RESEARCH ARTICLE

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

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Abstract

North-Western Palaearctic species of *Pristiphora* Latreille, 1810 are revised. Altogether, 90 species are treated, two of which are described as new: *P. caraganae* Vikberg & Prous, **sp. n.** from Finland and *P. dedeara* Liston & Prous, **sp. n.** from Germany. Host plant of *P. caraganae* is *Caragana arborescens* Lam. *Pristiphora dasiphorae* (Zinovjev, 1993) (previously known from East Palaearctic) and *P. cadma* Wong & Ross, 1960 (previously known from North America) are recorded for the first time from Europe. *Nematus nigricans* Eversmann, 1847 [= *Pristiphora nigricans* (Eversmann, 1847), **comb. n.**], *N. breviusculus* Eversmann, 1847 [= *Euura melanocephalus* (Hartig, 1837)], and *N. caudalis* Eversmann, 1847 [= *E. caudalis* (Eversmann, 1847), **comb. n.**] are removed from synonymy with *P. pallidiventris* (Fallén, 1808), *N. paralellus* Hartig, 1840 [= *P. paralella* (Hartig, 1840), **comb. n.**] is removed from synonymy with *P. bufo* (Brischke, 1883), and *P. mesatlantica* Lacourt, 1976 is removed from synonymy with *P. insularis* Rohwer, 1910. The following 29 new synonymies are proposed: *P. nigropuncticeps* Haris, 2002, **syn. n.** with *P. albitibia* (Costa, 1859); *Lygaeonematus karvoneni* Lindqvist, 1952, **syn. n.** with *P. alpestris* (Konow, 1903); *P. (P.) anivskiensis* Haris, 2006, **syn. n.** with *P. appendiculata* (Hartig, 1837); *Nematus canaliculatus* Hartig, 1840, **syn. n** with *P. carinata* (Hartig, 1837); *P. nigrogroenblomi* Haris, 2002, **syn. n.** with *P. cincta* Newman, 1837; *Tenthredo flavipes* Zetterstedt, 1838, **syn. n.**, *Nematus congener* W.F. Kirby, 1882, **syn. n.**, and *P. thomsoni* Lindqvist, 1953, **syn. n.** with *P. dochmocera* (Thomson, 1871); *P. atrata* Lindqvist, 1975, **syn. n.** with *P. friesei* (Konow, 1904); *P. gelida* Wong, 1968, **syn. n.** with *P. frigida* (Boheman, 1865); *Pachynematus nigricorpus* Takagi, 1931, **syn. n.** with *P. laricis* (Hartig, 1837); *Nematus (Pikonema) piceae* Zhelochovtsev in Zhelochovtsev and Zinovjev, 1988, **syn. n.** and *P. (P.) hoverlaensis* Haris, 2001, **syn. n.** with *P. leucopodia* (Hartig, 1837); *Mesoneura arctica* Lindqvist, 1959, **syn. n.**, *Pachynematus incisus* Lindqvist,

1970, **syn. n.**, *Pachynematus intermedius* Verzhutskii, 1974, **syn. n.**, and *P. mongololaricis* Haris, 2003, **syn. n.** with *P. malaisei* (Lindqvist, 1952); *Nematus anderschi* Zaddach, 1876, **syn. n.**, *P. inocreata* Konow, 1902, **syn. n.**, and *P. discolor* Lindqvist, 1975, **syn. n.** with *P. nigricans* (Eversmann, 1847); *Lygaeonematus tenuicornis* Lindqvist, 1955, **syn. n.** with *P. paralella* (Hartig, 1840); *Lygaeonematus concolor* Lindqvist, 1952, **syn. n.** with *P. pseudocoactula* (Lindqvist, 1952); *P. flavipicta* Lindqvist, 1975, **syn. n.**, *P. flavopleura* Haris, 2002, **syn. n.**, *P. mongoloexigua* Haris, 2002, **syn. n.**, and *P. mongolofausta* Haris, 2003, **syn. n.** with *P. punctifrons* (Thomson, 1871); *P. listoni* Lacourt, 1998, **syn. n.** with *P. sootryeni* Lindqvist, 1955; *P. gaunitzi* Lindqvist, 1968, **syn. n.** with *P. testacea* (Jurine, 1807); and *Nematus breviusculus* Eversmann, 1847, **syn. n.** with *Euura melanocephalus* (Hartig, 1837). The valid name of *Pachynematus (Pikonema) carpathiensis* Haris, 2001 is *Nematinus carpathiensis* (Haris, 2001) **comb. n.** Lectotypes are designated for 43 taxa. An illustrated electronic key made with Lucid and a traditional dichotomous key are provided to facilitate identification of the species. Species belonging to the *carinata* (previously *Lygaeotus*), *micronematica* (previously *Lygaeophora*), and *rufipes* (also known as *thalictri* or *aquilegiae*) groups are not keyed to the species level, because additional research is needed to delimit the species more reliably in these groups. Phylogeny of *Pristiphora* is reconstructed based on one mitochondrial (COI) and two nuclear (NaK and TPI) genes. Remarkably, around 50–60% (depending on the exclusion or inclusion of the *carinata*, *micronematica*, and *rufipes* groups) of the species cannot be reliably identified based on COI barcodes. Limited data from nuclear genes indicate a better identification potential (about 20% remain problematic).

Keywords

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Introduction

Pristiphora Latreille, 1810, as defined by Prous et al. (2014), is the second largest genus in Nematinae (Tenthredinidae), including about 240 species (Taeger et al. 2010). About half of these (120) are known in the West Palaearctic. The main keys available for the majority of West Palaearctic species are those of Benson (1958) and Zhelochovtsev and Zinovjev (1988). Benson's (1958) key is outdated and geographically restricted (British Isles). The key by Zhelochovtsev and Zinovjev (1988) includes more species because of wider geographic scope and new species described since Benson (1958). The most comprehensive key for *Pristiphora* in terms of number of species and geographic scope (Palaearctic) was published by Haris (2006b), but it is mostly based on previous keys and species descriptions. Both Haris (2006b) and Zhelochovtsev and Zinovjev (1988), studied only few types, included many species based on literature, and uncritically accepted characters used in previous keys. Problems in identifying species of

Pristiphora, and Nematinae in general, are exacerbated by inherent difficulties caused by the large number of species and a lack of discrete characters suitable for separating them. Here we revise the species found in the North-Western Palaearctic Region (defined here as Scandinavia and its neighbouring regions) and delimit several species groups (some of them previously treated as genera or subgenera) using molecular and morphological data. We provide photos of lancets and penis valves, an electronic key employing a large number of characters, and a dichotomous key using the most reliable characters for species identification. For convenience, the recently revised *ruficornis* species group (Prous et al. 2016) is also included. However, delimiting species belonging to the *carinata* (*Lygaeotus*), *micronematica* (*Lygaeophora*), and *rufipes* (also known as *thalictri* or *aquilegiae* group) groups requires additional research.

The most comprehensive phylogenetic analyses of *Pristiphora* so far published were part of broader analyses dealing mainly with higher level relationships of Nematinae (Nyman et al. 2006, Nyman et al. 2010, Prous et al. 2014). Here we estimate the phylogeny of *Pristiphora* based on expanded taxon sampling and three genes: one mitochondrial (COI) and two nuclear (NaK and TPI).

Mitochondrial COI barcodes are widely used for species identification. This often works rather well (Pentinsaari et al. 2014, Mutanen et al. 2016), but there are indications of significant barcoding failure in some groups of sawflies (Schmidt et al. 2017), particularly in Nematinae (table 2 in Schmidt et al. 2017). However, as there are also numerous taxonomic problems within Nematinae, the exact nature of barcoding failure is in many cases uncertain. The application of COI barcoding to *Pristiphora* revealed that COI cannot be reliably used for species identification in roughly half of the species, and that nuclear genes seem to work better for that purpose.

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;
CMH	Collection of Mikk Heidemaa, Tartu, Estonia;
CMV	Collection of Matti Viitasaari, Helsinki, Finland;
CNC	Canadian National Collection of Insects, Ottawa, Canada;
COL	Collection of Ole Lønnve, Oslo, Norway;
CVV	Collection of Veli Vikberg, Turenki, Finland;
CTN	Collection of Thierry Noblecourt, Quillan, France;
EJC	Collection of Ewald Jansen, Leipzig, Germany;
ETHZ	Eidgenössische Technische Hochschule-Zentrum, Zurich, Switzerland;
HMUG	Hunterian Museum, University of Glasgow, United Kingdom;
HNHM	Hungarian Natural History Museum, Budapest, Hungary;

INHS	Illinois Natural History Survey, Champaign, USA;
INRA	Institut National de la Recherche Agronomique, Centre de Biologie pour la Gestion des Populations (CBGP), Montferrier-sur-Lez Cedex, France;
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium;
LPNC	Collection of Pierre-Nicolas Libert, Somal, Belgium;
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, USA;
MNCN	Museo Nacional de Ciencias Naturales, Madrid, Spain;
MNHN	Muséum National d'Histoire Naturelle, Paris, France;
MZH	Finnish Museum of Natural History, Helsinki, Finland;
MZLU	Lunds Universitet, Lund, Sweden;
MZPW	Museum of the Institute of Zoology, Polish Academy of Science, Warsaw, Poland;
NFVG	Niedersächsische Forstliche Versuchsanstalt, Göttingen, Germany;
NHRS	Naturhistoriska Riksmuseet, Stockholm, Sweden;
NMPC	National Museum (Natural History), Prague, Czech Republic;
NMW	Naturhistorisches Museum Wien, Wien [= Vienna], Austria;
NFRC	Northern Forestry Centre, Edmonton, Canada;
NSM	University of Nebraska State Museum, Lincoln, USA;
NSMT	National Museum of Nature and Science, Tokyo, Japan;
NUORTJ	Collection of Juoko Nuorteva, Helsinki, Finland;
RMNH	Nationaal Natuurhistorische Museum, Leiden, Netherlands;
RSME	National Museums of Scotland, Edinburgh, United Kingdom;
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;
UEF	University of Eastern Finland, Joensuu, Finland;
USNM	National Museum of Natural History, Smithsonian Institution, Washington D.C., USA;
ZIN	Russian Academy of Sciences, Zoological Institute, St. Petersburg, Russia;
ZMAN	Universiteit van Amsterdam, Instituut voor Taxonomische Zoologie, Zoologisch Museum, Amsterdam, Netherlands;
ZMHB	Museum für Naturkunde der Humboldt-Universität, Berlin, Germany;
ZMUC	Zoological Museum of the University of Copenhagen, Denmark;
ZMUM	Zoological Museum, Moscow State University, Moscow, Russia;
ZMUO	Zoological Museum, University of Oulu, Finland;
ZSM	Zoologische Staatssammlung, München [= Munich], Germany.

Names of the mentioned host plants follow The Plant List (http://www.theplantlist.org/). Unless otherwise stated, species distribution data at the level of zoogeographic regions is taken from Taeger et al. (2010).

Collection data of the examined specimens is included in an excel file available at figshare (http://dx.doi.org/10.6084/m9.figshare.5235835).

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 (Danielsson 1985) was used (these specimens are labelled as 'PR.XXXVV', e.g. PR.579VV). 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 created using the program Image Composite Editor (Microsoft), or in few cases with plugin MosaicJ (Thévenaz and Unser 2007) implemented in ImageJ version 1.46r (Wayne Rasband; http://imagej.nih.gov/ij/). Morphological terminology follows Vikberg (1978, 2006) and Viitasaari (2002). We do not use the term "ctenidia" to denote the bands of setae on the annuli of female lancets (Fig. 129), as used previously by Prous et al. (2016) following Viitasaari (2002, Fig. 134). The term "ctenidia" (singular "ctenidium") correctly refers to rows of spines (i.e. protrusions of the cuticle); superficially they resemble bands of setae, which are composed of sensilla (Smith 1968, Blank and Schönitzer 1994, fig. 131 in Viitasaari 2002). Therefore we use the more neutral term "setae".

Rearing of larvae and adults

All the rearing data newly published here were obtained by VV. These data are given under *Rearing notes* in the *Taxonomy* section. Plants chosen for ovipositing experiments were mainly those from which females were collected in the field or reared from larvae. Our main intention was to find at least one acceptable host plant for rearing particular species. Ovipositing experiments were carried out indoors, at room temperature. Suitable parts of plants were cut, the cut end put in water or wrapped in moistened filter paper (paper towel), and the leaves offered to the sawfly in a closed container. Larvae were fed with fresh leaves that were changed every day or every second day. Cocoons were placed in glass vials and overwintered outdoors in a wooden chest.

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 two nuclear regions 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. The nuclear markers used are fragments of triose-phosphate isomerase (TPI) and sodium/potassium-transporting ATPase subunit alpha (NaK). The TPI fragment used is the nearly complete gene region, containing 676 bp of three exons and two short introns (each around 50–100 bp) in Nematinae, altogether 795–833 bp. The NaK fragment used is a nearly complete sequence of its longest exon, 1654 bp. New NaK primers were designed mainly based on four sawfly genomes and one transcriptome available in GenBank (accessions AOFN01001568, GAWW02019159, LGIB01000323, AMWH01001469, AZGP01005167), or using sequences published by Malm and Nyman (2015). Numbers in the new NaK primer names refer to the binding position of the primer's 3' end in the coding region of *Athalia rosae* mRNA (accession XM_012414227). Seven sequences of four specimens (4b, 9t, DG, DH) newly reported here were obtained from the VoSeq database (Peña and Malm 2012) maintained by Tommi Nyman (University of Eastern Finland). For these four specimens, 810 bp of COI and 997 bp of NaK had been sequenced as described previously (Nyman et al. 2006, Leppänen et al. 2012).

PCR reactions were carried out in a total volume of 15–25 µl containing 1–2 µl of extracted DNA, 1.0–1.5 µl (5.0–7.5 pmol) of primers and 7.5–12.5 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 47–59 °C depending on the primer set used, and 30–120 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). 1.0–1.8 U of both enzymes were added to 12–22 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. Some TPI sequences were polymorphic for intron length and in those cases heterozygous insertions/deletions (indels) were reconstructed using the program In*d*elligent v.1.2 (Dmitriev and Rakitov 2008), available at http://dmitriev.speciesfile.org/indel.asp. Only the longest haplotype was submitted to Genbank, because Genbank does not accept more than one sequence per specimen and marker. Ambiguous positions (i.e. double peaks in chromatograms of both strands) due to heterozygosity or heteroplasmy were coded using IUPAC symbols. The COI sequence of one sequenced specimen (*Pristiphora friesei*

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 PCR annealing temperature, utilization (PCR/ sequencing), and reference. Primer annealing temperatures used for sequencing at Macrogen were 47°C for COI and 50°C for nuclear genes.

Gene Region	Primer name	F/R i/o	Primer sequence 5'–3'	PCR annealing temperature (°)	PCR/ Sequencing	Reference
COI	SymF1	F o	TTTCAACWAATCATAAARAYATTGG	47	PCR, seq	Prous et al. (2016)
COI	SymF2	F o	TTTCAACAAATCATAAARAYATTGG	47	PCR, seq	Prous et al. (2016)
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	Prous et al. (2016)
COI	C1-N1760	R i/o	GGTARAAATCARAATCTTATATTAT	47	PCR, seq	(Prous et al. 2011)
COI	SymR1	R i/o	TAAACTTCWGGRTGICCAAARAATC	47	PCR, seq	Prous et al. (2016)
COI	SymR2	R i/o	TAAACTTCTGGRTGTCCAAARAATCA	47	PCR, seq	Prous et al. (2016)
COI	A2590	R o	GCTCCTATTGATARWACATARTGRAAATG	49	PCR, seq	(Normark et al. 1999)
TPI	TPI_29Fi	F o	GYAAATTYTTYGTTGGNGGIAA	52	PCR, seq	Prous et al. (2016)
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	Prous et al. (2016)
TPI	TPI 275Ri	R o	GCCCANACNGGYTCRTAIGC	56	PCR, seq	(Malm and Nyman 2015)
TPI	TPI706R	R o	ACNATYTGTACRAARTCWGGYTT	52	PCR, seq	Prous et al. (2016)
NaK	NaK_263F	F o	CTYAGCCAYGCRAARGCRAARGA	59	PCR, seq	This study
NaK	NaK_809F	F i/o	GCWTTYTTCTCNACSAAYGCSGTNGARGG	55	PCR, seq	This study
NaK	NaK_907Ri	R i/o	TGRATRAARTGRTGRATYTCYTTIGC	54	PCR, seq	This study
NaK	NaK_910R	R i/o	TGRATRAARTGRTGRATYTCYTT	50	PCR, seq	This study
NaK	NaK_1250Fi	F i	ATGTGGTTYGAYAAYCARATYATIGA	56	Seq	This study
NaK	NaKFor470	F i	ATGTGGTTYGAYAAYCARATYATCGA	56	Seq	Leppänen et al. (2012)
NaK	NaKRev475	R i	TCGATRATYTGRTTRTCRAACCACAT	56	Seq	Leppänen et al. (2012)
NaK	NaK_1918R	R o	GATTTGGCAAITNGCTTTGGCAGTDAT	59	PCR, seq	This study

DEI-GISHym11558) had a single bp deletion, which was replaced with N before submitting to GenBank.

Sequences reported here have been deposited in the GenBank (NCBI) database (accession numbers KY698031–KY698412 and MF426916–MF426924). Some of the sequences analysed here were originally published by Nyman et al. (2006, 2010), Prous et al. (2014, 2016), and Schmidt et al. (2017).

Sequences of COI, NaK, and TPI without introns were aligned manually, among which only one COI sequence of *P. friesei* (DEI-GISHym11558) had a single bp deletion.

For concatenation of separate alignments of different genes we used FASconCAT-G (Kück and Meusemann 2010) (https://www.zfmk.de/en/research/research-centres-and-groups/fasconcat-g). To minimize the missing cells in the dataset, a few composite COI sequences were created from different specimens of the same species. A nearly complete 1078 bp region of COI was created in these cases by combining the barcoding region (up to 658 bp) with the 810 bp region (423 bp of which overlaps with the barcoding region) when the overlapping part was identical between the sequences. Both ID numbers of the specimens used to create the composite COI sequences are given in the figures.

For phylogenetic analyses we used the maximum likelihood method (ML) implemented in RAxML v. 8.2.9 (Stamatakis 2014) through CIPRES Science Gateway V. 3.3 (Miller et al. 2010) at https://www.phylo.org/. Robustness of reconstructed trees was estimated with 1000 rapid bootstrap replicates. For tree search, GTRCAT model with 25 site-specific rate categories was used and the final tree evaluated with the GTRGAMMA model (Stamatakis 2006; http://sco.h-its.org/exelixis/web/software/raxml/). The concatenated dataset was partitioned by genes, and model parameters estimated separately for each gene. Additionally, MEGA7 (Kumar et al. 2016) was used to calculate p-distances (proportion of nucleotide differences) between specimens and net synonymous divergence between species. Unless stated otherwise, TPI introns were excluded from calculations. Minimal p-distances between and maximal distances within BIN (Barcode Index Number) clusters were taken from BOLD (http://www.boldsystems.org/) BIN database. Alignment files and output files from phylogenetic analysesare available at figshare (http://dx.doi.org/10.6084/m9.figshare.5235832).

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).

Preparation of the keys

The electronic identification key for the species of *Pristiphora* was prepared in Lucid 3.5 Builder (http://www.lucidcentral.org/) and a zip file containing all the Lucid data

files is available at figshare (http://dx.doi.org/10.6084/m9.figshare.5235805). If the licence for Lucid 3.5 is lacking, the free version of Lucid 3.3 can be used to run the key. In case of ambiguities or polymorphisms in character states, we conservatively coded these as multiple states. The key contains 90 morphological features with 244 character states, and 68 male and 71 female entities (species or groups). 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 to suggest the most efficient sequence of characters for identification. A traditional dichotomous key was constructed manually to emphasise the most reliable characters (usually penis valve for males, and valvula 3 or lancet for females).

Results

Definition of *Pristiphora* and its separation from other Nematinae

The genus was recently delimited mainly by phylogenetic analyses of DNA sequence data by Prous et al. (2014), which is here confirmed with the addition of the nuclear gene TPI. Phylogenetic analysis of mitochondrial COI and nuclear NaK and TPI sequences (altogether 3408 bp) strongly support monophyly of *Pristiphora* (Fig. 1). There are no unambiguous morphological characters that define *Pristiphora*, but the combination of the following characters can be used to distinguish most of the species from the similar genera *Nematus* and *Euura* (see Prous et al. 2014): clypeus usually more or less truncate (Fig. 9); apex of vein C usually swollen; head length behind eyes usually small; claws often with small subapical tooth or simple; in females, valvula 3 (apical sawsheath) often with scopa (e.g. Figs 75, 86, 104–107, 127) and tangium of lancet nearly always with campaniform sensilla (Fig. 177); in males, posterior end of tergum 8 without distinct apical projection in most species (except *P. armata* and *P. leucopus*), and penis valve usually with valvispina arising close to the ventral margin. Vikberg (1982) lists larval characters that might more reliably distinguish *Pristiphora* from *Nematus* and *Euura* with morphologically similar adults: 3rd abdominal segment with 6 annulets, annulets 2 and 4 with setae; no cerci; and maxillary stipes with or without seta. However, not all of these characters apply to all *Pristiphora*. For example, larvae of *P. dasiphorae* have only 3 visible annulets on abdominal segments and both species of the *P. malaisei* group (*arctica* group in Prous et al. 2014), *P. malaisei* and *P. dasiphorae*, have setae also on annulet 1 (Zinovjev 1993). More *Pristiphora* species should be scored for the larval characters mentioned by Vikberg (1982) to test the reliability of these characters for defining the genus.

Possible diploid males

Some of the nuclear sequences from males included polymorphic sites (double peaks in chromatograms) indicating heterozygosity or the presence of paralogous genes.
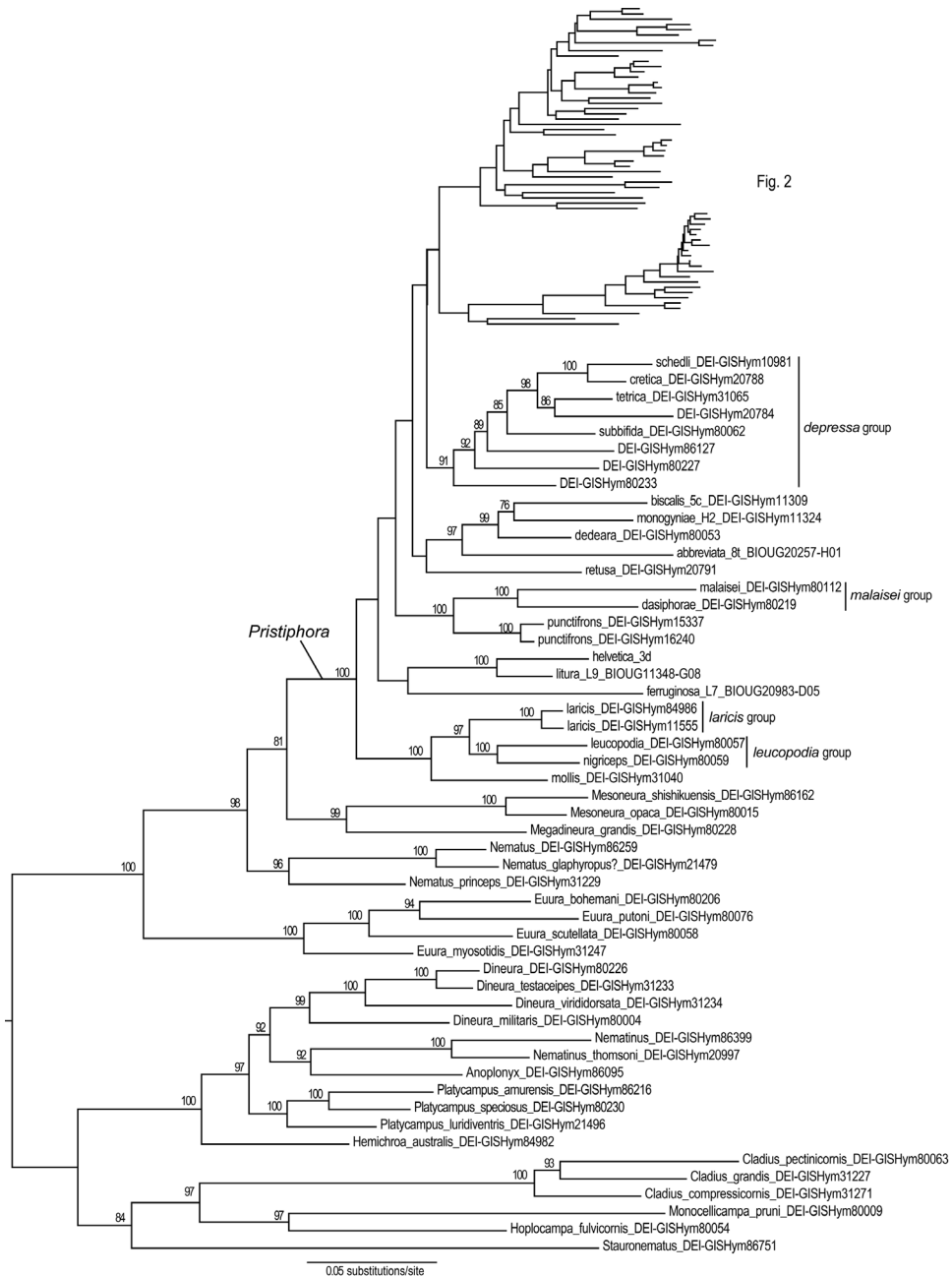
Figure 1. Maximum likelihood tree of *Pristiphora* and nematine outgroups based on three genes (3408 bp). Specimens having at least two of the three genes were included. Numbers above branches show bootstrap proportions (%). Support values for weakly supported branches (BP<70) are not shown. Part of *Pristiphora* is shown without support values and tip labels, which are shown in Fig. 2. The scale bar shows the number of estimated substitutions per nucleotide position.

Because these few polymorphic sites are restricted to synonymous positions (i.e. not affecting protein sequence) and so far there is no evidence for paralogous NaK and TPI genes at least in sawflies, these polymorphic sites might indicate heterozygosity because of diploidy. This can happen if there is no heterozygosity at the complementary sex determination (CSD) locus, preventing female development from a diploid embryo (Naito and Suzuki 1991, Heimpel and de Boer 2008, Harper et al. 2016). Survival of diploid males is known in sawflies (Naito and Suzuki 1991, Cook et al. 2013, Harper et al. 2016) and is common in nature at least in some species of Apocrita (Liebert et al. 2005, Retamal et al. 2016).

Possible frameshift mutation in COI

COI sequence of one *P. friesei* specimen (DEI-GISHym11558) had a single bp deletion, which was caused by shortening of 8 bp repeat of thymines (T) to 7 thymines, compared to a different *P. friesei* specimen and closely related *P. laricis*. Because the *P. friesei* sequence with the deletion was of good quality (trace files at figshare http://dx.doi.org/10.6084/m9.figshare.5235832), was found in amplicons obtained with two sets of different primers, and did not show anomalous phylogenetic position, it is possible that this COI sequence is functional despite the frameshift mutation (Beckenbach et al. 2005, Rosengarten et al. 2008). Barcode sequences of two additional *P. friesei* specimens in BOLD that are labelled as NUMT (nuclear mitochondrial pseudogene), DEI-GISHym4993 and DEI-GISHym11557, have identical sequence to specimen DEI-GISHym11558.

Phylogeny of *Pristiphora* and definitions of some species groups

Phylogenetic relationships at the base of *Pristiphora* are not well resolved by our three-gene dataset (Fig. 1), because most of the deeper splits receive bootstrap support less than 70%. Many of the more derived clades that receive strong bootstrap support (more than 90%) are also morphologically well-supported (see group definitions below). Generally, our results strengthen the conclusions of Nyman et al. (2010) that only a minority of lineage splits correlate with host plant shifts. Species in the groups which monophyly is well supported (Figs 1–2) tend to share the same host plant genus or family (see group definitions below and Nyman et al. 2010 for details). We will not repeat the quantitive analysis of Nyman et al. (2010), but our broader taxon sampling yields additional support for their conclusions, e.g. we recover a *Quercus*-feeding clade composed of *P. fausta, P. calliprina*, and *P. parnasia* (Figs 2, 5), and an *Acer*-feeding *depressa* group (Figs 1, 3), although host plants are not known for all the species involved.

     To enable easier discussion of relationships among *Pristiphora* species, we define the following informal species groups based on morphology and the phylogenetic analysis: *abietina, alpestris, carinata, depressa, erichsonii, laricis, leucopodia, malaisei,*
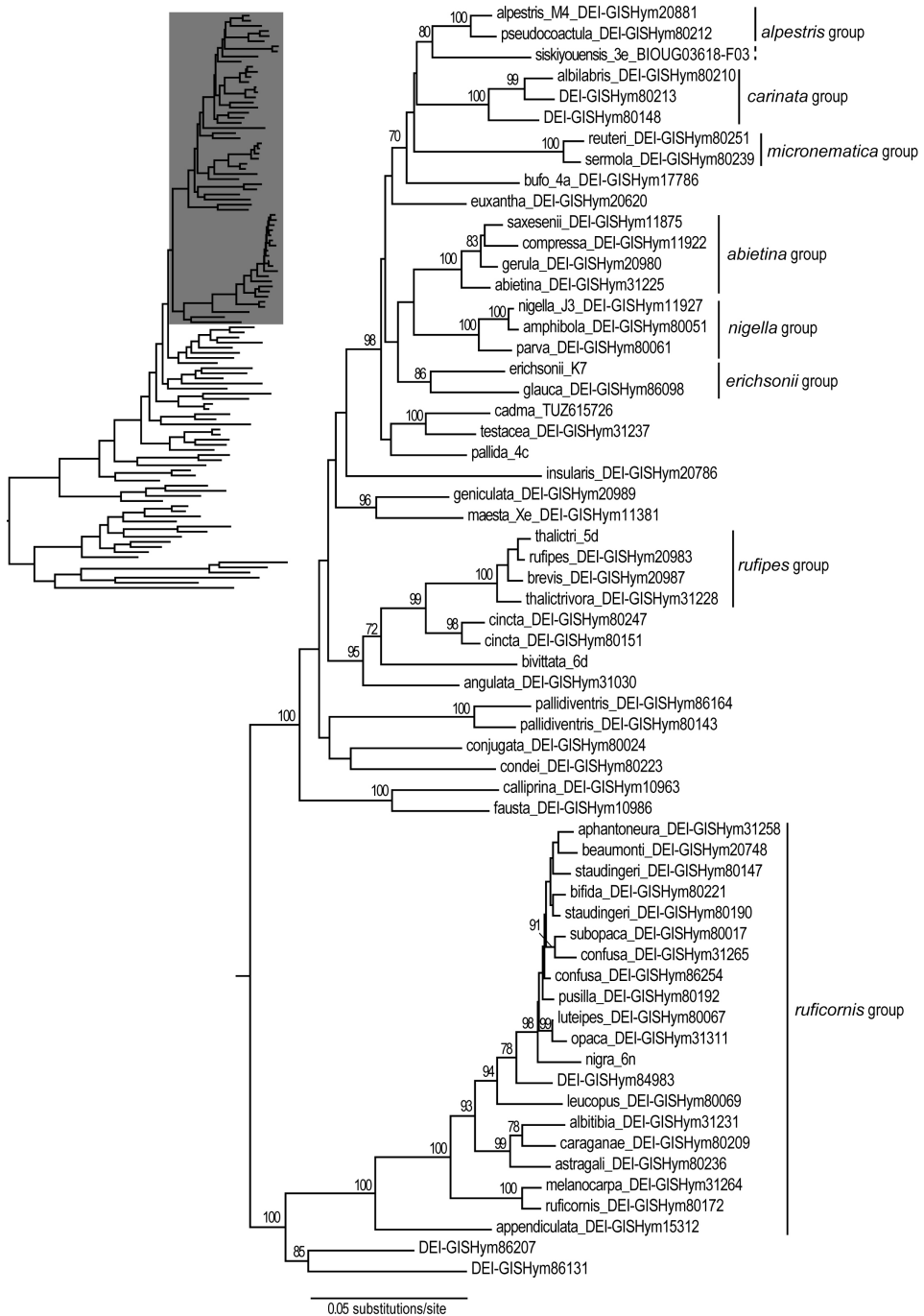
Figure 2. Part of the maximum likelihood tree shown in Fig. 1. Numbers above branches show bootstrap proportions (%). Support values for weakly supported branches (BP<70) are not shown. Outline of the full tree is shown upper left, with the part shown here highlighted. The scale bar shows the number of estimated substitutions per nucleotide position.
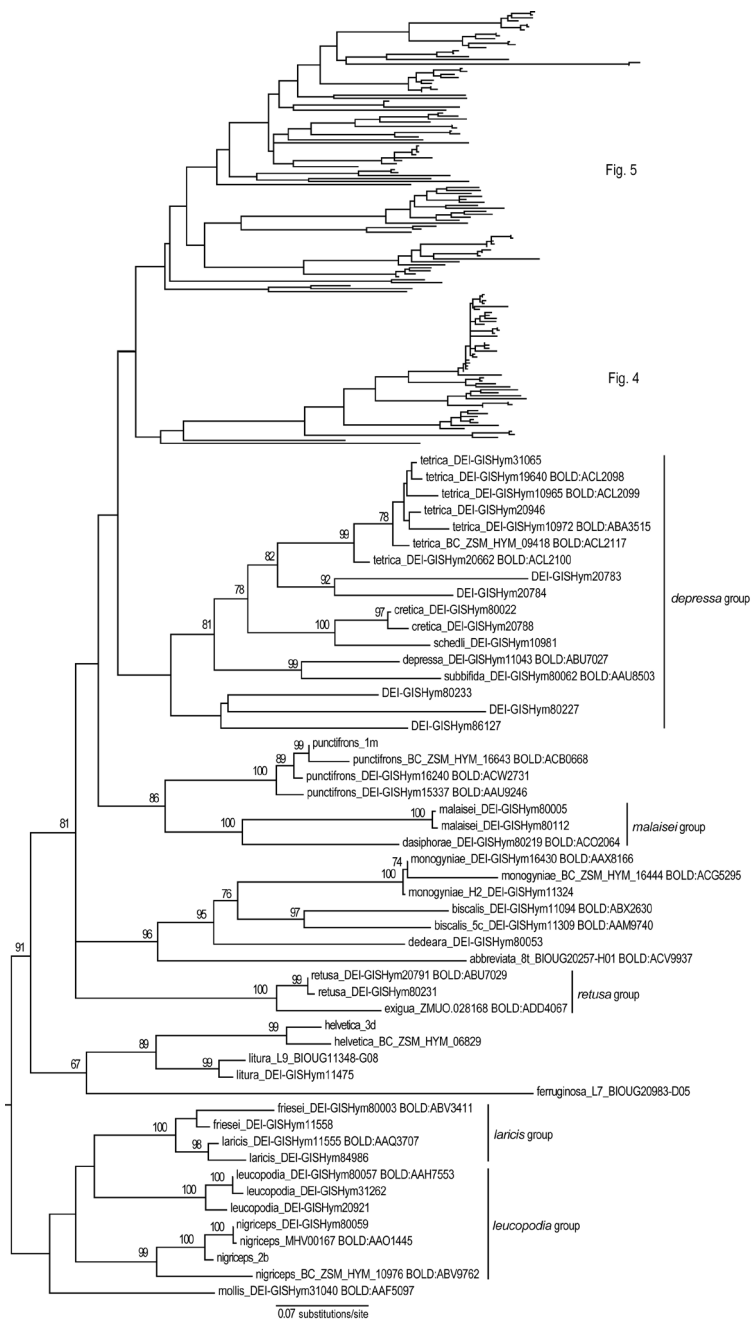
Figure 3. Maximum likelihood tree of *Pristiphora* based on COI gene (1078 bp). Shortest sequence included was 462 bp (*subarctica* MHV00166). Numbers above branches show bootstrap proportions (%). Support values for weakly supported branches (BP<70) are not shown. BIN numbers (BOLD:XXXXXXX) referred to in the text are shown for representative specimens. Part of *Pristiphora* is shown without support values and tip labels, which are shown in Figs 4–5. The scale bar shows the number of estimated substitutions per nucleotide position.

micronematica, *nigella*, *pallida*, *pallidiventris*, *retusa*, *ruficornis*, and *rufipes* group. The names of the groups are based on the oldest valid species name in that group.

