least three important considerations in making these decisions: (1) the majority of the collection was considered legally Hedqvist's and many descriptions of new taxa listed the type depository as being the Hedqvist collection; however (2), BMNH would want certain principles to be upheld regarding the acquisition and disposal of natural history collections held by employees of BMNH and other major collections; (3) it is generally a good principle, for increased accessibility, that paratypes should be deposited in more than one collection.

An agreement of exchange of material was established between the two museums which extends beyond the allocation of parts of the Hedqvist material to NHRS. This will hopefully lead to enrichment of the entomological collections in both countries as well as continued open communication and collaboration.

b) Redistribution of specimens from the Hedqvist collection

An overview of the types from the Hedqvist collection transferred to NHRS during 2011 is given in the type calalogue section of this paper. As a general principle, types of species described by Hedqvist during the periods when he was employed at NHRS (1959–1963 and 1971–1984) have been divided, whenever possible, between NHRS and BMNH. For a number of specimens, it could be demonstrated that they were obviously part of the collection at NHRS, and seemed like undocumented loans into the Hedqvist collection, or material received from individual entomologists for identification, either to be returned to the collector or deposited at the NHRS. Return of such specimens is normal curation procedure. As a part of the exchange agreement between the two museums, NHRS received unique voucher specimens for Swedish Chalcidoidea records where numbers of specimens allowed and BMNH will receive material from the Swedish Malaise Trap Project as well as material from other collecting events and expeditions in the near future.

A few types that were deposited in the Hedqvist collection were published as being elsewhere and a fair amount of other material was on loan from individuals and institutions; these specimens were indisputably the property of others and are being returned to these institutions. In numerous cases, the number of specimens labelled as types did not match the number of types stated in the original descriptions. A smaller number of types in the collection than stated in the original publication probably reflects the practice of sharing or trading specimens after publication, and the missing types will hopefully resurface sooner or later. On the other hand, where the number of specimens labelled as types exceeds the number specified in the original publication, it will be necessary to ascertain which specimens belong to the type series. For taxa published before 2000, all specimens of a species known to the author at the time of description are part of the type series (unless explicitly excluded from it in the original publication or by being separated, for example as varieties or of uncertain identity), regardless of whether they are labelled as such and of whether they were listed as such in the original publication (§72.4).

c) Recommendations to prevent future disputes

Problematic cases similar to this are known to the staff of most major museums, although not many have received as much attention, mainly because the collections concerned have not been sold but have instead ‘found their way’ into private and other collections. The Hedqvist case highlights a number of critical issues facing entomological taxonomy today, concerning the deposition of type specimens and the information published regarding type depositories, and concerning general practices revolving around private insect collections of amateur as well as professional entomologists.

Many museums have policies that staff should not keep private collections, at least not in groups they are working on professionally, but very often these policies are enforced only informally and not implemented in employment contracts. We recommend that institutions that house collections and the funding bodies that employ people to work at these institutions should give more thought to stipulations in employment contracts and staff handbooks, that specimens cannot be retained in employees’ private collections when there is a possibility of a conflict of interest arising. Normally this would mean that a person curating or researching a particular group of organisms should not continue to add to a personal collection of that group. We recognise that many curators and collections-based researchers have assembled collections prior to their employment in collections-based institutions and it cannot reasonably be expected that these collections should be relinquished (although such specimens will generally be gratefully received). It should be stressed that this applies not just to the collections of taxonomists/systematists but also to other fields of research carried out in museums and other institutes with large collections; ‘research’ collections are frequently neglected, poorly curated and sometimes disposed of, despite the obvious importance of these specimens as vouchers, and often their importance as specimens for taxonomic and faunistic work.

From both the viewpoint of scientists and of the public who largely fund science through taxation, science belongs to everybody, and it is a very reasonable line of argument that collections gathered and worked on by publicly funded scientists should belong either to the state funding the research or to the scientific community, and in both cases be deposited in public museum collections. It is of fundamental importance that scientific material is retained and curated in a way that ensures its availability to the scientific community, and ideally to reasonable public access. There are few reasons why such collections should be made available to private buyers. In the case of professionals, the practice of keeping large personal collections at home and offering them for sale rather than donating them to a scientific institution appears, in the light of these arguments and of widespread current trends, to be an outdated and hopefully soon obsolete practice.

Some concerns raised focused on the sale of Hedqvist's collection outside Sweden (perhaps a reminder of the sale of the Linnaeus collection to England). Indeed many Swedish species of Hymenoptera are represented only by Hedqvist's specimens and thus they are crucial to Swedish faunistics and conservation concerns. This is an area for which it is difficult to devise practical guidelines. All major museum collections hold material from a large number of countries, and of course, the crucial thing is that specimens and the information they represent are made available to the international community and available for various uses, including taxonomic and ecological research and national as well as global faunistics and conservation.

The International Code of Zoological Nomenclature (ICZN, 1999) codifies a minimum praxis needed to be agreed on by all workers. It provides an ethical discussion and many examples promoting good practice, but no mandatory rules other than those governing the validity of names. It states that for taxa described after 1999, type specimens must be distinguished in the published descriptions (§72.3) but it remains only a recommendation and not a strict rule that name-bearing types should be properly labelled (72D), all relevant information given in the publication (72E), and type specimens safely preserved and accessible for study (72F). It would not be unreasonable for all these recommendations to be treated as rules, and to adopt as strong recommendations the best parts of current practice, such as the deposition of type specimens and all other scientifically interesting specimens in natural history museums or other public collections. Today, this practice is standard also among many amateur entomologists with no formal association with a scientific institution.

We advise systematists to be careful when designating type specimens, publishing the relevant data about them, ensure they are properly labelled, and from the moment of publication available in named public collections. Even though museum collections are supposed to last forever, they are not immobile, and the statement of repositories in the description of a taxon does not mean that all the type specimens must remain in the specified collections forever. Sometimes public collections are fused, donated or divided; many museums encourage a practice of exchanging scientifically important material; dividing long type series over many museums is a highly beneficial way of increasing access to types and reducing risk of loss of crucial information by accidents or poor maintenance. The general good for research, education and advancement of knowledge must be more important than the arbitrary will of individuals in the end.

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Allochthonous blue spruce in Central Europe serves as a host for many native species of sawflies (Hymenoptera, Symphyta)

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Abstract

In air-polluted mountain areas of the Czech Republic, including the Ore Mountains, pure forest stands of introduced blue spruce (*Picea pungens*) were established in the 1980's. We studied the Symphyta (Hymenoptera) fauna in the canopies of these trees at four sites and in the canopies of adjacent *Picea abies* trees at one of these sites by beating tree branches. For the first time, Nearctic blue spruce is reported as a host for 17 European species of Symphyta (sawflies). Diprionids in the genus *Gilpinia* were the most abundant sawflies on *P. pungens* and were more abundant on *P. pungens* than on the native *Picea abies*. Spruce pamphiliids in the genus *Cephalcia* were also more abundant on *P. pungens* than on *P. abies*, while the abundances of representatives of the tenthredinid genera *Pikonema*, *Pachynematus*, and *Pristiphora* were similar on *P. pungens* and *P. abies*. Our results indicate that many species of European spruce Symphyta are able to use the allochthonous species *P. pungens* as a host.

Keywords

Picea pungens, *Picea abies*, Symphyta, Diprionidae, Tenthredinidae, Pamphiliidae, larvae

Introduction

In Central Europe, *P. abies* (L.) Karst is the only native species of spruce (Schwenke 1978). Many introduced spruce species including of the blue spruce, *Picea pungens* Engelm, are occasionally cultivated in urban areas. Beginning in the 1980s, pure stands of *P. pungens* have been planted in an area of about 100 km^2 in the air-polluted mountain regions of the Czech Republic. *P. pungens* was thought to require only modest soil resources, to have a high tolerance to sulfur oxide air pollution, and to have the ability to resist or avoid ungulate herbivores (Šika 1976, Tesař 1981, Balcar 1986, Jirgle et al. 1983, Kubelka et al. 1992). The assumption about high resistance to air pollution was found to be incorrect, however, because the needles of young *P. pungens* and *P. abies* exhibit the same degree of damage in response to air pollutants (Soukupová et al. 2001).

Many forest pests including many defoliators feed on spruce (Pschorn-Walcher 1982).

At least 34 species belonging to three families of Symphyta (32 species in Central Europe) feed on needles of native spruce in Europe. These feeders include Pamphiliidae with at least nine species of *Cephalcia* (Viitasaari 2002), Diprionidae with four *Gilpinia* species and *Microdiprion fuscipennis* (Forsius, 1911) (Kontuniemi 1960, Viitasaari and Varama 1987), and Tenthredinidae with 15 *Pristiphora* s.l. (Beneš and Křístek 1979, Kajmuk 1988), two *Pikonema* and three *Pachynematus* s.l. (Taeger et al. 1998). *Pristiphora tenuiserra* (Lindqvist, 1959), for which the host plant is unknown, may also be a spruce feeder (Holuša and Roller 2000). New generic nomenclature of Nematinae (Prous et al. 2014) has been omitted (*Pikonema* and *Pachynematus* are currently treated as members of a vast genus *Euura*) with respect to applied entomology.

Although the blue spruce *P. pungens* is planted in the extensive, air-polluted areas of the Czech Republic, the Symphyta fauna developing on this allochthonous plant have not been thoroughly studied. One reason is that serious outbreaks of pests have not occurred during the 25- to 30-year period following the establishment of pure stands of *P. pungens* in the Ore Mountains (Holuša and Holuša 2003).

The host status of *P. pungens* for European native Symphyta is unknown. The goals of this study were (i) to identify the sawflies that feed on *P. pungens* in the Czech Republic and (ii) to compare the abundances of these sawflies on the native *P. abies* and on the introduced *P. pungens.*

Methods

Sawflies were studied in three localities in the Ore Mountains (NW Czech Republic) (Table 1). Two localities (Jirkov, Dlouhá louka) had pure stands of *P. pungens*, and one locality (Sněžník) had a pure stand of *P. pungens* and a pure stand of *P. abies* that were 100 m apart.

Sawfly larvae and adults were sampled by beating tree branches and collecting the falling insects on a sheet stretched on a 0.5 × 1 m metal frame. On each sampling date, 10 samples were collected at each of the four stands. For each sample, two branches

Table 1. Characteristics of studied stands.

Locality	Tree species	Geographic characteristics	Altitude (m asl)	Stand density [%]	Age of stand [years]	Area/percentage of spruce forest in district	Native forest type	Annual mean temperature and total precipitation
Jirkov	*P. pungens*	50°33'11"N, 13°22'59"E	875	90	25–36	14.43 km^2/ 15.4%	*Fageto - Piceetum acidophilum*	4–4.5 °C 1050–1200 mm
Dlouhá louka	*P. pungens*	50°39'00"N, 13°38'04"E	865	70	34	29.37 km^2/ 22%	*Fageto - Piceetum acidophilum*	4–4.5 °C 1050–1200 mm
Sněžník	*P. pungens*	50°47'28"N, 14°04'33"E	576	70	27–31	4.87 km^2/ 4.5%	*Piceeto - Fagetum acidophilum*	4.5–5.5 °C 900–1050 mm
Sněžník	*P. abies*	50°47'30"N, 14°04'15"E	576	70	19	28.76 km^2/ 26.6%	*Piceeto - Fagetum acidophilum*	4.5–5.5 °C 900–1050 mm

were selected at random in the crowns of 10 trees, the branches were located from 0.7 to 2.5 m above the ground, and the sampled trees were in a line with 10 m between adjacent trees. Trees were sampled on 17 May, 15 June, 14 July, 15 August, 15 September, and 15 October 2007. Thus, one sample consisted of insects collected from one stand (a total of 20 branches on 10 trees) across all six sampling dates.

The collected insects were stored in 75% ethanol. Larvae were identified using the keys of Beneš and Křístek (1979), Battisti and Jiang-hua Sun (1996), Battisti and Zanocco (1994), Martinek (1988), and Zanocco and Battisti (1995). Very young larvae (first and second instars) were identified only to genus (*Cephalcia*, *Gilpinia*, and *Pristiphora*). The current knowledge of larvae allows the identification of some *Pachynematus* s.l. and *Pristiphora* s.l. only to the subgeneric level and are here referred to as the *Epicenematus* and *Sharliphora* species groups, respectively. Adult sawflies were identified using the keys of Beneš and Křístek (1979), Viitasaari (2002), and Zhelokhovtsev (1988). The nomenclature follows Taeger and Blank (2011), and host plants are given according to Taeger et al. (1998) unless stated otherwise.

The data of larvae per locality were not normally distributed. When the abundance of a sawfly species was > 10 on both *P. abies* and *P. pungens* at Sněžník, the values were compared with a Wilcoxon pair test in Statistica 12.0.

Results

In total, 748 larvae and 79 adults of 36 species of sawflies were collected (Table 2). Among the 36 species, 23 have been previously associated with spruce, and the 13 have been previously associated with other plant species (Table 2). Larvae obtained from the branches of *P. abies* (N=127) and *P. pungens* (N=621) belonged to 12 and 18 species of Symphyta, respectively.

Table 2. Total numbers of sawflies (Hymenoptera: Symphyta) collected on *P. abies* and *P. pungens* in the Czech Republic (plus information on known host plants for each species of sawfly). The sawflies were collected from 20 branches per stand (two branches on each of 10 trees) in three *P. pungens* stands (at Jirkov, Dlouhá louka, and Sněžník) and in one *P. abies* stand (at Sněžník) on six sampling dates from spring to fall in of 2007. Sawfly species feeding on spruce are in bold. When the abundance of a sawfly species (larvae + adults) was > 10 on both *P. abies* and *P. pungens* at Sněžník, the values were compared with a Wilcoxon pair test (an asterisk indicates a significant difference, and n.s. indicates a non-significant difference). The information on known host plants is from Taeger et al. (1998) unless indicated otherwise.

Sawfly species	Number of larvae		Wilcoxon pair test	Number of adults		Known hosts
	On *P. abies* at Sněžník	On *P. pungens* at all three stands (and at Sněžník in brackets)		On *P. abies* at Sněžník	On *P. pungens* at all three stands	
Arge fuscipes (Fallén, 1808)				1	1	*Salix*, *Betula*
***Cephalcia* sp.**	**5**	**17(4)**				
***Cephalcia abietis* (Linné, 1758)**		**11(1)**			**6**	***P. abies*, *P. obovata*, *P. koraiensis***
***Cephalcia alpina* (Klug, 1808)**	**2**	**16(2)**				***P. abies*, *P. obovata*, *P. koraiensis*, *P. jezoensis***
***Cephalcia arvensis* Panzer, 1805**		**16(7)**		**4**	**11**	***P. abies*, *P. obovata*, *P. koraiensis*, *P. jezoensis***
***Cephalcia erythrogaster* (Hartig, 1837)**		**1(0)**		**1**		***P. abies*, *P. koraiensis***
***Cephalcia fulva* Battisti & Zanocco, 1994**	**1**	**6(2)**				***P. abies*, *P. koraiensis***
Dineura virididdorsata (Retzius, 1783)					1	*Betula*
Dolerus gonager (Fabricius, 1781)					1	Poaceae
Dolerus nigratus (O.F.Müller, 1776)					2	Poaceae
***Gilpinia* sp.**	**17**	**84 (42)**	**2.36***			
***Gilpinia abieticola* (Dalla Torre, 1894)**	**19**	**98 (19)**	**0.00 n.s.**		**2**	***P. abies*, *P. obovata*, *Pinus pumila* (probably missidentification, Karel Beneš pers. comm.)**
***Gilpinia hercyniae* (Hartig, 1837)**	**2**	**134 (4)**	**0.80 n.s.**			***P. abies*, *P. obovata* (In N. America *P. glauca*, *P. sitchensis*, *P. pungens*, *P. mariana*, *P. rubens*, *P. pungens* (Quarantine PEST data Sheet))**
***Gilpinia polytoma* (Hartig, 1834)**	**7**	**19 (19)**	**1.85 n.s.**			***P. abies*, *P. obovata*, and *P. smithiana* (Viitasaari (1987)**
Macrophya sanguinoleta (Gmelin, 1790)					1	*Veronica*, *Galeopsis*, *Senecio*
Pachynematus lichtwardti Konow, 1903					2	unknown
***Pachynematus* (*Epicenematus*) sp.**	**21**	**95(17)**	**0.65 n.s.**			

Sawfly species	Number of larvae		Wilcoxon pair test	Number of adults		Known hosts
	On *P. abies* at Sněžník	On *P. pungens* at all three stands (and at Sněžník in brackets)		On *P. abies* at Sněžník	On *P. pungens* at all three stands	
Pachynematus montanus **(Zaddach, 1883)**					**1**	***P. abies, and P. obovata*** **(Popov & Kajmuk 2010)**
Pachynematus styx **(Benson, 1958)**					**1**	***P. abies***
Pachyprotasis rapae (Linné, 1767)					7	oligophagous
Pamphilius hortorum (Klug, 1808)					1	*Rubus*
Pikonema insigne **(Hartig, 1840)**		**1(1)**				***P. abies*****, and** ***P.obovata*** **(Popov & Kajmuk 2010)**
Pikonema scutellatum **(Hartig, 1840)**	**11**	**11(1)**	**1.94 n.s.**	**1**	**1**	***P. abies, P. obovata***
Pristiphora **sp.**	**17**	**39(12)**	**1.40 n.s.**			
Pristiphora abietina **(Christ, 1791)**	**2**	**6(4)**				***P. abies, P. obovata*** **(Popov & Kajmuk 2010) ,** ***P. obovata*** **and** ***P. sitchensis*** **(Kollar 2007, Austara et al 1984)**
Pristiphora compressa **(Hartig, 1837)**	**8**	**41 (12)**	**0.92 n.s.**		**2**	***P. abies*****, and** ***P. obovata*** **(Popov & Kajmuk 2010)**
Pristiphora decipiens **(Enslin, 1916)**	**4**	**15(6)**			**1**	***P. abies***
Pristiphora gerula **(Konow, 1904)**	**1**	**2(0)**				***P. abies***
Pristiphora leucopodia **(Hartig, 1837)**	**2**	**2(0)**				***P. abies***
Pristiphora pallida **(Konow, 1904)**					**1**	***P. abies***
Pristiphora pseudodecipiens **Beneš &** ***Křístek, 1976***	**6**	**6(0)**		**1**	**1**	***P. abies***
Pristiphora robusta **(Konow, 1895)**		**1(0)**				***P. abies*****, and** ***P.obovata*** **(Popov & Kajmuk 2010)**
Pristiphora saxesenii **(Hartig, 1837)**		**7(0)**				***P. abies***
Pristiphora **(*****Sharliphora*****) sp.**	**2**	**9(2)**				
Pristiphora nigella **(Förster, 1854)**					**2**	***P. abies***
Pristiphora parva **(Hartig, 1837)**				**1**		***P. abies***
Tenthredo atra Linné, 1758					1	oligophagous
Tenthredo mesomela Linné, 1758					3	oligophagous
Tenthredo olivacea Klug, 1817					2	oligophagous
Tenthredopsis ornata (Serville, 1823)					3	*Brachypodium*
Tenthredopsis scutellaris (Fabricius, 1804)				1	15	*Festuca, Poa, Dactylis, Elytrigia*
Total	127	621		10	69	

Five species in the genus *Cephalcia* were only found in small numbers and on several specimens of *P. pungens*, and two of these five species were found on *P. abies* (Table 2). The abundance of larvae belonging to *Cephalcia* species did not differ between samples from *P. abies* and *P. pungens* (Table 2).

Diprionids of the genus *Gilpinia* were the most abundant sawflies in the samples and represented 51.8% and 35.4% of the specimens collected from *P. pungens* and *P. abies*, respectively. *Gilpinia abieticola* and *G. hercyniae* were the most numerous species, while *G. polytoma* was recorded exclusively in the *P. abies* and *P. pungens* stands at Sněžník. Although the *Gilpinia* abundancy did not differ between *P. abies* and *P. pungens* stands, more first and second instar larvae of *Gilpinia* were found on *P. pungens* than on *P. abies* at Sněžník (Table 2).

Almost identical species (both larvae and adults) of spruce tenthredinids (*Pristiphora*, *Pachynematus*, and *Pikonema*) were found in the *P. abies* and the *P. pungens* samples, and the abundance of larvae of each species did not differ on *P. abies* vs. *P. pungens*. Based on larvae, *Pachynematus* (*Epicenematus*) sp. followed by *Pristiphora compressa* were the most abundant species in *P. pungens* samples (Table 2).

Across all species, sawfly abundance did not statistically differ on *P. abies* vs. *P. pungens* at Sněžník (z=0.59, p>0.05).

Discussion

In the current study, a total of 18 sawfly species were collected from *P. pungens* in the Ore Mountains of the Czech Republic. This represents 56% of the species of needle-feeding spruce sawflies in Central Europe (N=32) (Beneš and Křístek 1979, Holuša 2005, Jachym et al. 2005). *P. pungens* was recorded as a new host for 17 of these Palaearctic species. The 13 additional species have not been associated with spruce as a host, and their occurrence in the samples was accidental (Table 2).

In Central Europe, eight species of Pamphiliidae are associated with *P. abies* (Holuša et al. 2007). We confirmed that *P. pungens* is a host for *C. abietis*, *C. arvensis*, *C. alpina*, *C. fulva*, and *C. erythrogaster*. In Europe, the most abundant sawfly has been *C. abietis* followed by *C. arvensis*, and mass outbreaks of *C. abietis* (Escherich 1942, Pschorn-Walcher 1982, Kula 1987, Liška et al. 1991) and local outbreaks of *C. arvensis* and *C. alpina* have been repeatedly reported (Křístek and Švestka 1986, Martinek 1991, 1992, Liška 1999, Zanocco and Battisti 1995).

The most abundant larvae collected from *P. pungens* were species of *Gilpinia*. All three spruce diprionids (*G. abieticola*, *G. hercyniae*, and *G. polytoma*) are common in spruce stands in Central Europe (Úradník and Kulfan 2002, Holuša and Roller 2004), but the three species can differ in abundance, dominance, and frequency (Martinek 1960, Úradník and Kulfan 2002, Holuša and Roller 2004). Untill this study, *G. hercyniae* has been the only European diprionid known to feed on *P. pungens* (Balch 1939).

The numbers of spruce tenthredinids in the genera *Pikonema*, *Pristiphora*, and *Pachynematus* were similar on *P. pungens* vs. *P. abies*. We suspect that the L1 and L2 larvae identified as *Pachynematus* (*Epicenematus*) sp. are *P. montanus*, although *Pachynematus* (*Epicenematus*) *pallescens* (Hartig, 1837) and the extremely rare *P. styx* may also be present in the studied stands. The former species has the ability to rapidly increase (Kolubajiv 1939, Martinek 1994, Reisenberger and Krehan 1993) and is widespread not only in *P. abies* stands (Holuša 2002) but also in *P. pungens* stands (this study). Another species that can rapidly increase, *Pikonema scutellatum*, was rarely collected in the study area, although it is common in Central Europe (summarised by Holuša and Lubojacký 2008). Because one adult of the very rare species *Pikonema insigne* was found in the *P. pungens* stand at Sněžník, we suspect that *P. pungens* is a host for this species.

The larvae of eight *Pristiphora* species plus adults of *P.* (*Sharliphora*) *pallida* and *P.* (*Sharliphora*) *parva* were collected on *P. pungens*, but it is very probable that larvae of *Pristiphora* (*Sharliphora*) sp. were represented mainly by the larvae of *Pristiphora nigella. P. abietina* is a pest of Norway spruce in Central Europe (Pschorn-Walcher 1982) and often occurs in high numbers with *Pikonema scutellatum* and *Pachynematus montanus* (Kolubajiv 1939, 1958). However, *P. abietina* prefers lower altitudes where it can rapidly increases (Martinek 1960, Holuša 2002). Thus, the low abundance of this species in the studied stands is in accordance with the aforementioned studies. *P. compressa*, the most common *Pristiphora* in *P. pungens* stands, could be even more abundant than *P. abietina* in mountain stands of *P. abies* (Úradník and Kulfan 2002). We also found *P. pallida* and *P. robusta*, that have been very seldom recorded in spruce stands (Forsius 1911, Křístek 1973).

In the investigated air-polluted areas the native *P. abies* stands are almost completely absent because this tree was not used for forest regeneration in the 1980's (Kubelka et al. 1992). Our study indicates that a range of *P. abies* defoliators use *P. pungens* as a substitute host plant. This phenomenon has also been documented for herbivorous moths. Of the 50 moth species that feed on *P. abies* in Europe, 31 have been found to develop on the needles and buds of *P. pungens* (Kulfan et al. 2010).

The spruce-feeding sawflies in Central Europe are not strictly monophagous on *P. abies*. Most of these species have been observed to feed on other Palaearctic spruces like *Picea obovata* (Ledeb.), *Picea koraiensis* Nakai, and *Picea jezoensis* (Sieb. & Zucc.) (Taeger et al. 1998). Before the current study, however, Nearctic spruces had not been reported as hosts for European Symphyta other than for *G. hercyniae* (Balch 1939).

Because the abundance of sawfly larvae and adults was low in the current study (compare with Holuša 1999, Holuša and Lubojacký 2008), we did not observe substantial defoliation of trees in the *P. pungens* stands in 2007. Severe defoliation of *P. pungens* was reported in the 1970s and early 1980s even at altitudes of 900 m (Holuša and Holuša 2003). Many sawfly outbreaks occurred throughout the Czech Republic in the early 1980s. The most recent instance of severe defoliation and subsequent chemical treatment was in 1982 (Holuša and Holuša 2003). The regeneration of *P. abies* stands has recently increased in the Ore Mountains (Šrámek et al. 2008), and thus populations of sawflies living on *P. pungens* may recolonize the *P. abies* stands in the future. Although sawflies have not recently caused extensive damage to spruce in Central Europe, the spruce sawflies are in a latency period in this region (Holuša et al. in prep.), and local outbreaks have occasionally occurred (Egginger et al. 2014).

Conclusions

Our results demonstrate that European spruce sawflies are able to use the diverse allochtonous spruce species as hosts and may show stronger preferences for the new host, here especially *P. pungens*, than for the native host, *P. abies*.

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A new species of *Ophrella* Middlekauff, 1985 (Hymenoptera, Orussidae) from French Guiana

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Abstract

Ophrella seagi **sp. n.** is described and illustrated from a female and a male collected in French Guiana. Additional Orussidae from this country are listed in an Appendix. The new species differs from other members of *Ophrella* in a number of features, and the diagnosis of the genus is revised accordingly. A key to *Ophrella* species is included. The new species is included in a continuously updated morphological data set assembled for the Orussidae and its phylogenetic position discussed.

Keywords

Parasitoid wasps, wood-living insects, taxonomy, phylogeny, biogeography

Introduction

The Orussidae are a small family of parasitoid wasps, currently with about 90 extant described species. They have a worldwide distribution (Vilhelmsen 2003, 2004), but they are very rarely collected, many species being known from only one or a few specimens. Orussidae have a fossil record spanning the Cretaceous and Tertiary, the radiation of the extant members of the family probably occurred in the mid-Cretaceous, approx. 100 Ma ago (Vilhelmsen and Zimmermann 2014). Detailed biological information is lacking for most species, but they are generally associated with dead wood, targeting woodboring insect larvae (e.g., Buprestidae, Cerambycidae) and completing their pre-adult development inside the wood (Vilhelmsen et al. 2001).

The genus *Ophrella* Middlekauff, 1985 is one of the smallest genera of Orussidae and until recently one of the least frequently collected. The first species was described from a single specimen from Panama as *Ophrella lingulata* by Middlekauff (1985). Smith (1988) transferred *Oryssus amazonicus* Westwood, 1874 (also based on a single specimen, from Brazil) to *Ophrella* as *Ophrella amazonica* (Westwood, 1874), citing the shape of the frontal setae and the position of fore wing cross wing cu-a relative to the discoidal cell as evidence for this taxonomic placement. Vilhelmsen (2003) in his cladistic treatment of the Orussidae confirmed this and added the presence of a longitudinal furrow on top of the head separating the posteriormost coronal teeth as further support for the monophyly of *Ophrella*. Vilhelmsen et al. (2013) cited the presence of only a single short hind tibial apical spur as additional corroboration for the monophyly of *Ophrella*.

Ophrella belongs to the ophrynopine clade (Vilhelmsen and Smith 2002), an assemblage currently comprising six genera and 33 extant species. The monophyly of the clade is usually retrieved as well supported in cladistics analyses of Orussidae, prominent putative autapomorphies being the presence of a triangular protrusion on the posteroventral corner of the hind femur (reversed in *Kulcania* Benson, 1935), the fore wing vein 2r inserting distally on the pterostigma, and the presence of spines or pegs on sternum 9 in the male. More than half the species occur in the Neotropical Region, but ophrynopines are also represented in the Nearctic, Australasian (Australia, New Guinea), Oceanic (Fiji, New Zealand), Oriental (Southeast Asia) and eastern Palaearctic (Japan, South Korea) regions. The ophrynopine clade probably radiated in the Tertiary (Vilhelmsen et al. 2013), but the biographic history of the clade is highly complex and likely involves multiple dispersal events (Vilhelmsen 2004).

The Société Entomologique Antilles Guyane (SEAG; see http://insectafgseag.myspecies.info/en) has for the past decade been inventorying the insect fauna in French Guiana. Various passive and active collecting techniques have been implemented in a series of projects in different localities around the country. These intensive collecting efforts aim, among other things, to produce and update checklists for the country (Brûlé and Touroult 2014). The SEAG efforts have also generated material of otherwise rarely collected insect taxa, including Orussidae (see Appendix and Vilhelmsen et al. 2013). Each of the orussid specimens collected by the SEAG surveys probably represents several thousand trapping hours. Only by an effort of this magnitude is it possible to get a more comprehensive impression of the true diversity of such rare taxa in an area.

Including the material reported in the present paper, about ten specimens of *Ophrella* species have been collected in French Guiana until now. This has led to substantial changes in the taxonomy of the genus. Vilhelmsen et al. (2013) described *Ophrella eldorado* Vilhelmsen as new and placed *O. lingulata* in synonymy with *O. amazonica*. Here, I describe a new species of *Ophrella*. The new species differs substantially from the previously recognized species and the diagnosis of the genus is adjusted accordingly.

Material and methods

All the material treated in the present paper (see also Appendix) is stored in the Natural History Museum of Denmark, University of Copenhagen (NHMD).

Specimens were examined with a Leica M205C dissection microscope both before (in ethanol) and after mounting and scored for the characters in the data set presented in Blank and Vilhelmsen (2016).

The following characters were added to the data set of Blank and Vilhelmsen (2016).

175. Shape of female antennomere 10: less than three times as long as wide = 0; at least three times as long as wide = 1.

State 1 is observed in all species of *Ophrella* (Fig. 4C, green arrow), but elsewhere in Orussidae only in scattered species outside the ophrynopine clade (*Leptorussus africanus* Benson, 1955; *Orussus punctulatissimus* Blank & Vilhelmsen, 2014; *Pseudoryssus henschii* Mocsáry, 1910).

176. Transverse carina dorsally on pronotum: at most weakly developed = 1; well developed, without median incurvation = 1; strongly developed, protruding anteriorly, with median incurvation = 2 (ordered).

Ophrella eldorado has been scored state 1, *Ophrella seagi* sp. n. state 2 (Fig. 5A, yellow arrow); all other Orussidae examined for this character have state 0.

The dataset produced in Mesquite (Maddison and Maddison 2011) was analyzed in TNT (Goloboff et al. 2000). The matrix is available from Figshare [https://figshare.com/articles/DataMatrixOrussidae2016/3458834]. Initial analyses were run with the male and female of *O. seagi* treated as separate terminals, for the final analyses they were merged. The following characters were treated as additive: 12, 19, 24, 31, 34, 35, 46, 65, 66, 70, 75, 77, 87, 96, 103, 104, 111, 113, 114, 119, 124, 125, 126, 137, 146, 147, 149, 152, 156, 157, 159, 160, 161, 164, 167, 173 and 176. Space for 1 000 000 trees was reserved in memory. Traditional searches in equal weights analyses and implied weights analyses with the concavity constant k set in turn to 1-15, 20, 25 and 30 were run. Analyses were run with collapsing rules set to max. length = 0. For each weighting scheme, analyses with 10 000 replications / 100 trees saved pr. replication were conducted.

Digital images were produced with a Visionary Digital imaging setup with flash lightning and P-51 Camlift Driver ver. 2.6.1 to control the camera. A cylinder of semitransparent plastic and a cone of semitransparent paper were placed around the specimen to disperse the light. Images were stored in Adobe Lightroom 2 and composite images were compiled from stacks with the software Zerene Stacker ver.1.04 by implementing the Pyramidal stacking method (PMax).

Phylogenetics

The phylogenetic analyses under various weighting schemes produced variable results, the shortest/most fit trees being retrieved in most in less than 10% of the replications.

The results of the implied weights analyses with concavity constant k set to 7, 10 and 20 are shown in Figs 1–3. In the following, only the results relevant to evaluating the monophyly of *Ophrella* and its placement within the ophrynopine clade will be discussed.

In all the analyses where the male and female of *O. seagi* were included as separate terminals, they were retrieved as a monophylum, corroborated by the presence of a prominent transverse carina dorsally on the pronotum with a median incurvation (char. 176:2). *Ophrella* is retrieved as monophyletic in the implied weighting analyses with k settings 1-15, usually with *Ophrella seagi* as sister to the two other *Ophrella* species (Figs 1, 2). When k = 1, *O. seagi* is the sister to *O. eldorado*; this relationship is supported by the presence of a transverse carina dorsally on the pronotum (char. 176:1/2). *Ophrella amazonica* + *O. eldorado* is corroborated by the presence of dense pilosity posterior to the eyes (char. 23:1) and on the mesoscutum (char. 69:1) and having only one short hind tibial apical spur (chars 108:1; 109:1). The monophyly of *Ophrella* is supported by the presence of a longitudinal groove on the top of the head between the posteriormost coronal teeth (char. 7:1), the insertion of fore wing cross vein cu-a on Cu at least 0.3 the length of the discal cell distal to vein M (char. 123:1) and antennomere 10 in the female being at least three times longer than wide (char. 175:1). When k = 20, 25 or 30, *O. seagi* is the sister to a monophyletic *Ophrynopus* Konow, 1897 (Fig. 3), and under equal weights, *O. seagi* is sister to all *Ophrynopus* species except *Ophrynopus carinatus* Vilhelmsen & Smith, 2002. When *Ophrella* is not monophyletic, *O. amazonica* + *O. eldorado* are sister to *Argentophrynopus* (Fig. 3).

The position of *Ophrella* within the ophrynopine clade is somewhat unstable. When k = 1, 3, or 7-9 (Fig. 1), it is sister to *Ophrynopus*. When k = 2, 4-6 or 10-15 (Fig. 2), *Ophrella* is inside *Ophrynopus*, being sister to *Ophrynopus carinatus*; this is corroborated by the absence of the lateral longitudinal frontal carina (char. 12:0) and the pronotum being of equal length medially and laterally in dorsal view (char. 48:0), but these characters are variable within the ophrynopine clade. *O. seagi* shares some characters with all or some members of *Ophrynopus*, e.g., the presence of a mesepisternal carina (char. 85:1) and the presence of a projection posteriorly on the male sternum 9 (char. 157:2) that are absent in other *Ophrella* species but has the effect of pulling the entire genus inside *Ophrynopus*.

Even with the inclusion of the somewhat aberrant *O. seagi*, *Ophrella* remains well supported and diagnosable (see below for adjustments). Vilhelmsen et al. (2013) synonymized *Stirocorsia* Know, 1897 with *Ophrynopus*, but the latter remains poorly supported and difficult to circumscribe. Some subgroups within *Ophrynopus* are well defined and at some point it might be useful to subdivide the genus, but based on the findings of this study this is premature. *Ophrella seagi* can be accommodated in the current generic classification of the Orussidae without necessitating major adjustments.

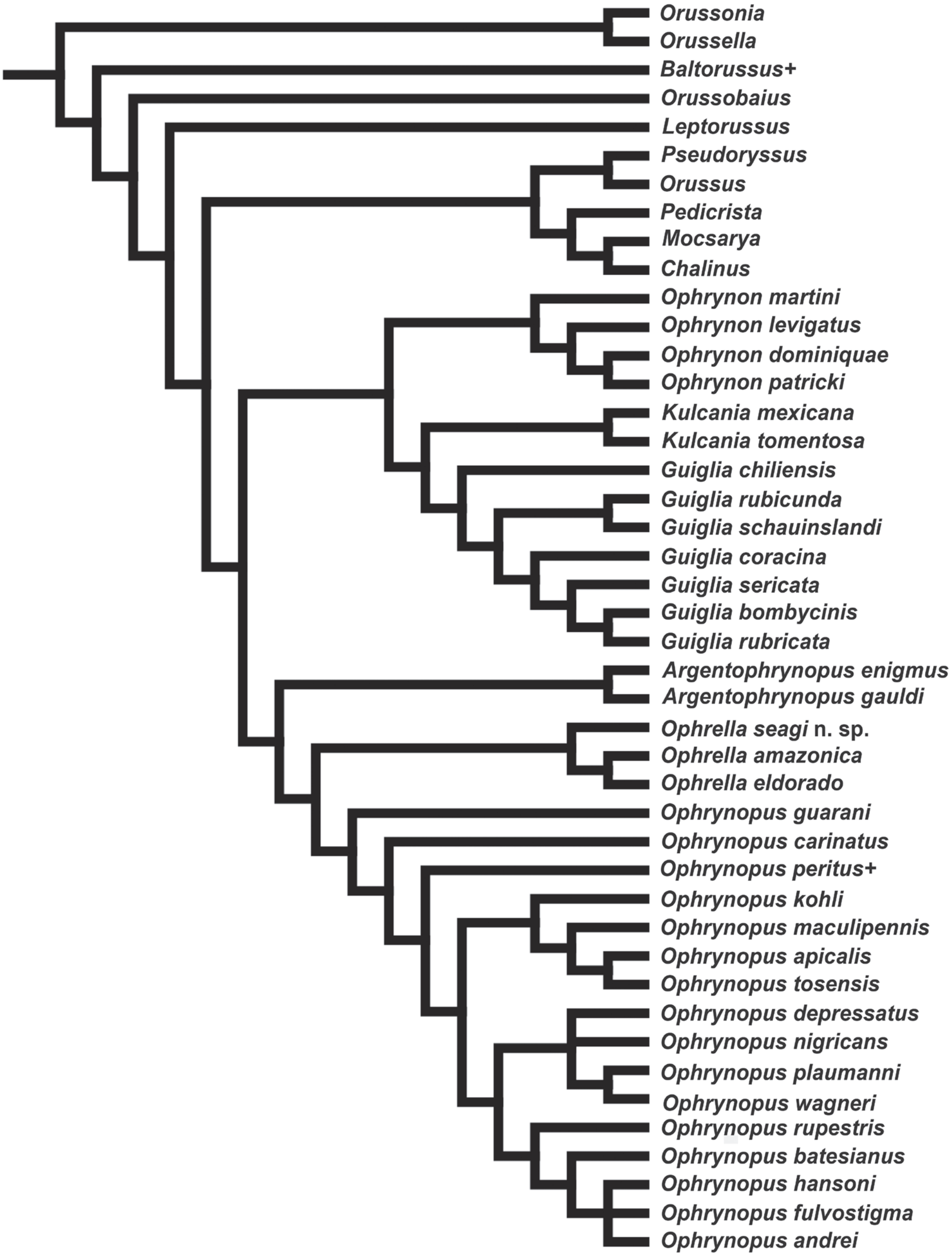

Figure 1. Consensus tree of 9 trees of fit 51,39931 produced by implied weighting analysis with k = 7. Only crown group Orussidae shown; genera outside the ophrynopine clade have been collapsed to single terminals.

Figure 2. Consensus tree of 9 trees of fit 41,51167 produced by implied weighting analysis with k = 10. Only crown group Orussidae shown; genera outside the ophrynopine clade have been collapsed to single terminals.

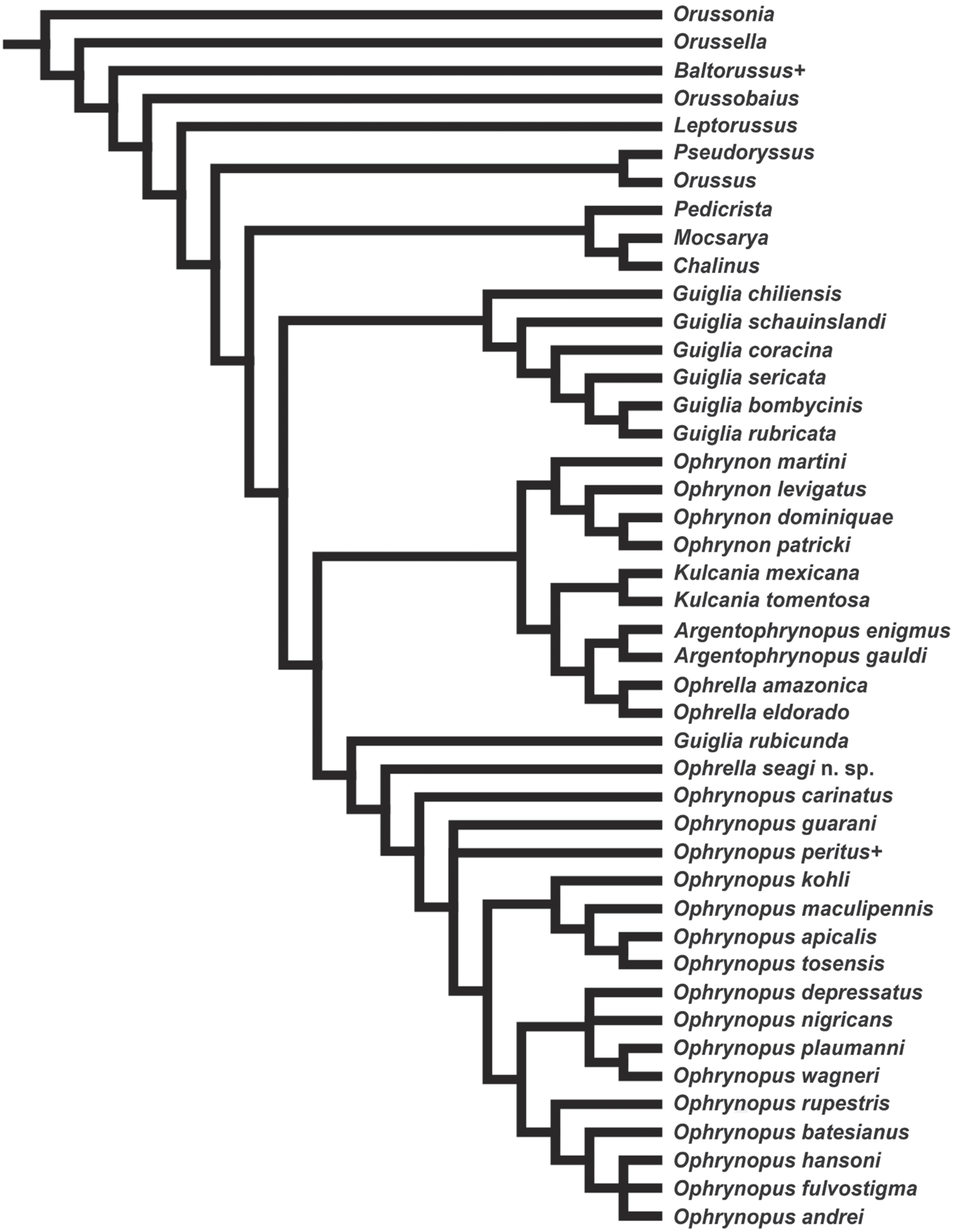

Figure 3. Consensus tree of 9 trees of fit 25,58786 produced by implied weighting analysis with k = 20. Only crown group Orussidae shown; genera outside the ophrynopine clade have been collapsed to single terminals.

Systematics

Ophrella seagi sp. n.

http://zoobank.org/F9659E25-6E4D-4FBF-A329-FEE6F0195029
Figs 4–6

Holotype. Female. 'FRENCH GUIANA, Montagne des Chevaux: 4°44'56"N - 52°26'28"W, alt. 75 m, Window Trap, SEAG leg., 4.ix.2013/*Ophrella seagi* Vilhelmsen, 2016 female det. L. Vilhelmsen 2016/Holotype/NHMD000071774'. NHMD.

Paratype. Male. FRENCH GUIANA, Montagne des Chevaux: 4°44'56"N - 52°26'28"W, alt. 75 m, Window Trap, SEAG leg., 28.xii.2013. NHMD000071775.

Description. Female. Body length 9.2 mm, fore wing length 5.9 mm. Body predominantly black (Fig. 4A). Small brownish spot situated laterally on frons, just median to lower part of eye (Fig. 4B). Antenna and mouthparts dark brown to black, Antennomeres 9-10 slightly paler (Fig. 4C). Fore femur black, fore tibia and tarsus dark brown; mid leg dark brown to black throughout, except for brown trochanters; hind coxa brown, hind femur laterally with large brown area, remainder of hind leg black (Fig. 5B). Fore wing predominantly heavily infuscated, with dense covering of short coarse dark hairs (Fig. 4A); pterostigma with basal half pale; small hyaline spot situated between basal parts of M+Cu and anal veins, narrowing hyaline band extending from pterostigma proximally of vein 2r to hind margin, apex of wing hyaline; venation predominantly dark brown, except for vein M clear in median hyaline band. Hind wing weakly infuscated in anterior and distal parts, otherwise more or less hyaline, venation dark to light brown (Fig. 4A).

Ocellar corona narrow, distance between median ocellus and lateral coronal tooth subequal to ocellar width (Fig. 4B); ocellar teeth raised on low swellings with finely imbricate sculpture forming drop-shaped concavity around median ocellus; swellings converge dorsally, dorsalmost coronal teeth situated dorsal to lateral ocelli, teeth separated medially by narrow longitudinal furrow. Frons coarsely areolate, without dorsal transverse and longitudinal carinae, irregular swelling present in middle; hairs on frons slender, inconspicuous; ventral transverse frontal carina with distinct median notch. Vertex and gena areolate-punctate, dense silvery pilosity on vertex posterior to dorsal part of eyes (Fig. 5A), pilosity on posterior part of head otherwise inconspicuous; postocular carina absent (Fig. 4C), occipital carina well developed, without concavity dorsally. Antennomeres 9-10 slender, antennomere 10 [missing on right antenna] more than three times as long as broad, tapering distally (Fig. 4C).