The following treated species were not assigned to any species groups: *abbreviata*, *angulata*, *biscalis*, *bufo*, *cadma*, *cincta*, *condei*, *conjugata*, *dedeara* sp. n., *fausta*, *geniculata*, *insularis*, *maesta*, *mollis*, *monogyniae*, *paralella*, *pseudogeniculata*, *punctifrons*, *tenuiserra*, and *testacea*.

P. *abietina* group (also known as the *compressa* complex)

Includes the following North-Western Palaearctic species: *abietina*, *compressa*, *decipiens*, *gerula*, *pseudodecipiens*, *robusta*, and *saxesenii*. All species feed on *Picea* (Beneš and Krístek 1979) and the females have a characteristically modified valvula 3 (Figs 116–118, 120–122), which is apparently correlated with oviposition in narrow conifer needles. Specifically, valvula 3 is relatively narrow in dorsal view, and in lateral view its dorsal and ventral margins are more or less parallel, with the posterior margin distinctly truncate (Figs 116–118, 120–122). In addition, the apical part of the abdomen of females is laterally compressed (Fig. 60), but this character is not reliable for unambiguous distinction of females of the *abietina* group from other species. Males are externally very similar to many other species outside the *abietina* group that are ventrally extensively pale and dorsally black, so that penis valves should be studied to recognise them. Penis valves of the *abietina* group have a similar structure (Figs 283–289) that can be distinguished from other *Pristiphora*: more or less straight ventral margin, similarly sized paravalva and pseudoceps with roughly convex dorsal margin, apically unmodified pseudoceps, and straight or slightly bent valvispina. Genetic data (no data yet for *P. robusta*) strongly support the monophyly of the *abietina* group (Figs 2, 5). We exclude the *erichsonii* and *pallida* groups from the *abietina* group (included in Wong 1975), because current phylogenetic analyses do not support such a clade (Figs 2, 5). Unusually, the divergence in mitochondrial sequences (maximum distance 2.2%, minimum between species distance 0.0%) in the *abietina* group is similar or lower than in nuclear sequences (maximum distance 2.7%, minimum between species distance 1.1%). This is a reversal of the typical condition in bilateral animals (Bilateria), in which the substitution rate in mitochondrial DNA is several-fold higher than in nuclear DNA (Ballard and Whitlock 2004, Lavrov 2007). It is unlikely that mitochondrial DNA (mtDNA) evolves more slowly than nuclear DNA in the *abietina* group (no reliable cases are known in Bilateria). More probable is that the reduced diversity of mtDNA is caused, for example, by infection with maternally transmitted *Wolbachia* (or some other Bacteria), a common occurrence in arthropods (e.g. Hurst and Jiggins 2005, Werren et al. 2008). *Wolbachia* infection can cause cytoplasmic incompatibility between infected males and uninfected females, meaning that mitochondria carried by infected females are preferentially spread within population or between closely related species via introgression. This could explain sharing of (near) identical COI sequences between different species in *abietina* group.

P. *alpestris* group

Includes the following North-Western Palaearctic species: *alpestris*, *pseudocoactula*, and possibly *dissimilis*. Penis valves and lancets are very similar in *alpestris* and *pseudocoactula* (Figs 203–204, 233–236), but females are not known for *dissimilis* and its penis valve is very distinctive compared to all other *Pristiphora* species (Fig. 237). Genetic data strongly supports monophyly of the *alpestris* and *pseudocoactula* clade (Figs 2, 5). Placement of *dissimilis* (no genetic data yet) in the *alpestris* group is tentative (Lindqvist 1971).

P. *carinata* group (previously *Lygaeotus*)

Includes the following North-Western Palaearctic species: *albilabris, borea, breadalbanensis, carinata, coactula, groenblomi, lativentris,* and *trochanterica*. Species of the *carinata* group have a distinctly matt mesepisternum, and completely or largely black body. Valvula 3 of females varies from simple (short, slightly tapering from base to apex, and without scopa; Figs 98–99) to somewhat square-shaped in dorsal view and with small scopa (Figs 93–97). Lancets are without setae and very similar to each other (Figs 210–217). Penis valves are also hardly distinguishable (Figs 238–242). Because of the high degree of similarity and the apparently continuous variation of (nearly) all characters, it is not clear how many species should be recognised and how they should be delimited. Genetic data strongly supports monophyly of the *carinata* group (Figs 2, 5). More research is need to associate males and females of different species, preferably by rearing experiments and sequencing of different nuclear genes, so that morphological variation within and between the species can be assessed more reliably.

P. *depressa* group (previously *subbifida* group)

Includes the following North-Western Palaearctic species: *depressa, subbifida,* and *tetrica*. This species group was reviewed by Liston and Späth (2008) and Liston et al. (2013). As far as is known, all species feed on *Acer* (Liston and Späth 2008). Females have usually a relatively short and narrow valvula 3 with a small scopa (Figs 82–83), but sometimes the scopa is practically absent. Most species have bifid or subbifid (Figs 24–25) claws. Males have a long and thin valvispina that can be strongly bent (Fig. 301), or nearly straight (in *P. ifranensis* Lacourt, 1973). Combined analysis of mitocondrial and nuclear genes moderately supports monophyly of the *depressa* group (Fig. 1). Genetic data (Figs 1, 3) indicates several additional, possibly undescribed, species in Europe (Mediterranean region and Central Europe; DEI-GISHym20783, 20784) and in the Far East (DEI-GISHym86127, 80227, 80233).

P. erichsonii group (previously *wesmaeli* complex)

Includes the following North-Western Palaearctic species: *erichsonii*, *glauca*, and *wesmaeli*. All species feed on *Larix* (Wong 1975). Characteristically for conifer-feeders, species of the *erichsonii* group have a narrow valvula 3 (Figs 124, 126). *P. erichsonii* has a different coloration (abdomen with a red band) and valvula 3 (not apically abruptly constricted; Fig. 124) from *P. glauca* and *P. wesmaeli* (abdomen ventrally yellow, valvula 3 apically abruptly constricted Fig. 126), but penis valves (Figs 290–292) and genetic data (Figs 2, 5) support monophyly of this group. The penis valves of the *erichsonii* group have a somewhat rhombus- (Fig. 290) or trapez-shaped (Figs 291–292) paravalva, a rather rectangular and unmodified pseudoceps, and small and slightly bent valvispina that is asymmetrical at apex.

P. laricis group (previously *Oligonematus*)

Includes the following North-Western Palaearctic species: *friesei* and *laricis*. Both species feed on *Larix* (Adam 1973, Huflejt and Sawoniewicz 1999, Liston et al. 2006). Females have a short valvula 3 (cerci clearly extend beyond its apex), with small scopa (Figs 79–81). The absence of a velum on the anterior protibial spur (Fig. 33), and usually mostly black body, can help in recognising this group. Lancets (Figs 174–178) and penis valves (Figs 277, 279–208) unambiguously distinguish the *laricis* group from other species (see the Key). Genetic data strongly supports monophyly of the *laricis* group (Figs 1, 3).

P. leucopodia group

Includes the following North-Western Palaearctic species: *leucopodia* and *nigriceps*. Both species feed on *Picea* (Beneš and Krístek 1979). As in many other species feeding on conifers, valvula 3 is narrow in the *leucopodia* group (Fig. 84). In lateral view, valvula 3 has a round outgrowth at the posterior margin (Fig. 85), which distinguishes the *leucopodia* group from other conifer-feeders. A relatively similar valvula 3 is found in *P. insularis* (Figs 86–87), but other characters distinguish this species from the *leucopodia* group (anterior protibial spur with velum and clearly different lancet; see Figs 33–34, 135, 181–183). A characteristic hump that is posteriorly constricted and situated at the base of the slightly bent valvispina (Figs 281–282) distinguish penis valves of the *leucopodia* group from other *Pristiphora* (see the Key). Combined mitochondrial and nuclear phylogenetic analysis strongly supports monophyly of the *leucopodia* group (Fig. 1), but mitochondrial COI sequences alone do not (Fig. 3).

P. malaisei group (previously *arctica* group, or *Pristicampus*)

Includes the following North-Western Palaearctic species: *malaisei* and *dasiphorae*. Both species feed on *Potentilla fruticosa* L. (=*Dasiphora fruticosa*) (Zinovjev 1993) and possibly *Comarum palustre* L. Quite characteristic for the group is its head shape, which is more evident in females (Fig. 58). Structure of the penis valves (apically truncate and without valvispina; Figs 297–298) is very distinct within *Pristiphora*, prompting Zinovjev (1993) to create even a separate tribe for the species of *malaisei* group. Genetic data strongly supports monophyly of the group (Fig. 1).

P. micronematica group (previously *Lygaeophora*)

Includes the following North-Western Palaearctic species: *affinis*, *atripes*, *kontuniemii*, *micronematica*, *nordmani*, *reuteri*, *sermola*, and possibly *lanifica*. In contrast to other group names, we use the name *micronematica* (Malaise 1931) for this group instead of the oldest name *lanifica* (Zaddach in Brischke 1883), because the identity of *lanifica* is uncertain and it might not belong to this group. As far as is known, species of this group feed on *Salix* (Lindqvist 1952, Kontuniemi 1960, 1972, Vikberg 1966, Liston 1982, Kangas 1985). Valvula 3 in females has a small scopa (Fig. 92), is more or less square-shaped in dorsal view and has two dense, lateral bundles of hairs at its apex (Fig. 91). Very similar are species in the *carinata* and *alpestris* groups, but lancets (with setae and serrulae not papilliform; Figs 205–209) and penis valves (pseudoceps in most species dorsally with loose membranous region covered with hair; Figs 303–310) of the *micronematica* group can be readily separated from these groups (see the Key). Genetic data strongly supports monophyly of the *micronematica* group (Figs 2, 5). Ecologically, and in some other biological characteristics, this group is similar to the phylogenetically distant *aphantoneura* subgroup (Figs 2, 4; Prous et al. 2016): the majority of species (perhaps all in the *micronematica* group) feed on *Salix*, are more abundant and species rich in boreal or (sub)arctic habitats (probably because of the host plants), have low diversity in mitochondrial DNA (maximum divergence in COI barcodes is 2.5% in *micronematica* group, 3.3% in *aphantoneura* subgroup) that does not correlate with species boundaries (tentative for *micronematica* group), and have phenotypically exceedingly similar females, while males can in most cases be identified by clear differences in penis valves. At least *ex ovo* rearings or sequencing of several nuclear markers from most species is needed to associate males and females confidently in the *micronematica* group.

P. nigella group (previously *Sharliphora*)

Includes the following North-Western Palaearctic species: *amphibola*, *nigella*, and *parva*. All species feed on *Picea* (Beneš et al. 1981). The structure of valvula 3 in the *nigella* group is unique among *Pristiphora*, with the scopa positioned dorsoapically (Figs 111, 115), rather
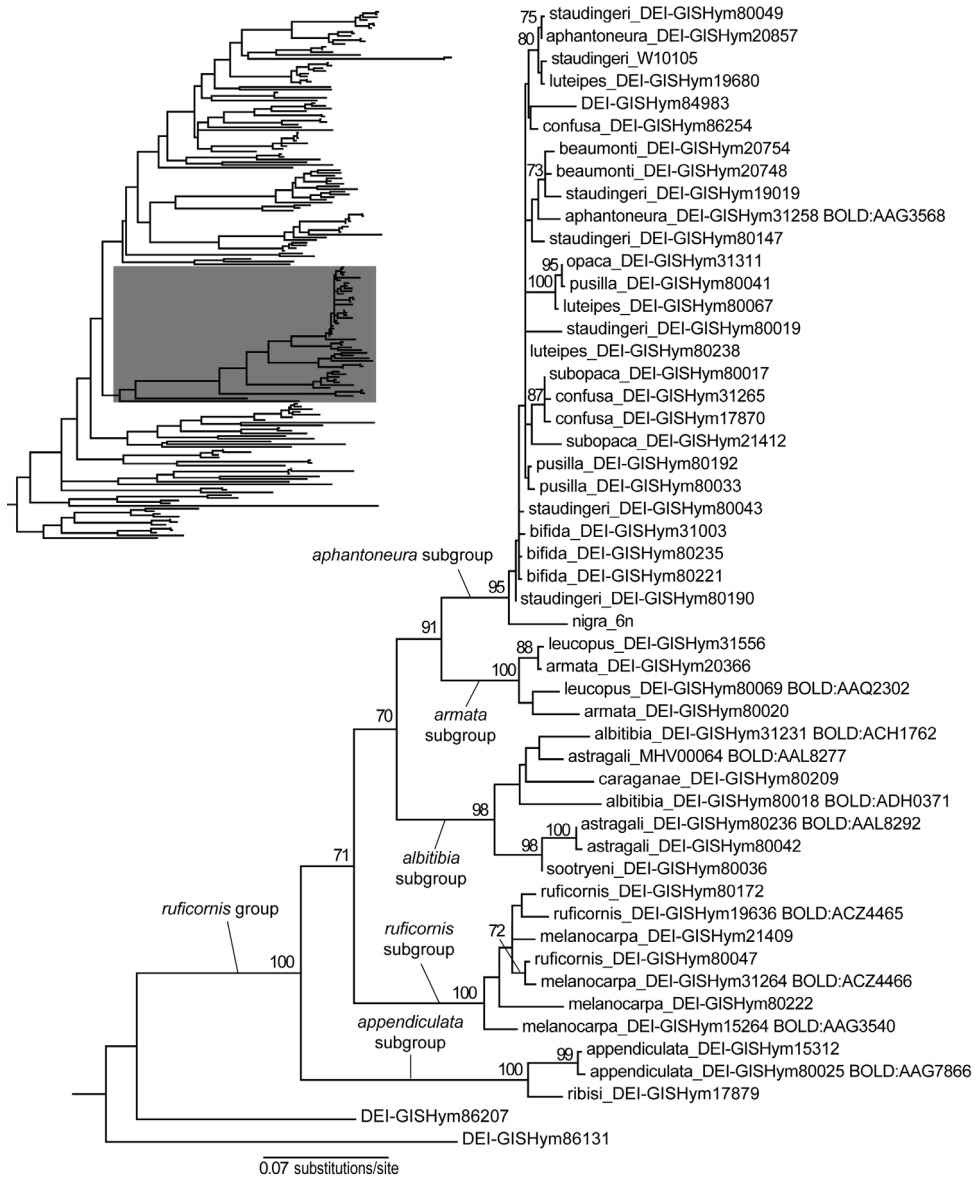
Figure 4. Part of the maximum likelihood tree shown in Fig. 3. Numbers above branches show bootstrap proportions (%). Support values for weakly supported branches (BP<70) are not shown. BIN numbers (BOLD:XXXXXXX) referred to in the text are shown for representative specimens. Outline of the full tree is shown upper left, with the part shown here highlighted. The scale bar shows the number of estimated substitutions per nucleotide position.

than just apically or ventroapically as in other species. This might be related to adaptation to ovipositing into closed or opening *Picea* buds (Nägeli 1936, Benson 1948, Grebenshchikova 1986), in contrast to other conifer-feeders which use already expanded needles.
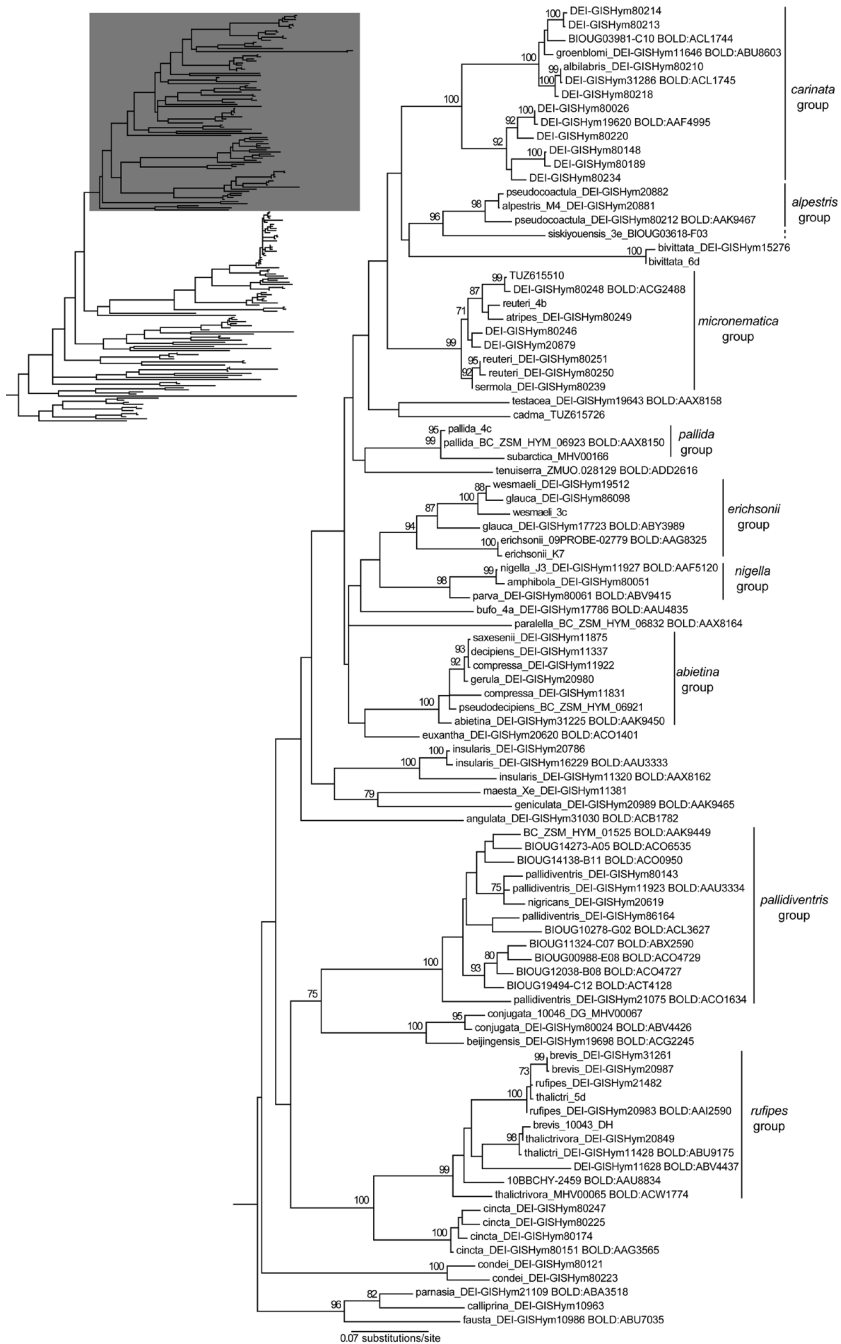
Figure 5. Part of the maximum likelihood tree shown in Fig. 3. Numbers above branches show bootstrap proportions (%). Support values for weakly supported branches (BP<70) are not shown. BIN numbers (BOLD:XXXXXXX) referred to in the text are shown for representative specimens. Outline of the full tree is shown upper left, with the part shown here highlighted. The scale bar shows the number of estimated substitutions per nucleotide position.

Lancets (long and narrow, with setae and flat serrulae; Figs 165–167) and penis valves (apically narrowed pseudoceps, paravalva dorsally somewhat s-shaped and with small dorsally directed valvispina; Figs 293–295) of the *nigella* group can also be distinguished from other species. Genetic data strongly supports monophyly of the *nigella* group (Figs 2, 5).

P. pallida group

Includes the following North-Western Palaearctic species: *pallida* and *subarctica*. Both species feed on *Picea* (Beneš and Krístek 1979). As in many other conifer-feeders, species of the *pallida* group have a narrow valvula 3 (as in Fig. 124) and both males and females are at least ventrally extensively pale yellow. The structure of valvula 3 cannot be distinguished from *P. erichsonii*, but this species has a different coloration (abdomen with a red band; as in Fig. 47). Very characteristic penis valves (Figs 276, 278) clearly distinguish this group from other similar conifer-feeders (see the Key). We cannot exclude the possible conspecifity of *pallida* and *subarctica*, because the differences between them are morphologically (Figs 171–172, 276, 278) and genetically (Fig. 5) small. Examination of more specimens and additional nuclear gene sequences are needed to decide this.

P. pallidiventris group

Includes the following North-Western Palaearctic species: *nigricans* and *pallidiventris*. Both species feed on herbaceous Rosaceae (Liston 2011, this study). Usually, in both species the abdomen is at least ventrally pale, but nearly completely black specimens of *pallidiventris* can occasionally be found. The structure of valvula 3 (deep scopa with long medial projection; Fig. 106) distinguishes this group from other species of Western Palaearctic *Pristiphora*, though the difference is small compared to many other species with similar valvula 3. When in doubt, lancets should be studied (Figs 141–144). Penis valves of both species are very similar (Fig. 223–226) and can be distinguished from other species: paravalva and pseudoceps are of similar size and shape, ventral margin of paravalva is more or less straight, and the valvispina is straight, small, and positioned in the middle or upper third of paravalva. Current genetic data (Fig. 5) does not allow separation of *P. nigricans* (only one COI sequence available) and *P. pallidiventris*.

P. retusa group

Includes the following North-Western Palaearctic species: *exigua* and *retusa*. A host plant is known only for *P. retusa* (*Prunus padus*; Kangas 1985). Characteristic for the group is small size (body length 3.0–4.5 mm), mostly black body, and distinctly asymmetrical labrum (Fig. 11). These two species appear to be rather closely related (only one COI sequence available for *P. exigua*) (Fig. 3).

P. ruficornis group

Includes the following North-Western Palaearctic species divided into five subgroups (Prous et al. 2016): *albitibia* subgroup (*albitibia, astragali, sootryeni, caraganae*), *aphantoneura* subgroup (*aphantoneura, bifida, confusa, luteipes, opaca, pusilla, staudingeri, subopaca*), *appendiculata* subgroup (*appendiculata*), *armata* subgroup (*armata, leucopus*), and *ruficornis* subgroup (*melanocarpa, ruficornis,* and possibly *frigida*). Species of the *albitibia* subgroup feed on Fabaceae, the *aphantoneura* subgroup mostly on *Salix* (except *P. aphantoneura* that feeds on *Lathyrus*), *P. appendiculata* on *Ribes*, the *armata* subgroup on *Crataegus* and *Tilia*, and the *ruficornis* subgroup on *Betula* (a host is not known for *P. frigida*). Morphologically, the *ruficornis* group is best characterised by the structure of penis valves, which have a large and usually strongly bent valvispina that almost completely (Figs 263–274) or largely (Fig. 262) replaces the paravalva. Several other species have a similarly large and bent valvispina (Figs 276, 278, 299, 301), but these penis valves can nevertheless be clearly distinguished from those of the *ruficornis* group, in combination with differences in body coloration (see the Key). Genetic data strongly supports monophyly of the *ruficornis* group (Figs 2, 4).

P. rufipes group (also known as *thalictri* or *aquilegiae* group)

Includes the following North-Western Palaearctic species: *brevis, dochmocera, rufipes, thalictri,* and *thalictrivora*. The species feed on *Aquilegia* (*P. rufipes*) or *Thalictrum* (*P. brevis, P. thalictri, P. thalictrivora,* and possibly *P. dochmocera*). Species of this group are usually black-bodied, valvula 3 of females has a distinct scopa, and lancets are without setae. Lancets and penis valves are very similar in all species. Penis valves of the *rufipes* group have a somewhat rectangular and unmodified pseudoceps, a somewhat oval-, rectangular- or square-shaped paravalva that is dorsoapically abruptly narrowed before the valvispina, a small and straight valvispina that arises on the ventral part of the paravalva, and a valvar strut that is distinct along its entire length (Figs 243, 245, 247–251). Very similar penis valves (Figs 244, 246), but somewhat more elongate than in the *rufipes* group, are found in the closely related *P. cincta* (Figs 2, 5). Species of the *rufipes* group are also genetically closely related to each other (Figs 2, 5). Species boundaries in the *rufipes* group are unclear, as well as the association of males and females. At least two species seem to be involved, one feeding on *Aquilegia* (*P. rufipes*) and the other one(s) on *Thalictrum*. The lancet of the *Aquilegia*-feeding *P. rufipes* seems to be slightly different from the other species. The most protruding part of the serrulae of *rufipes* tends to be relatively acute, usually with denticles along the entire margin (Fig. 222), while the most prominent part of the serrulae of the other species tends to be relatively blunt, with denticles concentrated mostly on the apical part of the serrula. Based on mitochondrial and nuclear sequences of larvae collected from *Aquilegia* sp. (DEI-GISHym20983 and DEI-GISHym21482), we were able to associate three additional adults (DEI-GISHym15263, DEI-GISHym19795, and 9t from VoSeq database) with

these larvae. Nuclear sequences from these adults (both genes, only NaK, or only TPI) and the larvae (both genes) form a monophyletic group to the exclusion of other species (not shown). Nuclear data suggests that there might be at least three additional lineages, which we have identified as *P. brevis*, *P. thalictri*, and *P. thalictrivora* (Fig. 2), but morphological separation of these forms is somewhat arbitrary. Although there is some variation in the shape of serrulae of lancets among the *Thalictrum*-feeders (Figs 218–221), this does not seem to correlate with external morphology, and the variation is continuous. Specimens with completely black (*P. thalictri*) or more or less completely pale legs (e.g. *P. thalictrivora*) can both have lancets of the two extreme forms (Figs 218, 221), but apparently also of intermediate form (Figs 219–220). Nevertheless, in addition to *P. rufipes*, we tentatively recognise four other species: *brevis*, *dochmocera*, *thalictri*, and *thalictrivora*. *Pristiphora thalictri* is the darkest, with completely or almost completely black body, including the legs and tegulae. *Pristiphora brevis* and *P. thalictrivora* have completely or nearly completely pale legs (at most with black hind tarsi) and tegulae. The only differences between *P. brevis* and *P. thalictrivora* may be the longer postocellar area (Fig. 7) and (usually?) rather smooth mesopostnotum (Fig. 19) in *P. brevis* (matt in *P. thalictrivora*; Fig. 20). *Pristiphora dochmocera*, which we tentatively keep as a separate species, might be a synonym of *P. thalictri* or *P. thalictrivora*, because its coloration is intermediate between them. *Pristiphora dochmocera* has black tegulae and pale (metafemur and metatibia nearly completely pale) or relatively dark legs (black metafemur and pale metatibia). Although specimens of the *rufipes* group usually have a completely black abdomen, we have studied numerous specimens from southern Ukraine, Armenia, and Russian Caucasus that have a mostly black to completely yellow abdomen (even the thorax is partly yellow in some specimens). Because length of postocellar area, sculpture of mesopostnotum, and coloration of tegula, pronotum, and labrum varies among these specimens, it is not clear if they can be associated with any of the species from Northern Europe (lancets are not different from those on Figs 219–220). Recently, Macek (2016) reared three species of this group: *P. rufipes* from *Aquilegia* and two species from *Thalictrum*. The species identified by Macek (2016) as *P. sareptana* Kuznetzov-Ugamskij, 1924 could actually be *P. brevis* or *P. thalictrivora* (if these are different species) based on the pictures given for adults (we have seen the types of *P. sareptana* and *P. similis* Kuznetzov-Ugamskij, 1924, which are most similar to *P. brevis* and could indeed be synonyms of this species). Additional studies are needed to resolve species boundaries (if there are any) of the *Thalictrum*-feeding complex, and to associate males with females.

Comment on species delimitation

If a well defined morphospecies corresponds to exclusive genetic clusters (not mixed with other morphospecies) based on more than one unlinked genetic marker (independently segregating gene regions that reside on different chromosomes or far from each other on the same chromosome) and individuals of that morphospecies have different relationships based on those different markers, then we are probably dealing with a single and

well separated species. Unfortunately, such extensive genetic data (many markers and individuals) are not available for most species (due to lack of suitable material or/and high costs associated with sequencing). Nevertheless, it is possible to get some idea about species boundaries based on much smaller amounts of genetic data. Based on our results (see Discussion), within species divergence of mitochondrial genes seems to remain within 5% and based on nuclear genes within 1%. Although divergence higher than 2% in COI barcode sequences is commonly regarded as good evidence for different species (Ratnasingham and Hebert 2013), our data suggest that it is not unusual for within species divergence to be more than 3% or 4%. An example of this is *P. albitibia*, which can have COI barcode divergence of 4.6%, although neither morphology nor nuclear genes indicate that more than one species is involved. Therefore we do not consider COI divergence of less than 5% as good evidence for the existence of different species if there is no support from morphological and / or nuclear data.

On the other hand, where we have consistent morphological (based on adults or larvae) or ecological (different hosts) evidence without clear genetic evidence (even if based on all three genes we sampled) for the existence of different species within groups of closely related species, we have not synonymised these species. In our view, the genetic evidence we have so far is not sufficient (too few specimens and gene regions sampled) to decide this.

Assessment of morphological characters of the adults

For females, the shape of valvula 3 (apical sawsheath) is an important and relatively stable character for identification, but nevertheless it was necessary to key many species more than once, because of variability or intermediate character states. Still, it might be difficult to key out some species or individiuals, especially when valvula 3 is distorted (which usually happens with specimens dried from alcohol). In these cases lancets should be examined, although they can sometimes be very similar, even among distantly related species.

Males in *Pristiphora* usually lack good external non-colour characters, and therefore penis valves should be studied in most cases, which are stable within species and often show good differences between the species.

Coloration is the easiest character to observe, but unfortunately it often varies quite a lot within species. The abdomen can be completely pale or (almost) completely black in some species. Thorax coloration varies somewhat less, but can occasionally still vary from completely black to extensively pale. Head coloration is the most stable, in most species being black or with small pale spots. In a minority of species the head tends to be extensively pale around the eyes. Leg coloration can also vary extensively within species, but can often still be used for identification (see the Key). Coloration of the pterostigma is often a useful character for species identification, but it can be problematic in older pinned specimens. In species that normally have a dark pterostigma, the dark coloration can fade, causing the pterostigma to appear pale.