Pronotum with prominent transverse carina anterodorsally, carina medially with distinct notch (Fig. 5A); pronotum areolate dorsally, glabrous with scattered punctures anterolaterally. Fore femur without ventral carina. Mesoscutum and mesoscutellum areolate, sculpture of equal density, no conspicuous pilosity (Fig. 5A); mesoscutellar sulcus deep, interrupted medially by small triangular projection from mesoscutellum; mesoscutellum raised relative to surrounding sclerites, laterally separated by narrow glabrous strip, posterior margin parallel with anterior margin of metanotum for some

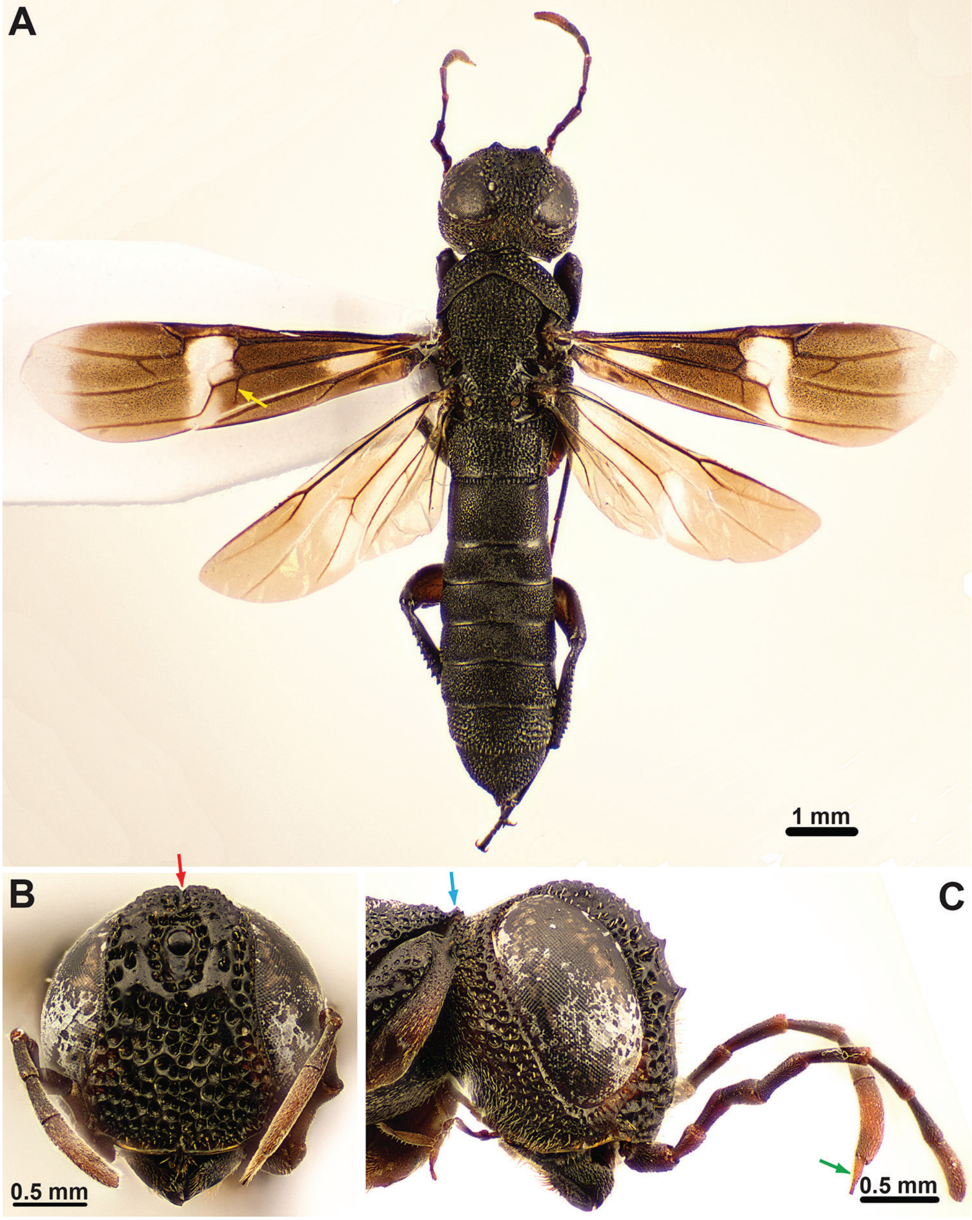

Figure 4. *Ophrella seagi* sp. n., female holotype, NHMD000071774. **A** Habitus dorsal **B** Head, anterior **C** Head and antenna, lateral. Yellow arrow = cross vein cu-a; red arrow = longitudinal furrow on top of head; blue arrow = pronotal transverse carina; green arrow = antennomere 10.

distance. Mesopleuron laterally coarsely areolate-punctate, ventrally micropunctate with slender pilosity; mesepisternal carina situated anterolaterally on mesopleuron. Metanotum coarsely areolate, with median longitudinal carina absent, lateral carina

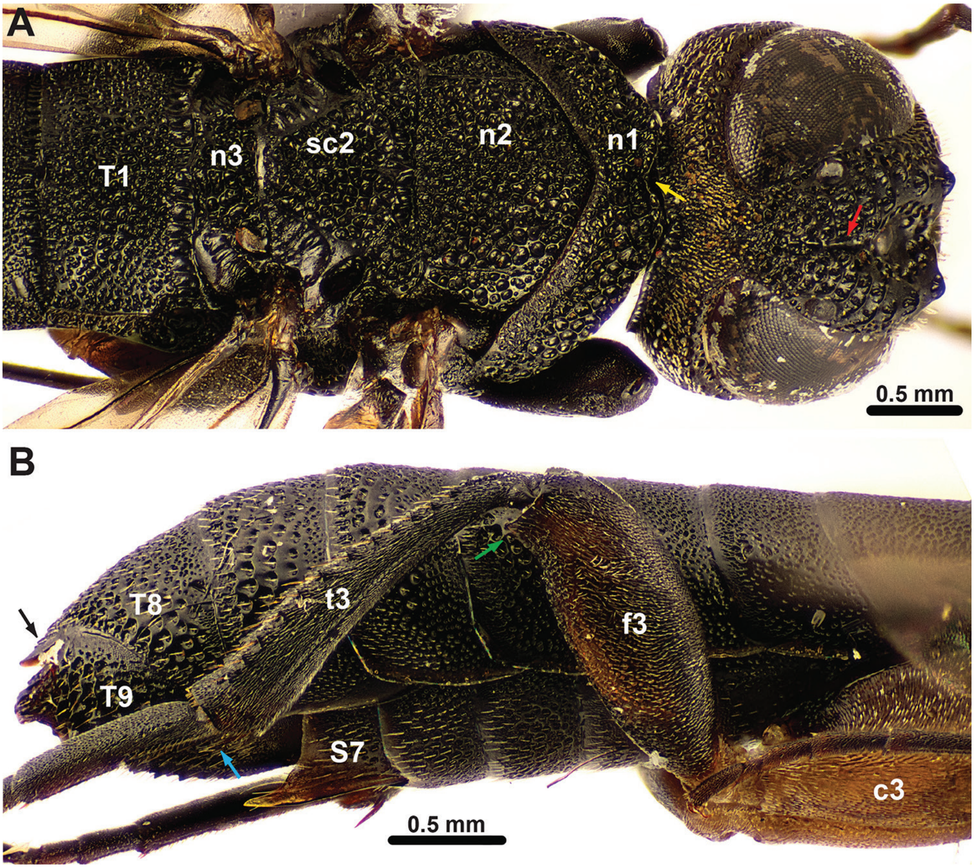

Figure 5. *Ophrella seagi* sp. n., female holotype, NHMD000071774. **A** Head and thorax, dorsal **B** Hind leg and abdomen, lateral. Yellow arrow = notch, pronotal transverse carina; red arrow = longitudinal furrow, top of head; black arrow = projection, tergum 8; blue arrow = hind tibial apical spur; green arrow = triangular projection on hind femur. c3 = hind coxa; f3 = hind femur; n1 = pronotum; n2 = mesoscutum; n3 = metanotum; sc2 = mesoscutellum; S7 = sternum 7; t3 = hind tibia; T[x] = tergum [x].

present; metepisternum predominantly glabrous. Hind coxa with dense pilosity laterally; hind femur with well-developed triangular protrusion laterodistally (Fig. 5B); hind tibia with 22-23 pegs in two rows dorsally, longitudinal carinae laterally and ventrally, and two apical tibial spurs.

Fore wing vein 2r arises 0.7 from base of pterostigma; vein cu-a inserts on Cu1 approx. 0.3 from proximal end of cell M (Fig. 4A).

Tergum 1 areolate (Fig. 5A), laterally with distinct postspiracular and subspiracular carina separated by prominent concavity with elongate hairs. Terga 2-6 finely areolate-punctate, without conspicuous pilosity, tergum 2 laterally with weakly developed carina in continuation of subspiracular carina on tergum 1, tergum 2 with smooth dark anterolateral area approx. twice as wide as long and adjacent to antecosta of tergum. Terga 7-8 more irregularly rugose, tergum 8 with prominent projection medially

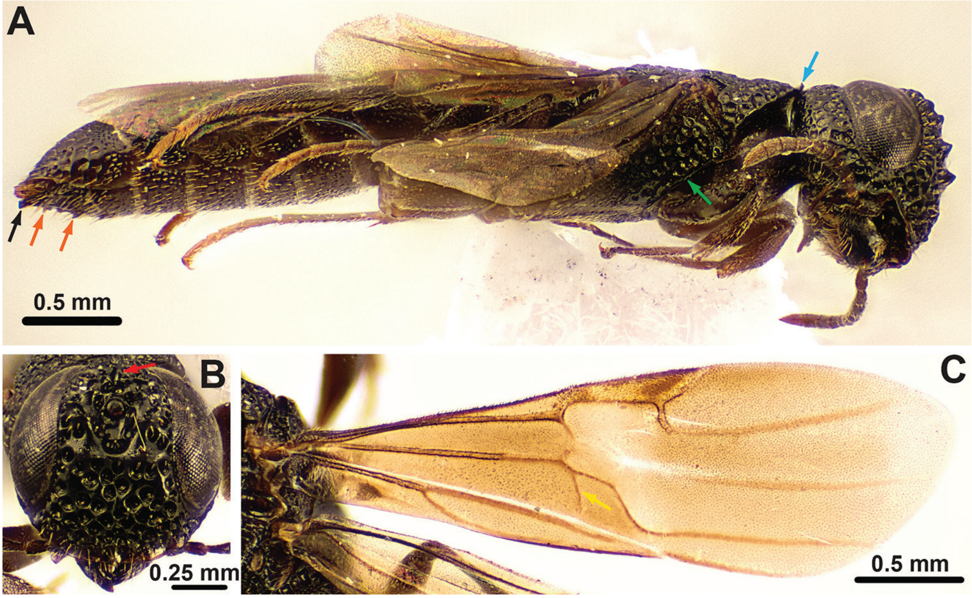

Figure 6. *Ophrella seagi* sp. n., male paratype, NHMD000071775. **A** Habitus lateral **B** Head, anterior **C** Fore wing. Black arrow = posterior projection on sternum 9; brown arrows = spines on sternum 9; blue arrow = pronotal transverse carina; green arrow = mesepisternal carina; red arrow = longitudinal furrow on top of head; yellow arrow = cross vein cu-a.

on posterior margin (Fig. 5B). Tergum 9 ventrally with spicules, longitudinal carina only present as short lobe posteriorly. Sterna 3-7 punctate.

Male. Body length 4.8 mm, fore wing length 3.2 mm. Body uniformly dark brown to black, even more so than female (Fig. 6A). Appendages and mouthparts dark brown to black, legs slightly paler towards apex, hind trochanters light brown. Fore wing infuscated almost throughout, not as heavily as in female, infuscation fades towards apex (Fig. 6C); pterostigma predominantly pale, with brown medial spot in distal half; venation dark brown proximally and anteriorly, light brown distally and posteriorly, vein M proximally hyaline.

Less pilose on top of head and on hind coxa than in female. Mesoscutellar sulcus not interrupted medially. Hind tibia with 22–23 pegs in two rows dorsally. Fore wing vein 2r arises 0.63 from base of pterostigma (Fig. 6C). Sternum 9 with three posteriorly directed spines, one anteromedially and two posterolaterally, sternum 9 terminating in stubby projection (Fig. 6A).

Etymology. Named to acknowledge the contributions of Société Entomologique Antilles Guyane (SEAG) to further the exploration of the diversity of Orussidae in the Neotropics.

Comments. The female and male that have been assigned to *Ophrella seagi* were collected in the same locality, albeit almost four months apart. There are some differences between the two specimens in the coloration of the body and appendages, and in the degree and pattern of infuscation of the fore wing (compare Figs 4–6), but this is within the degree of variation observed in other known species of Orussidae, especially between sexes (e.g., Vilhelmsen and Smith 2002, Blank et al. 2010).

Ophrella seagi has a unique combination of characters that differs somewhat from the other members of *Ophrella*. The generic placement is based on the presence of a median longitudinal furrow between the posteriormost coronal teeth (Figs 4B, 6B; less developed in *O. seagi* than in *O. amazonica* and *O. eldorado*), the presence of an elongate antennomere 10 (at least three times as long as broad; Fig. 4C), and the position of the fore wing vein cu-a on Cu1 some distance from vein M (Figs 4A, 6C); all these characters are unique within the ophrynopine clade. Previously diagnostic features suggested for *Ophrella*, e.g., the presence of flattened, leaf-shaped setae (Middlekauff 1985) and the presence of only one hind tibial apical spur (Vilhelmsen et al. 2013) are not observed in *O. seagi* and cannot be upheld as potential autapomorphies for *Ophrella*. Nevertheless, the monophyly of the genus, including *O. seagi*, is well supported, and it is still possible to identify *O. seagi* correctly to *Ophrella* in the genus key in Vilhelmsen et al. (2013).

Ophrella seagi is a very distinct species, especially when compared to the other two species in *Ophrella*. The most distinctive feature is the prominent, medially subdivided transverse carina on the dorsal part of the pronotum (Figs 4C, 5A, 6A); *O. eldorado* also has a transverse carina, but it is less developed and not subdivided medially (Vilhelmsen et al. 2013, fig. 7d). Like many other morphological features observed in Hymenoptera pupating in wood, the carina might help the wasp escaping from the wood after eclosion (see Vilhelmsen and Turrisi 2011), probably acting as a brace when the wasp is digging its escape tunnel with the mandibles. A possible analogue occurs in several species of Aulacidae, another family of woodliving parasitoid wasps. Some species of *Pristaulacus* Kieffer, 1900 have a prominent, medially interrupted transverse crest anteriorly on the mesoscutum (Turrisi and Vilhelmsen 2010, fig. 14). Topologically it is in a similar position, i.e., anterodorsally on the thorax, indicating a similar function; morphologically it is developed on a different part (mesoscutum in the Aulacidae, pronotum in Orussidae), perhaps because the pronotum is weakly developed medially in most Aulacidae (Turrisi et al. 2009; char. 25).

Ophrella seagi also differs from the other *Ophrella* species in having slender setae on the frons and around the ocellar corona (Fig. 4A,B) (the setae are leaf-shaped in *O. amazonica* Vilhelmsen et al. (2013, fig. 4d), flattened and elongate in *O. eldorado* Vilhelmsen et al. (2013, fig. 4e)); not having dense pilosity behind the eyes and not having a postocular carina (Fig. 4C; compare with Vilhelmsen et al. 2013, figs 5c, 7a); this carina is present in most other members of the ophrynopine clade. The 9th antennomere in the female is slender and without a lateral carina in *O. seagi* (Fig. 4C), unlike *O. amazonica* and *O. eldorado*. The mesoscutum is less pilose, and the mesoscutellum is more coarsely sculptured in *O. seagi* and it is delimited more clearly from the surrounding sclerites (Fig. 5A; compare with Vilhelmsen et al. 2013, figs

6c, 7c). A ventral longitudinal carina is absent from the fore femur in *O. seagi*, whereas the mesepisternal carina is well developed (Fig. 6A). There is only one short hind tibial apical spur present in *O. amazonica* and *O. eldorado* (Vilhelmsen et al. 2013, figs 6d, 7e), whereas *O. seagi* has two larger spurs. *O. seagi* has at least the basal part of the fore wing pterostigma pale in both sexes (Figs 4A, 6C), the other *Ophrella* species have at most a pale spot basally (Vilhelmsen et al. 2013, fig. 8b). In the male of *O. seagi*, the fore wing is more evenly infuscate than in *O. eldorado* and abdominal sternum 9 has a distinct stubby projecting (Fig. 6A) as opposed to a raised rim in *O. eldorado* (Vilhelmsen et al. 2013, fig. 8e); males of *O. amazonica* have still not been collected.

Key to species of *Ophrella*

1 Longitudinal furrow on top of the head separating the posteriormost coronal teeth present (Figs 4B, 5A, 6B). Fore wing cross vein cu-a inserts on Cu at least 0.3 the width of the discal cell distal to vein M (Figs 4A, 6C). Female with antennomere 10 at least three times as long as broad (Fig. 4C) ....**2 (*Ophrella*)**

– Not with the character combination above ....**other Orussidae**

2 Pronotum with distinct transverse carina anterodorsally, with median notch (Figs 4C, 5A, 6A). Head with setae on lower frons slender, inconspicuous (Fig. 4B, C). Dense pilosity posterior to eye and postocular carina absent (Fig. 4C). Mesepisternal carina present (Fig. 6A). Hind tibia with two apical tibial spurs. Fore wing pterostigma with at least basal half pale (Figs 4A, 6C) .... ***O. seagi* Vilhelmsen, sp. n.**

– Pronotum at most with low transverse carina anterodorsally (Vilhelmsen et al. 2013, fig. 7d), without median notch. Setae on lower frons flattened, either leaf-shaped or elongate (Vilhelmsen et al. 2013, fig. 4d, e). Dense pilosity present posterior to eye and postocular carina present (Vilhelmsen et al. 2013, figs 6a, c; 7a, c). Mesepisternal carina absent (Vilhelmsen et al. 2013, figs 4d, 7d). Hind tibia with only one short apical tibial spur (Vilhelmsen et al. 2013, figs 6d, 7e). Fore wing pterostigma at most with pale spot basally (Vilhelmsen et al. 2013, fig. 8b)...**3**

3 Setae on lower frons leaf-shaped (Vilhelmsen et al. 2013, fig. 4d). Pronotum without transverse carina dorsally (Vilhelmsen et al. 2013, figs 4c, 6a). Female predominantly dark brown to black (Vilhelmsen et al. 2013, figs 4a, 6a) .... ***O. amazonica* (Westwood)**

– Setae on lower frons elongate (Vilhelmsen et al. 2013, fig. 4e). Pronotum with low transverse carina anterodorsally (Vilhelmsen et al. 2013, fig. 7d), without median notch. Female extensively reddish brown on legs and abdomen (Vilhelmsen et al. 2013, fig. 7a, d, e)............. ***O. eldorado* Vilhelmsen**

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Appendix

Additional material from French Guiana

Ophrella amazonica (Westwood, 1874): FRENCH GUIANA. Montagne des Chevaux: 4°44'56"N - 52°26'28"W, alt. 75 m, Malaise Trap, SEAG leg., iii.2012; female, NHMD000071770.

Ophrynopus batesianus (Westwood, 1874): FRENCH GUIANA, Montagne des Chevaux: 4°44'56"N - 52°26'28"W, alt. 75 m, Malaise trap, SEAG leg., 23.x.2011; female, NHMD000071771.

Ophrynopus fulvostigma (Westwood, 1874): FRENCH GUIANA. Kourou, Savane Matiti, 5°5'N - 52°37'W, SEAG leg., 9.iii.2013; female, NHMD [ethanol]. Montagne des Chevaux: 4°44'56"N - 52°26'28"W, alt. 75 m, SEAG leg., window trap, SEAG leg., 16.vii.2012; male, NHMD000071773. Montagne des Chevaux: 4°44'56"N - 52°26'28"W, alt. 75 m, window trap, SEAG leg., 28.ix.2013; female, NHMD000071772. Regina, SEAG leg., vi.2012; female, NHMD [ethanol].

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Nesting ecology of *Polistes nimpha* (Hymenoptera, Vespidae): a preliminary study in western Poland

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Abstract

In 2014 and 2015 we investigated the nesting ecology of *Polistes nimpha*, one of the paper wasp species common in western Poland. In three selected study plots we collected data about plant species on which *P. nimpha* foundresses initiate nests, nest height above ground, and nest azimuth. We have observed some preferences of foundresses in relation to these three parameters. Nests are most often initiated on *Hypericum, Tanacetum, Daucus* and *Achillea* plants. The preferred range of nest height above ground is 15 to 25 cm, while the preferred nest azimuth is about 110°.

Keywords

Nesting ecology, host plant species, *Polistes nimpha*, Poland

Introduction

Most of the available information on nesting sites of the paper wasp *Polistes nimpha* (Christ, 1791) (Hymenoptera: Vespidae) and its host plant species and nest height above ground is scattered in various publications and usually placed in the description of the study area (Blüthgen 1961, Reed and Vinson 1979, Reeve 1991, Pekkarinen and Gustafsson 1999, Hunt 2007). Differences in nesting site preferences within some groups of species of the genus *Polistes* has been treated as an auxiliary diagnostic feature (Rau 1943).

Polistes nimpha is one of three species of the genus *Polistes* Latreille, 1802 found in Poland (Oleksa and Wiśniowski 2005). The foundresses usually build nests at a height of 10–20 cm above ground, on various plants, including dwarf shrubs of *Calluna vulgaris* (L.) Hull, twigs of *Rubus* spp., thickets of *Salix* spp., reed beds of *Phragmites australis* (Cav.) Trin. ex Steud., young *Picea* sp. (Blüthgen 1961), as well as *Achillea millefolium* L., *Amegdalus nana* L., *Caragana frutex* L., *Centaurea jacea* L., *C. orientalis* L., *Cirsium ukranicum* Bess., *Crepis micranhta* Czer., *Daucus carota* L., *Hypericum perforatum* L., *Elytriga elongate* (Host) Nevsky, *Salvia verticillata* L., *Tanacetum vulgare* L., *Silaum alpestre* L., *Phlomis tuberosa* L., *Koeleria cristata* L., and *Panicum capillare* L. (Rusina and Bogutskiy 2008, Rusina et al. 2008, Rusina and Orlova 2011). *P. nimpha* builds an approximately horizontal petiole so that the comb faces to the side. *P. nimpha* is also associated with man-made structures, such as eaves of various buildings (Blüthgen 1961, Cervo and Turillazzi 1985) or attics (Rusina et al. 2007). Nesting at natural or synanthropic sites (man-made structures) may markedly affect how the wasps establish their colonies. In *P. nimpha*, colonies on natural vegetation are usually haplometric (i.e., founded by a single queen), while some of the colonies found on or in buildings are pleometric (i.e., with two or more queens assisting each other) (Cervo and Turillazzi 1985, Rusina et al. 2007).

The available data on the nesting ecology of *Polistes nimpha* are mostly very brief descriptions of the general vegetation types where the nests were found, although some cited earlier lists of plant species. Only two studies of the paper wasp *P. chinensis antennalis* Pérez, 1905 from Japan and *P. nimpha* from Ukraine included a list of host plant species and precise numbers of nests on individual plant species (Yamane 1972, Rusina and Bogutskiy 2008).

This study's focus was to determine on which plant species the paper wasps of this species build their nests and to identify the possible preferred features of the plant species during nesting site selection by the foundress. We also took into account the height at which the nest was located and its orientation in relation to the north (azimuth). Additionally, our objective was to verify tentatively whether paper wasp colony survival depends on the plant species on which the nest is located. The collected data allowed us to analyse the nesting ecology by means of determining the wasps' preferences regarding host plant species and nest height above ground and its orientation in relation to the north. This is the first study to analyse the effect of host plant species selection on the survival rate of paper wasp colonies at the pre-emergence phase.

We tested the hypothesis that selection of the plant species on which the nest is located and nest height above ground and its orientation in relation to the north were not accidental, but rather served to maximize the chances of colony survival by improving the thermoregulatory capacity of the wasp nest. The population described in this paper is located at the edge of the general range of this species in Europe, although we know of at least one population of *Polistes nimpha* located on the Baltic Sea coast (about 250 km north of Poznań) (Kozyra et al. in press). Nests in both populations were initiated on similar species of plants, and both produced workers, males, and queens. From earlier observations we can infer that the climatic conditions for paper wasps in Poland were favourable but not optimal. These ecological characteristics can provide information on how populations of *P. nimpha* act at the edge of its range in Europe (Pekkarinen and Gustafsson 1999) and whether *P. nimpha* shows the ecological plasticity observed in *Polistes biglumis* (Yamane and Kawamichi 1975). Furthermore, it can be a potential tool for testing the hypothesis about the selective basis of variation in foundress behaviour and thus clarify the proximate causes of adaptiveness of the natural population organization.

Materials and methods

We conducted field research in 2014–2015 in three permanent plots located near Suchy Las, at the edges of the military training area in Biedrusko: plot A (52.495892°N, 16.874196°E, 17,400 m^2), plot B (52.493527°N, 16.873038°E, 5,300 m^2), and plot C (52.495657°N, 16.867265°E, 14,200 m^2). We selected these plots because of the favourable conditions for paper wasp nesting (sunny grasslands abandoned for several years), as in similar habitats *Polistes nimpha* particularly frequents (Szczepko et al. 2009). All the plots were surrounded by spontaneously regenerating wooded habitats. In the immediate vicinity, there were no man-made structures where paper wasps could build their nests.

We started our field research in late April. Initially, we searched for nests along line transects spaced 2 m apart and marked each nest with a numbered flag. Next, we recorded the host plant species and measured two major parameters of the nests: height at which the nest was located and its orientation in relation to the north (azimuth). We measured nest height as the distance between the ground surface below the nest and its petiole. With a portable magnetic compass, we measured the azimuth as the angle between a line oriented toward the magnetic north and the axis of the wasp nest petiole. We measured (to the nearest 5°) the azimuth of each nest three times and took the mean into account. To calculate the geographic azimuth, we added the local magnetic declination (Kryński 2013, 2014) to the measured magnetic azimuth values.

Paper wasp colony survival was studied in 2014. We controlled the observed nests weekly to determine their condition. We regarded a colony as dead if at least one of the following criteria was met:

- lack of a comb in a place where it was observed before;
- colony destruction (e.g., due to ant predation; without appearance of any new eggs, larvae, and pupae within 2 weeks after predation).

Colony causes of mortality and patterns of changes of *Polistes* nest numbers are the subject of a separate paper (Kozyra and Baraniak 2016). We did not find a significant impact of temperature on colony mortality; however, some aspects of the impact of weather conditions are described in another paper (Kozyra in prep.).

We analysed survival rate in the period between the first record of each nest until the first week of June (inclusive). This period spanned nearly the whole pre-emergence phase (i.e., before the appearance of the first worker wasps). We identified wasps' species when we found a nest for the first time or later during measurements or plant identification.

We performed all statistical analyses using GraphPad Prism 5 software. Because the distributions of azimuth and nest height values were not normal, we used nonparametric Kruskal-Wallis and Mann-Whitney tests. We compared the numbers of nests built on different plant species with the chi-squared test.

Results

During field research in the study area we found 157 nests of *P. nimpha* in 2014 and 127 nests in 2015. In 2014, we assessed nest azimuth and height for 124 nests and plant species for 129 nests, and in another 14 species, identified only the plant family (Poaceae, true grasses). In 2015, we assessed azimuth for 120 nests, height for 127 nests, and plant species for 121 nests.

In total, for both seasons, we found paper wasp nests on 30 plant species (Table 1). Most frequently, the wasps chose *Hypericum perforatum*, especially in 2014, when we located about 44% of their nests on the lignified stems of this species, compared to 19% in 2015. In the first year, paper wasps nested on lignified stems of 16 species, whereas a year later the number of plant species increased to 23 (Table 1). The wasps particularly preferred 6 plant species: *Hypericum perforatum*, *Daucus carota*, *Tanacetum vulgare*, *Achillea millefolium*, *Artemisia vulgaris*, and *Juncus effusus* (Table 1). Out of the 129 nests for which we identified plant species, only 18 survived the pre-emergence phase (Table 2). They were located on the stems of only 4 species: *Hypericum perforatum*, *Daucus carota*, *Artemisia vulgaris*, and *Elymus repens*.

The geographic orientation of combs was nearly identical and did not differ significantly between the years (Mann-Whitney test, $U = 6{,}899$; $P = 0.326$) (Fig. 1). For both years the mean azimuth was about 110°, which means that the cell openings in the combs usually faced the east or southeast (Fig. 2). Different nest orientations (i.e., with cell openings facing the west or another direction) were very rare (Fig. 1).

Nest height above ground was similar in both years, although the difference between years was significant (Mann-Whitney test, $U = 5{,}663$; $P = 0.0001$). The mean height in 2014 was 19.6 cm, whereas it was about 17 cm in 2015 (Fig. 3).

Nest azimuth on the most frequent plant species was similar in both years (Fig. 4), and the differences were not significant (Kruskal-Wallis test, $H = 6.75$, $P = 0.344$ in 2014 and $H = 7.095$, $P = 0.312$ in 2015). Nest height above ground was also similar irrespective of the host plant species (Fig. 5). In 2014 it did not differ significantly between plant species (Kruskal-Wallis test, $H = 11.8$, $P = 0.086$), but in 2015 the differences in this parameter between plant species were significant (Kruskal-Wallis test, $H = 16.54$, $P = 0.011$). The most remarkable difference was observed between *Juncus*

Table 1. List of plant species on which we found paper wasp nests of *Polistes nimpha* in 2014–2015.

Plant species	Family	Number of nests	
		2014	**2015**
Hypericum perforatum L.	Clussiaceae	57	24
Daucus carota L.	Apiaceae	20	7
Tanacetum vulgare L.	Asteraceae	5	20
Achillea millefolium L.	Asteraceae	9	9
Artemisia vulgaris L.	Asteraceae	12	3
Juncus effusus L.	Juncaceae	0	11
Holcus lanatus L.	Poaceae	1	8
Dactylis glomerata L.	Poaceae	7	2
Rosa canina L.	Rosaceae	7	1
Galium verum L.	Rubiaceae	0	7
Picris hieracioides L.	Asteraceae	0	5
Rumex acetosa L.	Polygonaceae	0	4
Artemisia campestris L.	Asteraceae	2	2
Centaurea stoebe L.	Asteraceae	0	3
Prunus domestica L. ssp. *syriaca* (Borkh.) Janch.	Rosaceae	0	3
Elymus repens (L.) Gould	Poaceae	3	0
Arrhenatherum elatius (L.) P. Beauv. ex J. Presl & C. Presl	Poaceae	0	2
Festuca rubra L.	Poaceae	0	2
Poa angustifolia L.	Poaceae	0	2
Pyrus pyraster (L.) Burgsd	Rosaceae	0	2
Agrimonia eupatoria L.	Asteraceae	0	1
Galium album Mill.	Rubiaceae	0	1
Lupinus polyphyllus Lindl.	Fabaceae	0	1
Phleum hubbardii D. Kováts	Poaceae	0	1
Calamagrostis epigejos (L.) Roth.	Poaceae	1	0
Festuca trachyphylla (Hack.) Krajina	Poaceae	1	0
Pinus sylvestris L.	Pinaceae	1	0
Populus sp.	Salicaceae	1	0
Quercus robur L.	Fagaceae	1	0
Senecio jacobaea L.	Asteraceae	1	0
Number of species		16	23
Total number of nests		129	121

effusus and *Holcus lanatus* (Dunn's post hoc test, $p < 0.05$). Nest height above ground for all nests jointly in 2014 did not differ significantly from the height of the nests that survived the pre-emergence phase (Mann-Whitney test, $U = 1{,}076$; $P = 0.54$) (Fig. 6).

The plant species composition and numbers of nests on plants of individual species differed between the two years (Fig. 7). The numbers of nests built on the most frequent plant species also differed significantly between years (chi-squared test, $\chi^2 = 53.54$, $P < 0.0001$).

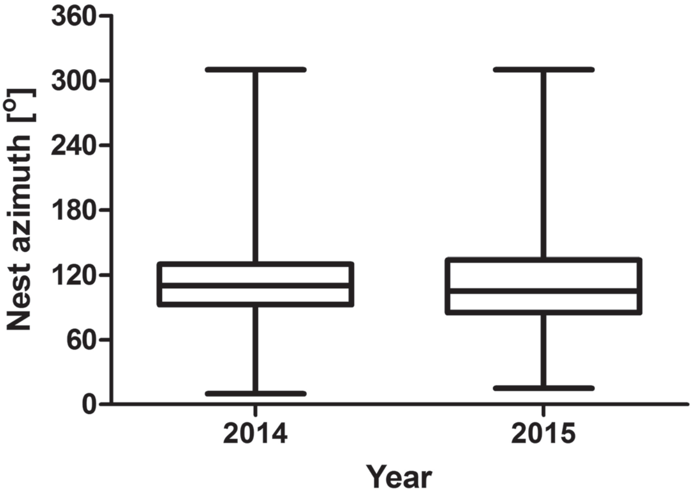

Figure 1. Orientation of nests of *Polistes nimpha* in relation to the north (azimuth) in 2014–2015.

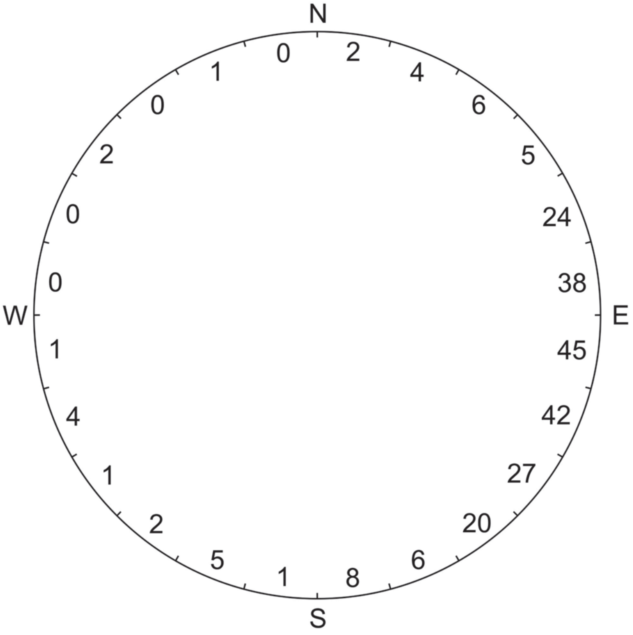

Figure 2. Number of nests with orientation in particular geographic directions in 2014–2015.

Discussion

The species composition of host plants of *Polistes nimpha*, especially in the upper part of Table 1, is very similar to that reported by Rusina and Orlova (2011), especially in relation to *Achillea millefolium*, *Hypericum perforatum*, and *Daucus carota*. Foundresses

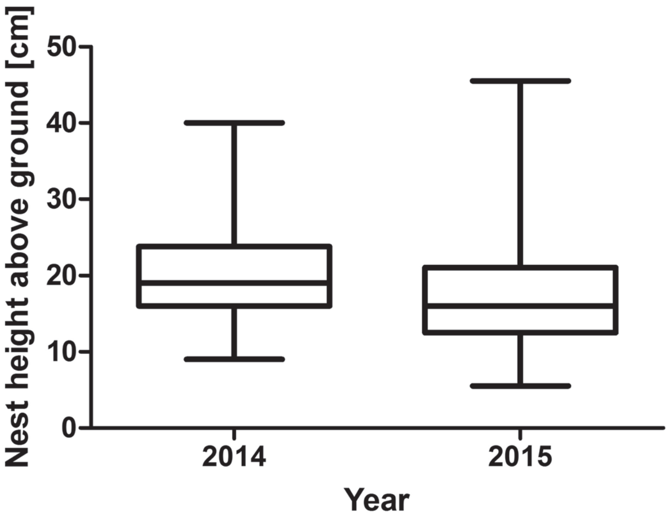

Figure 3. Height at which the nests of *Polistes nimpha* were built in 2014–2015.

Table 2. Survival rate of colonies of *Polistes nimpha*, depending on the plant species on which the comb was built in 2014.

Plant species	Number of nests		Survival [%]
	Initiated	Survived until worker emergence	
Hypericum perforatum	57	11	19
Daucus carota	20	4	20
Artemisia vulgaris	12	2	17
Achillea millefolium	9	0	0
Dactylis glomerata	7	0	0
Rosa canina	7	0	0
Tanacetum vulgare	5	0	0
Elymus repens	3	1	33
Artemisia campestris	2	0	0
Holcus lanatus	1	0	0
Calamagrostis epigejos	1	0	0
Festuca trachyphylla	1	0	0
Pinus sylvestris	1	0	0
Populus sp.	1	0	0
Quercus robur	1	0	0
Senecio jacobaea	1	0	0
Total	129	18	14

of *P. nimpha* emerge and start to build their nests from April until early May (Kozyra unpubl. data). At that time, the only available nesting sites for wasps in the analysed plots were young trees, shrubs, lignified parts of herbaceous plants, or grass culms

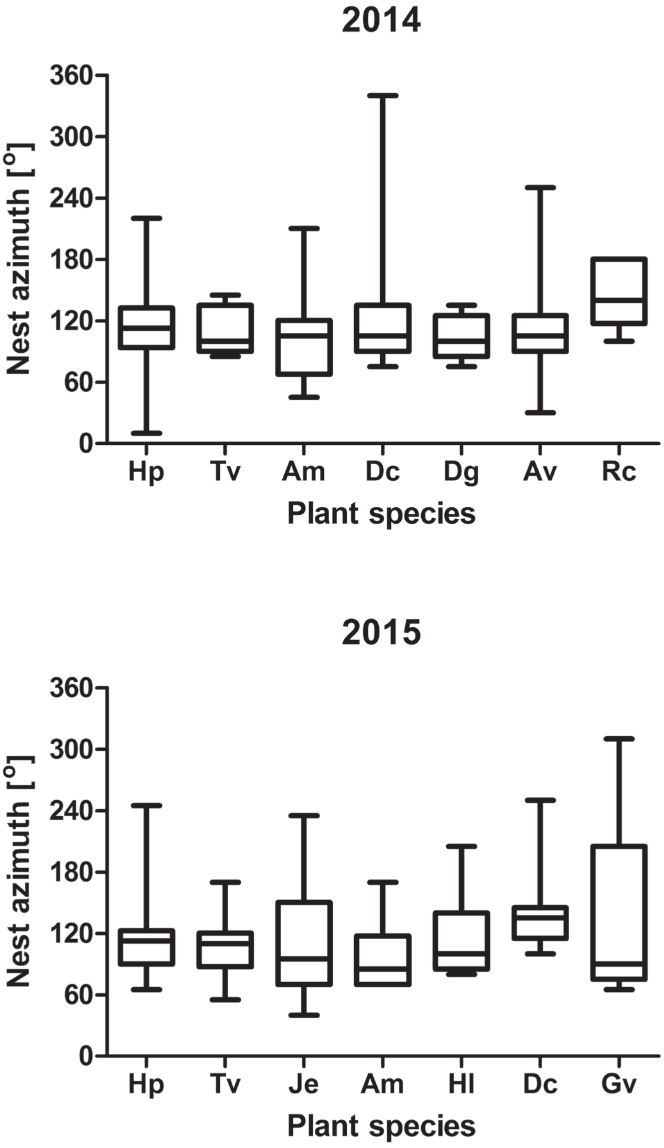

Figure 4. Values of the azimuth of nests of *P. nimpha*, depending on the plant species on which they were built in 2014–2015. Abbreviations: Hp—*Hypericum perforatum*; Tv—*Tanacetum vulgare*; Am—*Achillea millefolium*; Je—*Juncus effusus*; Dc—*Daucus carota*; Dg—*Dactylis glomerata*; Hl—*Holcus lanatus*; Rc—*Rosa canina*; Gv—*Galium verum*.

remaining after the winter period. During our study, paper wasps preferred plants characterized by strong, lignified stems (Table 1) that offered them good support.

The wasps also built many nests on culms of various grasses (e.g., *Holcus lanatus*, *Dactylis glomerata*, *Elymus repens*, and *Calamagrostis epigejos* (Table 1), but grass culms

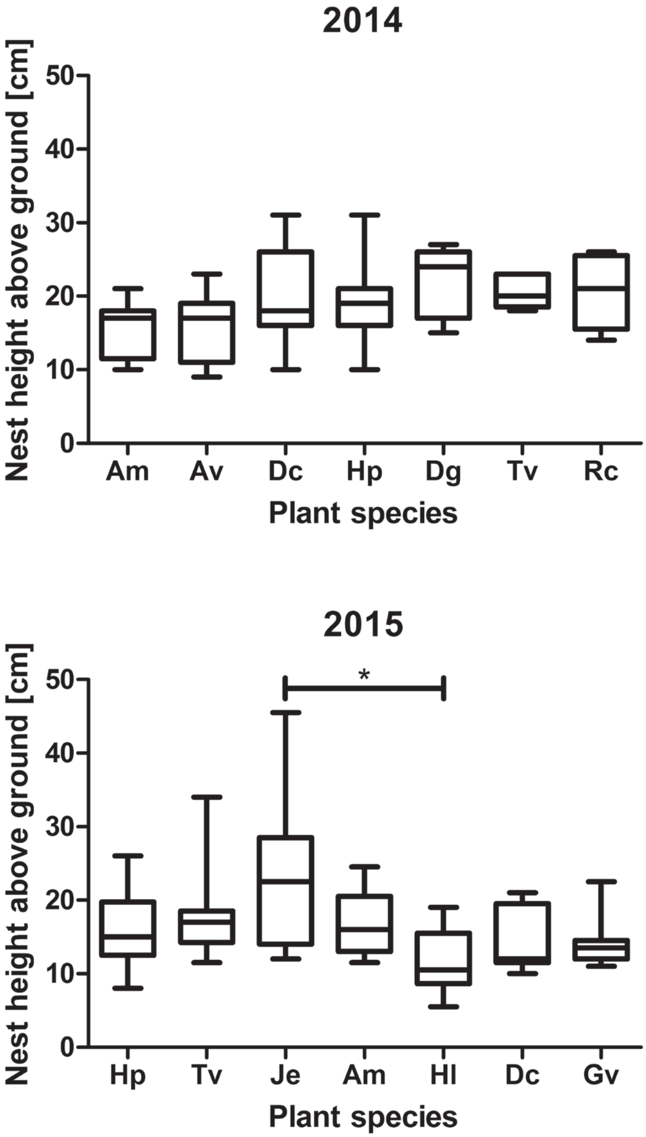

Figure 5. Height at which the nests of *P. nimpha* were built in 2014–2015, depending on plant species. *Dunn's post hoc test, $p < 0.05$. Abbreviations: Hp—*Hypericum perforatum*; Tv—*Tanacetum vulgare*; Am—*Achillea millefolium*; Je—*Juncus effusus*; Dc—*Daucus carota*; Dg—*Dactylis glomerata*; Hl—*Holcus lanatus*; Rc—*Rosa canina*; Gv—*Galium verum*.

are much more delicate than lignified stems of other plants so the nests built on the former are unlikely to survive. In 2014, after the pre-emergence phase, which is the most dangerous phase for colony development, only 1 of the 18 survived colonies was located on a grass (*Elymus*); the other 17 nests were on plants of the genera *Hypericum*,

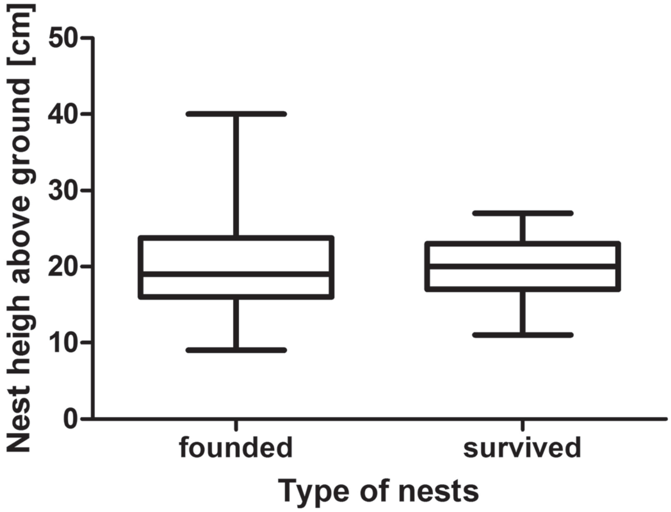

Figure 6. Comparison of the height above ground of all nests founded by *Polistes nimpha* in the study area with that of the colonies that survived the preemergence phase in 2014.

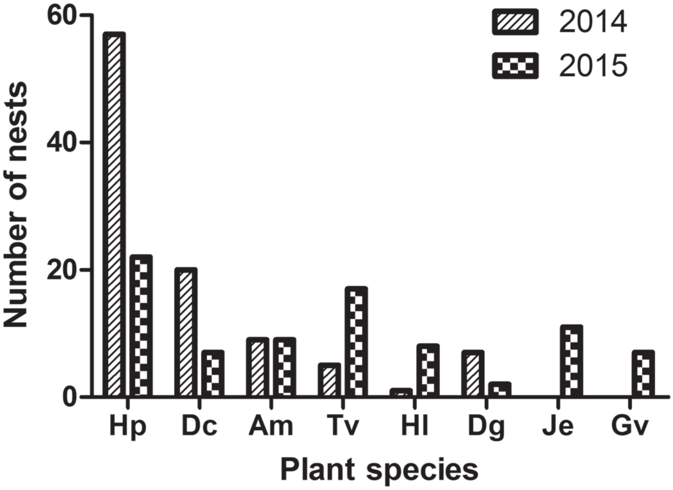

Figure 7. Number of nests of *P. nimpha* built on several most frequent plant species in 2014–2015. Abbreviations: Hp—*Hypericum perforatum*; Tv—*Tanacetum vulgare*; Am—*Achillea millefolium*; Je—*Juncus effusus*; Dc—*Daucus carota*; Dg—*Dactylis glomerata*; Hl—*Holcus lanatus*; Rc—*Rosa canina*; Gv—*Galium verum*.

Daucus, and *Artemisia* (Table 2). Colonies located on shrubs and other grasses did not survive that phase. Nests during their development increased in size and weight. In case of unfavourable weather (e.g., rain, strong winds), weaker substrates such as grass culms are much more exposed to destruction than strongly lignified stems of other herbaceous plants. Ant predation can be another reason for the high mortality of colonies, especially of those located on shrubs and young herbs. In contrast to lignified stems of herbaceous plants or the previous year's culms of grasses, the twigs of shrubs and young herbs are living structures, so they are more often penetrated by ants, which search for honeydew, aphids, and other insects. The third, probably major factor is the vegetation located near the nest. If its density is low, the vegetation can be easily penetrated by larger predators, such as wild boars or foxes, which are numerous in the study area. In the analysed plots in 2014, plants of the genera *Hypericum*, *Daucus*, *Artemisia,* or *Achillea* formed mixed patches. Nesting on plants of this group could reduce the risk of mammal predation and thus increase the chances of colony survival. We never observed foundresses of *Polistes nimpha* to build their nests in dense patches of grasses; their combs were built mostly in small, isolated clumps. The fourth, undoubtedly significant factor affecting colony survival is nest height above ground. Potential predators can more easily spot nests located high above the ground surface, so this nest location increases the risk of damage to the shoot on which it was built, which leads to colony destruction. Very low nest location can be a problem; most probably it increases the risk of ant predation. The data we collected in 2014 (Fig. 6) show that during the pre-emergence phase, the extreme values were eliminated (the lowest and highest located nests in the observed population declined) and the height of the nests that survived ranged from 15 cm to 25 cm. The final survival rate of *P. nimpha* colonies was most probably affected by all the above-mentioned factors. Observed mortality during the pre-emergence phase was much higher than in *P. biglumis* (Linneaus) (Yamane and Kawamichi 1975). Probably it is an effect of stronger activity of predators on study plots near Poznań (Kozyra and Baraniak 2016). Nevertheless the pattern of changes in number of nests during one season still fits the theoretical model of survivorship for paper wasps (Starr 2006).

The pattern of colony mortality during the season we observed in Poland is very similar to results of studies conducted in Italy for *Polistes nimpha* (Cervo and Turillazzi 1985) and in Japan for *P. chinensis antennalis* Pérez (Miyano 1980). In both localities mortality during the first phase of the colony cycle was significant but lower than that observed near Poznań. In fact, the number of living nests was certainly a bit higher than that which we observed during our research. In our study we focused only on nests that we located at the beginning of the season. After the nest was destroyed, we did not search for it again to check for possible comb rebuilding. However, in a previous study in the same plots, the researcher had observed some cases in which *P. nimpha* nests were rebuilt (Kozyra unpublished).