Unreliable characters. We have not used the length of the inner spur of the metatibia (in relation to the length of metatarsus for example) in species identification (e.g. Benson 1958; Zhelochovtsev and Zinovjev 1988, Haris 2006b) because the differences between the species (if there are any) are too small to be easily applied. Shape of the posterior margin of sternum 9 can be quite misleading. Several examined specimens of different species have a distinct notch, compared to other conspecific specimens with the margin entire, but because a notch is very sporadically present and does not correlate with other characters (which might indicate the existence of additional species), it seems to have no value in species identification and was therefore excluded from the key. However, in one exceptional case, the notch is large and deep and even has an outgrowth at the bottom of the notch (Fig. 52). Because it is a single specimen (based on penis valves, it is *P. biscalis*), it is not clear if this too is an aberration or there is an additional species involved. Vein 2r-rs of the forewing (see Fig. 1 in Prous et al. 2014) is another character that sporadically appears in some specimens, but without any phylogenetic correlation (we have observed it in *P. malaisei*, *P. robusta* [http://id.luomus.fi/GL.5198], and *P. staudingeri*), making it difficult to even recognise these specimens as *Pristiphora*.

Dichotomous key to *Pristiphora* adults

The key for females relies heavily on sawsheaths and ovipositors, and for males on penis valves, as these are most reliable for species identification. For females it is advisable to dissect the saw of one or more specimens of a series and for males it is in most cases necessary to pull out the genital capsule to see at least the tip of the penis valve. Fresh and clean specimens greatly help in species identification: particularly in females, where the shape of sawsheath can be of critical importance. Generally we recommend using the electronic key, which can be significantly faster (when using 'Best' and 'Next Best' options), easier to use, and more reliable because of the possibility to check more characters.

Females

Females of *P. dissimilis* are unknown.

1	a	Head dorsally extensively pale (Fig. 8) **2**
–	aa	Head dorsally black or with small brown or pale spots (Figs 6–7) **21**
2(1)	a	In dorsal view, valvula 3 with distinct scopa (e.g. Figs 104–107, 110–111, 115–116)..**3**
–	aa	In dorsal view, valvula 3 without distinct scopa (e.g. Figs 82–83, 93–99, 108–110, 112–114, 116, 120–122, 124, 126–127)...............................**11**
3(2)	a	Scopa partly positioned dorsally (Figs 111, 115)
	b	Claws without or with small subapical tooth (Figs 21–22)................**23**

–   aa   Scopa positioned posteriorly or posteroventrally (e.g. Figs 104–107, 110, 116)

bb   Claws with large subapical tooth (Figs 23–24) or if as 3b, consider other characters..**4**

4(3)   a   In lateral view, posterior margin of valvula 3 truncate (Fig. 117) **5**
–   aa   In lateral view, posterior margin of valvula 3 round (Fig. 109)...........**7**

5(4,14)   a   Hypopygium posteriorly excised (Fig. 63) .... ***P. decipiens***
–   aa   Hypopygium posteriorly not excised (Fig. 62) **6**

6(5)   a   Mesopleuron (mesepisternum + mesepimeron) extensively pale (Fig. 28)

b   Ventral margin of lancet not curved upwards (Fig. 163)

c   Body length 6.0–9.0 mm .... ***P. pseudodecipiens***
–   aa   Mesopleuron black (Fig. 27) or slightly pale

bb   Ventral margin of lancet apically strongly curved upwards (Fig. 157)

cc   Body length 4.0–6.5 mm..***P. abietina***

7(4)   a   Metatibia black (Fig. 29)

b   Claws with large subapical tooth or bifid (Fig. 24)

c   Valvula 3 with deep scopa (Fig. 107) ....***P. fausta***
–   aa   Metatibia at least with basal 2/3 pale (Fig. 47)

bb   Claws with large or small subapical tooth (Figs 22–24)

cc   Valvula 3 with shallow scopa (e.g. Figs 104–106, 110) **8**

8(7)   a   Mesepisternum completely or nearly completely pale (Fig. 336)

b   Thorax dorsally extensively pale to completely black (Figs 35–36, 51)

c   Claws with large subapical tooth (Fig. 335)

d   Lancet with numerous setae and apical serrulae protruding (Figs 331, 333) ... . ***P. cadma***
–   aa-dd   Combination of characters not as in a–d   9

9(8)   a   Scopa of valvula 3 shallow (Figs 108, 110)

b   Claws with small subapical tooth (Fig. 22)

c   Lancet with few setae and apical serrulae flat (Fig. 168)...............***P. bufo***
–   aa   Scopa of valvula 3 not shallow (104–105)

bb   Claws ***usually*** with large subapical tooth (Figs 23–24)

cc   Lancet without or with numerous setae, and apical serrulae more protruding (Figs 147–148, 153–155)..**10**

10(9,37) a   Pterostigma bicoloured (Fig. 43)

b   Mesepisternum black or partly pale (Figs 27–28)

c   Abdomen dorsally black or pale (Figs 49–50)

d   Lancet with numerous setae (Figs 153–155) .... ***P. conjugata***
–   aa   Pterostigma unicoloured (Fig. 42)

bb   Mesepisternum black (Fig. 27)

cc   Abdomen ***nearly always*** completely pale (Fig. 50)

dd   Lancet without setae (Figs 147–148) ....***P. testacea***

11(2)   a   Claws bifid or subbifid (Figs 24–25)

b   Abdomen completely pale (Figs 28, 50) ....***P. subbifida***

–   aa   Claws with small subapical tooth (Fig. 22)
            bb   Abdomen dorsally at least partly black (Figs 49, 51) **12**

12(11)   a   In lateral view, posterior margin of valvula 3 distinctly truncate and about
            as long as ventral margin (Fig. 118), and in dorsal view, slightly tapering
            from base to apex (Fig. 120) **13**

–   aa   Valvula 3 with different combination of characters (e.g. Figs 94, 98,
            108–110, 112–114, 116–117, 124–127)...**14**

13(12)   a   In posterior view, valvula 3 without scopa (Fig. 122)
            b   Pterostigma ***usually*** pale (Fig. 39) ....***P. gerula***

–   aa   In posterior view, valvula 3 with small scopa (Fig. 121)
            bb   Pterostigma ***usually*** dark (Fig. 42)....................................***P. saxesenii***

14(12)   a   In dorsal view, valvula 3 elongate, not tapering from base to apex, and
            with distinct scopa (Fig. 116)
            b   In lateral view, valvula 3 distinctly truncate (Fig. 117) **5**

–   aa   In dorsal view, valvula 3 with different combination of characters (Figs
            93, 95, 97, 99, 108, 112, 124, 126)
            bb   In lateral view, valvula 3 round or indistinctly truncate (Figs 109, 113,
            125)..**15**

15(14)   a   In dorsal view, valvula 3 abruptly constricted at apex, but not tapering
            completely (Fig. 126)
            b   In lateral view, valvula 3 indistinctly truncate (Fig. 113) **16**

–   aa   In dorsal view, valvula 3 not abruptly constricted (Figs 93, 97, 99, 108,
            112, 124) at apex, or tapering completely (Fig. 95)
            bb   In lateral view, valvula 3 round or indistinctly truncate (Figs 109, 113,
            125)..**17**

16(15)   a   Ovipositor (valvula 3 + valvifer 2, Figs 61–62) about 0.9 times as long as
            protibia (Benson, 1958)
            b   Distance between cenchri more than one and half times the breadth of
            one of them (Benson, 1958) ....***P. wesmaeli***

–   aa   Ovipositor about 1.1 times as long as protibia (Benson, 1958)
            bb   Distance between cenchri less than one and half times the breadth of
            one of them (Benson, 1958) ....***P. glauca***

17(15)   a   In dorsal view, valvula 3 narrow (Fig. 124)
            b   In lateral view, valvula 3 indistinctly truncate (Fig. 125)
            c   Mesepisternum smooth (Fig. 44)
            d   Abdomen sometimes dorsally extensively pale (Fig. 50) **18**

–   aa-dd   Combination of characters not as in a–d **19**

18(17)   a   Gap between basal serrulae small, and basal annuli with more numerous
            setae (Fig. 171)
            b   Abdomen (usually?) dorsally extensively pale (Fig. 50) ....***P. pallida***

–   aa   Gap between basal serrulae large, and basal annuli with fewer setae (Fig.
            172)
            bb   Abdomen (usually?) dorsally extensively black (Fig. 49) ...***P. subarctica***

19(17)   a   Mesepisternum matt and black (Fig. 46) ..... few specimens of ***carinata*** group
–   aa   Mesepisternum smooth and partly pale (Figs 28, 44).......................**20**
20(19)   a   In lateral view, valvula 3 not truncate (Fig. 109)
            b   Anterior protibial spur with velum (Fig. 34) ....***P. bufo***
–   aa   In lateral view, valvula 3 indistinctly truncate (Fig. 113)
            bb   Anterior protibial spur without velum, but with hairs (Fig. 33) ....
            ....***P. paralella***
21(1)   a   In dorsal view, valvula 3 with distinct scopa (Figs 75, 78, 86, 88, 100,
            104, 106–107, 111, 116)..**22**
–   aa   In dorsal view, valvula 3 without distinct scopa (Figs 67, 69, 72, 74–75,
            77–79, 82, 84, 86, 88–89, 91, 93, 95, 97, 99, 101, 103, 116, 119, 124)....**63**
22(21)   a   Scopa partly positioned dorsally (Figs 111, 115)
            b   Claws without, or with small subapical tooth (Figs 21–22)
            c   Body length 3.0–4.5 mm **23**
–   aa   Scopa positioned posteriorly or posteroventrally (Figs 75, 78, 86, 88,
            100, 104–107, 116)
            bb   Claws with large subapical tooth (Figs 23–25) or if as 22b consider
            other characters
            cc   Body length 3.0–11.0 mm..**25**
23(22,3)   a   Sawsheath (valvula 3 + valvifer 2; Figs 61–62) about 1.11 times longer
            than metatibia (Beneš et al. 1981), in dorsal view elongate
            b   Head dorsally black (Fig. 6)
            c   Posterior margin of pronotum black or narrowly pale (Fig. 35) ....
            ....***P. amphibola***
–   aa   Sawsheath about 0.93–1.03 times longer than metatibia (Beneš et al.
            1981), in dorsal view short or elongate
            bb   Head dorsally black to extensively pale (Figs 6–8)
            cc   Posterior margin of pronotum black to extensively pale (Fig. 35–36) **24**
24(23)   a   Sawsheath about 0.93–0.97 times longer than metatibia (Beneš et al.
            1981), in dorsal view short
            b   Tegula black or slightly pale (Fig. 35).......................................***P. nigella***
–   aa   Sawsheath about 1.00–1.03 times longer than metatibia (Beneš et al.
            1981), in dorsal view elongate
            bb   Tegula extensively pale (Figs 36–37) ....***P. parva***
25(22)   a   In lateral view, posterior margin of valvula 3 truncate (Fig. 117) **26**
–   aa   In lateral view, posterior margin of valvula 3 round (Figs 85, 87, 109) ...**29**
26(25)   a   Head, thorax, and abdomen black (Fig. 26)
            b   Hypopygium posteriorly not excised (Fig. 62)
            c   Body length 9–11 mm ....***P. robusta***
–   aa   Head, thorax, and abdomen ventrally at least partly pale (Figs 27–28)
            bb   Hypopygium posteriorly excised (Fig. 63) or if as 26b, consider other
            characters
            cc   Body length 4–9 mm..**27**

27(26)   a   Hypopygium posteriorly excised (Fig. 63)
           b   Ventral margin of lancet not strongly curved upwards (Figs 158–160) ... **28**
–   aa   Hypopygium posteriorly not excised (Fig. 62)
           bb   Ventral margin of lancet apically strongly curved upwards (Fig. 157)...
           ....***P. abietina***
28(27)   a   Mesopleuron ***usually*** extensively pale (Fig. 28)
           b   Ventral margin of lancet and its annuli more distinctly curved upwards
           (Fig. 160)... ***P. decipiens***
–   aa   Mesopleuron ***usually*** black or slightly pale (Fig. 27)
           bb   Ventral margin of lancet and its annuli less distinctly curved upwards
           (Figs 158–159) ....***P. compressa***
29(25)   a   In lateral view, valvula 3 with round outgrowth at posterior margin (Figs
           85, 87)
           b   In dorsal view elongate and with distinct or indistinct scopa (Figs 84, 86) **30**
–   aa-bb   Combination of characters not as in a–b **32**
30(29,67) a   In lateral view, valvula 3 more abruptly narrowed at apex (Fig. 87)
           b   In dorsal view, valvula 3 broader (Fig. 86)
           c   Anterior protibial spur with velum (Fig. 34).........................***P. insularis***
–   aa   In lateral view, valvula 3 less abruptly narrowed at apex (Fig. 85)
           bb   In dorsal view, valvula 3 narrower (Fig. 84)
           cc   Anterior protibial spur without velum, but with hairs (Fig. 33) **31**
31(30)   a   Thorax and abdomen extensively pale (Figs 28, 37, 50–51)..***P. nigriceps***
–   aa   Thorax and abdomen mostly black (Fig. 26), only sometimes abdomen
           nearly completely pale (Figs 49–50) and thorax slightly pale (Fig. 36) ....
           ....***P. leucopodia***
32(29)   a   Abdomen with red band (rarely in dorsal aspect entirely reduced), terga
           1 and 9–10 black (Figs 47–48)
           b   Scopa of valvula 3 with short medial projection (Figs 100, 104) **33**
–   aa–bb   Abdomen without red band (Figs 26–28, 49–51) ***or*** scopa of valvula
           3 with long medial projection (Fig. 106)..**34**
33(32)   a   Antenna ventrally partly paler than dorsally (Fig. 15)
           b   Supraclypeal area pale (Fig. 12)
           c   Postocellar area 1.5–2.5 times longer than diameter of lateral ocellus
           (Fig. 7) ....***P. condei***
–   aa   Antenna ***usually*** uniformly black (Fig. 14)
           bb   Supraclypeal area ***usually*** black (Figs 9–10)
           cc   Postocellar area 1.0–1.5 times longer than diameter of lateral ocellus
           (Fig. 6)... ***P. cincta***
34(32)   a   Valvula 3 with deep scopa and without long medial projection (Fig. 107)
           b   Claws without, or with minute subapical tooth (Figs 21–22)
           c   Abdomen ***usually*** ventrally black or partly pale (Fig. 27)
           d   Terga 9–10 ***usually*** extensively pale (Fig. 62)...................***P. punctifrons***

–   aa   Valvula 3 with shallow scopa *or* with long medial projection (Figs 75, 78, 100, 104, 106)
            bb   Claws with large subapical tooth (Figs 23–25) or if as 34b, consider other characters
            cc   Abdomen ventrally completely pale (Fig. 28) or if as 34c, consider other characters
            dd   Terga 9–10 black (Fig. 61) or if as 34d, consider other characters **35**
35(34)   a   Height of eye in lateral view *often* about 2–3 times as long as distance from dorsal margin of eye to dorsalmost point of head (Fig. 58)
            b   Clypeus emarginate (Fig. 13)
            c   Claws with small subapical tooth (Fig. 22)
            d   Abdomen *usually* ventrally black or partly pale (Fig. 27)
            e   Metatibia and often metatarsus nearly completely pale (Fig. 30)...***P. malaisei***
–   aa   Height of eye in lateral view about 3–4 times as long as distance from dorsal margin of eye to dorsalmost point of head (Fig. 59)
            bb   Clypeus truncate or slightly emarginate (Figs 9–10, 12)
            cc   Claws without, or with small or large subapical tooth (Figs 21–25)
            dd   Abdomen ventrally completely pale (Fig. 28) or if as 35d, consider other characters
            ee   Metatibia and metatarsus black (Fig. 29) or if as 35e, consider other characters...**36**
36(35)   a   Abdomen ventrally completely or nearly completely pale (Fig. 28).....**37**
–   aa   Abdomen ventrally black or partly pale (Figs 26–27).......................**38**
37(36)   a   Scopa of valvula 3 with long lateral lobes *and* long medial projection (Fig. 106)
            b   Claws *usually* with small subapical tooth (Fig. 22) **39**
–   aa   Scopa of valvula 3 with short lateral lobes *and / or* short medial projection (100, 104)
            bb   Claws *usually* with large subapical tooth (Figs 23–24) **10**
38(36)   a   Scopa of valvula 3 with long lateral lobes *and* long medial projection (Fig. 106)
            b   Postocellar area 1.0–1.5 times longer than diameter of lateral ocellus (Fig. 6)
            c   Claws *usually* with small subapical tooth (Fig. 22) **39**
–   aa   Scopa of valvula 3 with short lateral lobes *and / or* short medial projection (Figs 75, 78, 100, 104)
            bb   Postocellar area 1.0–2.5 times longer than diameter of lateral ocellus (Figs 6–7)
            cc   Claws without, or with small or large subapical tooth (Figs 21–25)...**40**
39(37,38) a   Metafemur (Fig. 28) and terga 9 and 10 (Fig. 62) completely yellow *or* at least metafemur apically slightly black
            b   Pterostigma dark (Fig. 42)
            c   Posterovenral tip of serrulae broader and gap between serrulae smaller (Figs 142–144) ....***P. pallidiventris***

–	aa	Metafemur completely yellow (Fig. 28) ***and*** terga 9 and 10 black (Fig. 61)
	bb	Pterostigma ***usually*** pale (Fig. 39)
	cc	Posterovenral tip of serrulae narrower and gap between serrulae larger (Fig. 141).. ***P. nigricans***

40(38) a   Abdomen laterally and ventrally with pale spots (Fig. 27)...................**41**
–   aa Abdomen laterally and ventrally black (Fig. 26)................................**42**
41(40) a   Clypeus at least partly pale (Figs 10, 12)
        b   Terga 9–10 pale (Fig. 62), ***often*** also valvula 3 pale (Fig. 65)
        c   Metafemur pale (Fig. 28)
        d   Serrulae papilliform (Fig. 203)..*P. alpestris*
–   aa Clypeus black (Fig. 9)
        bb Tergum 10 at least partly black (Fig. 61), valvula 3 completely black (Figs 61, 64)
        cc Metafemur extensively black (Figs 26–27)
        dd Serrulae flat (Fig. 130) ....*P. maesta*
42(40) a   Postocellar area 2.0–2.5 times longer than diameter of lateral ocellus (Fig. 7)
        b   Claws with large subapical tooth (Figs 23–24) **43**
–   aa-bb Combination of characters not as in a–b **44**
43(42) a   Flagellum about 2.4–2.5 times as long as width of head
        b   Metatarsomere 1 at least in apical 2/3 black (Fig. 29)
        c   Valvifer 2 pale (Fig. 62)
        d   Lancet with few setae and ventral margin of serrulae straight (Fig. 150) ....
            ....*P. geniculata*
–   aa Flagellum about 1.9–2.0 times as long as width of head
        bb Metatarsomere 1 completely or nearly completely pale (Fig. 31)
        cc Valvifer 2 black (Fig. 61)
        dd Lancet with numerous setae and ventral margin of serrulae slightly concave (Fig. 151) .... ***P. pseudogeniculata***
44(42) a   Mesopostnotum smooth (Fig. 19)
        b   Claws without subapical tooth (Fig. 21)
        c   Mesepisternum smooth (Fig. 44)
        d   Antenna ***usually*** ventrally paler than dorsally (Fig. 15) ....*P. appendiculata*
–   aa-dd Combination of characters not as in a–d 45
45(44) a   Postocellar area 1.5–2.5 times longer than diameter of lateral ocellus (Fig. 7)
        b   Mesepisternum smooth (Fig. 44)
        c   Lancet without setae (Figs 218–222)................................ ***rufipes* group**
–   aa Postocellar area 1.0–1.5 times longer than diameter of lateral ocellus (Fig. 6)
        bb Mesepisternum matt (Figs 45–46) or if as 45b, consider other characters
        cc Lancet with setae (Figs 188–202) or if as 45c, consider other characters...**46**
46(45) a   Metafemur mainly pale (Figs 27–28) **47**
–   aa Metafemur mainly black (Fig. 26) **49**

47(46)   a   Claws with large subapical tooth (Figs 23–24)
           b   Antenna ventrally paler than dorsally (Fig. 15)
           c   Metafemur whitish (Fig. 22 in Prous et al. 2016) .... ***P. leucopus***
–   aa   Claws with small subapical tooth (Fig. 22)
           bb   Antenna uniformly black (Fig. 14)
           cc   Metafemur yellowish (Fig. 28) **48**
48(47)   a   Lancet without setae (Figs 218–222)............................... ***rufipes*** **group**
–   aa   Lancet with numerous setae (Fig. 195) ....***P. aphantoneura*** (on
           Lathyrus) and ***P. luteipes*** (on *Salix*) (see Vikberg 2006 for minor characters
           for separating these species)
49(46)   a   Claws with long subapical tooth close to apical one (bifid) (Fig. 25)...**50**
–   aa   Claws with small or large subapical tooth clearly separated from apical
           one (Figs 22–24)..**51**
50(49)   a   Hind trochanters, trochantelli, and tibiae partly pale
           b   Antenna (usually?) ventrally at least slightly paler than dorsally (Fig. 15)
           c   Apical serrulae of lancet short and protruding, and tangium long and
           narrow (Fig. 199)...***P. bifida***
–   aa   Hind trochanters, trochantelli, and ***usually*** tibiae uniformly black or
           brown
           bb   Antenna uniformly black (Fig. 14)
           cc   Apical serrulae of lancet long and flat, and tangium short and broad
           (Fig. 200)... ***P. frigida***
51(49)   a   Tangium of lancet with distinct lobe (Fig. 191)
           b   Mesepisternum smooth (Fig. 44)
           c   Claws with small subapical tooth (rarely with large) (Fig. 22).............**52**
–   aa   Tangium of lancet without distinct lobe (Figs 188–190, 192–194, 196–198,
           201–202, 218–222)
           bb   Mesepisternum matt (Figs 45–46) or if as 51b, consider other characters
           cc   Claws with large subapical tooth (Figs 23–24) or if as 51c, consider
           other characters..**53**
52(51)   a   Antenna ventrally distinctly paler than dorsally (Fig. 15).... ***P. ruficornis***
–   aa   Antenna ***usually*** uniformly black (Fig. 14), but sometimes ventrally
           slightly paler than dorsally .... ***P. melanocarpa***
53(51)   a   Lancet without setae (Figs 218–222)
           b   Mesepisternum smooth (Fig. 44)
           c   Claws with small subapical tooth (Fig. 22) .... ***rufipes*** **group**
–   aa   Lancet with numerous or few setae (Figs 188–190, 192–194, 196–198,
           201–202)
           bb   Mesepisternum matt (Figs 45–46) or if as 53b, consider other characters
           cc   Claws with large subapical tooth (Figs 23–24) or if as 53c, consider
           other characters..**54**
54(53)   a   Inner surface of lancet with small spiny pectines (or dentes semicircu-
           lares) that reach sclerora (Figs 188–190, 194) **55**

–   aa   Inner surface of lancet without small spiny pectines (Figs 192–193, 196–198, 201–202)...**58**

55(54) a Pterostigma basally dark brown and apically brown (Fig. 40)
        b Mesepisternum smooth (Fig. 44)
        c Lancet with numerous setae (Fig. 188)
        d Apical serrulae of lancet short (Figs 188, 194)....................................**56**
–   aa Pterostigma uniformly yellow or brown (Fig. 39)
        bb   Mesepisternum ***usually*** at least slightly matt (Figs 45–46)
        cc Lancet with few setae (Fig. 189) or if as 55c, consider other characters
        dd   Apical serrulae of lancet long (Fig. 190), or if as 55d, consider other characters...**57**

56(55) a Antenna (usually?) ventrally paler than dorsally (Fig. 312)
        b Trochanters and trochantelli (usually?) pale (Fig. 312)
        c Pronotum (usually?) extensively pale (Fig. 311)
        d Inner surface of lancet with (usually?) indistinct spiny pectines (or dentes semicirculares) that reach sclerora (Fig. 194)................***P. caraganae* sp. n.**
–   aa   Antenna uniformly black (Fig. 14)
        b   Trochanters and trochantelli black (Fig. 26)
        c   Pronotum black or posterior margin narrowly pale (Fig. 35)
        d   Inner surface of lancet with distinct spiny pectines (or dentes semicirculares) that reach sclerora (Fig. 188)...***P. albitibia***

57(55) a Lancet with numerous setae (Fig. 190)
        b Apical serrulae of lancet long (Fig. 190) .... ***P. sootryeni***
–   aa   Lancet with few setae (Figs 189)
        bb   Apical serrulae of lancet short (Figs 189)...........................***P. astragali***

58(54) a Lancet with few setae (Fig. 201)
        b Serrulae of lancet flat (Fig. 201)
        c Mesepisternum at least slightly matt (Fig. 45)
        d Antenna ***usually*** ventrally slightly paler than dorsally (Fig. 15)....***P. pusilla***
–   aa Lancet with numerous setae (Figs 192–193, 196–198, 202)
        bb   Serrulae of lancet protruding (Figs 192–193, 196, 202) or if as 58b, consider other characters
        cc Mesepisternum smooth (Fig. 44) or if as 58c, consider other characters
        dd   Antenna uniformly black (Fig. 14) or if as 58d, consider other characters...**59**

59(58) a Mesepisternum (usually?) strongly matt (Fig. 46)
        b Antenna uniformly black (Fig. 14)
        c Pterostigma (usually?) uniformly yellow or brown (Fig. 39)
        d Arctic habitats...***P. staudingeri***
–   aa   Mesepisternum (usually?) smooth or slightly matt (Figs 44–45)
        bb   Antenna ventrally paler than dorsally (Fig. 15) or if as 59b, consider other characters

	cc	Pterostigma uniformly yellow to dark brown (Figs 39, 42), or basally dark brown and apically brown (Fig. 40)
	dd	***Usually*** non-arctic habitats..**60**
60(59)	a	Apical serrulae protruding (Figs 192–193, 196)
	b	Antenna ***often*** ventrally paler than dorsally (Fig. 15) **61**
–	aa	Apical serrulae flat (Figs 197–198)
	bb	Antenna uniformly black (Fig. 14) or if as 60b, consider other characters..**62**
61(60)	a	Pterostigma ***usually*** basally dark brown and apically brown (Fig. 40)
	b	Setae of lancet more distinct (Fig. 196)...................................***P. confusa***
–	aa	Pterostigma ***usually*** uniformly dark brown (Fig. 42)
	bb	Setae of lancet less distinct (Figs 192–193) ....

......***P. armata*** (on *Crataegus*) and ***P. leucopus*** (on *Tilia*) (see Grearson and Liston 2012 and Prous et al. 2016 for discussion separating these species)

62(60)	a	Tangium of lancet without fold (Fig. 198)
	b	Antenna uniformly black (Fig. 14)
	c	Pterostigma uniformly yellow (Fig. 39) ....***P. subopaca***
–	aa	Tangium of lancet with fold (Fig. 197)
	bb	Antenna ventrally slightly paler than dorsally (Fig. 15)
	cc	Pterostigma (usually?) basally dark brown and apically brown (Fig. 40)....

....***P. opaca***

63(21)	a	Claws bifid or subbifid (Figs 24–25) **64**
–	aa	Claws without or with small or large subapical tooth (Figs 21–23) ...**66**
64(63)	a	Pterostigma dark (Fig. 42)
	b	Mesepisternum smooth (Fig. 44)
	c	Valvula 3 in dorsal view more or less square-shaped or tapering towards apex, and longest setae not concentrated in two dense, lateroapically positioned bundles (Fig. 82)..**65**
–	aa	Pterostigma pale (Fig. 39)
	bb	Mesepisternum ***often*** matt (45–46)
	cc	Valvula 3 in dorsal view more or less square-shaped, and longest setae concentrated mainly in two dense, lateroapically positioned bundles (Fig. 91)...***P. sermola***
65(64)	a	Supraclypeal area black (Figs 9–10)
	b	Head dorsally ***usually*** black (Fig. 6)
	c	Legs ***often*** extensively black...***P. tetrica***
–	aa	Supraclypeal area pale (Fig. 12)
	bb	Head dorsally with pale spots (Fig. 7)
	cc	Legs mostly pale (Fig. 28) ....***P. depressa***
66(63)	a	Abdomen with red band, terga 1 and 7–10 black (Fig. 47)
	b	In dorsal view, valvula 3 narrow (Fig. 124)
	c	In lateral view, posterior margin of valvula 3 somewhat truncate, and without round outgrowth (Fig. 125).......................................***P. erichsonii***

–   aa   Abdomen without red band (Figs 26–27), or if present (few specimens of *P. laricis*), then valvula 3 not narrow in dorsal view (Fig. 79) and posteriorly not truncate in lateral view (Fig. 109)

            bb   In dorsal view, valvula 3 broad (Figs 67, 69, 72, 74–75, 77–79, 88–89, 91, 93, 95, 97, 101, 116) or if as 66b, consider other characters

            cc   In lateral view, posterior margin of valvula 3 with different combination of characters (Figs 73, 85, 87, 109) or if as 66c, consider other characters **67**

67(66)   a   In lateral view, valvula 3 with round outgrowth at posterior margin (Figs 85, 87)

            b   In dorsal view elongate and with distinct or indistinct scopa (Figs 84, 86)..**30**

–   aa-bb   Combination of characters not as in a–b **68**

68(67)   a   In lateral view, posterior margin of valvula 3 distinctly truncate (Fig. 117)

            b   In dorsal view valvula 3 elongate and with scopa (Fig. 116) **69**

–   aa-bb   Combination of characters not as in a–b **71**

69(68)   a   Head, thorax, and abdomen black (Fig. 26)

            b   Hypopygium posteriorly not excised (Fig. 62)

            c   Body length 9–11 mm ....***P. robusta***

–   aa   Head, thorax, and abdomen ventrally at least partly pale (Fig 27–28)

            bb   Hypopygium posteriorly excised (Fig. 63) or if as 69b, consider other characters

            cc   Body length 4–9 mm...**70**

70(69)   a   Hypopygium posteriorly excised (Fig. 63)

            b   Ventral margin of lancet not strongly curved upwards (Figs 158–159) ... .***P. compressa***

–   aa   Hypopygium posteriorly not excised (Fig. 62)

            bb   Ventral margin of lancet apically strongly curved upwards (Fig. 157) ... .***P. abietina***

71(68)   a   Height of eye in lateral view *often* about 2–3 times as long as distance from dorsal margin of eye to dorsalmost point of head (Fig. 58)

            b   Clypeus emarginate (Fig. 13)

            c   In lateral view, posterior margin of valvula 3 round (Fig. 73) **72**

–   aa   Height of eye in lateral view about 3–4 times as long as distance from dorsal margin of eye to dorsalmost point of head (Fig. 59)

            bb   Clypeus truncate or slightly emarginate (Figs 9–10, 12)

            cc   In lateral view, posterior margin of valvula 3 slightly truncate (Figs 70, 123) or if as 71c, consider other characters **73**

72(71)   a   Valvula 3 without scopa but with indistinct or distinct carina posteriorly (Figs 73, 74)

            b   Lancet without setae (Fig. 136)

            c   Pronotum extensively pale (Figs 36–37) .... ***P. dasiphorae***

–   aa   Valvula 3 with small scopa (Fig. 75)

            bb   Lancet with numerous setae (Fig. 137)

| | cc | Pronotum *usually* darker...*P. malaisei* |

73(71)   a   Labrum asymmetrical with right lobe much longer than left (Fig. 11)
          b   Mesepisternum smooth (Fig. 44)
          c   Claws without subapical tooth (Fig. 21)
          d   Pterostigma *sometimes* basally paler than apically (Fig. 41)
          e   Body length 3.0–4.5 mm **74**
–   aa Labrum *usually* symmetrical, or asymmetrical with right lobe slightly
          longer than left (Figs 9–10, 12)
          bb Mesepisternum matt (Figs 45–46) or if as 73b, consider other characters
          cc Claws with small or large subapical tooth (Figs 22–23), or if as 73c,
          consider other characters
          dd Pterostigma *usually* unicoloured (Figs 39, 42)
          ee Body length 3.0–8.0 mm..**75**
74(73)   a   Valvula 3 narrow (Fig. 103)
          b   Metafemur *usually* mostly black (Fig. 26) ....*P. retusa*
–   aa Valvula 3 broader (Figs 101–102)
          bb Metafemur completely pale (Fig. 28) ....*P. exigua*
75(73)   a   Valvula 3 without scopa and distinct posterior carina, and slightly taper-
          ing from base to apex (Figs 95, 99), *or* valvula 3 long and narrow and with
          indistinct scopa (Fig. 119) **76**
–   aa Valvula 3 with distinct posterior carina (Figs 66–69) *or* more or less
          square shaped in dorsal view and *usually* with small scopa (Figs 71–72,
          76–81, 88–94, 96–97)...**79**
76(75)   a   Valvula 3 long, not tapering from base to apex, and with or without in-
          distinct scopa (Figs 119, 123)
          b   Mesepisternum smooth (Fig. 44) ....*P. tenuiserra*
–   aa Valvula 3 short, slightly tapering from base to apex and without scopa
          (Figs Figs 95, 99)
          bb Mesepisternum matt (Fig. 46) or if as 76b, consider other characters ...**77**
77(76)   a   Mesepisternum smooth (Fig. 44)
          b   Pterostigma dark (Fig. 42)
          c   Claws without subapical tooth (Fig. 21)...................... *P. dedeara* **sp. n.**
–   aa Mesepisternum matt (Fig. 46)
          bb Pterostigma *usually* pale (Fig. 39)
          cc Claws with small subapical tooth (Fig. 22) **78**
78(77)   a   Valvifer 2 black (Fig. 61)
          b   Tergum 10 *usually* black (Fig. 61)
          c   Clypeus black (Fig. 9)
          d   Metatarsus *usually* mostly pale (Figs 30–31)
          e   Lancet with numerous setae (Fig. 156)....................................*P. mollis*
–   aa Valvifer 2 *often* pale (Fig. 62)
          bb Tergum 10 *often* pale (Fig. 62)
          cc Clypeus *often* partly pale (Fig. 10)

           dd Metatarsus mostly black (Fig. 29) or if as 78d, consider other characters

           ee Lancet without setae (Figs 210–217) .... ***carinata* group**

79(75)   a   In lateral view, ventral margin of valvula 3 straight along most of its length (Fig. 70)

           b Valvula 3 posteriorly with distinct carina (Figs 68–69)

           c Metatibia only with small dark area at apex (Fig. 30) ....***P. angulata***

–   aa   In lateral view, ventral margin of valvula 3 bending gradually upwards (Figs 66, 71, 109)

           bb Valvula 3 posteriorly without distinct carina (Figs 71–72, 76–81, 88–94, 96–97) or if as 79b, consider other characters

           cc Metatibia with small dark area at apex to completely black...............**80**