Nest height above ground generally did not differ significantly between host plant species (in 2014, no differences; in 2015, a difference between only *Juncus effusus* and *Holcus lanatus*) (Fig. 5), so values of this parameter do not seem to depend on host plant species. For the major plant species in 2014–2015, nest height values fit within the above-mentioned range (15–25 cm), which confirms the hypothesis that nest height is not accidental. This range of height may protect nests against strong, cold winds at the beginning of the season, at the turn of April and May, especially at high latitudes. On the other hand, foundresses should not build nests too low because of further problems with thermoregulation. When daily temperatures increase, the ground accumulates heat and starts to emit thermal energy from the surface. This may cause nests built too low to get not only thermal radiation from the sun but also excessive amounts of thermal energy emitted by the heated ground. The foundress avoids additional costs connected with active nest thermoregulation (fanning and deposition of drops of water in cells) through the choice of proper nest height above the ground (Jones and Oldroyd 2006).

Changes in host plant species composition which may alter the wasps' preferences for some species as nesting sites (Table 1 and Fig. 7) are caused by two major factors. The first factor was the ecological succession of plant communities and the decline of some plant species, which are replaced by others. The second factor was the activity of wild boars in 2014–2015. In plot C, where 94 nests were located in 2015, wild boars were very active. This probably resulted in significant changes in the abundance of individual plant species through the elimination of some patches, which could modify the wasps' preferences regarding host plant selection for nest construction.

The third parameter we analysed was the geographic orientation of the comb. In many social insects, such as ants and termites, the geographic orientation of nests is not accidental and is of great significance for their thermoregulation (for a review, see Jones and Oldroyd 2006). The lack of significant differences in nest azimuth in the population analysed between the years 2014 and 2015 (Fig. 1) and the lack of differences in nest azimuth between the most preferred plant species (Fig. 4) indicate that the foundresses oriented the comb in space in a specific way. Most of the values recorded in both years are within very narrow ranges (Fig. 1), oscillating around 110°. Thus, the cell openings in the combs nearly always face east or southeast, so this orientation does not seem to be accidental. The nests of *Polistes nimpha* built under the eaves of buildings were usually located on the southern side of buildings (Blüthgen 1961, Cervo and Turillazzi 1985). Yamane (1969) reported that a vast majority of the paper wasps that he studied (i.e., *P. snelleni* [de Saussure, 1862] and *P. biglumis*) nested on southern and southeastern slopes. The observed orientation of nests of *P. nimpha* is probably linked with passive mechanisms of nest thermoregulation: probably, if the cell openings face the east or southeast, in the pre-emergence phase of colony development the cells with developing offspring are heated more quickly in the morning by the energy from the rising sun. In early spring, the vegetation around the nests starts to develop, and only after some time they are shaded by the growing plants. Longer periods of high temperature in the nest are a factor enabling faster development of paper wasp larvae (Jeanne and Morgan 1992). This is crucial for the wasps because most of the colonies die during the pre-emergence phase, when there is only one queen (or, rarely, several queens) in the nest, so the defensive potential of the colony is very limited (Miyano 1980, Cervo and Turillazzi 1985, Kozyra et al. 2015).

Yamane and Kawamichi (1975) conducted similar studies for *Polistes biglumis* at the northern edge of its range in Japan. *P. nimpha* and *P. biglumis* are closely related species and, as expected, we observed some similarities between these two species. The life cycles of both species are similar. *P. nimpha* in Poland, similar to *P. biglumis*, initiates nests at the turn of April and May, and its colonies disappear in September. Furthermore, colonies of both species at the northern limit of their ranges produce full generations of both workers and sexual individuals. A more detailed comparison of life cycles of these two species is forthcoming in a separate paper (Kozyra in prep.).

In conclusion, this study shows that foundresses of *P. nimpha* demonstrate specific preferences for nesting sites regarding their host plant species, nest height above ground, and geographic orientation (azimuth) of the combs. The first 2 factors are important to maximize the chances of colony survival in preemergence phase, the most dangerous, initial part of the colony life cycle, while azimuth most likely functions as a passive mechanism of nest thermoregulation at an early stage of its development, when the surrounding vegetation is still low and allows direct access of sunlight to the comb. Although the nests were built on plants of more than 10 species (Table 2), the vast majority were located on only three species that offer them the greatest chances of colony survival. We made similar observations for nest height: while the range of variation is wide, only the middle part is optimal for colony survival (Fig. 6). Most probably, only the best-adapted foundresses are able to build their nests on a suitable plant species and at an appropriate height, maximizing the chances of colony survival and perpetuating the pattern of preferences in successive generations.

Both height above ground and azimuth seem to play important roles in the passive thermoregulation of paper wasp colonies. In some *Polistes* species spectacular adaptations to cold climates have been found, such as life cycle plasticity (Yamane and Kawamichi 1975) or a special nest construction called a functional envelope (Yamane 1972). It is very likely that the observed preferences in nest azimuth in *P. nimpha* play a role similar to that of the functional envelope in *Polistes* species from the northern part of Japan.

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RESEARCH ARTICLE

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Exotic ants (Hymenoptera, Formicidae) of Ohio

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Abstract

The worldwide transfer of plants and animals outside their native ranges is an ever increasing problem for global biodiversity. Ants are no exception and many species have been transported to new locations often with profound negative impacts on local biota. The current study is based on data gathered since the publication of the "Ants of Ohio" in 2005. Here I expand on our knowledge of Ohio's myrmecofauna by contributing new records, new distributional information and natural history notes. The list presented here contains 10 species with origins in a variety of geographic regions, including South America, Europe, Asia, and Indo-Australia. Two distinct groups of exotics, somewhat dissimilar in their geographic origin, occur in Ohio: a) 3 species of temperate Eurasian origin that have established reproducing outdoor populations; and b) 7 tropical tramp species currently confined to man-made structures. Only *Nylanderia flavipes* (Smith, 1874) is currently seen to be of concern although its effects on local ant communities appear to be restricted largely to already disturbed habitats. A systematic sampling of disturbed areas, urban sites, plant nurseries and conservatories, where new arrivals can be expected, would extend and build upon our current knowledge of Ohio's exotic ant fauna.

Keywords

Formicidae, non-native species, distribution, natural history, eastern US, Ohio

Introduction

People rarely travel alone and the worldwide human-mediated transfer of organisms is well documented. In the current era of enhanced commerce, improved transportation and globalization, more and more species are being transported to areas where they did not occur previously. A large number of plant and animal species have been transferred to new locations either purposefully (for food, medicine, landscaping, or as pets) or unintentionally (in ballast water, via potted plants, top soil, or fire wood) (Vitousek et al. 1997). We refer to such organisms that have completed the first step of the introduction process (i.e., initial "dispersal") as non-native, alien or exotic species. Ants are no exception, and most regions of the world now are known to harbor at least a few non-native species. Of the approximately 14 000 described species of ants, over 200 have established populations outside their known native range and even more species have been detected but not established (Sarnat et al. 2016).

Owing to their small body size, social behavior and often pronounced tolerance to, and association with, human-altered habitats, many non-native ants now are widely distributed across the globe and have become an integral part of their new homes (Holway et al. 2002). Non-native ants are not a new problem but their frequency of occurrence has been increasing due to increased rates of travel and trade, along with modification of natural habitats and urbanization. Islands are especially prone to accumulate exotic species and high proportions of non-native ants are known from a number of island systems. For example, the current myrmecofauna of the state of Hawaii includes at least 57 species (Krushelnycky 2015), none of which is native to the Hawaiian Islands. Similar trends have been noted also for certain continental areas where climatic conditions are appropriate for the establishment of a high number of tropical and subtropical ant species. With over 50 established species of non-native ants, Florida harbors the largest known exotic ant fauna of any continental US state (Deyrup et al. 2016).

Many established non-native species (i.e., species that have completed the second step of the dispersal process; "exotic established species" in Wittenborn and Jeschke 2011) possess invasive attributes and constitute a major part of the global environmental change. Such species have the potential to spread, often considerably, upon establishment and affect native ecosystems with devastating ecological consequences to local communities and ecosystem processes (i.e., invasive species; Mack et al. 2000; Mooney and Hobbs 2000, Pimentel et al. 2005). Next to habitat loss and degradation, invasive species are among the most significant drivers of biodiversity loss (Didham et al. 2007).

The Global Invasive Species Database shows that five ant species currently are listed among the World's 100 worst invasives (ISSG 2015). An emerging problem, at least in regard to ants, is the recent increased interest in keeping various ants species as pets. In Europe, where restrictions generally are lacking, Internet-stores offer living ant colonies, formicaries, and various accessories (Buschinger 2004). These shops advertise and sell ants from nearly all over the world, including some well-known ant invaders (Wild 2011). This unfortunate practice has the potential to increase the number of imported colonies and contribute to the spread of additional species. There is, therefore, a clear need for a better documentation of the current and future distribution of such exotic species if we are to better understand and to be able to mitigate the effects associated with their spread. That said, it is important to stress that not all exotic species are, or are likely to become, invasive or to attain a pest status. Aside from the more practical aspect of documenting the spread and the effects of non-native ants, the discovery and study of these species informs our understanding of general ecological principles.

In the context of this paper, I apply the term "exotic species" to designate any species detected outside the confines of its known native range. As such this definition includes both species with well-established populations in natural or human-altered settings as well as species which have been encountered only infrequently, or in low numbers, and whose current status therefore is uncertain. The focus of this paper, accordingly, is on the species that have concluded the first, fundamental, step in the invasion process, namely the completion of human-aided dispersal.

The first known record of an ant exotic in Ohio is from 1917 when *Monomorium pharaonis* (Linnaeus, 1758) was collected by M.R. Smith in Columbus (unpublished material housed at the Ohio State University Collection; in Wetterer 2010). Two additional species, *Tetramorium caespitum* (Linnaeus, 1758) and *Hypoponera ragusai,* (Emery, 1894) subsequently were reported from south-central Ohio by Wesson and Wesson (1940). *Linepithema humile* (Mayr, 1868) (Arnett 1993) and *Paratrechina longicornis* (Latreille, 1802) (Hedges 1998) were added to the list in the next 60 years, thus raising the number of exotic ant species known from Ohio to five prior to 2000. In 1996 a statewide survey of the ant fauna of Ohio was undertaken by Gary Coovert and Brian Rayburn, which resulted in two additional species (*Pheidole bilimeki* Mayr, 1870 and *Tetramorium atratulum* (Schenck, 1852)) reported for Ohio (Coovert 2005). Thus prior to the onset of the current study a total of seven non-native ant species were known from the state (although *P. longicornis* was not included in the Ohio ant list at that time).

Here I extend the current knowledge of the ant fauna of Ohio and provide a summary of the exotic species known to occur in the state at present. I expand the list with the inclusion of species newly discovered or species not included in Coovert (2005) and provide new distributional and/or ecological data. It is my intent that this paper will serve as a stepping stone and will encourage future explorations of Ohio's myrmecofauna.

Methods

The work for this study began in late 2005, following the publication of Coovert (2005) and is ongoing. The methods I used are not precise and most of my survey work, and that of my colleagues, was qualitative. One exception is the formicine *Nylanderia flavipes* (Smith, 1874), for which quantitative data are available (see Uno et al. 2010, Ivanov et al. 2011). The use of tuna baits, Winkler litter extraction and careful observations allowed for a more rigorous assessment of this species' current status in northern Ohio.

During my work I concentrated on documenting as many species as possible at each survey site primarily through the use of hand collecting. I divided my sampling time between natural and human altered habitats alike as disturbed areas are often prone to the accumulation of ant exotics. A substantial part of my sampling was conducted in human-modified habitats including parks, gardens, yards and other urban landscapes. In addition, various man-made structures such as greenhouses, conservatories, plant nurseries and people's homes also were examined. At each site I inspected the ground and vegetation (including flowers and seed pods) looked under bark, stones, logs and other cover objects. I also broke open stems and branches that have fallen on the ground and inspected them for the presence of ant colonies. On a number of occasions I augmented this sampling scheme by checking lights on buildings or by using black light for the collection of alate reproductives. New materials accumulated in the invertebrate collection at the Cleveland Museum of Natural History (CMNH) since 2005 also were examined. Much material, in the form of specimens and/or photographs, was sent to me by friends and colleagues to whom I am indebted (see Acknowledgements).

Voucher specimens of all recorded species are in the invertebrate collections at CMNH and the Virginia Museum of Natural History (VMNH). Nomenclature follows Bolton et al. (2007), except for the *Prenolepis* genus-group and for *Tetramorium* which are based on LaPolla et al. (2010) and Ward et al. (2014), respectively.

All species included here can be identified using the taxonomic keys in Coovert (2005), Ellison et al. (2012), and Sarnat et al. (2015). Additionally, representative high resolution photographs of at least the worker's caste of Ohio's non-native species can be found on AntWeb (www.antweb.org), AntWiki (www.antwiki.org) and on Discover Life (www.discoverlife.org).

Results

As a result of the current work three non-native ant species are newly recorded from the state – *Nylanderia flavipes* (first record in Ivanov and Milligan 2008), *Tapinoma melanocephalum* (Fabricius, 1793) and *Cardiocondyla obscurior* Wheeler, W.M., 1929 bringing the number of known ant exotics in Ohio to ten. New distributional data are added for most of Ohio's non-natives with the exception of *Paratrechina longicornis*, *Pheidole bilimeki* and *Hypoponera ragusai* which were not encountered during the survey, and have not been collected in Ohio since their original discovery. *Linepithema humile* (the Argentine ant) is confirmed for Ohio (Arnett 1993 was the first one to mention this ant for the state but didn't provide locality information) and now has established indoor colonies in at least one location in northeastern Ohio. *Paratrechina longicornis*, originally reported in 1998 but not present in Coovert (2005), also is included in the Ohio list. Two of the species (*Tapinoma melanocephalum*, *Cardiocondyla obscurior*) on this list have not previously been reported from Ohio, and as such represent new state records.

Taxa are arranged alphabetically by subfamily, genus and species. Each species name is followed by the taxon's currently known Ohio distribution, habitat, known area of origin and brief natural history notes. Precise distributional records of these species for North America and elsewhere can be found in Coovert (2005), Bolton et al. (2007), Klotz et al. (2008), Wetterer (2008, 2009, 2010, 2011), Wetterer et al. (2009), Ellison et al. (2012), Guénard et al. (2012), and Sarnat et al. (2015).

Dolichoderinae

Linepithema humile (Mayr, 1868)

The Argentine ant

Distribution in Ohio. Northern Ohio. Counties: **Cuyahoga** (Cleveland, 27.x.2005 [KI 1176], 15.xi.2005 [KI 1177], and 01.iii.2015 [observed, not coll.], same locality, leg. K. Ivanov, in a greenhouse) and an unspecified Ohio record in Arnett (1993), (Fig. 1).

Where found/Habitat. Indoors, in greenhouses and conservatories.

Origin. The Paraná River drainage basin of South America.

Natural history. The Argentine ant is amongst the world's most successful invasive species and is a nuisance everywhere it occurs. It is established primarily in regions with Mediterranean climate where it has been shown to have profound negative impacts on native biota (Suarez et al. 1998; Touyama et al. 2003). Workers of this genus can be identified by their broadly concave clypeus and the peculiar mandibular dentition arranged in a series of small denticles interspersed with larger single teeth. In the Northeast *L. humile* can be separated from the superficially similar *Tapinoma* by the presence of a well-developed petiolar scale and the vertical orientation of the first gastral segment which does not project over the petiole.

This cosmopolitan species often thrives in disturbed habitats with abundant moisture. Nests are most often in soil, but also under cover objects, refuse piles and more rarely under tree bark. The main dietary component is honeydew from hemipterans, although these ants will also take other sweet substances including household food items, and occasionally will feed on insects (Smith 1965).

Throughout its introduced range Argentine ant colonies are polygynous with pronounced unicoloniality (i.e., the formation of large colonies with multiple nests). A key attribute to the ecological success of this species thus is the absence of intraspecific aggression within the large colony (Tsutsui and Case 2001). These characteristics give argentine ant colonies remarkable capacity to expand, and populations can reach extremely large sizes and cover extensive geographic areas to the detriment of other, less populous, species (Giraud et al. 2002).

Ohio's only confirmed record of this species comes from a greenhouse in Cleveland where I have observed large numbers of ground foragers on paved surfaces, exposed soil, and on tropical plant debris on the ground. In many cases foragers were accumulating around sugar syrup stations, banana, apple and other fruit pieces used for feeding tropical butterflies. Due to logistical limitations, I was not able to conduct

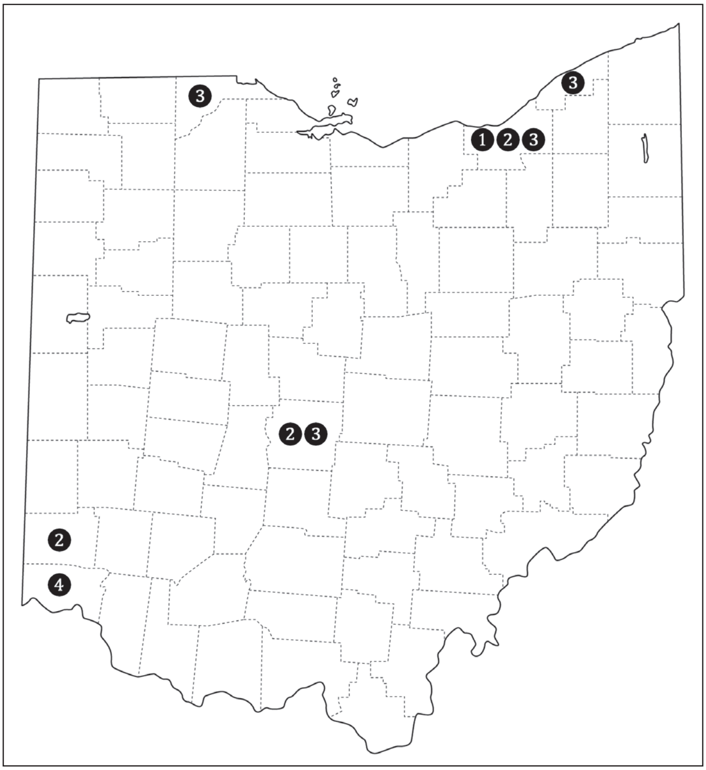

Figure 1. Distribution of *L. humile* (**1**), *T. melanocephalum* (**2**), *N. flavipes* (**3**), and *P. longicornis* (**4**) in Ohio.

nest searches at this location. The very high worker densities observed, however, suggest that this species now has well-established indoor colonies at this site. At present, this species can survive in the north only in heated buildings, where occasionally it can be a persistent and troublesome pest.

Tapinoma melanocephalum (Fabricius, 1793)

The ghost ant

Distribution in Ohio. Widespread in Ohio. Counties: **Butler** (material examined: Oxford, Miami University, Belk Greenhouse, 25.ii.2014, leg. S. Mays), **Cuyahoga** (material examined: Cleveland, 07.ii.2008, leg. K. Ivanov, and 04.iii.2008, leg. B. Poynter, same locality, in an animal care zoo facility), and **Franklin** (photographs examined: Columbus 25–29.ii.2008, photos by S. Heideman, in a conservatory), (Fig. 1).

Where found/Habitat. Indoors, abundant in greenhouses, conservatories and zoo buildings.

Origin. Indo-Pacific.

Figure 2. *Tapinoma melanocephalum* workers from a conservatory in Franklin Co. (Photo: S. Heideman).

Natural history. This widely distributed tramp species is more prevalent in disturbed areas but also has been encountered in natural habitats in its introduced range (Wetterer 2009 and references therein). Unlike many other exotic ants, this species can be distinguished easily by its minute size, peculiar coloration (Fig. 2), and the rapid, erratic movements when disturbed.

Colonies are moderate to large in size, and polygynous, with queens distributed in multiple nests. Additional features characteristic of this ant include unicoloniality, intranidal mating, and colony formation via budding (Bustos and Cherix 1998). Ghost ants are opportunistic nesters, usually in disturbed areas, and frequently relocate their nests (Wetterer 2009). Inside buildings, nests can be found in flowerpots, in small cracks and crevices, beneath baseboards, and in wall spaces (Klotz et al. 2008).

Where it occurs this ant is a major nuisance pest, both indoors and outdoors, that tends mealybugs and scale insects and scavenges for dead insects and food scraps (Smith 1965). The ghost ant is confined to greenhouses and other heated buildings in northerly states, which provide the high temperature and environmental humidity needed for the survival of this tropical species. According to Wetterer (2009), at latitudes greater than 30° this species is largely restricted to living inside buildings.

I have only seen this species at a single animal care facility in the greater Cleveland area where I observed multiple nests in wall spaces and crevices. In addition, numerous foragers were noted near and at reptile feeding stations. In Ohio, this ant is a known conservatory and zoo pest, likely distributed via potted plants or animal feed. Unpublished observations suggest that this ant has been present in the state since at least the early 2000s (B. Poynter and M. Vincent pers. communication).

Formicinae

Nylanderia flavipes (Smith, 1874)

The yellow-footed *Nylanderia*

Distribution in Ohio. Northern Ohio. Counties: **Cuyahoga** (material examined: Cleveland Heights, 12–14.x.2004 and 22–24.x.2004, leg. H. Clebsch, yellow pan traps in residential area; Cleveland, 19.v.2013 [KI 2319] and 23.iv.2014 [KI 2345], leg. K. Ivanov, in a greenhouse; Cleveland, Case Western Reserve University, main campus, 17.v.2015, leg. A. Perez, pitfall trap, mulch bed adjacent to a concrete path; Shaker Heights, Doan Brook Gorge, multiple records since original discovery in 2005 with last collection event on 06.v.2014 [KI 2346], leg. K. Ivanov, hand collecting, Winkler litter extraction, and baiting in open woodlands; Euclid Creek Reservation, Wildwood Park, 16.ix.2014 [KI 2348], leg. K. Ivanov, open woodland), **Franklin** (Columbus 17.viii.2015, leg. A. Perez, Winkler litter extraction, flower bed adjacent to public library), **Lake** (material examined: Kirtland, multiple records from July and August 2009 and 2010, leg. T. Webster, suburban lawn) and **Lucas** (Uno et al. 2010), (Fig. 1).

Where found/Habitat. This species is abundant in urban and suburban areas including forested green spaces, gardens, yards and vacant lots. It is also found indoors, in conservatories.

Origin. Temperate Asia.

Natural history. This temperate formicine was first reported for Ohio based on material collected at the Doan Brooke Gorge of Shaker Heights in July 2005 (Ivanov and Milligan 2008). Previously unknown material collected via yellow pan traps extends the first known date for Ohio to mid-October 2004 (leg. H. Clebsch). This species has well-established reproducing populations in, at least, northeastern Ohio where I first observed mating leks in July 2005. More recently, colonies containing alate reproductives were collected in May 2014 at the Doan Brook Gorge of Shaker Heights. This species can be relatively easily distinguished by its small size, the presence of paired macrochaetae on the mesosomal dorsum, the indistinct but visible ocelli, and the yellowish color of the antennae, mesosoma and legs.

This is a monogynous species that frequently develops polydomous colonies (Ichinose 1986). While quite common in its native range, this opportunistic species has not been reported as a pest, or as an ecologically dominant species, in its introduced range although data largely are lacking. Observed impacts have been mostly anecdotal and related to the disappearance of the ecologically similar native *Nylanderia faisonensis* (Forel, 1922) along the east coast of the US. New data (Ivanov et al. 2011) seem to contradict earlier views regarding the inconspicuous incorporation of this ant into local ant communities. See Ivanov and Milligan (2008) and Ivanov et al. (2011) for additional ecological data and natural history notes.

In Ohio I have observed and collected this species in a variety of different situations including urban woodlots, residential lawns, flower gardens, on concrete/pavement, as well as inside a greenhouse where I have seen foragers on *Oncidium* flowers. In all outdoor situations nests were in the soil, and were rather small and inconspicuous. Colonies most often were found under small rocks and less frequently under bark and tree limbs on the ground. On few occasions, workers readily came and took tuna in oil placed in open, rather degraded, mesic urban woodlots. *Nylanderia flavipes* maintained high abundance at the baits in the absence of native ants. However, when baits were discovered by native species, *N. flavipes* workers were displaced quickly. Our observations suggest that this species does not engage in aggressive interactions with native ants, and does not recruit to defend food resources.

Paratrechina longicornis **(Latreille, 1802)**

The longhorn crazy ant

Distribution in Ohio. Southern Ohio. Counties: **Hamilton** (Hedges 1998), (Fig. 1).

Where found/Habitat. Ohio's single record is from a warehouse in Cincinnati, although this species is undoubtedly more widespread in the state where it should be sought after in heated buildings.

Origin. Southeast Asia or Melanesia.

Natural history. Along with *Monomorium pharaonis* and *Tapinoma melanocephalum*, this is one the most widespread tramp ant species and perhaps the most widespread ant in the world (Wetterer 2008). It is found throughout the Old and the New Worlds where it appears to be a specialist of disturbed and degraded habitats, seemingly absent from undisturbed natural settings. This species can be identified on sight and relatively easily distinguished from other ant species by its erratic movements and the extraordinarily elongated scapes, head, and tibiae.

Longhorn crazy ants are highly adaptable and exhibit pronounced ability to survive even in extremely anthropogenically modified environments including nesting sites with very low humidity (Trager 1984). Nests are usually under cover objects, under dry litter and mulch, in rotten wood, less often in plant cavities, under refuse and debris piles, as well as in wall gaps inside buildings (Smith 1965). Colonies are moderate to large, polygynous, and occupy temporary nests which are highly mobile (Trager 1984). Workers are omnivorous, feeding on live and dead invertebrates, small seeds, fruits, honeydew, and a variety of household food items (Smith 1965).

A contributing factor to the colonizing success of this species is its mode of reproduction with lack of nuptial flights. Wings of queens are removed while still callow.

Dealate queens and winged males usually gather around the nest entrance, where mating occurs (Trager 1984). A process known as double cloning allows members of this species to mate with their siblings without exhibiting any of the negative effects associated with inbreeding (Pearcy et al. 2011).

This species is a known household and garden pest across tropical and subtropical areas, where it can also attain a significant agricultural pest status via its symbiotic relationships with sap feeding Hemiptera (Wetterer 2008). It has become established in temperate localities by living in buildings and other man-made structures.

Myrmicinae

Cardiocondyla obscurior Wheeler, W.M., 1929

Distribution in Ohio. Single record from southern Ohio. Counties: **Hamilton** (material examined: Cincinnati, 27-28.vii.2008, leg. R. Gibson and M. Gates, in a conservatory), (Fig. 3).

Where found/Habitat. Indoors, in a conservatory.

Origin. Australasia.

Natural history. This is an Old World genus of small, omnivorous ants that contains several cosmopolitan tramp species (Seifert 2003). Whereas most invasive and pest ants readily make themselves apparent, the presence of these minute ants in a given area often can remain undetected. *Cardiocondyla obscurior* is a species with well-known dispersal ability that has established populations in many parts of the world (Heinze et al. 2006). Individuals are readily distinguished by their swollen, heart-shaped postpetiole and the lack of erect hairs on the body (Fig. 4).

This is a species with arboreal nesting habits and its small colonies (usually <500 individuals) are typically located in nest cavities on low (2–5m) vegetation, or in folded leaves above ground. Similar to many other ants with small colonies, workers of this species do not defend foraging areas or food resources thus colonies can reach very high densities (Heinze et al. 2006). The members of this genus are ecologically subordinate and avoid competition with larger and more aggressive ants. As such they are among the few ants that can coexist with known invasives such as the Argentine ant (Carpintero et al. 2004).

It appears that colonies of all tramp *Cardiocondyla* species are polygynous and new colonies are formed via budding (Seifert 2003). In at least *Cardiocondyla obscurior*, enhanced propagation rates have been attributed to this species' ability to develop complete and fully functional colonies from very small colony fragments (Heinze et al. 2006). Given the small size of both workers and colonies of this species, such fragments can be easily transported to new localities in small samples of soil or plant material. Unusual among ants, species of this genus have long-lived ergatoid males (in addition to winged males) which usually stay and mate in their natal nests (intranidal mating) resulting in rigorous competition for virgin queens even among closely related males (Seifert 2003).

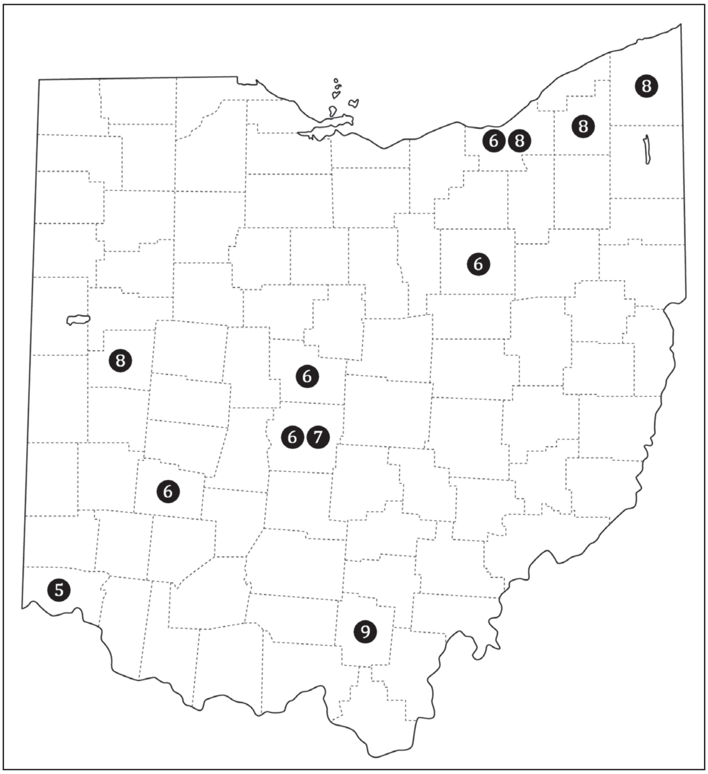

Figure 3. Distribution of *C. obscurior* (**5**), *M. pharaonis* (**6**), *P. bilimeki* (**7**), *T. atratulum* (**8**), and *H. ragusai* (**9**) in Ohio.

Due to their small colony size, and the fact that workers forage mostly solitary, members of *Cardiocondyla* are generally not considered pest species (Heinze et al. 2006). This tropical tramp species can survive in Ohio only in heated buildings.

Monomorium pharaonis (Linnaeus, 1758)

The pharaoh ant

Distribution in Ohio. Widespread in Ohio. Counties: **Cuyahoga** (material examined: Cleveland, iii.2007, leg. J.B. Keiper, inside a building, CMNH; also in Headley 1943), **Delaware**, **Franklin** (M.R. Smith material in the Ohio State University collection; in Wetterer 2010), **Greene** and **Wayne** (see Coovert 2005 and references therein for all listed counties), (Fig. 3).

Where found/Habitat. Indoors, in heated buildings.

Origin. Asia.

Natural history. The pharaoh ant is arguably one of the world's most widespread house-infesting ants and there is a large body of literature on the pest status of this spe-

Figure 4. Lateral view of *Cardiocondyla obscurior* worker (www.antweb.org, specimen CASENT0103429, photo: A. Nobile).

cies. According to Wetterer (2010) this ant is by far the most common species encountered indoors in both North America and in Europe. In tropical and subtropical regions it occurs both indoors and in natural settings, although it is rarely collected outdoors in most parts of the world (Wetterer 2010). Members of the genus *Monomorium* can be identified by their minute size, 12 segmented antennae with a three segmented club, and the dorsally smooth unarmed propodeum. Workers of *Monomorium pharaonis* can be separated from other *Monomorium* species by the densely punctate head and thorax, the yellowish body color, and the often infuscated posterior portion of the gaster.

Like other tramp species *Monomorium pharaonis* possesses features that facilitate its transport and establishment including highly polygynous and extensively polydomous colonies with little intercolony aggression (Passera 1994). A major contributing factor to the invasiveness of this ant is the formation of daughter colonies via fragmentation of the main nest. Newly formed nests remain in contact with the natal nest and may continue to exchange individuals after budding (Buczkowski and Bennett 2009). This results in large polydomous colonies that can quickly monopolize available resources. Inside buildings pharaoh ants breed continuously throughout the year. Mating occurs in the nest and no mating flights have been observed in this species (Passera 1994). In temperate areas nests are located exclusively inside buildings including wall spaces and foundations, under floors, in potted plants, around household items and in furniture. Workers are omnivorous and form pronounced foraging trails. They scavenge for both dead and live insects, as well as household food items, often exhibiting marked fondness for fats and meats (Smith 1965, Collingwood 1979).

In northern temperate regions, this small ant is highly synanthropic and depends on humans for food and shelter (Buczkowski and Bennett 2009). In Ohio, it is known only from people's homes and other heated buildings. In hospitals, this species can be a major nuisance and a serious health threat due to its ability to spread pathogenic bacteria onto sterile equipment and supplies (Beatson 1972).

Pheidole bilimeki Mayr, 1870

Distribution in Ohio. Single record from south-central Ohio. Counties: **Franklin** (Coovert 2005), (Fig. 3).

Where found/Habitat. Indoors. The single Ohio record was discovered in a greenhouse in Franklin Co.

Origin. Neotropics.

Natural history. This is a synanthropic species with pronounced tolerance to disturbed habitats.

Longino and Cox (2009) and Sarnat et al. (2015) provide the most relevant and up to date treatment of this species and its close relatives. This species can be easily confused with members of the *Pheidole punctatissima* clade (*P. anastasii* Emery, 1896; *P. punctatissima* Mayr, 1870) as well as with members of the *Pheidole flavens* complex (Economo et al. 2015; Sarnat et al. 2015). In the southeastern United States, where outdoor colonies of this species can be found, it has often been misidentified as *Pheidole floridana* Emery, 1895. According to Sarnat et al. (2015), the latter often results from the misapplication of the name *P. floridana* to collections of North American *P. bilimeki*. Identification of this species is difficult but the following characteristics may be useful in separating it from other closely related species: antennal scapes relatively short, head margin somewhat flattened posteriorly, anterior half of first gastral tergite foveolate and opaque, body color brown and only occasionally yellow-brown. In addition, it can be separated from the closely related *P. anastasii* by its preference for open, disturbed habitats (see Longino and Cox 2009; Sarnat et al. 2015 for additional information).

According to Longino and Cox (2009), this is an abundant species of open areas regularly found in recently, or frequently, disturbed habitats in its native range. Although it is often associated with anthropogenically altered areas and can be common along roadsides, it is also an abundant house pest. This ant is highly adaptable in its nest site preferences with nests located in dead rotten wood (including fence posts) and under stones. In Costa Rica Longino and Cox (2009) have observed this species in a variety of forested lowland and montane habitats. According to Wilson (2003; as *Pheidole floridana*) this species nests in soil, leaf-litter, and rotten wood in both xeric and mesic woodland habitats with colonies being monogynous and sometimes polydomous. In his account of the biology of *Pheidole bilimeki* (as *Pheidole anastasii*) in Florida Naves (1985) reports that this ant most often nests under the bark at the base, or along the roots, of pines, and only rarely in the soil. The observed colonies were monogynous and contained 600 workers. Naves (1985) also reports that *P. bilimeki* feeds on seeds, fruits, dead insects, and also preys on small live arthropods.

This species has a history of human-mediated dispersal, which is not surprising given its abundance and synanthropic habitat preferences. In northern regions, both in North America and in Europe, this species occasionally is found in greenhouses, and other heated buildings (Sarnat et al. 2015).

Tetramorium atratulum (Schenck, 1852)

Distribution in Ohio. Records from western and northeastern Ohio. Counties: **Ashtabula** (material examined: North Kingsville Sand Barrens, 20.vii.–11.viii.2007, leg. T. Pucci., Malaise trap, CMNH); **Cuyahoga** (material examined: Cleveland, Cleveland State University, main campus, 10.v.2007 [KI 1730], leg. K. Ivanov), **Geauga** (material examined: Observatory Park, 20.viii.2010, leg. E. Neff, CMNH), and **Shelby** (Coovert 2005 as *Anergates atratulus* (Schenck, 1852)), (Fig. 3).

Where found/Habitat. Along with host *Tetramorium caespitum* (see habitat description below).

Origin. Europe.

Natural history. This workerless inquiline social parasite is rarely observed and collected in both its native and introduced ranges, presumably because of its parasitic lifestyle or simply because it is indeed rare. This species' known distribution includes Europe and North America broadly following that of its host *Tetramorium caespitum*. In North America it is mostly found in the eastern part of the continent (Dash and Sanchez 2009). The pupoid wingless males are found only inside the host nests while the queens can be easily recognized by their small size and the unique, conspicuous median longitudinal depression on the dorsal surface of the gaster (Fisher and Cover 2007).

Colonies consist of males and females that live with their hosts on which they rely for work and food. Unlike many other obligate social parasites, queens of this species are adopted by queen-less host colonies (Buschinger 2009). As such every parasitized colony has a limited lifespan determined by the lifespan of the youngest host members present. See Wheeler (1908) and Francoeur and Pilon (2011) for excellent natural history notes and images.

My only encounter with this species in Ohio was in downtown Cleveland in early May 2007 when my attention was attracted by a single dealate queen which was swiftly running on the soil surface exploring exposed entrances to what later turned out to be *Tetramorium* cf. *caespitum* colonies. I was unable to observe any interactions between the two species in the short period of time before I collected the specimen. The location where this observation occurred is urban and heavily dominated by impervious surfaces, including pavement and mowed grass, interspersed with a multitude of non-native flowering plants and few scattered crab apples (*Malus* sp.), serviceberries (*Amelanchier* sp.), and tulip trees (*Liriodendron tulipifera* L.).

***Tetramorium* cf. *caespitum* (Linnaeus, 1758), (*Tetramorium* sp. E of Schlick-Steiner et al. 2006)**

The pavement ant

Distribution in Ohio. Statewide in Ohio. Counties: Listed for 74 of Ohio's 88 counties in Coovert (2005); **Geauga** (material examined: multiple records from well-separated localities within the county [KI 1206, 1219, 1261, 1281, 1322, 1351, 1356, 1375, 1411, 1427, 1454, 1509, 1601, 1986], leg. K. Ivanov)

Where found/Habitat. Along roadsides, in cracks in driveways, pavement and roads, under rocks and logs in open woodlands and wood edges, in grassy fields and many disturbed areas. Also in gardens, lawns and inside residences.

Origin. Europe.

Natural history. A temperate species commonly found in urban habitats and adjacent natural settings in Ohio. *Tetramorium* cf. *caespitum* has been continuously documented in the state since its first discovery and undoubtedly occurs in all of Ohio's counties. In North America this species has been reported as an agricultural pest, and shown to expand into natural habitats where it displaces native ants (Steiner et al. 2008 and references therein). Despite its wide ranging distribution it is relatively unstudied especially in its native habitats. This is a dark brown to black ant that can be identified by its 12 segmented antennae, the lateral portion of the clypeus which is raised into a sharp ridge anterior to the antennal insertion, the presence of abundant unbranched hairs on the mesosomal dorsum, and the regular longitudinal rugulation on the head behind the eyes. The East Asian *Tetramorium tshushimae* Emery, 1925 (known from Missouri and Illinois; Steiner et al. 2006) is smaller and typically has light colored individuals in addition to dark ones.

Pavement ant colonies are large to very large and usually monogynous. Nests are initiated by a single reproductive queen that carries out reproduction for the lifespan of the colony. In North America nuptial flights most commonly occur in mid-summer and generally one sex predominates in the reproductives produced by a particular colony (Bruder and Gupta 1972). In spring, large-scale battles between workers from unrelated colonies commonly can be observed when pavement ants are developing their territories (Ellison et al. 2012). This is an omnivorous species whose diet includes live and dead animal matter, seeds, plant exudates, occasional honeydew gathering, and kitchen food items (Smith 1965). Although common in outdoor situations this species is also an abundant indoor pest in parts of eastern North America (Klotz et al. 2008).

I have observed this species in every Ohio County in which I have had the opportunity to collect material. This is undoubtedly one of the most common ants I have encountered in the state although it is largely restricted to human-modified environments where workers are nearly ubiquitous on paved surfaces, near and inside buildings and in open grass situations (including mowed lawns). I have rarely encountered this ant in natural, relatively undisturbed, settings in Ohio. Nearly all colonies I have seen were located in open situations usually under some type of cover object, most commonly large rocks, or at the bases of grasses. Notable exceptions include two rather large colonies from northeastern Ohio, the first of which [KI 1375] was found in a naturalized open grass field at Eldon Russel Park in Geauga County and comprised a large, de-vegetated, soil mound akin to those of young *Formica exsectoides* Forel, 1886 colonies. The second colony [KI 2332] was found inside a very large rotten stump in the park manager's service area of Acacia Reservation in Cuyahoga County.

Ponerinae

Hypoponera ragusai (Emery, 1894)

Distribution in Ohio. Southern Ohio. Counties: **Jackson** (Wesson and Wesson 1940, as *Ponera oblongiceps* Smith, M.R., 1939), (Fig. 3).

Where found/Habitat. The following quote from Wesson and Wesson (1940) summarizes all the information we have for the single record of this species in Ohio - "A few workers of this species were found under a stone in partial shade, on moist but well drained soil, in Jackson."

Origin. Old World, with assumed African origin. The current confirmed distribution includes Europe, Africa and India (Bolton and Fisher 2011).

Natural history. The genus *Hypoponera* includes small cryptic ants with global distribution, although the highest diversity of the group occurs in the tropics. *Hypoponera ragusai* is a species with known tramping ability widespread in most parts of the world (Bolton and Fisher 2011). This species can be easily separated from most other North American *Hypoponera* by its smooth and shiny mesopleuron which lack punctures; and from the closely related *Hypoponera punctatissima* (Roger, 1859) by its smaller body size, and the lower and relatively longer petiolar node.

The success of this ant as a tramp species is attributed to the presence of unusual ergatoid males which remain in their natal nest where they mate with virgin queens (Taylor 1967). These ants are predators of small soil arthropods with nests usually located in soil, leaf-litter or rotting wood (Fisher and Cover 2007). This species was also found nesting under rocks and guano deposits inside caves in the Iberian Peninsula (Tinaut 2001). Workers of this relatively nondescript small ant are rarely collected due to their subterranean habits.

This species often has been refferred to as *Hypoponera gleadowi* (Emery, 1895) in the literature (including Coovert 2005), and often has been misidentified as the closely related *Hypoponera punctatissima* (Bolton and Fisher 2011). It is likely that this species shares natural history with *H. punctatissima*, which is often found in association with disturbed habitats, in addition to buildings in colder climates. Generaly neither *Hypoponera ragusai*, or any of its synonyms, have been reported as nuisance species in their introduced ranges.

Discussion

Biological invasions by plants and animals are an ever increasing problem for global biodiversity and ants are no exception. Many ant species have been transported to new locations with often profound negative impacts on local biota (e.g., *Linepithema humile, Solenopsis invicta* Buren, 1972). The collection of precise distributional records is the first, fundamental, step in establishing the extent of the current spread of these species. Such data are critical if we are to better understand the factors that govern the spread and establishment of these exotics and their potential to disturb native ecosystems.

In general, the majority of the world's known established non-native ants come from tropical and subtropical areas and the spread of temperate ant exotics is rather limited (Sarnat et al. 2016). The exotic ant fauna of virtually all northern US states and Canadian provinces is depauperate and relatively few non-native species occur in this region, especially those capable of living outdoors. Patterns observed in Ohio are consistent with this general trend as the state's climate and weather conditions offer little opportunity for the establishment of exotic ants. The rather poor representation of non-native ants in more northern latitudes likely is a result of the fact that ants as a group have their greatest diversity in tropical and subtropical areas. As a result, the pool of species which can be transferred and become established in temperate regions is much smaller as compared to that of tropical and subtropical areas. In addition, ecological reasons such as more aggressive competition from native species of similar ecological function, and reduced variability in nesting ecology in temperate conditions may be as important in determining the establishment of exotic ant species in higher latitudes.

As a result of the current work three ant exotics are added to the state's species list (but see *Paratrechina longicornis* comments above) thus increasing the number of known ant taxa in Ohio to 135 (Ivanov 2016). At present, the exotic ant fauna of Ohio comprises 10 species from 9 genera, and 4 of the 7 subfamilies known to occur in the state (Table 1). Ohio's exotic ant fauna contains 4 of the 19 ant species currently listed on the Global Invasive Species Database (*Linepithema. humile*, *Paratrechina longicornis*, *Monomorium pharaonis*, and *Tapinoma melanocephalum*; ISSG 2016). The presence of major nuisance pests and notorious invaders in the state leaves no doubt regarding their economic impact on the pest control industry and the general public. However, most of Ohio's non-native species probably have little ecological impact (but see *Nylanderia flavipes* comments below) due to their current confinement to man-made structures.

Two rather distinct groups of ant exotics with somewhat dissimilar geographic origin occur in Ohio. The first group comprises species of temperate Eurasian origin (*Nylanderia flavipes*, *Tetramorium* cf. *caespitum*, and *Tetramorium atratulum*) that have established outdoor populations in the state. The first two of these species were found to be common inhabitants of street medians in New York City by Pećarević et al. (2010). The ecology of *T. caespitum* has received relatively little attention, despite its wide-ranging distribution outside of its native range. This is likely due to its propensity

Table 1. List of Ohio's exotic ant species.

Species	First record (year, source)	Last record (year, source)	# localities	Where found
Dolichoderinae				
Linepithema humile (Mayr)	1993, Arnett	2015, this study	1	Indoors only
Tapinoma melanocephalum (Fabricius)	2008, this study	2014, this study	2–5	Indoors only
Formicinae				
Nylanderia flavipes (Smith)	2004, this study	2015, this study	6–9	Outdoors, occasionally indoors
Paratrechina longicornis (Latreille)	1998, Hedges	1998, Hedges	1	Indoors only
Myrmicinae				
Cardiocondyla obscurior Wheeler	2008, this study	2008, this study	1	Indoors only
Monomorium pharaonis (Linnaeus)	1917, OSU collection	2007, this study	6–9	Indoors only
Pheidole bilimeki Mayr	2005, Coovert	2005, Coovert	1	Indoors only
Tetramorium atratulum (Schenck)	2005, Coovert	2010, this study	2–5	Outdoors
Tetramorium cf. *caespitum* (Linnaeus)	1940, Wesson and Wesson	2015, this study	>10	Outdoors/ indoors
Ponerinae				
Hypoponera ragusai (Emery)	1940, Wesson and Wesson	1940, Wesson and Wesson	1	Unspecified, likely indoors

to nest in highly disturbed and human-modified environments. The second group includes seven tropical tramp species currently confined to man-made structures (Table 1). Not surprisingly the majority of these records in the state come from the major metropolitan areas of Cleveland, Columbus, and Cincinnati (Figs 1 and 3). With the exception of *Tapinoma melanocephalum* and *Monomorium pharaonis*, the remaining five of these species are restricted in their distribution in the state and are known only from a single locality or a single collecting event.