80(79)   a Valvula 3 with distinct posterior carina and without scopa (Figs 66–67)

           b Pronotum extensively pale (Fig. 36)

           c Basal 1/3 or less of metatibia pale (Fig. 26)

           d Clypeus black (Fig. 9)

           e Body length 3.0–5.0 mm ....***P. abbreviata***

–   aa   Valvula 3 without posterior carina, but ***usually*** with small scopa (Figs 71–72, 76–81, 88–94, 96–97)

           bb Pronotum black to extensively pale (Figs 35–37)

           cc Metatibia completely pale to completely black

           dd Clypeus pale (Figs 10, 12) or if as 80d, consider other characters

           ee Body length 3.0–8.0 mm..**81**

81(80)   a Claws with large subapical tooth (Fig. 23)

           b Abdomen completely black (Fig. 26)

           c Metatarsomere 1 completely or nearly completely pale (Figs 30–31)

           d Postocellar area 2.0–2.5 times longer than diameter of lateral ocellus (Fig. 7)

           e Mesepisternum smooth (Fig. 44)

           f Body length 7–8 mm.. ***P. pseudogeniculata***

–   aa-ff Combination of characters not as in a–f.......................................**82**

82(81)   a Cercus clearly extends beyond apex of valvula 3 (Fig. 79)

           b Anterior protibial spur without velum (Fig. 33)

           c Mesepisternum smooth (Fig. 44) **83**

–   aa-cc Combination of characters not as in a–c **84**

83(82)   a Labrum pale (Figs 10, 12)

           b Pronotum extensively pale (Fig. 36)

           c Tangium with (usually?) two campaniform sensilla and lancet with numerous setae (Figs 177–178)...***P. laricis***

–   aa Labrum black or dark brown (Fig. 9)

           bb Pronotum black or only posterior margin narrowly pale (Fig. 35)

           cc Tangium without (usually?) campaniform sensilla and lancet with fewer setae (Figs 174–176) .... ***P. friesei***

84(82)   a Mesepisternum smooth (Fig. 44) **85**

–   aa Mesepisternum matt (Fig. 46) **90**

85(84) a   Abdomen completely black (Fig. 26)
        b   Claws without subapical tooth (Fig. 21)
        c   Pronotum black
        d   Body length 3.0–4.0 mm...*P. monogyniae*
–   aa-dd   Combination of characters not as in a–d. **86**
86(85) a   Abdomen laterally and ventrally with pale patches (Fig. 27)
        b   Valvula 3 in dorsal view more or less square-shaped and longest setae not
        concentrated in two dense, lateroapically positioned bundles (Figs 77–78,
        88–89)...**87**
–   aa   Abdomen black (Fig. 26) *or* only terga 9–10 and valvifer 2 pale (Fig. 62)
        bb   Valvula 3 in dorsal view more or less square-shaped and longest setae
        concentrated mainly in two dense, lateroapically positioned bundles (Fig.
        91)..*micronematica* **group**
87(86) a   Serrulae of lancet flat (Figs 129–130)
        b   Pterostigma *usually* dark (Fig. 42)..**88**
–   aa   Serrulae of lancet distinctly papilliform (Figs 203–204)
        bb   Pterostigma pale (Fig. 39) **89**
88(87) a   Cercus black (Fig. 77)
        b   Clypeus at least partly pale (Fig. 10)
        c   Valvula 3 somewhat narrower (Figs 76–77) .... *P. biscalis*
–   aa   Cercus *usually* pale (Fig. 78)
        bb   Clypeus black (Fig. 9)
        cc   Valvula 3 somewhat broader (Fig. 78)....................................*P. maesta*
89(87) a   Valvula 3 somewhat narrower (Fig. 89)
        b   Middle serrulae small compared to height of lancet (ratio around 1/10–1/7)
        (Fig. 204)...*P. pseudocoactula*
–   aa   Valvula 3 somewhat broader (Fig. 88)
        bb   Middle serrulae large compared to height of lancet (ratio around 1/6–1/4)
        (Fig. 203) ....*P. alpestris*
90(84) a   Serrulae of lancet distinctly papilliform (Fig. 204)
        b   Lancet with setae (Fig. 204)......................................*P. pseudocoactula*
–   aa-bb   Combination of characters not as in a–b 91
91(90) a   Valvula 3 in dorsal view more or less square-shaped *and* longest setae con-
        centrated mainly in two dense, lateroapically positioned bundles (Fig. 91)
        b   Lancet with setae (Figs 205–209).........................*micronematica* **group**
–   aa   Valvula 3 in dorsal view tapering towards apex *and / or* with longest
        setae not concentrated in two dense, lateroapically positioned bundles
        (Figs 93–99)
        bb   Lancet without setae (Figs 210–217) ....*carinata* **group**

Males

Males of *P. aphantoneura*, *P. astragali*, *P. depressa*, and *P. subbifida* are unknown.

1	a At least mesepisternum partly pale (Fig. 28) **2**
–	aa At least mesepisternum black (Figs 26–27) **22**
2(1)	a Metatibia black (Fig. 29)
	c Metafemur black (Fig. 26)
	b Claws with large subapical tooth or bifid (Fig. 24) .... *P. fausta*
–	aa At least basal 2/3 of metatibia pale (Figs 26, 30–31)
	bb Metafemur *usually* pale (Figs 27–28)
	cc Claws *usually* with small subapical tooth (Fig. 22) **3**
3(2)	a Abdomen with red band dorsally
	b Paravalva somewhat rhombus-shaped, pseudoceps somewhat rectangular and unmodified, valvispina small, slightly bent and asymmetrical at apex (Fig. 290) .... *P. erichsonii*
–	aa Abdomen without red band
	bb Penis valve different **4**
4(3)	a Supraclypeal area black (Figs 9–10)
	b Antenna uniformly black (Fig. 14)
	c Antenna with numerous stout black setae among finer paler ones (Figs 16, 18)
	d Paravalva rectangular, with straight ventral margin, and apically distinctly shorter than pseudoceps; pseudoceps somewhat rectangular and unmodified; relatively large and straight valvispina forming right or acute angle with paravalva (Fig. 254) .... *P. insularis*
–	aa Supraclypeal area pale (Fig. 12)
	bb Antenna uniformly black to uniformly pale (Figs 14–18)
	cc Antenna without or apparently without numerous stout black setae among finer paler ones (Fig. 17), or if as 4c, consider other characters
	dd Penis valve different **5**
5(4)	a Mesepisternum completely or nearly completely pale (Fig. 336)
	b Valvispina straight and positioned in middle or upper third of paravalva (Fig. 337)
	c Paravalva somewhat oval shaped or rectangular (Fig. 337)
	d Pseudoceps unmodified, more or less rectangular (Fig. 337) .... *P. cadma*
–	aa-dd Combination of characters not as in a–d **6**
6(5)	a Paravalva and pseudoceps more or less rectangular (Figs 224–226)
	b Valvispina straight or slightly bent and positioned in middle or upper third of paravalva (Figs 224–226) .... *P. pallidiventris*
–	aa-bb Combination of characters not as in a–b **7**
7(6)	a Claws *usually* with large subapical tooth (Fig. 23)
	b Paravalva basally much broader than apically (Figs 255, 257, 259)

        c   Pseudoceps more or less rectangular, not distinctly modified (Figs 255,
        257, 259)
        d   Valvispina simple and straight or slightly bent and positioned close to but
        nevertheless distinctly removed from ventral margin of paravalva (Figs 255,
        257, 259)..*P. conjugata*
–   aa-dd   Combination of characters not as in a–d **8**
8(7)   a   Valvispina absent or indistinct (Figs 303–305)
        b   Pseudoceps dorsally with loose membranous region covered with hair
        (Figs 303–305)
        c   Propleuron black (Fig. 26)
        d   Claws *sometimes* bifid (Fig. 25)...........................*micronematica* **group**
–   aa   Valvispina distinct (Figs 275–276, 278, 283–289, 291–296, 302)
        bb   Pseudoceps without loose membranous region (Figs 275–276, 278,
        283–289, 291–296, 302)
        cc   Propleuron *often* pale (Fig. 28)
        dd   Claws without or with small subapical tooth (Figs 21–22)................**9**
9(8)   a   Valvispina small, simple, and bent dorsally (Figs 293–295)
        b   Paravalva and pseudoceps similar in size and shape (Figs 293–295)
        c   Paravalva dorsally concave, and ventrally convex or more or less straight
        (Figs 293–295)
        d   Body length 3.0–4.5 mm..**84**
–   aa-dd   Combination of characters not as in a–d **10**
10(9)   a   Pseudoceps with spines, and narrow tip extending far from valvispina
        (Fig. 275)
        b   Valvispina small, simple, and straight (Fig. 275) ....*P. bufo*
–   aa   Pseudoceps without spines, and with broad or narrow tip not extending
        far from paravalva (Figs 276, 278, 283–289, 291–292, 296, 302)
        bb   Valvispina variously shaped (Figs 276, 278, 283–289, 291–292, 296,
        302)..**11**
11(10) a   Valvispina large and bent, replacing half of paravalva (Figs 276, 278).**86**
–   aa   Valvispina smaller and paravalva less modified (Figs 283–289, 291–292,
        296, 302)..**12**
12(11) a   Valvispina large, gradually bent, *and* simple (Fig. 296) ....*P. paralella*
–   aa   Valvispina smaller, straight, abruptly bent, *or* dorsally serrate (Figs 283–
        289, 291–292, 302)..**13**
13(12) a   Pseudoceps with distinctly narrow tip (Fig. 302)
        b   Valvispina simple *and* more or less straight (Fig. 302) ....*P. tenuiserra*
–   aa   Pseudoceps with broad tip (Figs 283–289, 291–292)
        bb   Valvispina bent, dorsally serrate (Figs 283–288, 291–292), or if as 13b,
        consider other characters..**14**
14(13) a   Valvispina sharply bent, and short and broad (Figs 291–292)
        b   Paravalva somewhat trapez-shaped (Figs 291–292) **15**
–   aa   Valvispina not sharply bent, and narrower (Figs 283–289)

bb   Paravalva not trapez-shaped, or less distinctly trapez-shaped (Figs 283–289)...**16**

15(14)   a   Ventral margins of paravalva and valvispina forming obtuse angle (Fig. 292)

b   Paravalva anteriorly (usually?) slightly more concave (Fig. 292)..............
....***P. wesmaeli***

–   aa   Ventral margins of paravalva and valvispina forming almost right angle (Fig. 291)

bb   Paravalva anteriorly (usually?) slightly less concave (Fig. 291) ...***P. glauca***

16(14)   a   Valvispina small, more or less straight, and almost simple (Fig. 289)

b   Paravalva broad (Fig. 289)

c   Body length 8–9 mm ....***P. robusta***

–   aa-cc   Combination of characters not as in a–c **17**

17(16)   a   Paravalva and pseudoceps relatively narrow (Fig. 283)

b   Valvispina distinctly bent, and with thin and non-serrate dorsal margin (Fig. 283)

c   Body length 3.5–5.0 mm ....***P. abietina***

–   aa-cc   Combination of characters not as in a–c 18

18(17)   a   Valvispina simple and angled in middle (Fig. 285) .... ***P. decipiens***

–   aa   Valvispina with at least serrate dorsal margin and angled or not angled in middle (Figs 284, 286–288) **19**

19(18)   a   Paravalva relatively broad and abruptly narrowing at apex (Figs 284, 288)...**20**

–   aa   Paravalva slightly narrower and more gradually narrowing at apex (Figs 286–287)...**21**

20(19)   a   Apical margin of paravalva more or less entirely convex (Fig. 284)

b   Valvispina smaller and more or less straight (Fig. 284) ....***P. compressa***

–   aa   Apical margin of paravalva with concave part followed by convex part (Fig. 288)

bb   Valvispina larger and slightly bent (Fig. 288) ....***P. saxesenii***

21(19)   a   Valvispina with dorsal and ventral thinned and serrate margins (Fig. 286)

b   Paravalva more elongate (Fig. 286)...***P. gerula***

–   aa   Valvispina only with dorsal thinned and serrate margin (Fig. 287)

bb   Paravalva less elongate (Fig. 287) ....***P. pseudodecipiens***

22(1)   a   Tergum 8 with distinct apical projection (Fig. 57)

b   Antenna ventrally distinctly paler than dorsally, or uniformly pale (Figs 16, 18)

c   Claws with large subapical tooth (Figs 23–24)

d   Mesepisternum smooth (Fig. 44) .... ***P. armata*** (on *Crataegus*) and ***P. leucopus*** (on *Tilia*) (see Grearson and Liston 2012 and Prous et al. 2016 for discussion separating these species)

–   aa   Tergum 8 without distinct apical projection (Figs 55–56)

bb   Antenna uniformly black to uniformly pale (Figs 14–18)

	cc Claws without or with small subapical tooth (Figs 21–22), or if as 22c, consider other characters
	dd Mesepisternum matt (Figs 45–46) or if as 22d, consider other characters..**23**
23(22)	a Terga and sterna 2–6 at least partly pale (Fig. 27) **24**
–	aa Terga and sterna 2–6 black (Fig. 26) **43**
24(23)	a Metatibia black (Fig. 29)
	b Metafemur black (Fig. 26)
	c Claws with large subapical tooth or bifid (Figs 23–25) **25**
–	aa At least basal 1/3 of metatibia pale (Fig. 26)
	bb Metafemur pale (Figs 27–28) or if as 24b, consider other characters
	cc Claws without or with small subapical tooth (Figs 21–22), or if as 24c, consider other characters..**26**
25(24)	a Head extensively pale around eyes (Fig. 8)
	b Paravalva and valvura almost forming right angle (Fig. 299)
	c Valvispina broad with curved anteroventral margin (Fig. 299) ...***P. fausta***
–	aa Head at most with small brown or pale spots (Figs 6–7)
	bb Paravalva and valvura more or less at the same level (Fig. 301)
	cc Valvispina thin and symmetrical (Fig. 301)..............................***P. tetrica***
26(24)	a Basal 1/3–1/2 of metatibia pale (Fig. 26)
	b Supraclypeal area pale (Fig. 12)
	c Abdomen with red band (Fig. 48)
	d Claws ***usually*** with large subapical tooth (Fig. 23)
	e Dorsoapical margin of paravalva and dorsal margin of valvispina forming distinct s-shape (Fig. 232)
	f Valvispina at ventral margin of paravalva, and gradually merging with paravalva at ventral and dorsal side ....***P. condei***
–	aa-ff Combination of characters not as in a–f.......................................**27**
27(26)	a Supraclypeal area black (Figs 9–10)
	b Claws ***usually*** bifid or subbifid (Figs 24–25)
	c Penis valve with long, bent, and symmetrical valvispina (Fig. 301) ....***P. tetrica***
–	aa-cc Combination of characters not as in a–c 28
28(27)	a Supraclypeal area pale (Fig. 12) **29**
–	aa Supraclypeal area black (Figs 9–10) **32**
29(28)	a Abdomen with red band dorsally
	b Antenna extensively pale (Figs 16, 18)
	c Claws with small subapical tooth (Fig. 22)
	d Paravalva somewhat rhombus-shaped, pseudoceps somewhat rectangular and unmodified, valvispina small, slightly bent, and asymmetrical at apex (Fig. 290).. ***P. erichsonii***
–	aa-dd Combination of characters not as in a–d **30**
30(29)	a Claws ***usually*** with large subapical tooth (Fig. 23)

b   Abdomen ***often*** completely pale (Fig. 50)

c   Pterostigma dark (Fig. 42)

d   Paravalva apically distinctly narrower than pseudoceps; pseudoceps more or less rectangular, unmodified; valvispina small, simple and bent upwards (Fig. 261)..***P. testacea***

–   aa-dd   Combination of characters not as in a–d **31**

31(30)   a   Dorsal margin of paravalva somewhat s-shaped (Figs 294, 296)

b   Valvispina small or large, and directed dorsally (Figs 294, 296)

c   Claws without, or with small subapical tooth (Figs 21–22)

d   Body length 3.0–5.5 mm...**76**

–   aa   Dorsal margin of paravalva not s-shaped (Figs 223–227, 231, 233–237, 243–251, 253–254, 303–309)

bb   Valvispina absent, or larger, ***or*** not directed dorsally (Figs 223–227, 231, 233–237, 243–251, 253–254, 303–309)

cc   Claws with large subapical tooth (Figs 23–25) or if as 31c, consider other characters

dd   Body length 4.0–7.0 mm...**32**

32(31,28)   a   Anterior margin of paravalva forming acute or right angle with valvispina (Figs 253–254)

b   Valvispina arising from ventral margin of paravalva (Figs 253–254)...**33**

–   aa-bb   Combination of characters not as in a–b **34**

33(32,53)   a   Valvispina larger (Fig. 254)

b   Ventral margin of paravalva not protruding (Fig. 254).........***P. insularis***

–   aa   Valvispina smaller (Fig. 253)

bb   Ventral margin of paravalva protruding (Fig. 253) ....***P. biscalis***

34(32)   a   Valvispina absent or indistinct (Figs 303–305)

b   Pseudoceps dorsally with loose membranous region covered with setae (Figs 303–305)

c   Claws ***sometimes*** bifid (Fig. 25) ....***micronematica*** **group**

–   aa   Valvispina distinct (Figs 223–227, 231, 233–237, 243–251)

bb   Pseudoceps without loose membranous region (Figs 223–227, 231, 233–237, 243–251)

cc   Claws without or with small subapical tooth (Figs 21–22)................**35**

35(34)   a   Valvispina long and ventrally bent (Fig. 237)

b   Pseudoceps apically relatively narrow and ventrally bent (Fig. 237)........
....***P. dissimilis***

–   aa   Valvispina not ventrally bent (Figs 223–227, 231, 233–236, 243–251)

bb   Pseudoceps not ventrally bent (Figs 223–227, 231, 233–236, 243–251) **36**

36(35)   a   Dorsal margin of penis valve from tip of valvura to tip of pseudoceps almost forming semicircle (Figs 233–236)

b   Paravalva and pseudoceps broad (Figs 233–236)

c   Mesepisternum ***sometimes*** matt (Figs 45–46) **37**

–	aa	Dorsal margin of penis valve not forming semicircle (Figs 223–227, 231, 243–251)
	bb	Paravalva and pseudoceps narrow (Figs 223–227, 231) or if as 36b, consider other characters
	cc	Mesepisternum *usually* smooth (Fig. 44) **38**
37(36)	a	Valvispina close to ventral margin of paravalva (Figs 234, 236) ....***P. pseudocoactula***
–	aa	Valvispina distinctly removed from ventral margin of paravalva (Figs 233, 235)..***P. alpestris***
38(36)	a	Penis valve relatively small and narrow (Fig. 231)
	b	Pseudoceps apically distinctly narrowed (Fig. 231)
	c	Valvispina starting from ventral margin of paravalva and dorsally with round hump (Fig. 231)...***P. punctifrons***
–	aa-cc	Combination of characters not as in a–c **39**
39(38)	a	Paravalva and pseudoceps of similar size and shape (Figs 223–226)
	b	Ventral margin of paravalva more or less straight (Figs 223–226)
	c	Valvispina positioned in middle or upper third of paravalva (Figs 223–226) **40**
–	aa-cc	Combination of characters not as in a–c **41**
40(39)	a	Penis valve elongate, paravalva and pseudoceps more or less rectangular (Figs 224–226)
	b	Pterostigma dark (Fig. 42) .... ***P. pallidiventris***
–	aa	Paravalva and pseudoceps broader, less rectangular (Fig. 223)
	bb	Pterostigma (usually?) pale (Fig. 39) .... ***P. nigricans***
41(39)	a	Valvispina positioned more or less in middle of paravalva (Fig. 227)
	b	Dorsally, paravalva narrowing gradually at apex (Fig. 227)......***P. maesta***
–	aa	Valvispina positioned in lower part of paravalva (Figs 243–251)
	bb	Dorsally, paravalva narrowing abruptly at apex (Figs 243–251)........**42**
42(41)	a	Paravalva more elongate (Figs 244, 246)
	b	Valvispina longer (Figs 244, 246)
	c	Abdomen *sometimes* with red band (Fig. 47)
	d	Mesepisternum *sometimes* matt (Fig. 45) .... ***P. cincta***
–	aa	Paravalva less elongate (Figs 243, 245, 247–251)
	bb	Valvispina *usually* shorter
	cc	Abdomen without red band
	dd	Mesepisternum smooth (Fig. 44) .... few specimens of ***rufipes*** group
43(23)	a	Penis valve apically truncate (Figs 297–298)
	b	Valvispina absent (Figs 297–298)
	c	Clypeus emarginate (Fig. 13) **44**
–	aa	Penis valve apically pointed or round (Figs 224–231, 234, 236, 238–254, 256, 258, 260, 262, 264, 266–274, 277, 279–282, 293–296, 300, 303–310, 317, 321)

bb   Valvispina ***usually*** present (Figs 224–231, 234, 236, 238–254, 256, 258, 260, 262, 264, 266–274, 277, 279–282, 293–296, 300, 303–310, 317, 321)

cc   Clypeus truncate or slightly emarginate (Figs 9–10, 12) **45**

44(43)   a   Penis valve apically strongly bent, L-shaped (Fig. 298)

b   Apical margin of penis valve with middle notch (Fig. 298) ...***P. malaisei***

–   aa   Penis valve apically weakly bent, not L-shaped (Fig. 297)

bb   Apical margin of penis valve without middle notch (Fig. 297) ....
.... ***P. dasiphorae***

45(43)   a   Claws with long subapical tooth close to apical one (bifid) (Fig. 25) ..**46**

–   aa   Claws without or with small or large subapical tooth clearly separated from apical one (Figs 21–24) **49**

46(45)   a   Valvispina absent or indistinct (Figs 303–305)

b   Pseudoceps dorsally with loose membranous region covered with setae (Figs 303–305) ....***micronematica*** group

–   aa   Valvispina merged with paravalva forming large spine (Figs 267, 274, 317)

bb   Pseudoceps with or without loose membranous region (Figs 267, 274, 317)...**47**

47(46)   a   Pseudoceps of penis valve short and broad (Figs 317)

b   Antenna ventrally paler than dorsally (Fig. 319) ......***P. caraganae* sp. n.**

–   aa   Pseudoceps of penis valve longer and narrower (Figs 267, 274)

bb   Antenna uniformly black (Figs 14, 17) or if as 47b, consider other characters **48**

48(47)   a   Hind trochanters, trochantelli, and tibia partly pale

b   Antenna (usually?) ventrally at least slightly paler than dorsally (Fig. 18)

c   Antenna with numerous and clearly visible stout black setae among finer paler ones (Fig. 18)

d   Penis valve without membranous fold near tip of valvispina and pseudoceps with distinct dorsal depression in middle or basal part (Fig. 267) ....***P. bifida***

–   aa   Hind trochanters, trochantelli, and tibia uniformly black or brown

bb   Antenna uniformly black (Figs 14, 17)

cc   Antenna with only some barely visible stout black setae among finer paler ones (Fig. 17)

dd   Penis valve with membranous fold near tip of valvispina and pseudoceps without dorsal depression in middle or basal part (Fig. 274) ....***P. frigida***

49(45)   a   Labrum asymmetrical with right lobe much longer than left (Fig. 11)

b   Mesepisternum smooth (Fig. 44)

c   Claws without subapical tooth (Fig. 21)

d   Penis valves as in Figs 258, 260

e   Body length 3.0–4.5 mm **50**

–   aa   Labrum ***usually*** symmetrical or asymmetrical with right lobe slightly longer than left (Figs 9, 10, 12)

　　　　　　bb　Mesepisternum matt (Figs 45–46) or if as 49b, consider other characters

　　　　　　cc　Claws with small or large subapical tooth (Figs 21–24), or if as 49c, consider other characters

　　　　　　dd　Penis valves different (Figs 224–231, 234, 236, 238–254, 256, 262, 264, 266, 268–273, 277, 279–282, 293–296, 300, 303–310, 317, 321)

　　　　　　ee　Body length 3.0–7.0 mm..**51**

50(49)　　a　Anterior margin of paravalva forming acute or right angle with valvispina (Fig. 260)

　　　　　　b　Valvispina short and bent (Fig. 260)

　　　　　　c　Posterior margin of pronotum black or narrowly pale (Fig. 35)

　　　　　　d　Metafemur black (Fig. 26)

　　　　　　e　Trochanters and trochantelli from black to pale (Figs 26–27, 32) .***P. retusa***

–　　　　　　aa　Anterior margin of paravalva forming obtuse angle with valvispina (Fig. 258)

　　　　　　bb　Valvispina long and straight (Fig. 258)

　　　　　　cc　Pronotum extensively pale (Fig. 35)

　　　　　　dd　Metafemur black or pale (Figs 26–28)

　　　　　　ee　Trochanters and trochantelli pale (Fig. 27).............................***P. exigua***

51(49)　　a　Pseudoceps with dorsal membranous region covered with setae *and / or* apically bent upwards (Figs 303–309)

　　　　　　b　Valvispina small and bent, small and straight, or absent (Figs 303–309)......
　　　　　　.. ***micronematica*** **group**

–　　　　　　aa　Pseudoceps not strongly modified (Figs 224–231, 234, 236, 238–254, 256, 262, 264, 266, 268–273, 277, 279–282, 293–296, 300, 310, 317, 321)

　　　　　　bb　Valvispina distinctly present (Figs 224–231, 234, 236, 238–254, 256, 262, 264, 266, 268–273, 277, 279–282, 293–296, 300, 310, 317, 321)**52**

52(51)　　a　Valvispina relatively small *and* more or less straight (Figs 224–231, 234, 236, 238–251, 253–254, 310, 321)..**53**

–　　　　　　aa　Valvispina large *and / or* bent (Figs 252, 256, 262, 264, 266, 268–273, 277, 279–282, 293–296, 300, 317)..**65**

53(52)　　a　Anterior margin of paravalva forms acute or right angle with valvispina (Figs 253–254)

　　　　　　b　Valvispina relatively broad *or* ventral margin of paravalva distinctly protruding (Figs 253–254)

　　　　　　c　Sternum 9 pale (Figs 52, 54) ***33***

–　　　　　　aa　Anterior margin of paravalva forms obtuse or rarely right angle with valvispina (Figs 224–231, 234, 236, 238–251, 310, 321)

　　　　　　bb　Valvispina thin *and* ventral margin of paravalva *usually* not distinctly protruding (Figs 224–231, 234, 236, 238–251, 310, 321)

　　　　　　cc　Sternum 9 black (Fig. 53), or if as 53c, consider other characters......**54**

54(53)　　a　Pseudoceps apically distinctly narrowed (Fig. 231)

　　　　　　b　Penis valve relatively small and narrow (Fig. 231)

c   Valvispina arising from ventral margin of paravalva and dorsally with round hump (Fig. 231) ....***P. punctifrons***

–   aa   Pseudoceps apically broad (Figs 224–230, 234, 236, 238–251, 310, 321)

bb   Penis valve longer or broader (Figs 224–230, 234, 236, 238–251, 310, 321)

cc   Valvispina arising from middle of paravalva, dorsally without round hump (Figs 224–230, 238–251, 310, 321), or if as 54c, consider other characters **55**

55(54)   a   Shape of paravalva more or less symmetrical around valvispina (Fig. 310)

b   Valvispina small and positioned in middle of paravalva (Fig. 310)

c   Posterior margin of pronotum and tegula extensively pale (Fig. 35)

d   Metafemur black (Fig. 26)

e   Mesepisternum smooth or slightly matt (Figs 44–45)..... ***P. kontuniemii*** (*micronematica* group)

–   aa   Shape of paravalva clearly asymmetrical around valvispina (Figs 224–230, 234, 236, 238–251, 321)

bb   Valvispina large, positioned close to dorsal or ventral margin (Figs 224–230, 234, 236, 238–251, 321), or if as 55b, consider other characters

cc   Posterior margin of pronotum and tegula black (Fig. 35), or if as 55c, consider other characters

dd   Metafemur pale (Figs 27–28), or if as 55d, consider other characters

ee   Mesepisternum matt (Fig. 46), or if as 55e, consider other characters.... **56**

56(55)   a   Paravalva and pseudoceps more or less rectangular (Figs 224–226)

b   Valvispina positioned in middle or upper third of paravalva (Figs 224–226)

c   Posterior margin of pronotum and tegula pale (Fig. 35)

d   Supraclypeal area, clypeus, antenna ventrally, metafemur, and sternum 9 ***often*** pale (Figs 12, 18, 28, 54) .... ***P. pallidiventris***

–   aa-dd   Combination of characters not as in a–d **57**

57(56)   a   Ventral margin of paravalva abruptly bent before valvispina (Fig. 228)

b   Dorsal margin of paravalva gradually tapering towards valvispina (Fig. 228)

c   Valvura slightly bent ventrally (Fig. 228) ....***P. angulata***

–   aa-cc   Combination of characters not as in a–c 58

58(57)   a   Vertical distance between dorsalmost part of paravalva and valvispina relatively long (Fig. 321)

b   Valvispina relatively large (Fig. 321)

c   Ventral margin of paravalva slightly protruding (Fig. 321)

d   Dorsobasal part of paravalva without angulate dark area (Fig. 321)

e   Metatibia in basal 1/3 pale

f   Mesepisternum smooth (Fig. 44) .... ***P. dedeara* sp. n.**

–   aa-ff   Combination of characters not as in a–f......................................**59**

59(58)   a   Vertical distance between dorsalmost part of paravalva and valvispina short (Figs 227, 229–230)
          b   Dorsal margin of paravalva gradually tapering towards valvispina (Figs 227, 229–230)
          c   Paravalva relatively narrow (Figs 227, 229–230)
          d   Mesepisternum smooth (Fig. 44) **60**
–   aa   Vertical distance between dorsalmost part of paravalva and valvispina long (Figs 234, 236, 238–251)
          bb   Dorsal margin of paravalva abruptly tapering towards valvispina (Figs 242–251) or if as 59b, consider other characters
          cc   Paravalva *usually* relatively broad (Figs 234, 236, 238–251)
          dd   Mesepisternum matt (Figs 45–46) or if as 59d, consider other characters..**62**
60(59)   a   Dorsobasal part of paravalva with angulate dark area (Fig. 227)...*P. maesta*
–   aa   Dorsobasal part of paravalva without angulate dark area (Figs 229–230) **61**
61(60)   a   Flagellum about 2.4–2.5 times as long as width of head
          b   Metatarsus mainly black (Fig. 29) .... *P. geniculata*
–   aa   Flagellum about 2.0–2.1 times as long as width of head
          bb   Metatarsus mainly pale (Fig. 31) .... *P. pseudogeniculata*
62(59)   a   Dorsal margin of penis valve from tip of valvura to tip of pseudoceps almost forming semicircle (Figs 234, 236)
          b   Paravalva and pseudoceps broad (Figs 234, 236).........*P. pseudocoactula*
–   aa   Dorsal margin of penis valve not forming semicircle (Figs 238–251)
          bb   Paravalva and pseudoceps narrow (e.g. Figs 244, 246) or if as 62b, consider other characters **63**
63(62)   a   Valvar strut not clearly evident at anterior margin (Figs 238–242)
          b   Mesepisternum matt (Fig. 46) .... *carinata* group
–   aa   Valvar strut distinct along its entire length (Figs 243–251)
          bb   Mesepisternum *usually* smooth (Fig. 44)..**64**
64(63)   a   Paravalva more elongate (Figs 244, 246)
          b   Valvispina longer (Figs 244, 246)
          c   Mesepisternum *sometimes* matt (Fig. 45) .... *P. cincta*
–   aa   Paravalva less elongate (Figs 243, 245, 247–251)
          bb   Valvispina *usually* shorter (Figs 243, 245, 247–251)
          cc   Mesepisternum smooth (Fig. 44)................................... *rufipes* group
65(52)   a   Mesopostnotum smooth (Fig. 19)
          b   Claws without subapical tooth (Fig. 21)
          c   Mesepisternum smooth (Fig. 44)
          d   Antenna *usually* ventrally paler than dorsally (Fig. 18)
          e   Paravalva largely present (Fig. 262)
          f   Valvispina large and strongly bent, about as long as apical margin of paravalva and more or less parallel to it (Fig. 262) ....*P. appendiculata*