Published accounts suggest that only a handful of temperate species have established outdoor populations in northeastern US. These include: *Brachyponera chinensis* (Emery, 1895), *Formica paralugubris* Seifert, 1996, *Lasius* cf. *niger* (Linnaeus, 1758), *Nylanderia flavipes*, *Myrmica rubra* (Linnaeus, 1758), *M. scabrinodis* Nylander, 1846, *Tetramorium atratulum*, *Tetramorium* cf. *caespitum*, *Tetramorium tsushimae*, and *Vollenhovia emeryi* Wheeler, W.M., 1906 (Deyrup et al. 2000; Ellison et al. 2012; J. Trager pers. communication). The populations of some of these species (*B. chinensis*, *M. rubra*, *T. tsushimae*) are expanding and it will not be surprising if any or all of them are found in Ohio in future surveys (Steiner et al. 2006; Wetterer and Radchenko 2011, MacGown 2016). In addition, the tropical invasive red imported fire ant (*Solenopsis invicta*) has been increasing its range northward along the coastal plain of the eastern US and has recently been found as far north as northern Virginia and Maryland (Wetterer 2013). Given predictions for future climate change it is possible that this species will be found farther north in the not so distant future (IPCC 2007).

Tropical and subtropical exotic ants are more widespread and a larger number of species have been reported from more northerly states. However, given physiological restrictions all of these species currently are confined to indoor situations, being unable to survive the cold, harsh winter conditions. Although I do expect that the number of these species in Ohio will increase, it is difficult to predict which of these warmer climate species will turn up in the state. However, given the astonishing amount of personal and commercial transport in the US, it is relatively easy to foresee that we have not yet seen the last members of these exotics in Ohio. It is most likely that the first individuals to arrive in Ohio will be members of some of the most abundant and widespread among the synanthropic species (i.e., *Technomyrmex difficilis* Forel, 1892, *Brachymyrmex patagonicus* Mayr, 1868), *Nylanderia bourbonica* (Forel, 1886), *Cardiocondyla emeryi* Forel, 1881, *Monomorium floricola* (Jerdon, 1851), *M. destructor* (Jerdon, 1851), *Pheidole anastasii*, *P. megacephala* (Fabricius, 1793), *P. moerens* Wheeler, W.M., 1908, *Tetramorium bicarinatum* (Nylander, 1846), *Wasmannia auropunctata* (Roger, 1863)). Future survey efforts should focus on plant nurseries, botanical gardens, zoo facilities and other heated buildings to document the arrival and establishment of these species.

In eastern US, there is a clear pattern of increasing number of both native and non-native ant species from north to south, with the peak in the number of ant exotics reached in the southeastern US. In total, only 10 of Ohio's ant species are non-native with even a smaller number of these established in the state at present (including indoor and outdoor populations). These records are comparable with the number of ant exotics known from other northerly states, such as Illinois (8 species; Trager and Rericha 2016), Michigan (2; Wheeler et al. 1994), Pennsylvania (5; Butler and Coulter 2016), and New England (14, Ellison et al. 2012). In comparison at least 67 ant exotics are known from the southeastern US (MacGown 2016), with 52 species occurring in the state of Florida alone (approximately 25% of the local fauna; Deyrup et al. 2016).

Ants often are inconspicuous immigrants, and may remain unnoticed until many years after their arrival in an area. This is most likely the case with the recent finding of *Nylanderia flavipes* in Ohio. This species has been present in the eastern US since at least the 1930s when it was first discovered in Philadelphia, PA (Trager 1984). Around the time of its first discovery in Ohio, colonies of this Asian formicine already were well established, abundant and reproducing. Quantitative data from baiting and leaf-litter extraction suggest that this ant is one of the most abundant ant species in the disturbed urban and suburban green spaces where it occurs. Colonies can reach extremely high densities and worker numbers accounted for over 85% of total ant abundance at a site in northeastern Ohio (Ivanov et al. 2011; Ivanov unpubl.). At present, I am unable to confirm if this ant is expanding its range in Ohio or if it has been present in all localities and has remained undetected due to lack of sampling effort in the areas where it occurs. Nonetheless I advocate that efforts should be made to monitor the spread and potential impact of this species in Ohio and elsewhere.

Despite nearly ten years of surveying, I have sampled a rather small portion of the potential habitats in the state and thus many “exotic-ant-friendly” areas remain unexplored. This work is not complete and there is still much to do. A more extensive systematic sampling of disturbed areas, urban and suburban sites, plant nurseries and conservatories would be worthwhile and undoubtedly reveal the presence of yet undiscovered species in Ohio.

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Living beyond the limits of survival: wood ants trapped in a gigantic pitfall

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Abstract

A unique accumulation of workers ('colony') of the wood ant *Formica polyctena* Först., trapped within an old bunker for storing nuclear weapons, is described. The source of the 'colony' is a large colony nesting outdoors, on top of the bunker. Individuals that have fallen down through a ventilation pipe are not able to find their way back to the mother nest. In total darkness, they have constructed an earthen mound, which they have maintained all-year-round by moulding it and keeping the nest entrances open. Judging from the huge deposits of wood-ant corpses in the bunker, the 'colony' has survived for years. Through these years, the mortality has been more than compensated by new workers that fall down during the active season of the free-living colony outside, and at present the number of the bunker workers is counted in hundreds of thousands. The 'colony' has evidently produced no offspring, which is due to low (though relatively stable) temperatures and scanty food in the bunker.

Keywords

Adaptability, caves, continuous darkness, flexibility of nesting, *Formica polyctena*, lifespan, low temperatures, marginal habitats, scarce food resources

Introduction

In the boreal and temperate coniferous and mixed forests, territorial wood ants of the genus *Formica* L. are organising centres of multi-species ant assemblages, wherever the physical environment is suitable for them (Dlussky 1981, Savolainen and Vepsäläinen 1988). Territorial species need a stable and productive environment for constructing nests and colonies of high energy demand (see Hölldobler and Wilson 1977). Consequently, the territory of typical wood-ant colonies – with several hundred thousand or a million workers – ranges over several hectares (Savolainen and Vepsäläinen 1988). The base food of workers, honeydew of aphids, is abundantly available especially on coniferous trees and harvested at a distance up to over 100 metres from the mound (Rosengren and Sundström 1991, Vepsäläinen and Savolainen 1994).

In studies of the ants in the Tvärminne archipelago, in the Gulf of Finland in the Baltic Sea, wood ants were found only on forested islands (Vepsäläinen and Pisarski 1982). The explanation for the finding seems evident: the high energy demand of wood ant colonies restricts them to the largest islands with a stable and productive environment. When, however, colonies were artificially established on smaller islands with no wood ants, to search for the limits of their living conditions, colonies were found to survive on islands with a seemingly suboptimal environment (Czechowski and Vepsäläinen 2010). At its extreme, a colony has survived close to 30 years on a barren islet of less than 0.2 ha, where the only permanent and relatively rich food is provided by aphids on the islet's only pine tree (Czechowski and Vepsäläinen 2009 and unpublished). It is possible that the harsh conditions on the islet do not allow production of sexual offspring; thus the continued survival of the colony may depend on replenishment of young, fertilised queens born in colonies on the nearby mainland or large islands. Especially after having lost its own queen(s) a wood-ant colony is open to adopting new wood-ant queens, whatever their species identity (Czechowski 1994, Pisarski and Czechowski 1994, Czechowski and Vepsäläinen 2010).

Here we report on a unique wood-ant 'colony', which has survived in conditions beyond the limits of existence of wood ant colonies. This paradoxical situation is caused by a gigantic pitfall trap in the forests of Poland, originally constructed by the Soviet military to store nuclear weapons. Although the aggregation of wood ants described in this report superficially looks like a colony, it is a far cry from a fully functional colony; thus we use here the notion of 'colony' only for convenience.

Study area and methods

The observations were made at Templewo (52°27'N; 15°23'E) near Międzyrzecz in western Poland, close to the German border. There, a Soviet nuclear base existed from the late 1960s to 1992. Part of this military complex ("Special object 3003 Templewo" according to military nomenclature) with a total area of ca. 370 ha was dismantled in the beginning of the present century. Two underground two-level ammunition

Figure 1. Partly blocked entrance to the bunker system. In the background, pine-spruce forest overgrowing the hillock built to camouflage the structure. Photo taken on 17.07.2014 (Wojciech Stephan).

bunkers, 300 metres apart (26 m × 42 m each), which constituted the core of the base and where nuclear weapons were kept, have survived (Sadowski 2011, Rutko 2015). From the outside they are visible as flat-topped hillocks overgrown with spruce forest, densely populated by the wood ant *Formica polyctena* Först. Until recently the entrances to the bunkers were blocked, and only openings for bats were left (Rutko 2015). At present, however, the bunkers are accessible – some illegally dug cracks allow volunteers to squeeze inside (Fig. 1), to count bats hibernating there. One-metre thick ferroconcrete walls and ceilings keep the temperature inside at a relatively steady level: around 10 °C in summer and a few degrees above zero in winter.

Within the bunker under discussion, a corridor leads to a small 2.3 m high room, with a base area of 3 m × 1.2 m. The room is connected to an adjacent, somewhat larger space by two openings in the wall – one at the bottom (Fig. 2) and another higher up (Fig. 3). The walls are covered with flaking paint and limewash (calcium hydroxide) swellings. The terracotta floor is covered with soil, concrete rubble and rubbish. A vertical ventilation pipe, 40 cm in diameter and about five metres long, connects the bunker chamber through an outlet in the ceiling with the outside world (Fig. 3).

The bunker interior has been visited annually since 2012 as part of a campaign to count overwintering bats. Starting from 2013, when the bunker population of ants was discovered, several summer inspections have been made. During these examinations, the temperatures, both internal in the bunker space with ants, and external, above the bunker, were measured.

Voucher samples are stored in the Museum and Institute of Zoology, PAS, Warsaw (a sample of *Formica polyctena*) and the Natural History Collections, Faculty of Biology, Adam Mickiewicz University in Poznań (samples of all arthropods collected in the bunker).

Figure 2. The earthen mound inhabited by the *F. polyctena* 'colony' in the bunker. Photo taken on 11.01.2015 (Wojciech Stephan).

Results

A 'colony' of *Formica polyctena* was found in January 2013, during winter counts of hibernating bats in the underground bunker. It nested in the small room mentioned above, under the ventilation pipe (Figs 2, 3). In the summer of 2015 it was revealed that the top of the ventilation pipe (slightly below the ground outside) was covered by a huge elliptical mound of *F. polyctena* (height 60 cm, conjugate diameters of the base ca. 3 m and 2 m; Fig. 4). A bottom sight of the pipe outlet suggested that formerly it was covered with a metal plate which had rusted almost completely over the course of time (Fig. 5). Thus the origin of the underground wood ant 'colony' under discussion became clear: inside of the bunker, ants falling down from the hole in the ceiling were seen every now and then.

A majority of the surface area of the floor of the chamber was occupied by a rather flat earthen mound (25 cm at the highest point), irregularly shaped but evidently constructed and inhabited by ants, with many entrance or exit holes (Figs 2, 6). The mound contained a negligible amount of nest material typical of wood ants. During observations, both in winter and summer, teeming crowds of *Formica polyctena* workers were seen in the space with the nest, in the adjacent room and partly in the corridor in between; they also dispersed around neighbouring spaces of the bunker. The ants were fairly active in winter, both in respect of their numbers and vigour (Fig. 7), though less than in summer. In summer, they were seen climbing walls (Fig. 3), probably stimulated by the temperature that increased upwards. For instance, on 24 July 2015, when the external temperature was about 30 °C, the internal temperature was 9.5 °C at a height of 45 cm, and 11.4 °C at a height of 160 cm above floor level. In turn, on 21 February 2016, the external temperature was 10 °C, and the internal ones were 6.7 °C and 7.7 °C respectively.

Figure 3. The upper part of the bunker space with the *F. polyctena* 'nest'. In the middle of the ceiling, the input of the ventilation pipe. Ants climbing walls (and hardly reaching the ceiling) en masse within and outside the room are visible (especially well on the door frame). Photo taken on 24.07.2015 (Wojciech Stephan).

The ants, however, were never seen walking on the ceiling (Fig. 3), and thus they were not in reach of the pipe inlet. Consequently, when once trapped underground, they could not find their way back to the maternal nest. Flat parts of the earthen

Figure 4. The mound of the free-living *F. polyctena* colony built on the outlet of the ventilation pipe; the source of the bunker 'colony'. Photo taken on 24.07.2015 (Wojciech Stephan).

Figure 5. Bottom sight of the ventilation pipe outlet. Photo taken on 21.02.2016 (Wojciech Stephan).

mound and the floor of the adjacent spaces (including the room with the mound, the neighbouring chamber and a part of the corridor) were carpeted with bodies of dead ants (Figs 6, 8). Locally the deposits were a few centimetres thick. Because the total volume of these wood-ant 'cemeteries' was at least 250–300 dm^3, and a one cubic decimetre sample contained ca. 8,000 ant corpses, the number of dead *Formica polyctena* workers probably amounted to about two million. The cemeteries comprised also remnants of other insects, most probably those caught by foragers of the free-living upper colony that had fallen down. Of other ants, only a head of the *Leptothorax* sp. worker was found. Extraction of the cemetery samples in a Tullgren funnel also included living invertebrates; acarids, mainly Prostigmata and Mesostigmata (normally living in dead plant material), occurred in large numbers. Interestingly, we also found some myrmecophiles alive even in winter. These included rarely met myrmecophilic spiders and numerous beetles (these findings will be described separately). No empty ant cocoons were found during a manual search of the cemetery material.

During an inspection made in July 2015, we estimated the size of the bunker 'population' of *Formica polyctena* to be at least several hundred thousand workers, perhaps close to a million. That time, the earthen mound was partly dug up, paying attention to the possible presence of ant brood (larvae, pupae or empty cocoons) and queens. Nothing like these was found. By the next visit in January 2016, the damage caused by us to the mound had been repaired by ants.

Discussion

Ants are known to be flexible in their choices of nest site and nest construction, and to take advantage of exceptional opportunities. For example, myrmicines have been found nesting in big mushrooms, *Myrmica rugulosa* Nyl. in *Sparassius crispa* Fr. (Czechowski 1979) and *M. rubra* (L.) in *Gyromitra esculenta* (Pers.) Fr. (K. Vepsäläinen, unpublished). A colony of *Lasius niger* (L.) nested in a chassis of an immobilised car, from where the ants found their way to the cabin. The nest was built of particles of mud and dry plant remnants stuck to the underbody of the car (P. Skórka, pers. comm.). Wood ants, with considerably larger nests than those of myrmicines, have been known to construct a mound in an abandoned barn (Yle uutiset 2015). A smaller mound has been found in almost complete darkness within a cubic wooden box with one-metre edges but no floor or openings apart from a narrow slit at the bottom of one side (W. Czechowski, unpublished). In all the above cases, however, the foragers of the colony had access to the outside world, and each specific mode of nesting was the choice of the ants. The masses of *Formica polyctena* workers trapped in the bunker had no choice. They were merely surviving and continuing their social tasks on the conditions set by the extreme environment.

Wood ants are able to adapt themselves to notably suboptimal living conditions, as told in the Introduction. Likewise, after severe degradation of their environment, e.g. after forest clear-cuttings or splitting of the habitat by urbanisation, the colonies

Figure 6. The mound of *F. polyctena*'s bunker 'colony' in close-up. In the background, against the wall, an ant 'cemetery' is visible. Photo taken on 24.07.2015 (Wojciech Stephan).

with large mounds move to new, smaller ones (Vepsäläinen and Wuorenrinne 1978, Sorvari and Hakkarainen 2007, Sorvari 2013). By such means they increase the probability of survival of at least some mound(s) through the period with not enough food

Figure 7. *Formica polyctena* workers active on their mound surface in winter, keeping nest entrances open. Photo taken on 11.01.2015 (Wojciech Stephan).

to maintain large, stationary nest units (Vepsäläinen and Wuorenrinne 1978). More generally, any kind of degradation of the environment – including the limits set by central place foraging of the growing colony – may lead to the founding of temporary nests ('food stations') which in favourable conditions can develop to permanent sister nests (e.g. Mabelis 1979, Savolainen and Vepsäläinen 1989).

The bunker ant 'colony' described here seems, however, to be unique in all respects. First, the old military bunker has served (and still serves) as a gigantic pitfall trap for wood ants nesting on the top of the bunker. Second, the workers involuntarily trapped in total darkness have maintained their basic activities of nest maintenance, constructing and moulding the earthen mound, and keeping nest entrances open (Figs 6, 7). Third, without access to the outside world, the foragers have not been able to feed the whole workforce, and consequently the mortality rate has probably been much higher than in natural conditions. Normally, workers of wood ants live up to ca. three years (Czechowski 1996, see also Godzińska et al. 1999). It is hard to tell how long an individual worker can survive under the bunker conditions, but the existence through years of the underground 'colony' shows that they have been able to survive at least from one vegetative season to another – up to the new supply of workers falling down through the ventilation pipe. Fourth, neither queens nor any ant brood was

Figure 8. View from the bunker corridor over the space with the *F. polyctena* 'colony'; in the foreground, a vast ant 'cemetery'. Photo taken on 19.01.2016 after reopening the repaired mound for a second search of offspring (Wojciech Stephan).

seen in the bunker 'colony', though their occasional falling down cannot be excluded. Nevertheless, the low temperatures prevailing inside the bunker would scarcely allow production of any offspring. True, it is known that wood ants are effective in managing the inner temperatures of the mound and optimise the nest environment of each developmental stage and caste (Horstmann and Schmid 1986, Rosengren et al. 1987, Kadachová and Frouz 2014), but that would necessitate huge amounts of food in order to raise the organisational level of the colony to that observed in natural environments (Vepsäläinen and Wuorenrinne 1978, Pisarski and Vepsäläinen 1989, Sorvari and Hakkarainen 2007, Sorvari 2013, Sorvari et al. 2014). Because wood-ant workers of queenless colonies as a rule produce workers (e.g. Czechowski 1996), the lack of male offspring in the bunker indicates extremely difficult conditions.

The amount of potential food in the bunker, suitable for wood ants, is not known, but the smaller arthropods living there could hardly be enough to allow the workers both temperature regulation of the mound and feeding of offspring. Under Central-European climatic conditions, development of permanent arthropod communities in the bunker under discussion is rather impossible. The mites which occur there seem to be first of all ant-dependent detritivores (mainly Mesostigmata) feeding amongst ant cemeteries. The amount of another possible resource, the bat guano, is too scarce there to play any role as substrate for a detritivore fauna. Predatory forms (Prostigmata) can forage on smaller mites. The question arises whether and to what extent these much larger wood ants (ca. 4–8 mm in length) are able to forage on such small mites. Although some exploitation by the ants cannot be excluded, it seems rather unlikely.

In all its uniqueness, the conditions within the bunker seem to be closest to deep caves. Wilson (1962) explained why it is unlikely that any truly cavernicolous (troglobiotic) ant species existed. Simply, social insects seem to be unable to maintain sufficiently large populations in caves (though see Roncin and Deharveng 2003). In spite of quite a few reports on ants found in caves (e.g. Espadaler and Gelabert 1983, López 1988, Cokendolpher et al. 2009), most of the many species reported seem to be stray individuals that have entered the cave through its entrance or dropped in through cavities (Espadaler and Gelabert 1983). For such species, the food supply of caves is too meagre to sustain even a single colony (Wheeler 1924). As a rule, the ants have been found close to the cave entrance, where there is still some light (Wilson 1962). This can be explained by the fact that the majority of 'cave ants' nest outside caves and only a few opportunistic foragers in search of food penetrate the cave. Finally, most of the caves harbouring ants are in the tropics or subtropical regions, where benign temperatures and copious nutrient (mainly guano) support a diverse fauna of cave arthropods. Indeed, the few finds of functional ant colonies nesting deep within a cave are from the tropics, where probably some species may have their nest far from the entrance in complete darkness (Wilson 1962, Roncin and Deharveng 2003) or, e.g. from the Mediterranean, like the cavernicolous *Hypoponera ragusai* (Em.) with all-year-round colonies of workers, queens and males (Tinaut 2001).

To conclude, the wood-ant 'colony' described here – although superficially looking like a functioning colony with workers teeming on the surface of the mound – is rather an example of survival of a large amount of workers trapped within a hostile environment in total darkness, with constantly low temperatures and no ample supply of food. The continued survival of the 'colony' through the years is dependent on new workers falling in through the ventilation pipe. The supplement of workers more than compensates for the mortality rate of workers such that through the years the bunker workforce has grown to the level of big, mature natural colonies.

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Pan traps and bee body size in unmanaged urban habitats

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Abstract

Pan traps are among the most popular methods employed to survey bees and changes in some functional traits, such as body size, are increasingly used to understand how bee communities and species respond to landscape changes. Herein we assess body size differences between bees captured at ground-level and elevated (70 cm) pan traps in unmanaged urban habitats in northwestern Turkey. We compare body size at the community level as well as for the sweat bee *Lasioglossum malachurum* (Kirby) (Halictidae: Halictini), the most abundant species. We also compare the diversity, richness and abundance of bees sampled at both heights. A total of 31 species (13 genera of three families) were captured. We did not find significant differences in the abundance nor in the species richness between heights, and Simpson's indices were similar. At the community level, average intertegular distance was significantly greater in bees collected at the elevated traps than on the ground. Intertegular distances in *L. malachurum* did not differ between elevated and ground-level pan traps. Our results show an effect of pan trap height on bee body size in the urban habitat surveyed, thus suggesting that assessing bee body size from samples collected with either ground-level or elevated pan traps alone might result in biased estimates of this functional trait.

Keywords

Anthophila, Halictidae, intertegular distance, sampling bias, urban ecology

Introduction

Pan traps of different colors placed at different heights have been successfully used as complementary methods in monitoring bee communities across a number of habitats and landscapes of both tropical and temperate environments (e.g., Wilson et al. 2008, Tuell and Isaacs 2009, Droege et al. 2010, Ulyshen et al. 2010, Nuttman et al. 2011, Gonçalves and Oliveira 2013, Geroff et al. 2014). These traps have become popular among bee ecologists and conservation biologists because they are readily available, inexpensive, and are not collector biased. In addition, a large number of traps can be used for long periods at multiple locations (Droege et al. 2010). The use of these traps has not only allowed rapid assessments of the richness, diversity, abundance, and phenology of bees but has also provided insights into their behavior. For example, some studies have revealed species- and sex-specific color preferences, which are similar to the color of their host flowers (Heneberg and Bogusch 2014). Studies using pan traps at different heights above the ground have also supported the idea that bees tend to forage in a horizontal stratum (Gumbert and Kunze 1999, Cane et al. 2000). Elevated pan traps often capture a greater abundance, as well as a different composition of bees, than those placed on the ground, including large-bodied bees that are never or rarely caught in ground-level pan traps (Tuell and Isaacs 2009, Geroff et al. 2014).

Body size affects bee foraging behavior (Greenleaf et al. 2007) and changes in this functional trait are increasingly used to understand how bee communities and species might respond to changes in landscape (Wray et al. 2014, Renauld et al. 2016). Herein we assess body size differences between bees captured at ground-level and elevated pan traps (70 cm) in unmanaged urban habitats in northwestern Turkey. This information might be useful when designing survey protocols aimed to assess body size distributions across habitats. We compare body size at the community level as well as for the sweat bee *Lasioglossum malachurum* (Kirby) (Halictidae: Halictini), the most common species captured at both heights. We also compare the diversity, richness and abundance of bees sampled at both heights.

Materials and methods

This study was conducted at two unmanaged areas separated by 900 m in the Görükle Campus of Uludağ University in Bursa, Turkey (40°13'35"N, 28°52'13"E, 56m). In addition to grasses, these sites were dominated by wild carrots (*Daucus carota* L., Apiaceae), whose primary umbels occasionally reached up to 2 m in height; *Heracleum platytaenium* Boiss (Apiaceae), *Echinops microcephalus* Sm. (Asteraceae), *Sonchus asper* (L.) Hill (Asteraceae), and *Cota tinctoria* (L.) J. Gay ex Guss (Asteraceae) were also common in both sites. On each site we set up two parallel transects of pan traps 1 m apart. Each stratified pair, one on the ground and one elevated, was 2 m apart, for a total of 10 pairs per transect. Each elevated pan trap was placed 70 cm above the pan trap on the ground. Pan traps consisted of plastic bowls spray-painted fluorescent yellow (Solo® plastics Soufflé Cup, 3.25 oz.) and half filled with soapy water. This color was chosen because preliminary observations suggest that it is the most effective color to capture bees at the study area. We built the elevated pan traps using a white PVC tube (2 cm in diameter, 86 cm in length) and the upper one-third of a transparent 0.5 L plastic bottle. The tube's lower end was cut at a diagonal with a pipe cutter so that it was easily inserted into the ground. At the upper end we placed the screw cap of a cut plastic bottle, which served as a support for the plastic bowl; the latter was secured to the bottle with clear adhesive tape. The PVC tube was inserted into the ground until the bottom of the bowl was 70 cm above the ground, a height that exceeded the minimum height of *D. carota*, the tallest surrounding flowering plant. We collected bees and refilled the pan traps with soapy water every two days from July 19 to July 24, 2015. We pinned all specimens and estimated their body size by measuring the minimum intertegular distance (Cane 1987) with an ocular micrometer on a Leica S6E stereomicroscope. Specimens are deposited in the Beekeeping Development and Research Center, Uludağ University, Bursa, Turkey.

We used a Chi-square analysis to test for differences in abundance and species richness of bees collected at different heights. We also calculated the Simpson (1-D) and Sørensen indices to estimate the diversity and similarity between the samples and used a two-sample t-test to detect differences in body size between the community of bees collected at the ground and elevated traps, as well as between specimens of *Lasioglossum malachurum* collected at both heights. Averages are given with standard errors.

Results

We collected 154 specimens representing a total of 31 species belonging to 13 genera and three families. Similar counts of individuals and species were captured at both heights (Abundance: X^2 (1, n = 154) = 0.234, p = 0.629; Richness: X^2 (1, n = 40) = 0.90, p = 0.343). Nine species were collected at both heights and, according to the Sørensen index (0.45), these communities moderately overlap; similar Simpson's indices were also obtained at both heights (Table 1). *Lasioglossum malachurum* was the most common species, accounting for 30.5% of all bees collected, and was equally captured at both heights, X^2 (1, n = 47) = 0.191, p = 0.662). Overall, average intertegular distance was 42.2% greater in bees collected at the elevated traps ($\bar{x}$ = 2.29 mm ± 0.216, 0.98–6.64, n = 42) than bees at ground-level traps ($\bar{x}$ = 1.61 mm ± 0.088, 0.83–3.05, n = 34, two-sample t-test, t= 2.91, df: 53, p = 0.003). For *L. malachurum*, average intertegular distance at elevated traps (1.41 ± 0.016 mm, 1.20–1.55, n = 24) was not significantly different from ground-level traps ($\bar{x}$ = 1.39 ± 0.017 mm, 1.25–1.53, n = 22, two-sample t-test, t= -0.70, df: 43, p= 0.489; Fig. 1).

Table 1. Average intertegular distance and number of specimens of each bee species collected from pan traps placed on the ground and at 70 cm above ground. Supraspecific classification follows Michener (2007).

Bee taxa	**Intertegular distance (mm)**	**Ground**	**Elevated**
Family Apidae			
Amegilla sp.	3.50	0	1
Apis mellifera L.	2.83	1	5
Ceratina sp. 1	1.27	4	1
Eucera sp. 1	2.60	0	1
Eucera sp. 2	3.05	0	1
Eucera sp. 3	3.50	0	1
Xylocopa iris (Christ)	4.28	0	3
Xylocopa violacea (L.)	6.03	0	3
Family Halictidae			
Halictus (*Seladonia*) sp.	1.22	1	6
Halictus scabiosae (Rossi)	3.10	0	2
Halictus sp. 1	1.91	0	3
Halictus sp. 2	1.60	2	0
Halictus sp. 3	1.11	0	2
Lasioglossum malachurum (Kirby)	1.40	22	25
Lasioglossum (*Evylaeus*) sp. 1	1.53	1	3
Lasioglossum (*Evylaeus*) sp. 2	1.23	0	2
Lasioglossum (*Evylaeus*) sp. 3	1.23	1	0
Lasioglossum (*Dialictus*) sp.1	1.49	1	2
Lasioglossum (*Dialictus*) sp. 2	1.25	1	0
Lasioglossum (*Dialictus*) sp. 3	1.06	0	3
Lasioglossum (*Dialictus*) sp. 4	0.83	1	0
Lasioglossum (*Dialictus*) sp. 5	1.02	2	1
Lasioglossum (s. str) sp. 1	2.00	24	11
Lasioglossum (s. str) sp. 2	2.10	0	1
Family Megachilidae			
Anthidium florentinum (Fabricius)	3.75	0	1
Hoplitis sp.	2.35	3	0
Hoplosmia sp.	1.46	3	0
Lithurgus chrysurus Fonscolombe	2.90	1	1
Osmia erythrogastra Ferton	1.57	5	0
Osmia bidentata Morawitz	1.63	1	0
Pseudoanthidium lituratum (Panzer)	2.03	0	1
Total specimens		74	80
Total species		17	23
Simpson's Index		0.80	0.87

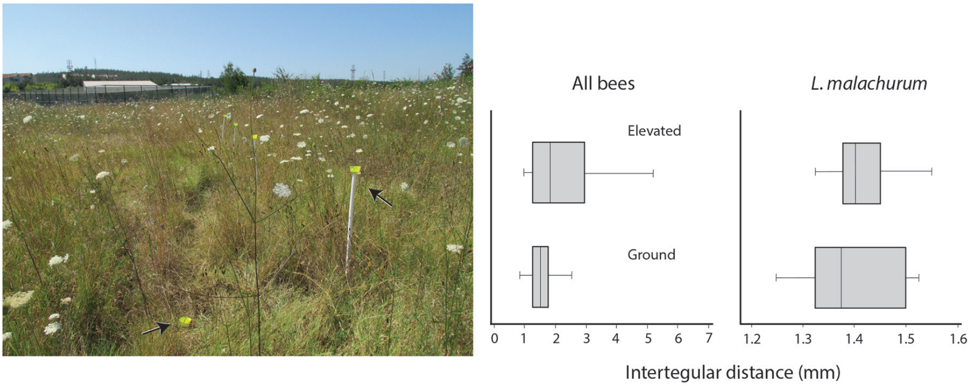

Figure 1. One of the unmanaged areas at Uludağ University in Bursa, Turkey, surveyed using pan traps placed on the ground and at 70 cm above ground (left); boxplots (right) showing the intertegular distance of all bees and *L. malachurum* collected at each height.

Discussion

We showed that, on average, larger bees are captured more often with elevated pan traps than with ground-level traps in the urban environments surveyed. As in previous studies, large-bodied bees such as *Xylocopa*, *Eucera* and *Anthidium* were captured exclusively or, in the case of honey bees, more frequently in elevated traps than at ground-level traps. Species of these groups were often seen either flying across the field or foraging at taller inflorescences, and had been previously collected at the same area with aerial nets only. Pan traps located at a height that exceeds the minimum height of the tallest surrounding flowering plants, as in our study, might act as beacons given that bees and other pollinators are naturally attracted to flowers or inflorescences of taller plants (e.g., Gumbert and Kunze 1999, Lortie and Aarssen 1999).

Differences in foraging behavior associated with intraspecific variations in body size have been documented in social species, such as bumble bees (e.g., Goulson et al. 2002). Social halictids often exhibit caste-associated size variation (e.g., Michener 1990) that could affect foraging. While size variation was observed in *Lasioglossum malachurum*, counter to our expectations, specimens collected in elevated pan traps were not, on average, larger than those collected at the ground level. However, as this was a short term experiment with small sample sizes, this result is hardly conclusive. Determining whether a similar pattern in the body size distribution across bees occurs in other habitats and ecosystems is an important consideration for understanding pollination services as well as providing appropriate resources for bee conservation efforts. From a practical point of view, our results suggest that assessing bee body size from samples collected with either ground-level or elevated pan traps alone might result in biased estimates of this trait. This is likely true for other sampling methods as well. For example, inexperienced or less-experienced collectors using aerial nets might be biased to capture large, slow-flying, noisy or conspicuous bees when compared with more experienced collectors. Our results also contribute to the increasing body of evidence demonstrating that a more complete picture of the bee communities can be obtained by incorporating multiple sampling methods and examining particular traits such as body size, even in disturbed, open, grassy habitats.

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SHORT COMMUNICATION

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Host-associated volatiles attract parasitoids of a native solitary bee, *Osmia lignaria* Say (Hymenoptera, Megachilidae)

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Abstract

Parasitoids use volatiles to recognize and locate suitable hosts. Numerous studies have investigated parasitoid host location from a pest management perspective, but comparatively little is known regarding parasitoid-pollinator interactions. Previous research has shown that parasitoids of some native bees respond to volatiles emitted by host frass and cocoons. We used a Y-tube bioassay to test whether two parasitoid species (*Monodontomerus torchioi* and *Melittobia acasta*) are attracted to volatiles associated with their host, the blue orchard bee, *Osmia lignaria*. Specifically, we tested attraction to (1) cocooned adult *O. lignaria* females (2) *O. lignaria* frass (3) methanol and (4) acetic acid. Both parasitoid species were attracted to host frass and acetic acid. Although *M. acasta* showed a strong attraction to volatiles from cocooned *O. lignaria* females, it was repelled by methanol, a chemical constituent of *Osmia* cocoons. In contrast, *M. torchioi* showed no response to cocooned *O. lignaria* and only a slight attraction to methanol. Both parasitoid species appear to be differentially attracted to specific host-associated volatiles, suggesting that they may respond to distinct olfactory cues when locating potential bee hosts.

Keywords

Y-tube bioassay, olfactory cues, solitary bee, Megachilidae, *Melittobia acasta*, *Monodontomerus torchioi*

Introduction

Parasitoids use a variety of chemical cues to identify and locate potential hosts, including those emitted by the host's habitat (Vet et al. 1984), host byproducts (i.e. frass, Agelopoulos et al. 1995), organisms living in association with the host (Sullivan et al. 2000), and the host itself (Wiskerke et al. 1992, Jumean et al. 2009). Numerous studies have investigated parasitoid attraction to host-associated volatiles in agroecosystems, often with the goal of developing more effective pest management strategies (Jones et al. 1973, Godfray 1994, Jumean et al. 2009). However, despite the ecological and economic importance of pollinators, few studies have investigated how parasitoids recognize and locate their bee hosts (but see Silva-Torres et al. 2005, Filella et al. 2011). A number of solitary bee species are currently used to pollinate commercial crops, including *Nomia melanderi* Cockrell (Halictidae) and *Megachile rotundata* Fabricius (Megachilidae) in alfalfa (Kemp and Bosch 2000, Cane 2008) and *Osmia* spp. (Megachilidae) in almonds (Bosch and Kemp 2001). Many solitary bee species are attacked by a diversity of hymenopteran parasitoids and brood parasites during development, sometimes resulting in high rates of mortality prior to adult eclosion (Vicens et al. 1994, Bosch and Kemp 2001, Wcislo and Cane 1996). Thus, building a more robust understanding of parasitoid host location is not only of interest from an ecological perspective, it may also aid efforts to control parasitism in commercially important pollinator species.

The blue orchard bee (*Osmia lignaria* Say, Megachilidae) is a univoltine solitary species that emerges in early spring and nests in hollow twigs and beetle burrows (Bosch and Kemp 2001). We focused on two geographically widespread ectoparasitoids commonly found in *O. lignaria* nests: *Monodontomerus torchioi* Grissell (Hymenoptera: Torymidae) and *Melittobia acasta* (Walker) (Hymenoptera: Eulophidae). We selected these species because they differ in both their oviposition strategy and the breadth of their host range. To parasitize the host, *Monodontomerus* females oviposit directly through the host cocoon onto the prepupa or pupa (Eves 1970, Bosch and Kemp 2001, Filella et al. 2011). In contrast, *Melittobia* parasitoids chew through nesting substrates and cocoons to feed on host hemolymph and/or oviposit (Hobbs and Krunic 1971, Cusumano et al. 2010). Unlike *Monodontomerus, Melittobia* spp. attack a wide diversity of insects, including Coleoptera, Diptera, and Hymenoptera (Hobbs and Krunic 1971, González et al. 2004, Silva-Torres et al. 2005, Cusumano et al. 2010).

Using *M. torchioi* and *M. acasta* reared from field-collected *O. lignaria*, we tested attraction to several host volatiles. Given that host bees are enclosed in a thick cocoon covered in layers of frass during the preferred life stages for parasitoid oviposition (prepupae, pupae), we expected both parasitoid species to be more attracted to volatiles associated with host frass and cocoons than volatiles emitted by the adult host. Our primary goals were (1) to determine which host-associated volatiles the two species use during host location and (2) to experimentally test parasitoid attraction to two previously-identified *Osmia* nest volatiles, acetic acid and methanol (Filella et al. 2011).

Materials and methods

Parasitoid collection and rearing

In February 2014, we attached seventy-five pine nests (15 × 14 × 15 cm) containing paper nest tubes to narrowleaf cottonwood trees (*Populus angustifolia*) on a 7 ha. tract of land in Mountain Green, Utah (41°10'2"N 111°41'35"W). In July 2014, we collected all nesting tubes and transferred them to an incubator for eight weeks (28°C) to allow occupants to complete development. Using benchtop digital x-ray analysis (8 sec exposure at 20 kVp), we identified and isolated parasitoids within the nests. The two most abundant parasitoids were *Monodontomerus torchioi* and *Melittobia acasta*. We stored parasitoids at overwintering conditions (3–4°C) from October 2014–March 2015. In March 2015, we transferred the larvae to an incubator (31°C, 60% RH) and reared them to adulthood in ventilated plastic soufflé cups (Dart Corporation, Lodi CA). Upon emergence, we transferred all adult parasitoids to a second incubator (21°C, 60% RH). We fed *M. torchioi* adults a 50% honey solution *ad libitum*. We did not provide honey solution to emerged *M. acasta* because this species feeds directly on host hemolymph (Silva-Torres et al. 2005). We isolated virgin females with three males in soufflé cups 24 hours prior to testing and tested them in a Y-tube bioassay 2–3 days after emergence.

Testing

We used a Y-tube bioassay to test parasitoid attraction to four host volatiles: *O. lignaria* frass (0.01 g), live female *O. lignaria* adult in cocoon with frass removed, pure methanol (0.5 ml), and pure glacial acetic acid (0.1 ml). Previous research has identified methanol and acetic acid as the primary chemical components of *Osmia* cocoons and frass, respectively (Filella et al. 2011). We applied the methanol and acetic acid treatments to filter paper and allowed it to dry in the fume hood for at least 10 minutes prior to testing. We tested all treatments against blank filter paper.

The Y-tube olfactometer consisted of an air source pumped over an activated charcoal filter (5×100 cc/min) connected to an air flow monitor and divided into two substreams using Nalgene tubing (Fig. 1; Takabayashi and Dicke 1992). Tubing was connected to two glass bell jars (47 cm height × 15 cm diameter), one containing an odor source and the other containing blank filter paper (control). Nalgene tubing connected the bell jars to a glass Y-tube (Y-tube arms 1.2 cm diameter, 6 cm in length). To create an airtight seal, we positioned each jar in a plastic well filled with 1-2 cm of distilled water.

Using a clean strip of filter paper, we introduced a single naïve female parasitoid into the vestibule of the Y-tube. We recorded a "choice" if the female traveled at least halfway down a Y-tube arm. If the female did not make a choice within 5 minutes, the trial was recorded as "no choice." We tested a total of 82 *M. torchioi* females (n=20–21

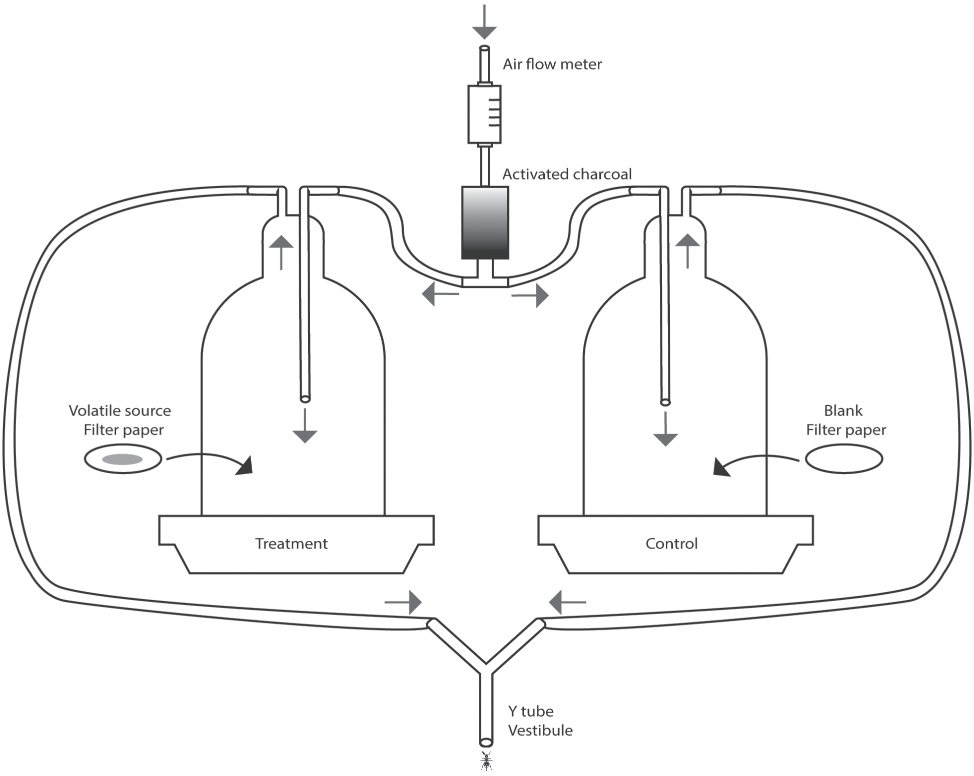

Figure 1. Schematic of the Y-tube olfactometer used to test parasitoid attraction to host volatiles.

per treatment) and 122 *M. acasta* females (n=30–32 per treatment). Although we initially planned to test the same number of individuals per treatment, two *M. torchioi* and six *M. acasta* escaped from containment prior to testing.

In an effort to maintain consistent environmental conditions, we placed visual blocks around the perimeter of the testing arena and used overhead full spectrum fluorescent lights to simulate natural light. In addition, ambient temperature within the testing arena remained at a constant 22°C throughout the study. After each trial, we washed glassware in detergent and rinsed it with distilled water and pure ethanol. To ensure volatile residue did not interfere with testing, tubing and glass bell jars were associated with a single treatment during testing. Lastly, we switched the position of the treatment and control bell jars following each trial to reduce directionality bias.

Data analysis

We tested whether the number of individuals that selected treatment over the control differed significantly from 1:1 using exact binomial tests, assuming a 50% chance of choosing either arm of the Y-tube (R Core Development Team 2016). Tests compared the number of parasitoids that chose (1) *Osmia lignaria* frass or control, (2) live cocooned *Osmia lignaria* female or control, (3) methanol or control, and (4) acetic acid or control. Individuals that did not make a choice were excluded from the analysis.

Results and discussion

Across all trials, 70–90% of *M. torchioi* and 73–93% of *M. acasta* made a choice. Both species showed strong attraction to several of the volatiles tested, suggesting that they respond to multiple olfactory cues when searching for a host. Significantly more *M. torchioi* and *M. acasta* females were attracted to host frass and its primary chemical component, acetic acid, than the control (Table 1). These results empirically confirm previous work suggesting these volatiles act as chemical cues for parasitoid females (Agelopoulos et al. 1995, Sullivan et al. 2000, Filella et al. 2011). Specifically, frass and its associated volatile components may indicate host suitability. In general, *Monodontomerus* and *Melittobia* parasitize host pre-pupae and pupae (Eves 1970, Dahms 1984). In this system, *O. lignaria* defecate as fifth instar larvae, later incorporating this frass into the cocoon with salivary strands (Torchio 1989). Thus, frass-associated volatiles may allow parasitoids to discriminate between host life stages.

In contrast, the parasitoid species showed substantially different reactions to methanol. We expected both species to be attracted to methanol because it is a primary chemical component of host cocoons (Filella et al. 2011) and a natural byproduct of wood rot (Arantes and Goodell 2014). Megachilid bees often nest in standing dead trees (Macivor and Salehi 2014), therefore we hypothesized that methanol may act as a general cue that allows parasitoids to locate host nests. Although a higher number of *M. torchioi* females selected methanol over the control, this difference was not statistically significant (Table 1a). Using exact binomial testing with a larger sample size would be needed to assess the significance of these trends. Contrary to our expectations, *M. acasta* appeared to be repelled by methanol (Table 1b). It is possible *M. acasta* females avoided the methanol treatment because the concentration was too high. An alternative explanation for this behavior is that methanol acts as a repellent when isolated from other host-associated volatiles. The ratio-specific odor recognition hypothesis presented in Bruce et al. (2005) stresses that correct ratios and combinations of common plant volatiles are more generally used by phytophagous insects than any one species-specific volatile source. Furthermore, Takemoto and Takabayashi (2015) observed repellent effects of an isolated compound, linalool, regardless of concentration. However, the parasitoid was attracted to linalool when in combination with other herbivore-induced plant volatile components. Additional studies that test attraction to multiple methanol concentrations and blends of host-associated volatiles are necessary to test this hypothesis.

Lastly, *M. acasta* was strongly attracted to cocooned *O. lignaria* females, but *M. torchioi* was not (Table 1). Our results for *M. acasta* are consistent with previous research showing *Melittobia* rely primarily on indirect host-associated chemical cues,

Table 1. Results of choice tests for *Monodontomerus torchioi* (Hymenoptera: Torymidae) (**A**) and *Melittobia acasta* (Hymenoptera: Eulophidae) (**B**) Mated females of both species were tested for attraction to four host-associated volatiles: acetic acid, frass, methanol, and cocooned *O. lignaria* adult female.

A.

	No. individuals that chose			
Volatile source (n)	**Treatment**	**Blank**	**Neither**	**P**
Acetic acid (20)	13	4	3	0.049*
Frass (21)	14	4	2	0.031*
Methanol (20)	11	3	6	0.057
Cocooned *O. lignaria* female (21)	11	8	2	NS

B.

	No. individuals that chose			
Volatile source (n)	**Treatment**	**Blank**	**Neither**	**P**
Acetic acid (32)	22	7	3	0.008**
Frass (30)	26	2	2	<0.0001***
Methanol (30)	4	20	6	0.002**
Cocooned *O. lignaria* female (30)	20	2	8	<0.0001***

rather than cues produced by the appropriate host stage (Cusumano et al. 2010). Because parasitoids in this group employ a ‘sit-and-wait’ strategy in the host nest (Cusumano et al. 2010) and are limited in their dispersal ability (Matthews 2009), a strong attraction to the adult host may also allow them to locate nests at short distances. Surprisingly, *M. torchioi* was not attracted to volatiles from cocooned host bees (Table 1). Given that the closely-related *M. aeneus* (Fonscolombe) does not respond to volatiles from uncocooned *Osmia* host prepupae but is attracted to host cocoons and frass (Filella et al. 2011), it is possible that *Monodontomerus* spp. rely on a combination of volatiles emitted by the host at the preferred life stage. To disentangle parasitoid response to adult hosts and cocoons, future studies could examine attraction to uncocooned *Osmia* adults.

Our study is among the first of its kind to test parasitoid attraction to pollinator-associated volatiles. Collectively, our results suggest that both *M. torchioi* and *M. acasta* use a number of volatile cues to locate hosts. By simultaneously comparing parasitoid attraction to multiple volatiles and combinations of volatiles, future studies may allow us to rank the relative importance of each cue and further elucidate the complexities of parasitoid host location.

Contribution of authors

SG contributed to data collection and writing. SF contributed to data collection and analysis, writing, and project design.

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