–   aa   Mesopostnotum (usually?) matt (Fig. 20)
        bb   Claws with subapical tooth (Figs 22–24) or if as 65b, consider other characters
        cc   Mesepisternum matt (Figs 45–46), or if as 65c, consider other characters
        dd   Antenna uniformly black to uniformly pale (Figs 14–18)
        ee   Paravalva nearly completely merged with valvispina (Figs 264, 266, 268–273, 317) or largely present (Figs 252, 256, 277, 279–282, 293–296, 300)
        ff   Valvispina smaller, or not strongly bent, or not parallel to apical margin of paravalva, or not as long as apical margin of paravalva (Figs 252, 256, 264, 266, 268–273, 277, 279–282, 293–296, 300, 317).......................**66**

66(65)   a   Paravalva nearly completely merged with valvispina, forming large spine (Figs 264, 266, 268–273, 317) **67**
–   aa   Paravalva largely present and valvispina *usually* smaller (Figs 252, 256, 277, 279–282, 293–296, 300)...**75**

67(66)   a   Penis valve with membranous fold near or covering tip of valvispina (Figs 264, 266)
        b   Claws with small subapical tooth (Fig. 22)
        c   Mesepisternum smooth (Fig. 44) **68**
–   aa   Penis valve without membranous fold (Figs 268–273, 317)
        bb   Claws with large subapical tooth (Figs 22–23) or if as 67b, consider other characters
        cc   Mesepisternum matt (Figs 45–46) or if as 67c, consider other characters...**69**

68(67)   a   Valvispina of penis valve less sharply bent (forming half circle) (Fig. 266)... ***P. ruficornis***
–   aa   Valvispina of penis valve more sharply bent (being almost L-shaped) (Fig. 264)... ***P. melanocarpa***

69(67)   a   Pseudoceps of penis valve short and broad (Figs 273, 317)
        b   Mesepisternum (usually?) smooth (Fig. 44) **87**
–   aa   Pseudoceps of penis valve longer and narrower (Figs 268–272)
        bb   Mesepisternum matt (Figs 44–46) or if as 69b, consider other characters...**70**

70(69)   a   Penis valve with weakly bent and broad valvispina, and with narrow pseudoceps without distinct dorsal depression in middle part (Fig. 268) ....
        P. confusa
–   aa   Penis valve with different combination of characters (Figs 269–272)...**71**

71(70)   a   Valvispina of penis valve narrow and with blunt tip (Fig. 270)
        b   Antenna ventrally paler than dorsally (Fig. 18) ....***P. opaca***
–   aa   Valvispina of penis valve broad or narrow and with sharp tip (Figs 269, 271–272)
        bb   Antenna uniformly black (Fig. 14) or if as 71b, consider other characters ..**72**

72(71)   a   Valvispina of penis valve narrow (Fig. 272)
          b   Antenna uniformly black (Fig. 14)..**73**
–   aa   Valvispina of penis valve broad (Figs 269, 271)
          bb   Antenna ventrally paler than dorsally (Fig. 18) or if as 72b, consider
          other characters..**74**
73(72)   a   Mesepisternum smooth to slightly matt (Figs 44–45)
          b   ***Usually*** non-arctic habitats..***P. luteipes***
–   aa   Mesepisternum ***usually*** strongly matt (Fig. 46)
          bb   Arctic habitats...***P. staudingeri***
74(72)   a   Pseudoceps of left and right penis valve without distinct dorsal depression
          in middle part and with weakly bent valvispina (Fig. 269)
          b   Antenna uniformly black (Fig. 14).................................... ***P. subopaca***
–   aa   Pseudoceps of left penis valve with distinct dorsal depression in middle
          part and with strongly bent valvispina (Fig. 271)
          bb   Antenna ventrally paler than dorsally (Fig. 18) .... ***P. pusilla***
75(66)   a   Dorsal margin of paravalva somewhat s-shaped (Figs 293–294, 296)
          b   Valvispina small and narrow or large and narrow (Figs 293–294, 296)
          c   Supraclypeal area pale (Fig. 12)
          d   Body length 3.0–5.5 mm...**76**
–   aa   Dorsal margin of paravalva not s-shaped (Figs 252, 256, 277, 279–282, 300)
          bb   Valvispina large and broad or small and narrow (Figs 252, 256, 277,
          279–282, 300)
          cc   Supraclypeal area black (Figs 9–10)
          dd   Body length 3.0–7.0 mm...**78**
76(75)   a   Valvispina large (Fig. 296)
          b   Body length 4.0–5.5 mm...***P. paralella***
–   aa   Valvispina small (Figs 293, 294)
          bb   Body length 3.0–4.5 mm...**77**
77(76)   a   Paravalva ventrally abruptly narrowed before valvispina (Fig. 294) ....
          .... ***P. nigella***
–   aa   Paravalva ventrally gradually narrowed before valvispina (Fig. 293) ......
          ....***P. amphibola***
78(75)   a   Valvispina broad (Fig. 300)
          b   Mesepisternum matt (Fig. 46) ....***P. mollis***
–   aa   Valvispina narrow (Figs 252, 256, 277, 279–282)
          bb   Mesepisternum smooth (Fig. 44) **79**
79(78)   a   Pseudoceps covered with setae and expanded apically (Fig. 256)
          b   Valvispina long and abruptly bent apically (Fig. 256)
          c   Claws without subapical tooth (Fig. 21)
          d   Pronotum black
          e   Body length 3.0–4.0 mm ....***P. monogyniae***
–   aa   Pseudoceps apparently without setae and not expanded apically
          (Figs 252, 277, 279–282)
          bb   Valvispina shorter or more gradually bent (Figs 252, 277, 279–282)

　　　　cc　Claws with subapical tooth (Fig. 22) or if as 79c, consider other characters
　　　　dd　Pronotum *often* pale (Fig. 35)
　　　　ee　Body length 3.0–7.0 mm...**80**
80(79)　　a　Valvispina long, *and* dorsally without posteriorly constricted hump (Fig. 252)
　　　　b　Claws without subapical tooth (Fig. 21)
　　　　c　Body length about 4.3 mm (based on a single male available for study) ...
　　　　...*P. abbreviata*
–　　　　aa　Valvispina short *or* dorsally with posteriorly constricted hump (Figs 277, 279–282)
　　　　bb　Claws with small subapical tooth (Fig. 22) or if as 80b, consider other characters
　　　　cc　Body length 5.0–7.0 mm...**81**
81(80)　　a　Valvispina long and with posteriorly constricted hump (Figs 281–282)....**82**
–　　　　aa　Valvispina short and without posteriorly constricted hump (Figs 277, 279–280)...**83**
82(81)　　a　Pseudoceps apically with narrow thickening (Fig. 282)
　　　　b　Paravalva distinctly angled dorsobasally (Fig. 282) ....*P. nigriceps*
–　　　　aa　Pseudoceps apically with broad thickening (Fig. 281)
　　　　bb　Paravalva not angled dorsobasally (Fig. 281) ....*P. leucopodia*
83(81)　　a　Labrum pale (Figs 10, 12)
　　　　b　Pronotum extensively pale or posterior margin narrowly pale (Figs 35–36)
　　　　c　Flagellum about 2.4–3.2 times as long as width of head...........*P. laricis*
–　　　　aa　Labrum black or dark brown (Fig. 9)
　　　　bb　Pronotum (usually?) black
　　　　cc　Flagellum about 3.6–3.8 times as long as width of head ....*P. friesei*
84(9)　　a　Paravalva ventrally abruptly narrowed before valvispina (Fig. 294) ...*P. nigella*
–　　　　aa　Paravalva ventrally gradually narrowed before valvispina (Figs 293, 295)...**85**
85(84)　　a　Tegula and pronotum extensively pale (Fig. 36)
　　　　b　Penis valve ventrally somewhat bent (Fig. 295) ....*P. parva*
–　　　　aa　Tegula and pronotum black (Fig. 35)
　　　　bb　Penis valve ventrally more or less straight (Fig. 293)........*P. amphibola*
86(11)　　a　Depression on apical part of valvispina absent (Fig. 276) ....*P. pallida*
–　　　　aa　Depression on apical part of valvispina present (Fig. 278) *P. subarctica*
87(69)　　a　Antenna ventrally paler than dorsally (Fig. 319)
　　　　b　Ventroapical part of pseudoceps only slightly extended beyond dorsalmost margin (Fig. 317)
　　　　c　Valvispina narrower and its posterior and anterior margin of similar shape (Fig. 317)..*P. caraganae* **sp. n.**
–　　　　aa　Antenna uniformly black (Fig. 14)
　　　　bb　Ventroapical part of pseudoceps distinctly extended beyond dorsalmost margin (Fig. 273; http://dx.doi.org/10.6084/m9.figshare.4690174)
　　　　cc　Valvispina broader and its posterior and anterior margin of distinctly different or of similar shape (Fig. 273; http://dx.doi.org/10.6084/m9.figshare.4690174)..**88**

88(87) a Pterostigma (usually?) basally dark brown and apically brown (Fig. 40)
        b Pseudoceps of penis valve somewhat broader (Fig. 273).......***P. albitibia***
–   aa Pterostigma (usually?) uniformly yellow (Fig. 39)
        bb   Pseudoceps of penis valve somewhat narrower (http://dx.doi. org/10.6084/m9.figshare.4690174) .... ***P. sootryeni***

Taxonomy

Pristiphora abietina group

Pristiphora abietina (Christ, 1791)
Figs 12,157, 283

Tenthredo Pini [sic!] Retzius, 1783: 73, by indication to Degeer (1771: 1001–1002, Pl. 38. figs 5–7). Primary homonym of *Tenthredo pini* Linné, 1758 [= *Diprion pini* (Linné, 1758)]. Syntype(s) possibly in NHRS. Type locality: possibly Lövstabruk, Uppland, Sweden (place of residence of Degeer; see Taeger and Blank 1998).
Tenthredo abietina Christ, 1791: 447, by indication to Degeer (1771: 1001–1002, Pl. 38. figs 5–7). Syntype(s) possibly in NHRS. Type locality: possibly Lövstabruk, Uppland, Sweden (place of residence of Degeer; see Taeger and Blank 1998).
Tenthredo abietum Hartig in Hartig and Hartig, 1834: 984–985. Lectotype ♀ (GBIF-GISHym3183; here designated) in ZSM, examined. Type locality: not stated.
Nematus (*Nematus*) *limbatus* Dahlbom, 1835b: 9. Not available. Nomen nudum. Note. Not available through an indication, only internal reference on "*Nematus abietinus* No. 86", without giving any differences.
Nematus (*Nematus*) *abietinus* Dahlbom, 1835b: 9. Note. Description by indication on "Mouche à scie du Sapin De Geer". Syntype(s) possibly in NHRS. Type locality: possibly Lövstabruk, Uppland, Sweden (place of residence of Degeer; see Taeger and Blank 1998).
Nematus truncatus Hartig, 1837: 207. Holotype ♀ possibly lost. Type locality: Harz, Germany. Synonymised with *Lygaeonematus pini* by Konow (1904b).

Similar species. The most similar species is *P. compressa,* which is on average larger (6.0–9.0 vs. 4.0–6.5 mm) and has hypopygium posteriorly excised (not excised in *P. abietina*) (Figs 62–63). Males are best recognised by examining penis valves (Fig. 283). See the Key for more details.

Genetic data. Based on COI barcode sequences, *P. abietina* belongs to the same BIN cluster (BOLD:AAK9450) as *P. compressa, P. decipiens, P. gerula, P. pseudodecipiens*, *P. saxesenii*, and possibly *P. robusta*. Maximum distance within the BIN is 2.18% and minimum between species distance is 0.00%. The nearest neighbour to BOLD:AAK9450, diverging by minimum of 3.92%, is BOLD:ACO1401 (*P. euxantha* Huflejt, 2006, a species not treated here). Based on nuclear data, within species

divergence is 0.1% (based on two specimens and NaK) and the nearest neighbour is 1.2% different (*P. saxesenii*, both genes combined).

Host plants. *Picea abies* (L.) Karsten (Schafellner et al. 1999, Pschorn-Walcher and Altenhofer 2000), *P. sitchensis* (Bong.) Carriere (Austarå et al. 1984), *P. pungens* Engelm. (Kollár 2007, Kula et al. 2016).

Distribution and material examined. West Palaearctic. Specimens studied are from Germany, Latvia, and Sweden.

Pristiphora compressa (Hartig, 1837)
Figs 158–159, 284

Nematus compressus Hartig, 1837: 213–214. Lectotype ♀ (GBIF-GISHym3223; here designated) in ZSM, examined. Type locality: Harz, Germany.

Similar species. The most similar species are *P. abietina* and *P. decipiens*. *Pristiphora abietina* is on average smaller (4.0–6.5 *vs* 6.0–9.0 mm) and has a posteriorly sinuate hypopygium (excised in *P. compressa*). *Pristiphora decipiens* tends to be paler (with extensively pale mesepisternum, while in *P. compressa* it is usually black). Lancets and penis valves of these species can also be distinguished (see the Key).

Genetic data. Based on COI barcode sequences, *P. compressa* belongs to the same BIN cluster (BOLD:AAK9450) as *P. abietina, P. decipiens, P. gerula, P. pseudodecipiens, P. saxesenii*, and possibly *P. robusta* (Fig. 5). Maximum distance within the BIN is 2.18% and minimum between species distance is 0.00%. The nearest neighbour to BOLD:AAK9450, diverging by a minimum of 3.92%, is BOLD:ACO1401 (*P. euxantha*). Based on nuclear data, within species divergence is 0.0% (based on three specimens and NaK or TPI) and the nearest neighbour is 1.3% different (*P. abietina*, only NaK).

Host plants. *Picea* sp. (Beneš and Krístek 1979), *P. pungens* Engelm. (Kula et al. 2016).

Distribution and material examined. Palaearctic. Specimens studied are from Germany, Slovakia, and Sweden.

Pristiphora decipiens (Enslin, 1916)
Figs 63, 116–117, 160, 285

Lygaeonematus compressus var. *decipiens* Enslin, 1916: 499. Lectotype ♀ (GBIF-GISHym3259; here designated) in ZSM, examined. Type locality: Mül. [abbreviation for an unidentified German locality].

Similar species. The most similar species is *P. compressa*, which tends to be darker (usually has a black mesepisternum, while in *decipiens* it is extensively pale), and has a different lancet and penis valve (see the Key).

Genetic data. Based on COI barcode sequences, *P. decipiens* belongs to the same BIN cluster (BOLD:AAK9450) as *P. abietina*, *P. compressa*, *P. gerula*, *P. pseudodecipiens*, *P. saxesenii*, and possibly *P. robusta*. Maximum distance within the BIN is 2.18% and minimum between species distance is 0.00%. The nearest neighbour to BOLD:AAK9450, diverging by minimum of 3.92%, is BOLD:ACO1401 (*P. euxantha*). No nuclear data are available.

Host plants. *Picea* sp. (Beneš and Krístek 1979), *P. pungens* Engelm. (Kula et al. 2016).

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

Pristiphora gerula (Konow, 1904)
Figs 118, 122, 161, 286

Lygaeonematus gerulus Konow, 1904a: 194, 199–200. Lectotype ♂ (GBIF-GISHym3898; here designated) in SDEI, examined. Type locality: Kalkhorst, Mecklenburg-Vorpommern, Germany.

Similar species. The most similar species is *P. saxesenii*, valvula 3 of which possesses a small scopa in posterior view (completely absent in *P. gerula*) and which usually has a dark brown pterostigma (usually pale in *P. gerula*). Males are best recognised by examining penis valves (see the Key).

Genetic data. Based on COI barcode sequences, *P. gerula* belongs to the same BIN cluster (BOLD:AAK9450) as *P. abietina*, *P. compressa*, *P. decipiens*, *P. pseudodecipiens*, *P. saxesenii*, and possibly *P. robusta* (Fig. 5). Maximum distance within the BIN is 2.18% and minimum between species distance is 0.00%. The nearest neighbour to BOLD:AAK9450, diverging by minimum of 3.92%, is BOLD:ACO1401 (*P. euxantha*). Based on nuclear data (one specimen and TPI), the nearest neighbour is 1.2% different (*P. abietina*).

Host plants. *Picea* sp. (Beneš and Krístek 1979), *P. pungens* Engelm. (Kula et al. 2016).

Distribution and material examined. West Palaearctic. Specimens studied are from Estonia, France, Germany, Slovakia, and Sweden.

Pristiphora pseudodecipiens Beneš & Křístek, 1976
Figs 62, 163, 287

Pristiphora pseudodecipiens Beneš & Křístek, 1976: 404–414. Holotype ♀ (Cat. No. 26 237) in NMPC, not examined. Kuničky, South Moravian Region, Czech Republic.

Similar species. The most similar species is *P. decipiens*, females of which can be distinguished by having a posteriorly excised hypopygium (not excised in *P. pseudodecipiens*). Males are best recognised by examining penis valves.

Genetic data. Based on COI barcode sequences, *P. pseudodecipiens* belongs to the same BIN cluster (BOLD:AAK9450) as *P. abietina, P. compressa, P. decipiens, P. gerula, P. saxesenii*, and possibly *P. robusta* (Fig. 5). Maximum distance within the BIN is 2.18% and minimum between species distance is 0.00%. The nearest neighbour to BOLD:AAK9450, diverging by minimum of 3.92%, is BOLD:ACO1401 (*P. euxantha*). No nuclear data available.

Host plants. *Picea abies* (L.) Karsten (Beneš and Krístek 1976), *P. pungens* Engelm. (Kula et al. 2016).

Distribution and material examined. West Palaearctic. Specimens studied are from Czech Republic, Germany, and Ukraine.

Pristiphora robusta (Konow, 1895)
Figs 26, 164, 289

Lygaeonematus robustus Konow, 1895: 53. Holotype ♀ (GBIF-GISHym3897) in SDEI, examined. Type locality: Bohemia, Czech Republic.

Similar species. Combination of the structure of valvula 3, nearly completely black coloration, and the large size (9–11 mm) enable easy identification of the females. Males are best recognised by examining penis valves. Interestingly, a reared male specimen from Finland (http://id.luomus.fi/GL.5198) has vein 2r-rs present on both wings.

Genetic data. No data.

Host plants. *Picea abies* (L.) Karsten (Perkiömäki 1969, Kajmuk 1988), *P. obovata* Ledeb. (Kajmuk 1988), *P. pungens* Engelm. (Kula et al. 2016).

Distribution and material examined. Palaearctic. Specimens studied are from Czech Republic, Finland, and Sweden.

Pristiphora saxesenii (Hartig, 1837)
Figs 60, 120–121, 162, 288

Nematus (*Nematus*) *hospes* Dahlbom, 1835b: 9. Not available. Nomen nudum.
Nematus saxesenii Hartig, 1837: 212–213. Lectotype ♀ (GBIF -GISHym3409; here designated) in ZSM, examined. Type locality: Harz, Germany.
Pristiphora thalenhorsti Wong, 1975: 453–454. Holotype ♂ in CNC, not examined. Type locality: Sieber, Lower Saxony, Germany. Synonymised with *P. saxesenii* by Beneš and Krístek (1976).

Similar species. The most similar species is *P. gerula*, valvula 3 of which lacks a scopa (present in posterior view in *P. saxesenii*) and which usually has a pale pterostigma (usually dark brown in *P. saxesenii*). Males are best recognised by examining penis valves (see the Key).

Genetic data. Based on COI barcode sequences, *P. saxesenii* belongs to the same BIN cluster (BOLD:AAK9450) as *P. abietina*, *P. compressa*, *P. decipiens*, *P. gerula*, *P. pseudodecipiens*, and possibly *P. robusta* (Fig. 5). Maximum distance within the BIN is 2.18% and minimum between species distance is 0.00%. The nearest neighbour to BOLD:AAK9450, diverging by minimum of 3.92%, is BOLD:ACO1401 (*P. euxantha*). Based on nuclear data (one specimen), the nearest neighbour is 1.1% different (*P. gerula*, only TPI).

Host plants. *Picea abies* (L.) Karste (Pschorn-Walcher and Altenhofer 2000, *ex ovo* rearing experiments by VV), *P. pungens* Engelm. (Kula et al. 2016).

Rearing notes. Ovipositing experiment no.19/1987: Finland, South Häme, Hämeenlinna (uniform grid reference 676:336). On 5–6.VI.1987 one captured female laid eggs on new needles of *Picea abies*, the eggs were on outer margin of needle near its middle and entirely visible. Larvae hatched on 9.VI.1987. Four to five larval instars were observed, the development of larvae was rapid and on 21.VI.1987 prepupae were seen. No extra moult after feeding.

Distribution and material examined. West Palaearctic. Specimens studied are from Czech Republic, Estonia, Germany, Slovakia, and Sweden.

Pristiphora alpestris group

Pristiphora alpestris (Konow, 1903)
Figs 65, 88, 203, 233, 235

Pachynematus alpestris Konow, 1903: 380 (key). Lectotype ♀ (GBIF-GISHym3921; here designated) in SDEI, examined. Type locality: Switzerland.

Lygaeonematus karvoneni Lindqvist, 1952: 116–117, **syn. n.** Holotype ♂ (DEI-GISHym20888) in MZH, examined. Type locality: Pasila-Moor, Helsinki, Finland.

Similar species. The most similar species is *P. pseudocoactula*, from which it can be distinguished by usually having paler coloration (yellow clypeus, labrum, metafemur, and valvula 3) and different lancet and penis valve (see the Key). The holotype of *karvoneni* Lindqvist is not separable from *P. alpestris* (Figs 233, 235) and the figure of the penis valve given for *karvoneni* by Lindqvist (1952) is misleading: the valvispina is drawn close to the ventral margin of paravalva (Fig. 51 in Lindqvist 1952), while in *alpestris* and in the holotype of *karvoneni* it is distinctly removed from the ventral margin (Figs 233, 235). Furthermore, the reported host plant (*Betula pendula*) of *karvoneni* is also used by *P. alpestris* (Kangas, 1985).

Genetic data. Based on COI barcode sequences, *P. alpestris* belongs to the same BIN cluster (BOLD:AAK9467) as *P. pseudocoactula* (Fig. 5). Maximum distance within the BIN is 1.62% and minimum between species distance is 0.00%. The nearest neighbour to BOLD:AAK9467, diverging by a minimum of 4.69%, is BOLD:ACO1401 (*P. euxantha*). Based on nuclear data (one specimen; NaK), the nearest neighbour is 0.7% different (*P. pseudocoactula*).

Host plants. *Betula pendula* Roth (Adam 1973, Kangas 1985, *ex ovo* rearing experiments by VV), *Betula pubescens* Ehrh. (Kangas, 1985).

Rearing notes. Ovipositing experiment no. 3/1983: Finland, Janakkala, Kalpalinna. One captured female laid eggs on 7.V.1983 in pockets on undersides of the young leaves of *Betula pendula*, the egg pockets are attached to side veins. Larvae hatched on 11.V.1983, four larval instars were observed. They grew rapidly and prepupae were seen on 20.V.1983 and the next days. No extra moult after feeding.

Distribution and material examined. West Palaearctic. Specimens studied are from Finland, Germany, Sweden, and Switzerland.

Pristiphora dissimilis **Lindqvist, 1971**
Fig. 237

Pristiphora dissimilis Lindqvist, 1971: 13–14. Holotype ♂ (DEI-GISHym20906) in MZH, examined. Type locality: Helsinge, Uusimaa, Finland.

Similar species. Possibly belongs to the *alpestris* group. Only the holotype male is known, which can easily be distinguished from other species by its distinct penis valve (Fig. 237).

Genetic data. No data.

Host plants. Unknown.

Distribution and material examined. West Palaearctic. One male specimen studied from Finland.

Pristiphora pseudocoactula **(Lindqvist, 1952)**
Figs 89–90, 204, 234, 236

Lygaeonematus pseudocoactulus Lindqvist, 1952: 115–116. Holotype ♀ not found in MZH. Type locality: Utsjoki, Lapland, Finland.

Lygaeonematus concolor Lindqvist, 1952: 117–118, **syn. n.** Holotype ♀ (DEI-GISHym31689) in MZH, examined. Type locality: Kilpisjärvi, Lapland, Finland.

Similar species. The most similar species is *P. alpestris*, from which it can be distinguished by usually having darker coloration (black clypeus, labrum, metafemur, and valvula 3) and different lancet and penis valve (see the Key). The differences Lindqvist (1952) mentioned between *concolor* and *pseudocoactula* (coloration of labrum, pronotum, metafemur, and the amount of setae on the lancet) are small and not reliable, because the variation is continuous.

Genetic data. Based on COI barcode sequences, *P. pseudocoactula* belongs to the same BIN cluster (BOLD:AAK9467) as *P. alpestris* (Fig. 5). Maximum distance within the BIN is 1.62% and minimum between species distance is 0.00%. The nearest neighbour to

BOLD:AAK9467, diverging by minimum of 4.69%, is BOLD:ACO1401 (*P. euxantha*). Based on nuclear data, maximum within species divergence is 0.4% (based on four specimens and TPI) and the nearest neighbour is 0.7% different (*P. alpestris*, only NaK).

Host plants. *Betula pubescens* Ehrh. (*ex ovo* rearing experiments by VV). Possibly also *B. nana* L. (incomplete *ex ovo* rearing experiments by VV) and *Salix* sp. (reared *ex larva* by Lindqvist 1952, as *P. concolor*).

Rearing notes. Rearing no. 56/1970 as *P. concolor*: Saana, Finnish Lapland. On 5.VII.1970 several larvae were found on *Betula pubescens* var. *pumila*. Next year one female emerged and buds of *B. pubescens* were offered her. She laid several eggs in pockets on underside of young leaves, egg pockets were near veins rather close to leaf margin.

Ovipositing experiment no. 12/1972 as *P. concolor*: Finland, North Karelia, Kontiolahti, Venejoki. One captured female laid two eggs in pockets on undersides of young leaves of *Betula nana*, young larvae died for technical reasons (food too old).

Ovipositing experiment 15/1972 as *P. pseudocoactula*: Finland, North Karelia, Kontiolahti, Venejoki. On 2.VI.1972 one captured female laid one egg in pocket near the midvein on underside of young leaf of *Betula pubescens*. She laid no eggs on *Betula nana* or *Salix aurita*. Four larval instars were observed and prepupa was seen on 16.VI.1972. No extra moult after feeding.

Distribution and material examined. West Palaearctic, Nearctic. Specimens studied are from Finland and Sweden.

Pristiphora carinata group

Pristiphora albilabris (Boheman, 1852)
Figs 210, 238

Nematus (*Nematus*) *albilabris* Dahlbom, 1835b: 7. Not available. Nomen nudum.
Nematus albilabris Boheman, 1852: 172. Syntype(s) not found in NHRS. Type locality: Wärnaby and Anneberg, Småland, Sweden.
Nematus albilabris Thomson, 1863: 622. Primary homonym of *Nematus albilabris* Boheman, 1852 [= *Pristiphora albilabris* (Boheman, 1852)]. Holotype ♀ (NHRS-
HEVA000003749) in NHRS, examined. Type locality: Bohuslän, Sweden.
Nematus collaris Stein, 1884: 305–308. 4 ♀ syntypes possibly in BMNH, not examined. Type locality: Chodov, Czech Republic. Synonymised with *Lygaeonematus
albilabris* by Konow (1892).

Similar species. Species limits in the *carinata* group are still unclear.

Genetic data. Based on COI barcode sequences, specimens of the *carinata* group are divided between four BIN clusters (BOLD:AAF4995, BOLD:ABU8603, BOLD:ACL1744, BOLD:ACL1745), which form a monophyletic group (Fig. 5). Minimal distances between these clusters are 1.2%–4.48%. Because of unresolved taxonomy, it is not yet clear how different species are divided among these BIN clusters.

Based on nuclear data, maximum divergence within the group is 2.2% (based on ten specimens and TPI) and the nearest neighbour is 1.5% (*P. pseudocoactula*, both genes combined) or 1.0% different (*P. wesmaeli*, only NaK).

Host plants. *Betula* sp. (Conde 1934, Benson 1958), *B. pubescens* Ehrh (*ex ovo* rearing experiments by VV).

Rearing notes. Ovipositing experiment no. 16/1972: Finland, North Karelia, Kontiolahti, Venejoki. One captured female laid eggs on 2–3.VI.1972 in pockets on underside of teeth (leaf edges) of young leaves of *Betula pubescens*. Larvae hatched on 8–9.VI.1972, four larval instars were observed. The final feeding instar lasted about 17 days. Rather small prepupae (male sex?) were seen on 4.VII.1972. No extra moult after feeding.

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

Pristiphora borea (Konow, 1904)
Fig. 212

Nematus astutus Cameron, 1885: 77–78. Nomen oblitum. Syntypes (♀♂) have not been found (Lindqvist 1952). Type locality: not stated. Synonymised with *P. borea* by Liston et al. (2006).

Lygaeonematus boreus Konow, 1904: 196–197 (key). Nomen protectum. See Liston, Taeger and Blank (2006). Syntype ♂ (GBIF-GISHym3908) in SDEI, examined (severely damaged, abdomen missing). Type locality: Kanin Peninsula, Nenets Autonomous Okrug, Russia, and Vassijaure, Torne Lappmark, Sweden.

Pachynematus lapponicus Enslin, 1916: 462–463. 2 ♀ and 1 ♂ syntypes in ZSM, examined. Type locality: Lappland, Europe. Synonymised with *Lygaeonematus boreus* by Lindqvist (1952).

Similar species. Species limits in the *carinata* group are still unclear.

Genetic data. Based on COI barcode sequences, specimens of the *carinata* group are divided between four BIN clusters (BOLD:AAF4995, BOLD:ABU8603, BOLD:ACL1744, BOLD:ACL1745), which form a monophyletic group (Fig. 5). Minimal distances between these clusters are 1.2%–4.48%. Because of unresolved taxonomy, it is not yet clear how different species are divided among these BIN clusters. Based on nuclear data, maximum divergence within the group is 2.2% (based on ten specimens and TPI) and the nearest neighbour is 1.5% (*P. pseudocoactula*, both genes combined) or 1.0% different (*P. wesmaeli*, only NaK).

Host plants. *Betula nana* L. (Bland and Liston 1999, *ex ovo* rearing experiments by VV).

Rearing notes. Ovipositing experiment no. 10/1970: Finland, North Karelia, Kontiolahti, Selkie. On 28–29.V. 1970 one captured female laid several eggs in pockets near leaf-margin on underside of the young leaves of *Betula nana*. Larvae hatched on 2.VI.1970 and 6 larval instars were observed; larvae eat margins of leaves. Last

instar was some 30–40 days long. No "extra" moult after feeding, prepupae were seen on 27.VII.–12.VIII.1970.

Ovipositing experiment no. 15/1970: Finland, North Karelia, Tuupovaara. One captured female laid several eggs on leaves of *Betula nana*; she did not lay any eggs on *Vaccinium uliginosum*. Larvae developed, as in earlier experiment.

Ovipositing experiments 17/1970 and 18/1970: Finland, North Karelia, Kontiolahti, Venejoki. Two females laid many eggs on *Betula nana*, but respectively no and only two eggs on *Vaccinium uliginosum*. Otherwise very similar results as in previous two experiments.

Ovipositing experiments no. 4/1988, 5/1988, 6/1988, and 7/1988: Finland, South Häme, Janakkala, Suurisuo. Four captured females laid eggs on 26–27.V.1988 in pockets on undersurface of leaves of *Betula nana*, four larval instars were observed in all rearings and last instar lasted long.

Larvae observed on *Betula pubescens* var. *pumila* (L.) Govaerts (=*Betula pubescens* ssp. *czerepanovii*) in Saana, Finnish Lapland on 27.VII.1971.

Distribution and material examined. West Palaearctic, Nearctic. Specimens studied are from Finland and Russia (Nenets Autonomous Okrug).

Pristiphora breadalbanensis (Cameron, 1882)
Fig. 214

Nematus breadalbanensis Cameron, 1882: 531–532. Syntypes possibly in BMNH, not examined. Type locality: Scotland, United Kingdom.

Lygaeonematus tromsöensis [sic!] Kiær, 1898: 48–49. 2 ♀ syntypes in TROM, not examined. Type locality: Flöifjeld and Mauken, Troms, Norway. Synonymised with *Lygaeonematus breadalbanensis* by Lindqvist (1952).

Lygaeonematus corpulentus Konow, 1904a: 196 (key). Syntype ♀ (GBIF-GISHym3909) in SDEI, examined. Type locality: Norway and Sweden (Konow 1904b).

Lygaeonematus arcticola Enslin, 1916: 514–515.1 ♀ and 1 ♂ syntype in ZSM, examined. Type locality: North Ural, Russia.

Similar species. Species limits in the *carinata* group are still unclear.

Genetic data. Based on COI barcode sequences, specimens of the *carinata* group are divided between four BIN clusters (BOLD:AAF4995, BOLD:ABU8603, BOLD:ACL1744, BOLD:ACL1745), which form a monophyletic group (Fig. 5). Minimal distances between these clusters are 1.2%–4.48%. Because of unresolved taxonomy, it is not yet clear how different species are divided among these BIN clusters. Based on nuclear data, maximum divergence within the group is 2.2% (based on ten specimens and TPI) and the nearest neighbour is 1.5% (*P. pseudocoactula*, both genes combined) or 1.0% different (*P. wesmaeli*, only NaK).

Host plants. Unknown.

Distribution and material examined. West Palaearctic, Nearctic. Specimens studied are from Norway, Russia (North Ural), and United Kingdom.

Pristiphora carinata (Hartig, 1837)
Figs 98–99, 216, 239

Tenthredo pallipes Fallén, 1808: 110–111. Primary homonym of *Tenthredo pallipes* Spinola, 1808 [= *Ametastegia* (*Protemphytus*) *pallipes* (Spinola, 1808)]. Syntype ♀ in MZLU, not examined. Type locality: Västergötland, Sweden.

Nematus carinatus Hartig, 1837: 199–200. Syntype ♂ (GBIF-GISHym4689) in NFVG, examined. Type locality: Harz, Germany.

Nematus canaliculatus Hartig, 1840: 23, **syn. n.** Lectotype ♀ (GBIF-GISHym4691; here designated) in NFVG, examined. Type locality: Clausthal-Zellerfeld, Lower Saxony, Germany.

Nematus denudatus Hartig, 1840: 23. Lectotype ♂ (DEI-GISHym80268; here designated) in ZSM, examined. Type locality: not stated.

Pachynematus alticola Enslin, 1916: 463. Lectotype ♀ (GBIF-GISHym3192; here designated) in ZSM, examined. Type locality: Praděd (Altvater), Czech Republic.

Similar species. Species limits in the *carinata* group are still unclear.

Genetic data. Based on COI barcode sequences, specimens of the *carinata* group are divided between four BIN clusters (BOLD:AAF4995, BOLD:ABU8603, BOLD:ACL1744, BOLD:ACL1745), which form a monophyletic group (Fig. 5). Minimal distances between these clusters are 1.2%–4.48%. Because of unresolved taxonomy, it is not yet clear how different species are divided among these BIN clusters. Based on nuclear data, maximum divergence within the group is 2.2% (based on ten specimens and TPI) and the nearest neighbour is 1.5% (*P. pseudocoactula*, both genes combined) or 1.0% different (*P. wesmaeli*, only NaK).

Host plants. *Vaccinium myrtillus* L. (*ex ovo* rearing experiments by VV).

Rearing notes. Ovipositing experiment no. 3/1986: Finland, South Häme, Janakkala, Kalpalinna. On 22.V.1986 one captured female laid 5 eggs in pockets near leaf-margin on underside of the leaves of *Vaccinium myrtillus*. Larvae hatched on 27–28.V.1986, 5 larval instars were observed. Larvae eat margins of shoots and margins of leaves near their bases. Last instar was more than 16 days long. No "extra" moult after feeding. Larvae were put in alcohol on 27.VI.1986.

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

Pristiphora coactula (Ruthe, 1859)
Fig. 217

Nematus coactulus Ruthe, 1859: 307–308. Holotype ♀ in NMW, not examined. Type locality: Iceland.

Nematus winnipeg Norton, 1867b: 198. Lectotype ♀ in ANSP (designated by Cresson 1928, spelt as "*winnepeg*"), not examined. Type locality: Lake Winnipeg, Manitoba, Canada. Synonymised with *P. coactula* by Benson (1962).

Nematus alpinus Thomson, 1871: 98. Lectotype ♀ (MZLU2014449; here designated) in MZLU, examined. Type locality: Skalstugan, Jämtland, Sweden.

Nematus winnipegensis W.F. Kirby, 1882: 143. Replacement name for *Nematus winnipeg* Norton, 1867.

Lygaeonematus pachyvalvis Konow, 1904a: 197 (key). Syntype ♀ (GBIF-GISHym3913) in SDEI, examined. Type locality: Mt Dore, France; Kanin Peninsula, Nenets Autonomous Okrug, Russia; and Vassijaure, Torne Lappmark, Sweden.

Pristiphora dawsoni Rohwer, 1908: 109. Holotype ♀ in NSM (Smith 1983), not examined. Type locality: Ute Creek, Costilla, Colorado, USA. Synonymised with *P. coactula* by Smith (1979).

Similar species. Species limits in the *carinata* group are still unclear.

Genetic data. Based on COI barcode sequences, specimens of the *carinata* group are divided between four BIN clusters (BOLD:AAF4995, BOLD:ABU8603, BOLD:ACL1744, BOLD:ACL1745), which form a monophyletic group (Fig. 5). Minimal distances between these clusters are 1.2%–4.48%. Because of unresolved taxonomy, it is not yet clear how different species are divided among these BIN clusters. Based on nuclear data, maximum divergence within the group is 2.2% (based on ten specimens and TPI) and the nearest neighbour is 1.5% (*P. pseudocoactula*, both genes combined) or 1.0% different (*P. wesmaeli*, only NaK).

Host plants. *Vaccinium uliginosum* L (*ex ovo* rearing experiments by VV).

Rearing notes. Ovipositing experiment no. 46/1969: Finland, North Karelia, Kontiolahti, Venejoki. On 14–15.VI.1969 one captured female laid several eggs in pockets near leaf-margin on underside of the young leaves of *Vaccinium uliginosum*. Larvae hatched on 20.VI.1969, 6 larval instars were observed. Larvae fed on the margins of leaves at night. During the day they hid near the bottom of the rearing container. The final feeding instar lasted some 30 days. No "extra" moult after feeding, prepupae were seen on 7.VIII.1969.

Distribution and material examined. West Palaearctic, Nearctic. Specimens studied are from Finland, France, and Sweden.

Pristiphora groenblomi (Lindqvist, 1952)
Figs 10, 211

Lygaeonematus (*Lygaeotus*) *grönblomi* [sic!] Lindqvist, 1952: 101. Note. The spelling *groenblomi* is in predominant usage, not *gronblomi*, which would be correct according to Article 32.5.2 (ICZN 1999). Following Article 33.3.1, the predominantly used spelling is maintained. Holotype ♀ (DEI-GISHym31602) in MZH, examined. Type locality: Luumäki, South Karelia, Finland.

Similar species. Species limits in the *carinata* group are still unclear.

Genetic data. Based on COI barcode sequences, specimens of the *carinata* group are divided between four BIN clusters (BOLD:AAF4995, BOLD:ABU8603, BOLD:ACL1744, BOLD:ACL1745), which form a monophyletic group (Fig. 5).

Minimal distances between these clusters are 1.2%–4.48%. Because of unresolved taxonomy, it is not yet clear how different species are divided among these BIN clusters. Based on nuclear data, maximum divergence within the group is 2.2% (based on ten specimens and TPI) and the nearest neighbour is 1.5% (*P. pseudocoactula*, both genes combined) or 1.0% different (*P. wesmaeli*, only NaK).

Host plants. Perhaps *Betula* sp. (Verzhutskii 1981), if the species was correctly identified.

Distribution and material examined. West Palaearctic, Nearctic. Specimens studied are from Finland.

Pristiphora lativentris (Thomson, 1871)
Figs 95–96, 215

Nematus lativentris Thomson, 1871: 99–100 Lectotype ♀ (DEI-GISHym31596; here designated) in MZLU, examined. Type locality: Kälahög, Jämtland, Sweden.

Nematus scoticus Cameron, 1881: 563–564. Syntype(s) ♀ possibly in BMNH, not examined. Type locality: Braemar, Aberdeenshire, Scotland, United Kingdom. Synonymised with *Lygaeonematus lativentris* by Lindqvist (1952).

Nematus extremus Holmgren, 1883: 148. Syntypes ♂♀ in NHRS, not examined. Type locality: Matotschkin Scharr, Novaja Zemlya, Russia. Synonymised with *Lygaeonematus lativentris* by Lindqvist (1952).

Pristiphora bucoda Kincaid, 1900: 350–351. Syntype ♀ (USNMENT00778160) in USNM, not examined. Type locality: Berg Bay and Sitka, Alaska, USA. Synonymised with *Pristiphora lativentris* by Benson (1962).

Lygaeonematus alpicola Konow, 1904: 197 (key). Syntypes ♂♀ lost (Lindqvist 1952). Type locality: Austria and Switzerland. Tentatively synonymised with *Lygaeonematus lativentris* by Lindqvist (1952).

Lygaeonematus pallipes var. *femoralis* Zirngiebl, 1953: 32. Holotype ♂ (GBIF-GISHym3275) in ZSM, not examined. Type locality: Ammergau Alps, Bavaria, Germany. Synonymised with *P. lativentris* by Blank (1996).

Similar species. Species limits in the *carinata* group are still unclear.

Genetic data. Based on COI barcode sequences, specimens of the *carinata* group are divided between four BIN clusters (BOLD:AAF4995, BOLD:ABU8603, BOLD:ACL1744, BOLD:ACL1745), which form a monophyletic group (Fig. 5). Minimal distances between these clusters are 1.2%–4.48%. Because of unresolved taxonomy, it is not yet clear how different species are divided among these BIN clusters. Based on nuclear data, maximum divergence within the group is 2.2% (based on ten specimens and TPI) and the nearest neighbour is 1.5% (*P. pseudocoactula*, both genes combined) or 1.0% different (*P. wesmaeli*, only NaK).

Host plants. Unknown.

Distribution and material examined. West Palaearctic, Nearctic. Specimens studied are from Norway and Sweden.

Pristiphora trochanterica (Lindqvist, 1952)
Fig. 213

Lygaeonematus (*Lygaeotus*) *trochantericus* Lindqvist, 1952: 101–102. Holotype ♀ (DEI-
    GISHym31566) in MZH, examined. Type locality: Utsjoki, Outakoski, Finland.

Similar species. Species limits in the *carinata* group are still unclear.

Genetic data. Based on COI barcode sequences, specimens of the *carinata*
group are divided between four BIN clusters (BOLD:AAF4995, BOLD:ABU8603,
BOLD:ACL1744, BOLD:ACL1745), which form a monophyletic group (Fig. 5).
Minimal distances between these clusters are 1.2%–4.48%. Because of unresolved tax-
onomy, it is not yet clear how different species are divided among these BIN clusters.
Based on nuclear data, maximum divergence within the group is 2.2% (based on ten
specimens and TPI) and the nearest neighbour is 1.5% (*P. pseudocoactula*, both genes
combined) or 1.0% different (*P. wesmaeli*, only NaK).

Host plants. Unknown.

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

Pristiphora depressa group

Pristiphora depressa (Hartig, 1840)
Figs 24, 82–83, 184

Nematus depressus Hartig, 1840: 24. Lectotype ♀ (designated by Liston and Späth
    2008) in ZSM, examined. Type locality: not stated.
Pristiphora Carpentieri [sic!] Konow, 1902: 18. Lectotype ♀ (GBIF-GISHym3902;
    designated by Oehlke and Wudowenz 1984), examined. Type locality: Amiens,
    Nord-Pas-de-Calais-Picardie, France.

Similar species. The most similar species are *P. subbifida* and *P. tetrica*. *Pristiphora
subbifida* has an extensively pale head in dorsal view (with only small pale spots in
P. depressa) and at least partly pale metapostnotum (Fig. 38) (black in *P. depressa*).
Pristiphora tetrica, on the other hand, has a darker head than *P. depressa* (with black
supraclypeal area and *usually* without pale spots dorsally in *P. tetrica*). For more details
see Liston and Späth (2008) and Liston et al. (2013). Male unknown.

Genetic data. Based on COI barcode sequences, *P. depressa* forms its own BIN
cluster (BOLD:ABU7027) (Fig. 3). Maximum distance within the BIN is 0.61%.
The nearest neighbour to BOLD:ABU7027, diverging by minimum of 7.06%, is
BOLD:AAU8503 (*P. subbifida*).

Host plants. *Acer* sp. (Carpentier 1901). Adults reared from the larvae mentioned
by Carpentier (1901) were described a year later as *P. carpentieri* by Konow (1902).

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

Pristiphora subbifida (Thomson, 1871)
Figs 28, 38, 185

Nematus subbifidus Thomson, 1871: 105. Lectotype ♀ in MZLU (designated by Lindqvist 1954), examined. Type locality: Östergöthland, Sweden.

Similar species. The most similar species is *P. depressa*, which has a black metapostnotum (at least partly pale in *P. subbifida*: Fig. 38) and head in dorsal view with small pale spots (extensively pale in *P. subbifida*). See Liston and Späth (2008) and Liston et al. (2013) for more details. Male unknown.

Genetic data. Based on COI barcode sequences, *P. subbifida* forms its own BIN cluster (BOLD:AAU8503) (Fig. 3). Maximum distance within the BIN is 2.29%. The nearest neighbour to BOLD:AAU8503, diverging by a minimum of 6.26%, is BOLD:ABU7027 (*P. depressa*). Based on nuclear data (one specimen and both genes combined), the nearest neighbour is 2.1% different (*P. tetrica*).

Host plants. *Acer campestre* L. (Liston 1996, Liston et al. 2013). No other *Acer* species has been unequivocally recorded as a host, because of previous confusion of *P. subbifida* with other closely related species.

Distribution and material examined. West Palaearctic, (Nearctic, see Smith 2016). Specimens studied are from Germany, Greece, and Sweden.

Pristiphora tetrica (Zaddach, 1883)
Figs 186, 301

Nematus tetricus Zaddach in Brischke, 1883b: 148–149. Holotype ♀ possibly destroyed (Blank and Taeger 1998). Type locality: Thüringen, Germany.
Nematus velatus Zaddach in Brischke, 1883b: 149. Holotype ♀ was not found in ZSM (Liston and Späth 2008). Type locality: Baiern, Germany. Synonymised with *P. tetrica* by Konow (1902).
Pristiphora nievesi Haris, 2004: 164–165. Holotype ♀ (DEI-GISHym20461) in MNCN, examined. Type locality: El Ventorillo, Madrid, Spain.

Similar species. The most similar species are *P. depressa* and *P. subbifida*, from which it can be distinguished by having a black supraclypeal area (pale in *P. depressa* and *P. subbifida*) and *usually* black head in dorsal view (at least with small pale spots in *P. depressa*). See Liston and Späth (2008) for more details.

Genetic data. Based on COI barcode sequences, specimens of this species are divided between five BIN clusters (BOLD:ACL2117, BOLD:ABA3515,

BOLD:ACL2098, BOLD:ACL2099, BOLD:ACL2100) (Fig. 3), four of which (i.e. not BOLD:ACL2117) were previously identified as *P. nievesi* Haris. Minimum distances between these clusters are 1.72%–1.90%. All these clusters form a monophyletic group (Fig. 3) and we treat them as one species, because there is a continuous variation in external morphological characters used to separate *P. nievesi* from *P. tetrica*, and no clear differences in penis valves and lancets (see Liston et al. 2015). Based on nuclear data (two specimens and both genes combined), within species divergence is 0.2% and the nearest neighbour is 1.7% different (*P. cretica* Schedl, 1981, a species not treated here).

Host plants. *Acer pseudoplatanus* L. (Macek 2012b) and *A. sempervirens* L. (Liston et al. 2015).

Distribution and material examined. West Palaearctic. Specimens studied are from France, Germany, Greece, Italy, Morocco, Russia (Karachay-Cherkess Republic), and Spain.

Pristiphora erichsonii group

Pristiphora erichsonii (Hartig, 1837)
Figs 35, 124, 170, 290

Nematus Leachii [sic!] Dahlbom, 1835a: 27–28. Suppressed. Note. Suppressed for the purposes of the Law of Priority but not for those of the Law of Homonymy. (Opinion 906, ICZN 1970). Described from larvae, no type probably available. Type locality: Skåne (Sweden) and Zealand (Denmark). Synonymised with *Nematus erichsonii* by Thomson (1863).

Nematus (*Nematus*) *leachei* Dahlbom, 1835b: 10. Not available. Nomen nudum.

Nematus erichsonii Hartig, 1837: 187–188. Holotype ♀ (GBIF-GISHym3272) in ZSM, examined. Type locality: Harz, Germany.

Nematus notabilis Cresson, 1880: 7. Lectotype ♀ in ANSP (designated by Cresson 1916), not examined. Type locality: Massachusetts, USA. Synonymised with *P. erichsonii* by Marlatt (1896).

Similar species. Females can be distinguished from other *Pristiphora* species relatively easily by the shape of the valvula 3 (Fig.124) and the colour of the abdomen (having a red band). Likewise, it should be possible to distinguish males (which are extremely rare) from other species by the dorsal red band on the abdomen and extensively pale antenna.

Genetic data. Based on COI barcode sequences (only one specimen in BOLD), *P. erichsonii* forms its own BIN cluster (BOLD:AAG8325). The nearest neighbour to BOLD:AAG8325, diverging by a minimum of 5.04%, is BOLD:ACO1401 (*P. euxantha*). Based on nuclear data (one specimen and NaK), the nearest neighbour is 0.7% different (*P. parva*).

Host plants. *Larix decidua* Mill. (Drooz 1960, Kangas 1985, Pschorn-Walcher and Altenhofer 2000), *L. kaempferi* (Lamb.) Carrière (Drooz 1960, Huflejt and Sawoniewicz 1999, Pschorn-Walcher and Altenhofer 2000), *L. sibirica* Ledeb. (Drooz 1960, Kangas 1985), *L. laricina* (Du Roi) K. Koch (Drooz 1960, Jardon et al. 1994), *L. occidentalis* Nutt. (Drooz 1960), *L. principis-rupprechtii* (Mayr) Pilger (Li et al. 2013).

Distribution and material examined. Palaearctic, (Nearctic). Specimens studied are from Finland, Germany, and Norway.

Pristiphora glauca **Benson, 1954**
Figs 126–127, 179, 291

Pachynematus laricivorus Takagi, 1931: 28–32 (Jap.), 8–11(Engl.). Secondary homonym of *Nematus laricivorus* Brischke, 1883a [= *Pristiphora laricis* (Hartig, 1837)]. Syntypes possibly in the National Institute of Forest Science (previously Forestry Experiment Station), Seoul, South Korea (Wong 1975), not examined. Type locality: North Korea. Synonymised with *P. glauca* by Vikberg (1975).

Pristiphora glauca Benson, 1954a: 113–114. Holotype ♀ in BMNH, not examined. Type locality: Mortimer Forest, Hereford, England, United Kingdom.

Pristiphora takagii Wong, 1975: 459. Replacement name for *Pachynematus laricivorus* Takagi, 1931.

Similar species. The most similar species is *P. wesmaeli*. The differences in adults are small and might not be always reliable. According to Benson (1958), the ovipositor is about 1.1 times as long as the protibia in *P. glauca* (0.9 times in *P. wesmaeli*). For males, the differences in penis valves are also very slight (see the Key). The differences in larval coloration, and earlier emergence of adults and earlier larval feeding period of *P. glauca* distinguish the species more reliably (Benson, 1954a).

Genetic data. Based on COI barcode sequences, *P. glauca* belongs to the same BIN cluster (BOLD:ABY3989) as *P. wesmaeli* (Fig. 5). Maximum distance within the BIN is 2.17% and minimum between species distance is possibly 0.00%. The nearest neighbour to BOLD:ABY3989, diverging by minimum of 3.75%, is BOLD:ACO1401 (*P. euxantha*). Based on nuclear data (one specimen), the nearest neighbour is 0.1% (only NaK) or 0.9% (only TPI) different (*P. wesmaeli*).

Host plants. *Larix decidua* Mill. (Kirkland and Styles 1955, Pschorn-Walcher and Altenhofer 2000), *L. kaempferi* (Lamb.) Carrière (Takagi 1931, Kirkland and Styles 1955, Pschorn-Walcher and Altenhofer 2000), *L. sibirica* Ledeb. (Verzhutskii 1966), *Larix gmelinii* (Rupr.) Kuzen. (Takagi 1931).

Distribution and material examined. Palaearctic. Specimens studied are from Germany and Russia (Primorsky Krai).

Pristiphora wesmaeli (Tischbein, 1853)
Figs 180, 292

Nematus Wesmaeli [sic!] Tischbein, 1853: 347–348. 34 ♀♀ and 32 ♂♂ syntypes prob-
     ably destroyed (Horn et al. 1990). Type locality: Herrstein, Rhineland-Palatinate,
     Germany.
Nematus solea Snellen van Vollenhoven, 1870: 59–60. Holotype ♂ in ZMAN (Thomas
     1987), not examined. Type locality: not stated. Synonymised with *Lygaeonematus
     wesmaeli* by Konow (1904a).

Similar species. The most similar species is *P. glauca*. The differences in adults are small
and might not always be clear. According to Benson (1958), the ovipositor is about
0.9 times as long as the protibia in *P. wesmaeli* (1.1 times in *P. glauca*). For males, the
differences in penis valves are also very slight (see the Key). The differences in larval
coloration, later emergence of adults, and later larval feeding period distinguish *P. wes-
maeli* from *P. glauca* more reliably (Benson, 1954a).
     Genetic data. Based on COI barcode sequences, *P. wesmaeli* belongs to the same
BIN cluster (BOLD:ABY3989) as *P. glauca* (Fig. 5). Maximum distance within the BIN
is 2.17% and minimum between species distance is possibly 0.00%. The nearest neigh-
bour to BOLD:ABY3989, diverging by a minimum of 3.75%, is BOLD:ACO1401 (*P.
euxantha*). Based on nuclear data (two specimens), the nearest neighbour is 0.1% (only
NaK) or 0.9% (only TPI) different (*P. glauca*).
     Host plants. *Larix decidua* Mill., *Larix gmelinii* (Rupr.) Rupr., *L. kaempferi*
(Lamb.) Carrière, *Larix×eurolepis* Henry (Huflejt and Sawoniewicz 1999), and *L. si-
birica* Ledeb. (Kangas 1985).
     Distribution and material examined. Palaearctic. One male specimen studied
from France. The second specimen mentioned under *Genetic data* is from a larva
(voucher 3c, Belgium, collected on 7.VIII.2000) that we have not studied.

Pristiphora laricis group

Pristiphora friesei (Konow, 1904)
Figs 33, 79–81, 174–176, 277

Lygaeonematus Friesei [sic!] Konow, 1904a: 195, 208. Lectotype ♀ (GBIF-
     GISHym3914; here designated) in SDEI, examined. Type locality: Airolo, Ticino,
     Switzerland (not in Tirol, Austria, as written by Konow 1904a, b; see also Enslin,
     1916: 509). Note. Enslin (1916: 509) and Muche (1974: 136–137) referred to the
     single female specimen in the SDEI as the type of *P. friesei* (under the name *P. frisei*
     [sic!] by Muche 1974). Neither reference constitutes a valid lectotype designation
     according to ICZN Article 74.5, because the specimen was not unambiguously
     selected from the syntype series. However, because Enslin and Muche based their

concept of the species on the specimen in the SDEI, we hereby designate this specimen as the lectotype.

Pristiphora atrata Lindqvist, 1975: 13, **syn. n.** Holotype ♀ (DEI-GISHym20834) in MZH, examined. Type locality: Goloustnoje, Irkutsk, Russia. Note. The holotype was reared by B. N. Verzhutskii from a larva found on *Vaccinium uliginosum* L. on May 29, 1966 (label data; see also Verzhutskii 1981), which we interpret as an accidental find, as the host plant of *P. friesei* is *Larix* (Schedl 1976, Liston et al. 2006). Lancet and external morphology of *atrata* does not differ from *friesei*.

Similar species. The most similar species is *P. laricis*, which tends to be paler, but darker specimens could be mistaken for *P. friesei*. There are small differences in the structure of the lancets: the tangium appears to be without campaniform sensilla and there are fewer setae in *P. friesei*, while campaniform sensilla are present and there are more setae in *P. laricis* (Figs 174–178). There appear to be no consistent differences in penis valves (Figs 277, 279–280), contrary to Chevin (1974), but the antennae are longer in *P. friesei* (see the Key).

Genetic data. Based on COI barcode sequences, *P. friesei* forms its own BIN cluster (BOLD:ABV3411). When specimens that have 1 bp deletion in the barcoding region (e.g. DEI-GISHym11558) are included (excluded from calculations in BOLD), maximum distance within *P. friesei* is 3.5% and the nearest *P. laricis* specimens are only 2.3% different (based on full barcodes), but *P. friesei* nevertheless forms a monophyletic group (Fig. 3). The nearest neighbour to BOLD:ABV3411 (excluding the specimens with 1 bp deletion), diverging by minimum of 4.67%, is BOLD:AAQ3707 (*P. laricis*). No nuclear data are available.

Host plants. *Larix decidua* Mill. (Schedl 1976), *Larix×eurolepis* (Liston et al. 2006).

Distribution and material examined. Palaearctic. Specimens studied are from Germany, Italy, Russia (Irkutsk Oblast), Switzerland, and United Kingdom.

Pristiphora laricis (Hartig, 1837)
Figs 64, 177–178, 279–280

Nematus laricis Hartig, 1837: 203–204. Lectotype ♀ (GBIF-GISHym3328; here designated) in ZSM, examined. Type locality: Germany according to the title of the publication.

Nematus ruficollis Hartig, 1840: 27. Lectotype ♀ (GBIF-GISHym3405; here designated) in ZSM, examined. Type locality: not stated.

Nematus leucocnemis Förster, 1854b: 433–434. Lectotype ♀ (GBIF-GISHym3333; designated by Liston 1995) in ZSM, examined. Type locality: Aachen, North Rhine-Westphalia, Germany.

Nematus oblongus Cameron, 1882: 539. Syntype(s) possibly in BMNH, not examined. Type locality: England, United Kingdom. Synonymised with *Lygaeonematus laricis* by Konow (1904a).

Nematus laricivorus Brischke, 1883a: pl. I, 1e. Described from larvae, types possibly destroyed (Blank and Taeger 1998). Type locality: not stated, but probably in former East Prussia (now Kaliningrad Oblast of Russia, or Poland). Synonymised with *Pristiphora laricis* by Konow (1898).

Nematus rusticanus Brischke, 1884: 128–129. Holotype ♀ possibly destroyed (Blank and Taeger 1998). Type locality: not stated, but probably in former East Prussia (now Kaliningrad Oblast of Russia, or Poland). Synonymised with *Lygaeonematus laricis* by Konow (1904a).

Pachynematus ravidus Konow, 1903: 382 (key). Lectotype ♀ (GBIF-GISHym3855; designated by Taeger and Blank 1998) in SDEI, examined. Type locality: Zermatt, Valais, Switzerland. Synonymised with *Pristiphora laricis* by Koch (1989).

Lygaeonematus paedidus Konow, 1904a: 195, 205. Lectotype ♀ (GBIF-GISHym3854; designated by Koch 1989 as "holotype") in SDEI, examined. Type locality: Ulm (Baden-Württemberg) or Erfurt (Thuringia), Germany (the specimen has two different labels, with locality names that do not match). Synonymised with *Pristiphora laricis* by Koch (1989).

Pachynematus nigricorpus Takagi, 1931: 32–33 (Jap.), 11–12(Engl.), **syn. n.** Syntypes possibly in the National Institute of Forest Science (previously Forestry Experiment Station), Seoul, South Korea, not examined. Type locality: North Korea.

Similar species. The most similar species is *P. friesei*, which tends to be darker (see the Key). There are small differences in the structure of the lancets: campaniform sensilla are present on the tangium and there are more setae in *P. laricis*, while campaniform sensilla appear to be absent and there are fewer setae in *P. friesei* (Figs 174–178). There appear to be no consistent differences in penis valves (Figs 277, 279–280), contrary to Chevin (1974), but the antennae are shorter in *P. laricis* (see the Key). One studied female from Scotland (DEI-GISHym31503) had a red band on the abdomen, like *P. cincta* and *P. erichsonii*, but all these species can be distinguished based on the shape of valvula 3 and the structure of the lancet (Figs 104–105, 145–146 for *P. cincta*; Figs 124–125, 170 for *P. erichsonii*; Figs 79–81, 177–178 for *P. laricis*). As already suspected by Vikberg (1975), we treat *nigricorpus* Takagi as synonym of *laricis* Hartig. The description by Takagi (1931) fits well with *P. laricis* (pale labrum, length of antenna in male 3–4 mm) rather than *P. friesei* (black or dark brown labrum and length of antenna in male about 5 mm). Haris (2006b) apparently misinterpreted *P. laricis*, because the figure of valvula 3 given for this species (Fig. 10 in Haris 2006b) belongs to the *leucopodia* group, *tenuiserra* or some other species where valvula 3 can extend or extends beyond cerci. However, the figure of valvula 3 (Fig. 30 in Haris 2006b) given for *nigricorpus* Takagi by Haris (2006b, as *P. nigrocarpa*) does fit with *P. laricis* (Fig. 79).

Genetic data. Based on COI barcode sequences, *P. laricis* forms its own BIN cluster (BOLD:AAQ3707). Maximum distance within the BIN is 2.09% (Fig. 3). The nearest neighbour to BOLD:AAQ3707, diverging by minimum of 4.31%, is BOLD:ABV3411 (*P. friesei*). Based on nuclear data (three specimens and TPI or NaK),

within species divergence is 0.2% (NaK) or 1.2% (TPI) and the nearest neighbour is 2.3% different (*P. nigriceps*, only NaK).

Host plants. *Larix decidua* Mill. (Adam 1973, Huflejt and Sawoniewicz 1999), *L. kaempferi* (Lamb.) Carrière (Pschorn-Walcher and Altenhofer 2000), *L. sibirica* Ledeb. (Kangas 1985, Huflejt and Sawoniewicz 1999), *L. gmelinii* (Rupr.) Kuzen., *L. laricina* (Du Roi) K. Koch, *L. occidentalis* Nutt., *Larix×eurolepis* A. Henry (Huflejt and Sawoniewicz 1999).

Distribution and material examined. Palaearctic. Specimens studied are from Austria, Finland, Germany, United Kingdom, Italy, Japan, Slovenia, and Switzerland.

Pristiphora leucopodia **group**

Pristiphora leucopodia **(Hartig, 1837)**
Figs 56, 181–182, 281

Nematus leucopodius Hartig, 1837: 200. Lectotype ♀ (GBIF-GISHym3336; here designated) in ZSM, examined. Type locality: Harz, Germany.

Nematus nitens Borries, 1896: 232. Primary homonym of *Nematus nitens* Thomson, 1888 [= *Euura respondens* (Förster, 1854b) **comb. n.**]. Syntypes ♀♂ have not been located in ZMUC (Blank et al. 2009). Type locality: Dyrehaven, Region Hovedstaden (Capital Region), Denmark. Synonymised with *P. leucopodia* by Blank et al. (2009).

Pachynematus sagulatus Konow, 1903: 382 (key). Lectotype ♀ (GBIF-GISHym3903; designated by Oehlke and Wudowenz 1984, as "Holotypus") in SDEI, examined. Type locality: Hungaria bor. Tatra [Tatra Mountains], Poland or Slovakia.

Lygaeonematus leucopodius ab. *flavipes* Lindqvist, 1941: 70. Not available. Infrasubspecific name.

Nematus (*Pikonema*) *piceae* Zhelochovtsev in Zhelochovtsev and Zinovjev, 1988: 170, **syn. n.** Holotype ♀ in ZMUM, not examined. Type locality: Srednyaya Usva [Средняя Усьва], Perm Krai, Russia.

Pristiphora (*Pristiphora*) *hoverlaensis* Haris, 2001: 82, **syn. n.** Holotype ♂ (DEI-GISHym80339; http://dx.doi.org/10.6084/m9.figshare.5091895) in HNHM, examined. Type locality: Bohdan (Богдан), Zakarpattia Oblast, Ukraine.

Similar species. The most similar species is *P. nigriceps*, females of which have an extensively pale thorax and abdomen. In *P. leucopodia*, thorax and abdomen are usually black, palest specimens have a nearly completely pale abdomen and slightly pale thorax. Males are best recognised by examining penis valves. Although we did not study the holotype of *piceae* Zhelochovtsev, differences mentioned by Zhelochovtsev and Zinovjev (1988) in lancet, coloration and length of antennae seem to be minute. Examination of female specimens that vary in coloration and length of valvula 3 did not allow separation of two forms, as the variation seems to be continuous. Neither

were reliable differences detected in the lancet. The penis valve of one male identified by Alexey Zinovjev as *piceae* is indistinguishable from *leucopodia*.

Genetic data. Based on COI barcode sequences, *P. leucopodia* belongs to its own BIN cluster (BOLD:AAH7553) (Fig. 3). Maximum distance within the BIN is 1.83%. The nearest neighbour to BOLD:AAH7553, diverging by minimum of 5.06%, is BOLD:AAQ3707 (*P. laricis*). Based on nuclear data, maximum within species divergence is 0.9% (based on three specimens and NaK) and the nearest neighbour is 2.4% different (*P. nigriceps*, both genes combined).

Host plants. *Picea abies* (L.) Karsten (Pschorn-Walcher and Altenhofer 2000), *P. pungens* Engelm. (Kula et al. 2016).

Distribution and material examined. West Palaearctic. Specimens studied are from Estonia, Finland, Germany, Norway, Slovakia, Sweden, Switzerland, and Ukraine.

Pristiphora nigriceps (Hartig, 1840)
Figs 37, 53, 84–85, 183, 282

Nematus nigriceps Hartig, 1840: 24. Lectotype ♀ (GBIF-GISHym3362; here designated) in ZSM, examined. Type locality: not stated.

Nematus bistriatus Thomson, 1871: 105–106. Lectotype ♀ (NHRS-HEVA000001950; here designated) in NHRS, examined. Type locality: Östergötland (Götaland), Sweden.

Similar species. The closest species is *P. leucopodia*, females of which usually have a black thorax and abdomen (extensively pale in *P. nigriceps*). In paler specimens of *P. leucopodia*, at least the thorax remains relatively dark compared to *P. nigriceps*. Males are best recognised by examining penis valves (see the Key).

Genetic data. Based on COI barcode sequences, specimens of this species are divided between two BIN clusters (BOLD:AAO1445 and BOLD:ABV9762), which form a monophyletic group (Fig. 3). Minimal distance between these two clusters is 2.87%. Based on nuclear data, within species divergence is 0.0% (based on two specimens and NaK) and the nearest neighbour is 2.3% (*P. laricis*, only NaK) or 2.4% different (*P. leucopodia*, both genes combined).

Host plants. *Picea abies* (L.) Karsten (Boevé 1990, Pschorn-Walcher and Altenhofer 2000, *ex ovo* rearing experiments by VV).

Rearing notes. Ovipositing experiment no.20/1987: Finland, South Häme, Janakkala (uniform grid reference 6757:3376). On 6.VI.1987 one captured female laid 2 eggs on new needles of *Picea abies*, the eggs were on outer margin of needle near its apex and mostly inside needle. Larvae hatched on 9.VI.1987. Four larval instars were observed, the development of larvae was rapid and on 22.VI.1987 one prepupa was seen. No extra moult after feeding.

Distribution and material examined. Palaearctic. Specimens studied are from Finland, Germany, Russia (Primorsky Krai), Slovakia, Sweden, Switzerland, and Ukraine.

Pristiphora malaisei group

Pristiphora dasiphorae (Zinovjev, 1993), comb. n.
Figs 73–74, 136, 297

Pristicampus dasiphorae Zinovjev, 1993: 81–84. Holotype ♀ in ZMUM, not examined. Type locality: Tibelti, Irkutsk Oblast, Russia.

Similar species. The most similar species is *P. malaisei*, which can be separated based on the valvula 3, the lancet, and the penis valve (see the Key).

Genetic data. Based on COI barcode sequences, *P. dasiphorae* belongs to its own BIN cluster (BOLD:ACO2064). Maximum distance within the BIN is 0% (based on two specimens). The nearest neighbour to BOLD:ACO2064, diverging by minimum of 8.45%, is *P. malaisei* (no BIN number has been assigned yet). Based on nuclear data, the nearest neighbour is 4.3% different (*P. punctifrons*, both genes combined).

Host plants. *Potentilla fruticosa* L. (=*Dasiphora fruticosa*) (Zinovjev 1993, our own observations on larvae in Öland).

Distribution and material examined. Palaearctic. Specimens studied are from Russia (Zabaykalsky Krai) and Sweden (Öland).

Pristiphora malaisei (Lindqvist, 1952)
Figs 13, 30, 58, 75, 137, 298

Lygaeonematus (*Lygaeophora*) *malaisei* Lindqvist, 1952: 112–113. Holotype ♀ (NHRS-HEVA000003753) in NHRS, examined. Type locality: Torneträsk, Torne Lappmark, Sweden.

Mesoneura arctica Lindqvist, 1959: 68–70, **syn. n.** Holotype ♂ (http://id.luomus.fi/GL.5218) in MZH, examined. Type locality: Malla, Lapland, Finland.

Pachynematus incisus Lindqvist, 1970: 103, **syn. n.** Holotype ♀ in MZH (http://id.luomus.fi/GL.5183), examined. Type locality: Popovo, Oljhonsk, Irkutsk, Russia.

Pachynematus intermedius Verzhutskii, 1974: 160, **syn. n.** Original paper not seen, cited in Zinovjev (1993): 81. Note. Described as "*Pachynematus intermedius* Lqv. sp. n." from larvae feeding on *Dasiphora*, type material not cited. Type locality: Baikal region, Russia.

Pristiphora mongololaricis Haris, 2003: 116–117, **syn. n.** Holotype ♀ (DEI-GISHym80350; http://dx.doi.org/10.6084/m9.figshare.5053627) in HNHM, examined. Type locality: Nukht, Bogd Khan Mountain, Ulaanbaatar, Mongolia.

Similar species. The most similar species is *P. dasiphorae*, which can be separated by differences in the valvula 3, lancet, and penis valve (see the Key). Contrary to Zinovjev (1993), we treat *P. incisa* (Lindqvist, 1970) as a synonym, because we are unable to find consistent differences between the arctic (*P. malaisei*) and non-arctic forms (*P. incisa*).

Genetic data. Based on COI barcode sequences, *P. malaisei* belongs to its own cluster (no BIN number has been assigned yet). Maximum distance within *P. malaisei* is 0.6% (based on full barcodes). The nearest neighbour to *P. malaisei*, diverging by minimum of 8.45%, is BOLD:ACO2064 (*P. dasiphorae*). Based on nuclear data, within species divergence is 0.4% (based on two specimens and both genes combined) and the nearest neighbour is 5.1% (*P. luteipes*, only TPI) or 5.3% different (*P. punctifrons*, both genes combined).

Host plants. *Potentilla fruticosa* L. (=*Dasiphora fruticosa*) (Lindqvist 1970, Verzhutskii 1981, *ex ovo* rearing experiments by VV) and possibly *Comarum palustre* L. (incomplete *ex ovo* and *ex larva* rearing experiments by VV).

Rearing notes. Ovipositing experiment no. 1/1994: Finland, South Häme, Janakkala, Turenki, Alanko. On 11.V.1994 two females were swept from *Potentilla fruticosa*, one of them in copula. On the same day they laid eggs in pockets on the underside of young leaves of *P. fruticosa*, the eggs were near the leaf margin. On 17.V.1994 larvae hatched. Four larval instars were observed, the development of larvae was rapid. On 31.V.1994 prepupae and three cocoons were found. No extra moult after feeding.

Ovipositing experiment no. 2/1998: the same locality as above. On 2.V.1998 one female was offered leaves of *Potentilla argentea* agg., in which she showed no interest. On the next day small leaves and buds of *Comarum palustre* were offered, and the female began immediately to lay eggs in petioles of young leaves and unopened buds. Larvae hatched but did not live many days.

Larval feeding experiment on 26.VI.1998. 11 larvae from *Potentilla fruticosa* were put into container with *Comarum palustre* and *Potentilla crantzii* (Crantz) Beck ex Fritsch. Within an hour 6 larvae were eating *Comarum* but not *Potentilla*. Inspection on the next day: many larvae were feeding on *Comarum* and many leaves of *Comarum* had large holes. In addition, no larvae were observed to feed on *Potentilla argentea* L. In the evening the larvae were put again on *Potentilla fruticosa*.

Larval feeding experiment in July 1998. Many rather large larvae were put into a container with *Potentilla anserina* L., *P. argentea*, and *P. erecta* (L.) Raeusch. After 3 hours no larva was feeding on them, but they walked around, seeking better food.

Distribution and material examined. Palaearctic. Specimens studied are from Finland, France, Mongolia, Russia (Irkutsk Oblast), and Sweden.

Pristiphora micronematica group

Pristiphora affinis (Lindqvist, 1952)
Fig. 206

Lygaeonematus (*Lygaeophora*) *affinis* Lindqvist, 1952: 109–110. Holotype ♀ (DEI-GISHym20898) in MZH, examined. Type locality: Utsjoki, Outakoski, Finland.

Similar species. Species limits in the *micronematica* group are still unclear.

Genetic data. Based on COI barcode sequences, specimens of the *micronematica* group belong to the BIN cluster BOLD:ACG2488. Maximum distance within the BIN is 2.45%. The nearest neighbour to BOLD:ACG2488, diverging by minimum of 4.1%, is BOLD:ACO1401 (*P. euxantha*). Based on nuclear data, maximum divergence within the group is 2.5% (based on four specimens and TPI) and the nearest neighbour is 4.7% (*P. nigella*, only TPI) or 0.6% different (*P. siskiyouensis* Marlatt, 1896, a Nearctic species not treated here; only NaK).

Host plants. *Salix* sp. (Lindqvist 1952, Kontuniemi 1972).

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

Pristiphora atripes (Lindqvist, 1952)
Figs 29, 205, 306

Nematus (*Lygaeonematus*) *lanificus* ab. *atripes* Hellén, 1948a: 46. Not available. Infrasubspecific name.

Lygaeonematus atripes Lindqvist, 1952: 111–112. Holotype ♀ (DEI-GISHym31610) in MZH, examined. Type locality: Lapponia, Europe.

Similar species. Species limits in the *micronematica* group are still unclear.

Genetic data. Based on COI barcode sequences, specimens of the *micronematica* group belong to the BIN cluster BOLD:ACG2488. Maximum distance within the BIN is 2.45%. The nearest neighbour to BOLD:ACG2488, diverging by minimum of 4.1%, is BOLD:ACO1401 (*P. euxantha*). Based on nuclear data, maximum divergence within the group is 2.5% (based on four specimens and TPI) and the nearest neighbour is 4.7% (*P. nigella*, only TPI) or 0.6% different (*P. siskiyouensis*, only NaK).

Host plants. Unknown, but could be *Salix herbacea* L. (Kontuniemi 1972).

Distribution and material examined. West Palaearctic. Specimens studied are from Sweden.

Pristiphora kontuniemii (Lindqvist, 1952)
Fig. 310

Lygaeonematus kontuniemii Lindqvist, 1952: 113–114. Holotype ♀ (DEI-GISHym20880) in MZH, examined. Type locality: Ivalo, Finland.

Similar species. Species limits in the *micronematica* group are still unclear.

Genetic data. Based on COI barcode sequences, specimens of the *micronematica* group belong to the BIN cluster BOLD:ACG2488. Maximum distance within the BIN is 2.45%. The nearest neighbour to BOLD:ACG2488, diverging by a minimum of 4.1%, is BOLD:ACO1401 (*P. euxantha*). Based on nuclear data, maximum diver-

gence within the group is 2.5% (based on four specimens and TPI) and the nearest neighbour is 4.7% (*P. nigella*, only TPI) or 0.6% different (*P. siskiyouensis*, only NaK).

Host plants. *Salix pentandra* L., *Salix daphnoides* Vill. (*ex ovo* rearing experiments by VV).

Rearing notes. Rearing no. 47/1987: Finland, South Häme, Hämeenlinna, Katinen. On 14.VI.1987 larvae on *Salix pentandra*; head coloration characteristic.

Ovipositing experiment no. 5/2009: Finland, South Häme, Janakkala. On 8.V.2009 one female was found ovipositing in a bud of *Salix pentandra*. When captured she laid 12 eggs in pockets on undersides of young leaves of *S. pentandra*. The eggs were close to the leaf margin. On 8.V.2009 the larvae hatched, and during the next days they gnawed holes in the leaf margins. Four larval instars were observed. Development of the larvae was rapid, and prepupae were found on 22–24.V.2009. No extra moult after feeding.

Rearing no. 2/1999: Finland, Uusimaa, Espoo, Överby school. On 29.V.1999 eggs were found in large buds of *Salix daphnoides* subsp. *acutifolia* (Willd.) Ahlfv., the eggs were on underside of outer leaves near the leaf margin in the apical part of the leaf. Larvae hatched and four instars were observed. Prepupae were seen on 1–3.VI.1999. No extra moult after feeding. In next March males and females emerged.

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

Pristiphora micronematica Malaise, 1931
Figs 207, 305

Pristiphora micronematica Malaise, 1931: 58–59. Lectotype ♀ (NHRS-HE-VA000003865; here designated) in NHRS, examined. Type locality: Lake Azhabachye (Ажабачье) near Nizhnekamchatsk (Нижнекамчатск), Kamchatka Krai, Russia.

Lygaeonematus (*Lygaeophora*) *leucostoma* Lindqvist, 1952: 108. Holotype ♀ (DEI-GISHym31675) in MZH, examined. Type locality: Munksnäs, Uusimaa, Finland.

Similar species. Species limits in the *micronematica* group are still unclear.

Genetic data. Based on COI barcode sequences, specimens of the *micronematica* group belong to the BIN cluster BOLD:ACG2488. Maximum distance within the BIN is 2.45%. The nearest neighbour to BOLD:ACG2488, diverging by a minimum of 4.1%, is BOLD:ACO1401 (*P. euxantha*). Based on nuclear data, maximum divergence within the group is 2.5% (based on four specimens and TPI) and the nearest neighbour is 4.7% (*P. nigella*, only TPI) or 0.6% different (*P. siskiyouensis*, only NaK).

Host plants. *Salix caprea* L. (Verzhutskii 1981), *S. phylicifolia* L. (Kangas 1985, *ex ovo* rearing experiments by VV), *S. pentandra* L. (Kangas 1985).

Rearing notes. Ovipositing experiment no. 1/1973: Finland, North Karelia, Joensuu, Purola. One female was captured and buds of *Salix phylicifolia* and young leaves of *Betula pubescens* were offered her. On 18–19.V.1973 several eggs were laid in buds

of *Salix*, the egg pockets were on undersides of leaves near the leaf margin. Four larval instars were observed, their development was rapid and on 28.V.1973 several prepupae were seen. No extra moult after feeding.

Distribution and material examined. Palaearctic, Nearctic. Specimens studied are from Finland and Russia (Kamchatka Krai).

Pristiphora nordmani (Lindqvist, 1949)
Fig. 309

Lygaeonematus nordmani Lindqvist, 1949: 85–86. Holotype ♀ (DEI-GISHym20890) in MZH, examined. Type locality: Finström, Åland, Finland.

Similar species. Species limits in the *micronematica* group are still unclear.

Genetic data. Based on COI barcode sequences, specimens of the *micronematica* group belong to the BIN cluster BOLD:ACG2488. Maximum distance within the BIN is 2.45%. The nearest neighbour to BOLD:ACG2488, diverging by minimum of 4.1%, is BOLD:ACO1401 (*P. euxantha*). Based on nuclear data, maximum divergence within the group is 2.5% (based on four specimens and TPI) and the nearest neighbour is 4.7% (*P. nigella*, only TPI) or 0.6% different (*P. siskiyouensis*, only NaK).

Host plants. Unknown.

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

Pristiphora reuteri (Lindqvist, 1960)
Figs 208, 308

Lygaeonematus (*Lygaeophora*) *reuteri* Lindqvist, 1960b: 33–34. Holotype ♀ (DEI-GISHym31676) in MZH, examined. Type locality: Munksnäs, Uusimaa, Finland.

Similar species. Species limits in the *micronematica* group are still unclear.

Genetic data. Based on COI barcode sequences, specimens of the *micronematica* group belong to the BIN cluster BOLD:ACG2488. Maximum distance within the BIN is 2.45%. The nearest neighbour to BOLD:ACG2488, diverging by a minimum of 4.1%, is BOLD:ACO1401 (*P. euxantha*). Based on nuclear data, maximum divergence within the group is 2.5% (based on four specimens and TPI) and the nearest neighbour is 4.7% (*P. nigella*, only TPI) or 0.6% different (*P. siskiyouensis*, only NaK).

Host plants. *Salix phylicifolia* L. (Vikberg 1966 and later *ex ovo* rearing experiments by VV). Records from *Spiraea* (Verzhutskii 1981) are doubtful, because of possible misidentifications.

Rearing notes. Ovipositing experiment no. 2/1973: Finland, North Karelia, Joensuu, Purola. One female was captured and offered buds of *Salix phylicifolia* and young

leaves of *Betula pubescens*. On 18–19.V.1973 several eggs were laid in buds of *Salix*, the egg pockets were on the undersides of leaves near the leaf margin. Larvae hatched on 22.V.1973. Four larval instars were observed, their development was rapid and on 30.V.1973 some prepupae were seen. No extra moult after feeding.

Distribution and material examined. West Palaearctic, Nearctic. Specimens studied are from Finland and Sweden.

Pristiphora sermola Liston, 1993
Figs 209, 304

Lygaeonematus (*Lygaeophora*) *variipes* Lindqvist, 1952: 106–107. Secondary homonym of *Pristiphora varipes* Serville, 1823. Holotype ♀ (DEI-GISHym20889) in MZH, examined. Type locality: Island Ruissalo (=Runsala), Turku, Finland.

Lygaeonematus (*Lygaeophora*) *variipes* ab. *xanthopus* Lindqvist, 1952: 107. Not available. Infrasubspecific name.

Lygaeonematus (*Lygaeophora*) *variipes* ab. *morio* Lindqvist, 1952: 107. Not available. Infrasubspecific name.

Pristiphora sermola Liston, 1993: 104. Replacement name for *Lygaeonematus* (*Lygaeophora*) *variipes* Lindqvist, 1952.

Similar species. Species limits in the *micronematica* group are still unclear.

Genetic data. Based on COI barcode sequences, specimens of the *micronematica* group belong to the BIN cluster BOLD:ACG2488. Maximum distance within the BIN is 2.45%. The nearest neighbour to BOLD:ACG2488, diverging by a minimum of 4.1%, is BOLD:ACO1401 (*P. euxantha*). Based on nuclear data, maximum divergence within the group is 2.5% (based on four specimens and TPI) and the nearest neighbour is 4.7% (*P. nigella*, only TPI) or 0.6% different (*P. siskiyouensis*, only NaK).

Host plants. *Salix caprea* L. [Liston 1982, as *Pristiphora* (*Lygaeophora*) *lanifica*], *S. phylicifolia* (*ex larva* and *ex ovo* rearings by J. Kangas and VV), *Salix starkeana* Willd. (*ex ovo* rearing experiments by VV). The report by Kontuniemi (1960) of *P. lanifica* from *Salix phylicifolia* L. possibly refers to *P. sermola*.

Rearing notes. Ovipositing experiment no. 2/1971 as *P. variipes*: Finland, North Karelia: Kontiolahti, Jaamankangas. On 30–31.V.1971 one captured female laid several eggs in pockets near leaf margin of *Salix phylicifolia*. Larvae hatched on 2–3. VI.1971. Four larval instars were observed, their development was rapid and prepupae were seen on 11–13.VI.1971. No extra moult after feeding.

Ovipositing experiment no. 23/1973: Finland, North Karelia, Kontiolahti, Jaamankangas. On 28–29.V.1973 one captured female laid several eggs in buds of *Salix starkeana*, in egg pockets on the undersides of leaves near the leaf margin. Larvae hatched on 1.VI.1973. Five larval instars were observed, their development was rapid and on 11.VI.1973 prepupae were seen. No extra moult after feeding.

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

Pristiphora nigella group

Pristiphora amphibola (Förster, 1854)
Figs 165, 293

Nematus amphibolus Förster, 1854b: 329–330. Lectotype ♀ (GBIF-GISHym3195) in ZSM, examined. Type locality: Aachen, North Rhine-Westphalia, Germany.

Nematus laetus Cameron, 1883: 194–195. Syntype(s) ♀ possibly in BMNH, not examined. Type locality: Mickleham, Surrey, United Kingdom. Synonymised as *fraternus* with *P. amphibola* by Benson (1948).

Nematus fraternus Cameron, 1885: 73–74. Replacement name for *Nematus laetus* Cameron, 1883.

Similar species. The most similar species are *P. nigella* and *P. parva*, from which females of *P. amphibola* can be distinguished by the combination of dark coloration (almost completely black) and long valvula 3 (see the Key, and Beneš et al. 1981). Males are best recognised by examining penis valves (see the Key).

Genetic data. Based on COI barcode sequences, *P. amphibola* belongs to the same BIN cluster (BOLD:AAF5120) as *P. nigella* (Fig. 5). Maximum distance within the BIN is 0.71% and minimum between species distance is possibly 0.00%. The nearest neighbour to BOLD:AAF5120, diverging by minimum of 2.26%, is BOLD:ABV9415 (*P. parva*). Based on nuclear data (one specimen; NaK), the nearest neighbour is 0.4% different (*P. nigella*).

Host plants. *Picea abies* (L.) Karsten (Crooke 1957, Beneš et al. 1981), *Picea sitchensis* (Bong.) Carriere (Crooke, 1957).

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

Pristiphora nigella (Förster, 1854)
Figs 34, 111, 115, 166, 294

Tenthredo ambigua Fallén, 1808: 112–113. Primary homonym of *Tenthredo ambigua* O.F. Müller, 1776. Lectotype ♂ (designated by Beneš et al. 1981) in MZLU, examined. Type locality: Sweden.

Nematus occultus Förster, 1854a: 331–332. Lectotype ♂ (GBIF-GISHym3371; designated by Beneš et al. 1981) in ZSM, examined. Type locality: Aachen, North Rhine-Westphalia, Germany. Synonymised with *Lygaeonematus ambiguus* by Konow (1904a).

Nematus nigellus Förster, 1854a: 328–329. Lectotype ♀ (GBIF-GISHym3361; designated by Beneš et al. 1981) in ZSM, examined. Type locality: near Aachen, North Rhine-Westphalia, Germany.

Nematus furvescens Cameron, 1876: 308–311. Syntype(s) possibly in BMNH, not examined. Type locality: East Dunbartonshire or Stirling ("old road between

Milngavie and Strathblane"), Scotland, United Kingdom. Synonymised with *Lygaeonematus ambiguus* by Konow (1904a).

Nematus obscurus Zaddach in Brischke, 1884: 126. Primary homonym of *Nematus obscurus* Norton, 1861 [= *Euura obscura* (Norton, 1861)]. Syntypes possibly destroyed (Blank and Taeger 1998). Type locality: Gdańsk [Danzig], Poland or Kaliningrad [Königsberg], Russia. Synonymised with *Lygaeonematus ambiguus* by Konow (1904a).

Nematus xanthomus Zaddach in Brischke, 1884: 138. Syntype ♂ and ♀ possibly destroyed (Blank and Taeger 1998). Type locality: Lüneburg, Lower Saxony, Germany. Synonymised with *Sharliphora nigella* by Beneš et al. (1981).

Nematus obscurior Dalla Torre, 1894: 246. Replacement name for *Nematus obscurus* Zaddach, 1884.

Similar species. The most similar species are *P. amphibola* and *P. parva*. In females, the shorter valvula 3 (see the Key) of *P. nigella* enables its separation from *P. amphibola*, but differences (slightly shorter valvula 3 and darker coloration) from *P. parva* might not always be evident. Penis valves of *P. nigella*, however, seem to show more reliable differences from *P. amphibola* and *P. parva*: in *nigella*, the paravalva is ventrally abruptly narrowed before the valvispina (Fig. 294), while in other species the narrowing is more gradual (Figs 293, 295).

Genetic data. Based on COI barcode sequences, *P. nigella* belongs to the same BIN cluster (BOLD:AAF5120) as *P. amphibola* (Fig. 5). Maximum distance within the BIN is 0.71% and minimum between species distance is possibly 0.00%. The nearest neighbour to BOLD:AAF5120, diverging by minimum of 2.26%, is BOLD:ABV9415 (*P. parva*). Based on nuclear data, the nearest neighbour is 0.3% different (*P. parva*, only TPI).

Host plants. *Picea abies* (L.) Karsten (Kontuniemi 1960).

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

Pristiphora parva (Hartig, 1837)
Figs 167, 295

Nematus parvus Hartig, 1837: 208–210. Lectotype ♂ (GBIF-GISHym3376; designated by Beneš et al. 1981) in ZSM, examined. Type locality: Germany.

Nematus nigricornis Zaddach in Brischke, 1883b: 146–147. Primary homonym of *Nematus nigricornis* Serville, 1823 [= *Euura nigricornis* (Serville, 1823)]. Holotype ♂ possibly destroyed (Blank and Taeger 1998). Type locality: Gacko [Dammhof], West Pomeranian Voivodeship, Poland. Synonymised with *Sharliphora parva* by Beneš et al. (1981).

Nematus germanicus Dalla Torre, 1894: 227, 7. Replacement name for *Nematus nigricornis* Zaddach, 1883.

Lygaeonematus ambiguus var. *flavater* Enslin, 1916: 503–504. Lectotype ♂ (DEI-GISHym31699; here designated) in ZSM, examined. Type locality: Gräfenberg, Bavaria, Germany.

Similar species. Most similar species is *P. nigella*. *Pristiphora parva* tends to be paler than *P. nigella*, and in females the valvula 3 is slightly longer in *P. parva* than in *P. nigella* (see the Key). Penis valves seem to show more reliable differences: in *P. parva*, the paravalva narrows distinctly more gradually than in *P. nigella* (Figs 294–295).

Genetic data. Based on COI barcode sequences, *P. parva* belongs to its own BIN cluster (BOLD:ABV9415) (Fig. 5). Maximum distance within the BIN is 0.32%. The nearest neighbour to BOLD:ABV9415, diverging by a minimum of 2.26%, is BOLD:AAF5120 (*P. amphibola* and *P. nigella*). Based on nuclear data, within species divergence is 0.0% (based on two specimens and both genes combined) and the nearest neighbour is 0.3% different (*P. nigella*, only TPI).

Host plants. *Picea abies* (L.) Karsten (Kangas 1985).

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

Pristiphora pallida group

Pristiphora pallida (Konow, 1904)
Figs 8, 125, 171, 276

Lygaeonematus pallidus Konow, 1904a: 195, 204. Lectotype ♀ (GBIF-GISHym3906; here designated) in SDEI, examined. Type locality: Thüringen, Germany.
Lygaeonematus Stecki [sic!] Nägeli, 1936: 218–219. No type specimens were found in ETHZ by Michael Greeff. Type locality: Bülach, Switzerland. Synonymised with *Lygaeonematus pallidus* by Forsslund (1939).

Similar species. The most similar species is *P. subarctica*. For females, there might be small differences in basal annuli of the lancet: in *P. pallida*, the gap between basal serrulae is smaller and setae are more numerous on basal three annuli than in *P. subarctica*. Additional differences mentioned by Forsslund (1939) are even smaller or do not seem to be reliable. For example, the lancet is supposed to be more bent in *P. pallida* (dorsally convex and ventrally concave) than in *P. subarctica* (somewhat evident also in Figs 171–172), but this difference seems to be absent according to drawings by Wong (1975: figs 17–18). Penis valves are also almost identical, the only difference being possibly the absence (*P. pallida*, Fig. 276) or presence (*P. subarctica*, Fig. 278) of a depression on the apical part of valvispina. More studies are needed to decide if *P. pallida* and *P. subarctica* are distinct species.

Genetic data. Based on COI barcode sequences, *P. pallida* forms its own BIN cluster (BOLD:AAX8150). Maximum distance within the BIN is 0.69%. The nearest neighbour to BOLD:AAX8150, diverging by minimum of 2.44%, is *P. subarctica* (no full barcode available, but possibly belonging also to BOLD:AAX8150). Based on nuclear data (one specimen and NaK), the nearest neighbour is 1.1% different (*P. parva*).

Host plants. *Picea abies* (L.) Karsten (Boevé 1990, Pschorn-Walcher and Altenhofer 2000).

Distribution and material examined. West Palaearctic. Specimens studied are from Germany.

Pristiphora subarctica (Forsslund, 1936)
Figs 172, 278

Lygaeonematus subarcticus Forsslund, 1936: 14–22. Holotype ♀ was not found in NHRS. Type locality: Tärna and Stensele, Lycksele Lappmark, Sweden.
Pristiphora pseudosaxesenii Lindqvist, 1968a: 138–139. Holotype ♀ (DEI-GISHym31526) in MZH, examined. Type locality: Forssa, Finland.

Similar species. The most similar species is *P. pallida*. For females, there might be small differences in basal annuli of the lancet: in *P. subarctica*, the gap between basal serrulae is larger and setae are less numerous on basal three annuli than in *P. pallida*. Additional differences mentioned by Forsslund (1939) are even smaller, or do not seem to be reliable. The penis valves are also almost identical, the only difference being possibly the presence (*P. subarctica*, Fig. 278) or absence (*P. pallida*, Fig. 276) of a depression on the apical part of valvispina. More studies are needed to decide if *P. pallida* and *P. subarctica* are distinct species.

Genetic data. No full COI barcode available, but a 462 bp fragment available in BOLD of one Finnish specimen (FISYM334-15, MHV000166) is closest to BOLD:AAX8150 (*P. pallida*) differing by a minimum of 2.44%. No nuclear data are available.

Host plants. *Picea abies* (L.) Karsten (Forsslund 1936, Rodeghiero 2006).

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

Pristiphora pallidiventris group

Pristiphora nigricans (Eversmann, 1847), comb. n.
Figs 141, 223

Nematus nigricans Eversmann, 1847: 16. Lectotype ♀ (DEI-GISHym30030; here designated) in ZIN, examined. Type locality: prov. Casan [Republic of Tatarstan], Russia.
Nematus Anderschi [sic!] Zaddach, 1876: 62–63, **syn. n.** Holotype ♀ possibly destroyed (Blank and Taeger 1998). Type locality: Uncertain, but possibly Tilsit, Kaliningrad Oblast, Russia. Note. The name *anderschi* has apparently not been used as valid more than 25 times during the last 50 years (we found 17 publications) and therefore Article 23.9.1 (ICZN 1999) cannot be applied in this case.

Pristiphora inocreata Konow, 1902: 181, **syn. n.** Lectotype ♀ (GBIF-GISHym3923; designated by Oehlke and Wudowenz 1984 as "Holotypus") in SDEI, examined. Type locality: Moravia, Czech Republic.

Pristiphora discolor Lindqvist, 1975: 13–14, **syn. n.** Holotype ♀ (GBIF-GISHym20870) in MZH, examined. Type locality: Popovo, Iljhonsk, Irkutsk Oblast, Russia.

Similar species. The most similar species is *P. pallidiventris*. Females of *P. nigricans* have a completely pale metafemur and black terga 9 and 10, while in *P. pallidiventris* metafemur and terga 9–10 are completely pale or at least the metafemur is apically slightly black. The lancet and penis valve also show consistent differences (see the Key).

Genetic data. Based on a COI barcode sequence of one confidently identified specimen (DEI-GISHym20619), *P. nigricans* belongs to the same BIN cluster (BOLD:AAU3334) as *P. pallidiventris* (Fig. 5). The nearest neighbour (BOLD:ACO0950, possibly *P. pallidiventris*, from China) is 2.26% different. No nuclear data available.

Host plants. *Sanguisorba* sp. (Verzhutskii 1981, as *P. discolor*). *Sanguisorba officinalis* L. according to the label data of the holotype of *discolor* Lindqvist.

Distribution and material examined. Palaearctic. Specimens studied are from Czech Republic, France, Germany, Kazakhstan, Russia (Irkutsk Oblast and Republic of Tatarstan), and Ukraine.

Pristiphora pallidiventris (Fallén, 1808)
Figs 54, 106, 142–144, 224–226

Tenthredo pallidiventris Fallén, 1808: 120–121. Lectotype ♀ (MZLU2014482; here designated) in MZLU, examined. Type locality: not stated.

Nematus (*Nematus*) *luridus* Dahlbom, 1835b: 7. Not available. Nomen nudum.

Nematus ephippiger Hartig, 1840: 24. Out of 7 ♀♀ and 2 ♂♂ syntypes, 2 ♀♀ and 2 ♂♂ were not found in ZSM. Type locality: not stated.

Nematus flavicomus Tischbein, 1846: 77. Types probably destroyed (Horn et al. 1990). Type locality: B. [Birkenfeld, Rhineland-Palatinate, Germany]. Synonymised with *P. pallidiventris* by Konow (1902).

Nematus gemellus Förster, 1854a: 425–427. Lectotype ♀ (GBIF-GISHym3288; here designated) in ZSM, examined. Type locality: near Aachen, North Rhine-Westphalia, Germany.

Nematus Marshalli [sic!] Cameron, 1875: 9. Syntype(s) possibly in BMNH, not examined. Type locality: Corsica, France. Synonymised with *P. pallidiventris* by Konow (1902).

Nematus cirrhostomus Zaddach in Brischke, 1883b: 195. Two syntypes possibly destroyed (Blank and Taeger 1998). Type locality: Finland. Synonymised with *P. pallidiventris* by Konow (1902).

Pristiphora pallidiventris var. *denudata* Konow, 1902: 165, 179. Lectotype ♀ (DEI-GISHym3905; here designated) in SDEI, examined (severely damaged, abdomen missing). Type locality: Barcelona, Spain.

Pristiphora zella Rohwer, 1909: 20. Holotype ♀ in NSM (Smith 1983), not examined. Type locality: Nebraska, USA. Synonymised with *P. pallidiventris* by Smith (1979).

Pristiphora pallicoxa Rohwer, 1910b: 200. Holotype ♀ (USNMENT00779341) in USNM, not examined. Type locality: Nerepis, New Brunswick, Canada. Synonymised with *P. pallidiventris* by Smith (1979).

Pristophora [sic!] *xanthotrachela* Rohwer, 1913: 281. Holotype ♀ (USNMENT00779593) in USNM, not examined. Type locality: Cabin John, Maryland, USA. Synonymised with *P. pallidiventris* by Smith (1979).

Pristiphora pallidiventris var. *haemorrhoidalis* Enslin, 1916: 526. Lectotype ♀ (GBIF-GISHym3291; here designated) in ZSM, examined. Type locality: Erlangen, Bavaria, Germany.

Pristiphora pallidiventris var. *stigmatica* Enslin, 1916: 526. Lectotype ♀ (GBIF-GISHym3444; here designated) in ZSM, examined. Type locality: Krefeld [Crefeld], North Rhine-Westphalia, Germany.

Pristiphora ostiaria MacGillivray, 1920: 236. Lectotype ♀ in INHS (http://inhsinsectcollection.speciesfile.org/InsectCollection.aspx) (designated by Frison 1927), not examined. Type locality: Ithaca, New York, USA. Synonymised with *P. pallidiventris* by Smith (1979).

Pristiphora atlantica Malaise, 1939: 1–3. Holotype ♀ in NHRS, examined. Type locality: Caramujo, Madeira, Portugal.

Nematus (*Pristiphora*) *pallidiventris* ab. *flaviapex* Hellén, 1948a: 45. Not available. Infrasubspecific name.

Nematus (Pristiphora) *pallidiventris* ab. *nigrofemoratus* Hellén, 1948a: 45. Not available. Infrasubspecific name.

Pristiphora pallidiventris atlantica Lacourt, 1987: 261–262. Primary homonym of *Pristiphora atlantica* Malaise, 1939 [= *Pristiphora pallidiventris* (Fallén, 1808)]. Holotype ♀ in CTN, examined. Type locality: Ifrane, Meknès-Tafilalet, Morocco.

Pristiphora pallidiventris megalpina Lacourt, 1987: 262–264. Holotype ♀ in CTN, examined. Type locality: St Véran, Provence-Alpes-Côte d'Azur, France.

Similar species. The most similar species is *P. nigricans*. Females of *P. pallidiventris* have a completely pale metafemur and terga 9–10, or at least partly black metafemur, while in *P. nigricans* the metafemur is completely pale and terga 9–10 are black. The lancets (Figs 141–144) and penis valves (Figs 223–226) have also consistent differences (see the Key). *P. pallidiventris* is rather variable (also discussed by Lacourt 1987): size of the subapical tooth of claws varies from small to large, the abdomen can be nearly completely black to completely yellow (sometimes even mesepisternum is partly pale), and the structure of the serrulae of the lancet and shape of the penis valve varies as well. Because the variation seems to be continuous and there is no unambiguous way to divide the variation into more than one taxon, we accept only one species.

Genetic data. Based on COI barcode sequences, specimens of this species are divided between at least two BIN clusters (BOLD:ACO1634 and BOLD:AAU3334)

(Fig. 5). Minimal distance between these two clusters is 4.94%. Eight additional BIN numbers available in BOLD fall between these two *P. pallidiventris* BIN clusters. One BIN cluster from Germany (BOLD:AAK9449), five from Canada (BOLD:ACT4128, BOLD:ACO4727, BOLD:ACO4729, BOLD:ABX2590, BOLD:ACL3627) and two from China (BOLD:ACO0950 and BOLD:ACO6535) may contain *P. pallidiventris* rather than *P. nigricans* based on the pictures available in BOLD (no specimens studied), although the existence of additional species cannot be excluded. A studied male specimen of *P. pallidiventris* from Primorsky Krai is closest to BOLD:ACL3627 (Canada), differing by a minimum of 2.3%. Based on nuclear data (two specimens, both genes combined), within species divergence is 0.9% and the nearest neighbour is 3.1% different (*P. testacea*). Large genetic diversity would be expected for a widespread species (BOLD:AAU3334 contains specimens from Europe and Canada). As the specimens belonging to BIN clusters BOLD:ACO1634 and BOLD:AAU3334, and the specimen from Primorsky Krai cannot be morphologically separated, we consider *pallidiventris* to be a single species, that is widespread and genetically diverse.

Host plants. *Filipendula ulmaria* (L.) Maxim. (Loiselle 1913), *Geum urbanum* L. (Loth 1913), *G. rivale* L. (Kangas 1985), *Rubus chamaemorus* L. (Liston 2011), *R. idaeus* L. (Loth 1913), *R. fruticosus* agg. (Loth 1913, Chambers 1961), *R. ulmifolius* Schott (Liston and Zerafa 2012, as *P. atlantica*).

Distribution and material examined. Palaearctic, Nearctic. Specimens studied are from Austria, Estonia, Finland, France, Germany, United Kingdom, Morocco, Poland, Portugal, Russia (Primorsky Krai), Spain, Sweden, Switzerland, and Ukraine.

Pristiphora retusa group

Pristiphora exigua (Lindqvist, 1955)
Figs 101–102, 133, 258

Lygaeonematus exiguus Lindqvist, 1955a: 143. Holotype ♂ (DEI-GISHym20912) in MZH, examined. Type locality: Espoo, Uusimaa, Finland.

Similar species. The most similar species is *P. retusa*, females of which usually have a mostly black metafemur in (pale in *P. exigua*) and narrower valvula 3 (Figs 101–103). Males are best recognised by examining penis valves (see the Key).

Genetic data. Based on COI barcode sequences (only one specimen in BOLD), *P. exigua* belongs to its own BIN cluster (BOLD:ADD4067). The nearest neighbour to BOLD:ADD4067, diverging by a minimum of 4.3%, is BOLD:ABU7029 (*P. retusa*). No nuclear data are available.

Host plants. Unknown.

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

Pristiphora retusa (Thomson, 1871)

Figs 11, 41, 103, 134, 260

Nematus retusus Thomson, 1871: 109–110. Lectotype ♀ (NHRS-HEVA000003756; here designated) in NHRS, examined. Type locality: Dalarna, Sweden.

Similar species. The most similar species is *P. exigua*, females of which have a completely pale metafemur (usually in most part black in *P. retusa*) and a broader valvula 3. Males are best recognised by examining penis valves (see the Key).

Genetic data. Based on COI barcode sequences, belongs to its own BIN cluster (BOLD:ABU7029) (Fig. 3). Maximum distance within the BIN is 0.3%. The nearest neighbour to BOLD:ABU7029, diverging by a minimum of 4.3%, is BOLD:ADD4067 (*P. exigua*). Based on nuclear data, maximum within species divergence is 0.3% (based on three specimens and NaK or both genes combined) and the nearest neighbour is 2.4% different [*P. bivittata* (Norton, 1861), a Nearctic species, only NaK].

Host plants. *Prunus padus* L. (Benson 1954b, Kangas 1985, *ex ovo* rearing experiments by VV).

Rearing notes. Ovipositing experiment no. 1/1978: Finland, South Häme, Janakkala, Hangastenmäki. On 22–23.V.1978 two captured females laid eggs into pockets on undersides of young leaves of *Prunus padus*. Larvae hatched on 27.V.1978, and ate holes into leaves. Four larval instars were observed, the development of larvae was rapid and on 7.VI.1978 prepupae were found. No extra moult after feeding.

Distribution and material examined. Palaearctic. Specimens studied are from Germany, Russia (Primorsky Krai), and Sweden.

Pristiphora ruficornis group

Pristiphora albitibia (Costa, 1859)

Figs 6, 20, 44, 188, 273

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. Synonymised with *P. albitibia* by Costa (1894).

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). Synonymised with *P. staudingeri* auct. by Konow (1905).

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

Pristiphora nigropuncticeps Haris, 2002: 75–76, **syn. n.** Holotype ♂ (DEI-GISHym80345; http://dx.doi.org/10.6084/m9.figshare.5057701) in HNHM, examined. Type locality: Nukht, Bogd Khan Mountain, Ulaanbaatar, Mongolia.

Similar species. Externally, the most similar species are *P. armata*, *P. confusa*, *P. leucopus*, *P. opaca*, *P. sootryeni*, and *P. subopaca*, from which it is best distinguished by the structure of the lancet (Fig. 188), the penis valve (Fig. 273), and the colour of pterostigma (Fig. 40) (see the Key).

Genetic data. Based on COI barcode sequences, specimens of this species are divided between two BIN clusters (BOLD:ACH1762 and BOLD:ADH0371) (Fig. 4). Minimum distance between the clusters is 4.6%. Based on nuclear data (four specimens and both genes combined), maximum within species divergence is 0.3% and the nearest neighbour is 0.8% different (*P. astragali* or *P. caraganae*). Two studied specimens (male and female) from Finland with a highly divergent barcode (BOLD:ADH0371; DEI-GISHym80018 and DEI-GISHym80357) are morphologically indistinguishable from other *P. albitibia* specimens and this is congruent with nuclear data (both genes) from the female DEI-GISHym80357 (divergence from the other three specimens is 0.1–0.3%).

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*), *V. baicalensis* Turcz., *V. unijuga* A. Br. (Verzhutskii 1981, as *P. puncticeps*).

Rearing notes. See Vikberg (2006).

Distribution and material examined. Palaearctic. Specimens studied are from Estonia, Finland, Germany, Mongolia, Russia (Irkutsk Oblast), and Sweden.

Pristiphora aphantoneura (Förster, 1854)
Fig. 195

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

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

Cryptocampus distinctus Costa, 1882: 198. Syntype(s) ♀ possibly in MZUN, not examined. Type locality: Oschiri, Sardinia, Italy. Synonymised with *P. fulvipes* by Costa (1894). 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. Synonymised with *P. aphantoneura* by Vikberg (2006).

Similar species. The most similar species is *P. luteipes*, from which it cannot be always distinguished morphologically. Vikberg (2006) mentioned that the mesepisternum is completely smooth unlike in *P. luteipes*, which should show at least slightly coriaceous

sculpture (Fig. 45 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), *P. aphantoneura* 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 Prous et al. 2016). Maximum distance within the BIN is 3.33% and minimum between species distance is 0.00%. The nearest neighbour to BOLD:AAG3568, diverging by minimum of 2.76%, is BOLD:AAQ2302 (*P. armata* and *P. leucopus*). Based on nuclear data (if the specimen DEI-GISHym31258 is correctly identified), the nearest neighbour is 0.2% different (*P. luteipes*, both genes combined).

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

Rearing notes. See Vikberg (2006).

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

Pristiphora appendiculata (Hartig, 1837)
Figs 19, 21, 61, 105, 187, 262

Pristiphora pallipes Serville, 1823: 75. Secondary homonym of *Tenthredo pallipes* Fallén, 1808 [= *Pristiphora 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 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.

Nematus appendiculatus Hartig, 1837: 202–203. Nomen protectum. See Blank et al. (2009). Lectotype ♀ (GBIF-GISHym3197; designated by Prous et al. 2016) 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. Synonymised with *Nematus appendiculatus* by Stein (1881).

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

Nematus cathoraticus Förster, 1854: 325–326. Lectotype ♀ (GBIF-GISHym3214; designated by Prous et al. 2016) 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. Synonymised with *P. pallipes* by Smith (1966).

Nematus pallicornis var. *labratus* Norton, 1861: 160. Holotype ♀ possibly in ANSP or MCZ. Type locality: Massachusetts, USA. Synonymised with *P. rufipes* auct. by Smith (1979).

Pristiphora grossulariae Walsh, 1866: 123. Neotype ♀ (designated by Zinovjev and Smith 2000) in ANSP, not examined. Type locality: possibly (if the neotype belongs to the syntype series) Davenport, Iowa, USA. Synonymised with *Nematus appendiculatus* by Dalla Torre (1894).

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

Nematus hypobalius Zaddach in Brischke, 1884: 154. Holotype ♀ possibly destroyed (Blank and Taeger 1998). Type locality: Hungary. Synonymised with *P. pallipes* by Konow (1905).

Nematus pumilus Zaddach in Brischke, 1884: 172. 2 ♂ syntypes possibly destroyed (Blank and Taeger 1998). Type locality: Chernyakhovsk [Insterburg], Kaliningrad Oblast, Russia. Synonymised with *P. pallipes* by Konow (1905).

Nematus Ghilianii [sic!] Costa, 1894: 73. Syntype(s) ♂ possibly in MZUN, not examined. Type locality: Alps [Alpi boreali], Europe. Synonymised with P. pallipes by Konow (1905).

Pristiphora (Pristiphora) anivskiensis Haris, 2006a: 194–195, **syn. n.** Holotype ♂ (DEI-GISHym80340; http://dx.doi.org/10.6084/m9.figshare.5100763) in HNHM, examined. Type locality: Novo-Aleksandrovsk, Sakhalin Oblast, Russia.

Similar species. Smooth mesopostnotum (Fig. 19), claws without subapical tooth (Fig. 21), and the structure of serrula (Fig. 187) or penis valves (Fig. 262) allow separation of this species from other similar species in the *ruficornis* and *rufipes* groups.

Genetic data. Based on COI barcode sequences, specimens of this species are divided between two BIN clusters (BOLD:AAG7866 and BOLD:AAU8684) (Fig. 1 in Prous et al. 2016). Minimum distance between the clusters is 3.26%. However, BOLD:AAU8684 might represent a cluster of nuclear mitochondrial pseudogenes (Prous et al. 2016). Based on nuclear data (two specimens and both genes combined), maximum within species divergence is 0.3% and the nearest neighbour is 1.8% different (*P. pusilla*).

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 (Republic of Bashkortostan, Sakhalin Oblast), and Sweden.

Pristiphora armata (Thomson, 1863)
Figs 16, 57, 193, 263

Nematus crassicornis Hartig, 1837: 204–205. Primary homonym of *Nematus crassicornis* Stephens, 1835 [= *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. Note. Because of difficulties separating *P. armata* from *P. leucopus* (see Prous et al. 2016), we refrain from selecting a lectotype at this stage.

Nematus crataegi Brischke, 1883b: 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). Synonymised with *P. crassicornis* by Konow (1905).

Nematus Fletcheri [sic!] Cameron, 1884: 26. Syntype(s) possibly in BMNH, not examined. Type locality: Worcester and Clydesdale, United Kingdom. Synonymised with *P. crassicornis* by Konow (1905).

Nematus melanostomus Zaddach in Brischke, 1884: 140–141. Holotype ♀ possibly destroyed (Blank and Taeger 1998). Type locality: Bautzen, Saxony, Germany. Synonymised with *P. crassicornis* by Konow (1905).

Nematus ensicornis Jacobs, 1884: XXIII. Syntype(s) ♀ possibly in IRSNB, not examined. Type locality: near Brussels, Belgium. Synonymised with *P. crassicornis* by Konow (1905).

Nematus nigricollis Cameron, 1885: 66. Syntype(s) possibly in BMNH, not examined. Type locality: Worcester, United Kingdom. Synonymised with *P. crassicornis* by Konow (1905).

Similar species. The most similar species is *P. leucopus*. Differences between these two species, which unfortunately are not very strong, were discussed by Grearson and Liston (2012) and Prous et al. (2016).

Genetic data. Based on COI barcode sequences, *P. armata* belongs to the same BIN cluster (BOLD:AAQ2302) as *P. leucopus* (Fig. 4). Maximum distance within the BIN is 2.41% and minimum between species distance is possibly 0.00%. The nearest neighbour to BOLD:AAQ2302, diverging by minimum of 2.76%, is BOLD:AAG3568 (*P. aphantoneura*, *P. bifida*, *P. confusa*, *P. luteipes*, *P. opaca*, *P. pusilla*, *P. staudingeri*, and *P. subopaca*). Based on nuclear TPI sequences, *P. armata* (one specimen) and *P. leucopus* (two specimens) cannot be separated either. The *P. armata* specimen is identical to one of the *P. leucopus* specimens when ambiguous positions due to heterozygosity are excluded.

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

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

Pristiphora astragali **Vikberg, 1978**
Figs 46, 189

Pristiphora astragali Vikberg, 1978: 133–137. Holotype ♀ (PR.354VV) in MZH, ex-
    amined. 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 189). The lancet has weak setae (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. 190) are rather small. Morpho-logically, the subapical tooth of the claws tends be smaller, the apical serrulae of the lancet are shorter, and the number of setae on the lancet is smaller than in *P. sootryeni* (Vikberg 2006). Male unknown.

    Genetic data. Based on a COI barcode sequences, specimens of *P. astragali* are di-vided between two BIN clusters (BOLD:AAL8292, BOLD:AAL8277), one of which (BOLD:AAL8292) includes also *P. sootryeni* (Fig. 4). Minimum distance between the two BINs is 2.4%. Based on nuclear data (one specimen and both genes combined), the nearest neighbour is 0.6% different (*P. caraganae*).

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

    Rearing notes. See Vikberg (1978, 2006).

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

Pristiphora bifida **(Hellén, 1948)**
Figs 9, 25, 199, 267

Nematus (*Pristiphora*) *bifidus* Hellén, 1948b: 116–117. Lectotype ♀ (http://id.luomus.
    fi/GL.5214; designated by Prous et al. 2016) 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. 18), while in *P. frigida* only a few black setae are barely visible (Fig. 17). The lancets (Figs 199–200) and penis valves (Figs 267, 274) are also different. The apical serrulae are somewhat shorter and more protruding, and the tangium of the lancet tends to be longer and narrower (Fig. 199) than in *P. frigida* (Fig. 200). The penis valve lacks (Fig. 267) a membranous fold near the tip of the valvispina (present in *P. frigida*; Fig. 274) 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. 4). Maximum distance within the BIN is 3.33% and minimum between species distance is 0.00%. The nearest neighbour to BOLD:AAG3568, diverging by minimum of 2.76%, is BOLD:AAQ2302 (*P. armata* and *P. leucopus*). Based on nuclear data, maximum within species divergence is 0.1% (based on two specimens and both genes combined) and the nearest neighbour is 0.0% different (*P. confusa*, *P. luteipes*, or *P. beaumonti*, only TPI). When including TPI introns, the nearest neighbour is still 0.0% different (*P. confusa* or *P. luteipes*).

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. West Palaearctic. Specimens studied are from Finland, Germany, Norway, and Sweden.

Pristiphora caraganae **Vikberg & Prous, sp. n.**
http://zoobank.org/084872FB-B38D-412F-844F-DF8CD20CDC45
Figs 194, 311–319

Description. Female (holotype DEI-GISHym80209 and one paratype), Figs 194, 311–313, 315. Body 6.1–6.3 mm. Colour mostly black. Labrum brown; labial and maxillary palps pale; mandibles reddish-brown at apex; flagellum ventrally slightly paler than dorsally or extensively pale; tibia and tarsi of fore and middle legs more or less entirely pale; apex of profemur pale; metatibia and metatarsomere 1 pale with small black area at apex; trochanters and trochantelli mainly pale; pterostigma bicoloured, basally darker than apically; pronotum and tegula extensively pale. Labrum more or less symmetrical; clypeus truncate; postocellar area about 1.4 times as long as diameter of lateral ocellus; flagellum length 3.9–4.0 mm, 2.3–2.4 times as long as width of head. Mesopostnotum matt; mesepisternum smooth; claws with large subapical tooth clearly separated from apical one; anterior protibial spur with velum. Hypopygium posteriorly not excised. Sawsheath (valvula 3 + valvifer 2) with distinct scopa directed posteriorly and with short medial projection. Lancet with numerous setae on annuli; serrulae protruding, more or less triangular, and with numerous denticles on ventro-apical surface; small spiny pectines on the inner surface (dentes semicirculares) that reach sclerora weak; tangium without lobe, campaniform sensilla present.

Male (31 paratypes), Figs 314, 316–319. Body 5.0–5.6 mm (n=6). Colour mostly black, similar to female. Flagellum ventrally distinctly paler than dorsally; labial and maxillary palps pale; mandibles reddish-brown at apex; tibia and tarsi of fore and middle legs more or less entirely pale; apex of pro- and mesofemur pale; metatibia pale with small black area at apex, trochanters and trochantelli slightly pale; pterostigma bicoloured, basally darker than apically; pronotum black or apically slightly brownish, tegula black to extensively pale. Labrum more or less symmetrical; clypeus truncate; postocellar area about 1.5 times as long as diameter of lateral ocellus; flagellomeres with numerous stout black setae among finer paler ones; flagellum length 4.0–4.3 mm,

2.6–3.1 times as long as width of head. Mesopostnotum matt; mesepisternum smooth; claws with long subapical tooth close to or clearly separated from the apical one; anterior protibial spur with velum. Tergum 8 without apical projection; sternum 9 without notch. Penis valve with large valvispina that nearly entirely replaces paravalva. Valvispina strongly bent in dorsal direction, narrow and with posterior and anterior margin of similar shape, apex sharp; pseudoceps relatively short and broad, apex distinctly narrowed and ventroapical part only slightly extending beyond dorsalmost margin, dorsally without depression, distinct spines, hair, and membranous regions or folds.

Etymology. The species name refers to the host plant *Caragana*.

Similar species. Externally, females of this species (only the holotype and one paratype known so far) are not distinguishable from many specimens of *P. confusa*, as well as from *P. armata* and *P. leucopus* that have completely black metafemora. However, the lancet has small spiny pectines on its inner surface (Fig. 194) as in other species of *albitibia* subgroup. Unfortunately, these spiny pectines might easily be overlooked, because they are rather weakly developed (at least in the holotype) compared to other species in the group. In the *albitibia* subgroup, the female as well as the male of *P. caraganae* differ from the other species by having the antenna ventrally pale. The female differs additionally from *astragali* and *sootryeni* by having a smooth mesepisternum and different lancet (see the Key). Males seem externally most similar to *P. bifida*, but the penis valves of *P. caraganae* (Fig. 317) clearly indicate a close relationship with the *albitibia* subgroup. Compared to other species in the group (although males of *P. astragali* are unknown), the penis valves seem to be sufficiently distinct (see the Key). There appears to be one more species belonging to the *albitibia* subgroup that has ventrally pale antennae. *Pristiphora nigromongolica* Haris, 2002 (http://dx.doi.org/10.6084/m9.figshare.5057791), which is so far known only from the holotype male, differs from *P. caraganae* by having a smaller subapical tooth of the claw, possibly darker pterostigma (uniformly dark) and a different penis valve that is most similar to *P. sootryeni* (http://dx.doi.org/10.6084/m9.figshare.4690174).

Genetic data. Based on two identical COI barcode sequences, *P. caraganae* possibly forms its own cluster (no BIN number has been assigned yet) (Fig. 4). Based on nuclear data (two specimens and both genes combined), within species divergence is 0.0% and the nearest neighbour is 0.6% different (*P. astragali*).

Host plants. *Caragana arborescens* Lam.

Rearing notes. The type specimens were collected from *Caragana arborescens* that grew intermixed with *Populus tremula*. One larva swept on 18.VI.2017 from the same spot as the adults was offered leaves of *Caragana*, *Populus*, and *Vicia cracca* L., but fed only on *Caragana*. The larvae made a cocoon on 22.VI.2017 and a female emerged on 2.VII.2017. The reared female laid 44 eggs in leaflets of *Caragana* and one egg in a leaflet of *Vicia*. The first larvae emerged on 7.VII.2017. The larva emerged from *Vicia* was also feeding on *Vicia*, but died the following day (8.VII.2017). The larvae feeding on *Caragana* had four instars and possibly a few (3?) had five instars and their development was rapid. On 17–19.VII.2017, 41 prepupae were counted (three larvae had died earlier as rather young) and they made brown cocoons in filter paper in petri dishes, except four prepupae which were stored in alcohol. On 31.VII.–5.VIII.2017, 30 males emerged.

Distribution and material examined. West Palaearctic. Finland.

Holotype. Female. Finland, Hame, Janakkala, Kuumola [ETRS-TM35FIN 67558:[8]3721], 60.91707°N 24.64196°E, 28.VIII.2016, leg. V. Vikberg (MZH). Paratypes. 1♂ (DEI-GISHym80356), same data as the holotype, except 30.V.2017 (MZH), 1♀, same data as the holotype, except reared *ex larva* from *Caragana arborescens* found on 18.VI.2017, emerged 2.VII.2017 (CVV), 30 ♂♂, same data as the holotype, except reared *ex ovo* from the reared female, emerged 31.VII.–5.VIII.2017 (15 in CVV, 5 in MZH, 8 in SDEI, 2 in UEF), 4 prepupae (♂), same data as the holotype, except reared *ex ovo* from the reared female (SDEI).

Pristiphora confusa Lindqvist, 1955
Figs 196, 268

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*. *Pristiphora confusa* is best distinguished by the structure of the male penis valve (Fig. 268). 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 192–193, 196–198). The apical serrulae are more protruding and shorter than in *P. opaca* and *P. subopaca* (Figs 196–198). *Pristiphora opaca* also has a fold at the base of the tangium of the lancet (Fig. 197) that is lacking in other species in the *ruficornis* group. *Pristiphora opaca* tends also to have a smaller subapical tooth than *P. confusa* (Figs 22–23). The pterostigma of *P. confusa* is apically brown and basally dark brown, like in *P. opaca* (Fig. 40), but unlike in *P. subopaca*, in which it is uniformly yellow (Fig. 39). In *P. armata* and *P. leucopus*, the pterostigma is usually dark brown (Fig. 42), 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 setae tend to be more distinct in *P. confusa* (Figs 192–193, 196). Among the males, the most similar penis valves are of *P. subopaca*. The valvispina in *P. confusa* is barely bent and the pseudoceps is narrower compared to *P. subopaca* (Figs 268–269).

Genetic data. Based on COI barcode sequences, 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. 4). Maximum distance within the BIN is 3.33% and minimum between species distance is 0.00%. The nearest neighbour to BOLD:AAG3568, diverging by minimum of 2.76%, is BOLD:AAQ2302 (*P. armata* and *P. leucopus*). Based on nuclear data, maximum within species divergence is 0.7% (based on two specimens and both genes combined) and the nearest neighbour is 0.0% different (*P. bifida* or *P. luteipes*, only TPI). If TPI introns are included, the nearest neighbour is still 0.0% different (*P. bifida*).

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

Distribution and material examined. Palaearctic. Specimens studied are from Estonia, Finland, France, Germany, Russia (Primorsky Krai), Sweden, and Switzerland.

Pristiphora frigida (Boheman, 1865)
Figs 17, 200, 274

Nematus frigidus Boheman, 1865: 568–569. Lectotype ♂ (NHRS-HEVA000005005; designated by Prous et al. 2016) in NHRS, examined. Type locality: "Middel Hook in Belsund" (Spitsbergen Island), Svalbard, Norway.

Pristiphora Adelungi [sic!] Konow, 1902: 162, 167–168. Lectotype ♀ (DEI-GISHym30151; designated by Prous et al. 2016) in ZIN, examined. Type locality: Hornsund (Spitsbergen Island), Svalbard, Norway.

Pristiphora gelida Wong, 1968: 185, syn. n. Holotype ♂ (USNMENT00778416) in USNM, not examined. Type locality: Point Barrow, Alaska, USA.

Similar species. Externally, perhaps the most similar species is *P. bifida*, from which it can be distinguished by having black or brown hind trochanters and trochantelli, and usually black tibiae (pale in *P. bifida*). In addition, antennae of males have only some barely visible stout black setae among finer paler ones (Fig. 17), while these are numerous and clearly visible in *P. bifida* (Fig. 18). On the other hand, the penis valve (Fig. 274) might indicate a closer relationship to *P. melanocarpa* and *P. ruficornis* (Figs 264, 266), because of a membranous fold near the tip of the valvispina that is missing in other species of the *ruficornis* group. The tangium of the lancet (Fig. 200) also resembles more closely the *Betula* feeding *P. melanocarpa* and *P. ruficornis* (Fig. 191) rather than *P. bifida* (Fig. 199): the dark sclerotized area is rather broader than long instead of longer than broad. Although we did not study the holotype of *gelida* Wong, six specimens from Canada identified by Wong as *P. gelida* could not be distinguished from *P. frigida*. The minute differences figured by Wong (1968: 186) between *gelida* and *frigida* penis valves and lancets are not reliable. Penis valves of one of the specimens that we studied from Canada are more similar to the figure given by Wong (1968) for *frigida*.

Genetic data. No data.

Host plants. Unknown.

Distribution and material examined. West Palaearctic, Nearctic. Specimens studied are from Canada and Norway (Svalbard).

Pristiphora leucopus (Hellén, 1948)
Figs 192, 265

Nematus vitreipennis Eversmann in Kawall, 1864: 295. Nomen oblitum (Prous et al. 2016). Lectotype ♀ (DEI-GISHym30027; designated by Prous et al. 2016) in ZIN,

examined. Type locality: In promontor. Uralensibus [foothills of Ural mountains], Russia.

Nematus (*Pristiphora*) *ruficornis* var. *leucopus* Hellén, 1948b: 116. Nomen protectum (Prous et al. 2016). No syntypes were found in MZH. Type locality: Joutseno, South-Eastern Finland, Finland and Pionerskoye [Kuolemajärvi], Leningrad Oblast, Russia.

Similar species. The most similar species is *P. armata*. Differences between these two species, which unfortunately are not very strong, were discussed by Grearson and Liston (2012) and Prous et al. (2016).

Genetic data. Based on COI barcode sequences, *P. leucopus* belongs to the same BIN cluster (BOLD:AAQ2302) as *P. armata* (Fig. 4). Maximum distance within the BIN is 2.41% and minimum between species distance is possibly 0.00%. The nearest neighbour to BOLD:AAQ2302, diverging by minimum of 2.76%, is BOLD:AAG3568 (*P. aphantoneura*, *P. bifida*, *P. confusa*, *P. luteipes*, *P. opaca*, *P. pusilla*, *P. staudingeri*, and *P. subopaca*). Neither does nuclear sequence data allow separation of *P. leucopus* from *P. armata*. Based on nuclear data, maximum within species divergence is 0.4% (based on three specimens and TPI or NaK) and the nearest neighbour is 0.0% different (*P. armata*, based on TPI including introns).

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

Distribution and material examined. West Palaearctic. Specimens studied are from Austria, Finland, Germany, United Kingdom, Russia (Ural mountains), and Sweden.

Pristiphora luteipes Lindqvist, 1955
Figs 14, 45

Pristiphora luteipes Lindqvist, 1955b: 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. Sometimes the separation of *P. luteipes* from *P. staudingeri* can also be problematic, when the colour of metafemur is intermediate between completely black and completely pale (e.g. specimen DEI-GISHym80238 from an arctic habitat in Sweden has a nearly completely pale metafemur). See Vikberg (2006) and Prous et al. (2016) for more detailed discussion.

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. 4). Maximum distance within the BIN is 3.33% and minimum between species distance is 0.00%. The nearest neighbour to BOLD:AAG3568, diverging by minimum of 2.76%, is BOLD:AAQ2302 (*P. armata* and *P. leucopus*). Based on nuclear data (four specimens and TPI or both genes com-

bined), maximum within species divergence is 0.3% (excluding DEI-GISHym80238, which could be *P. staudingeri*) or 0.4% (including DEI-GISHym80238) and the nearest neighbour is 0.0% different (*P. bifida*, *P. confusa*, or *P. subopaca*, only TPI). When including TPI introns, the nearest neighbour is still 0.0% different (*P. bifida*).

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*).

Rearing notes. See Vikberg (2006).

Distribution and material examined. West Palaearctic. Specimens studied are from Finland, France, Germany, United Kingdom, Italy, Norway, Portugal, Spain, and Sweden.

Pristiphora melanocarpa (Hartig, 1840)
Figs 191, 264

Nematus melanocarpus Hartig, 1840: 27. Lectotype ♀ (GBIF-GISHym3349; designated by Prous et al. 2016) 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. Synonymised with *P. wustneii* [sic!] by Ghigi (1905).

Nematus wuestneii Stein, 1885 [mandatory correction of incorrect original spelling *N. Wüstneii*]: 304. Lectotype ♀ (designated by Prous et al. 2016) 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. Synonymised with *P. melanocarpa* by by Smith (1979).

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. 14) or only slightly paler, while *P. ruficornis* has a distinctly paler ventral side (Fig. 15). 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 valvispina of the penis valve bends distinctly more sharply (being almost L-shaped) and is usually narrower (Fig. 264) than in *P. ruficornis* (Fig. 266).

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 in Prous et al. 2016). These BIN clusters form a monophyletic group (Fig. 4) and minimum distances between them are only 1.13–1.50%. Based on nuclear data, maximum within species divergence is 0.9% (based on seven specimens and NaK, TPI,

or both genes) and the nearest neighbour is 0.0% different (*P. ruficornis*, only TPI including introns).

Host plants. *Betula pendula* Roth (Kangas 1985), *B. pubescens* Ehrh., *B. nana* L. (Prous et al. 2016). The records from *Salix* are doubtful (Prous et al. 2016).

Distribution and material examined. Holarctic. Specimens studied are from Canada, Estonia, Finland, France, Germany, Norway, Russia (Primorsky Krai), and Sweden.

Pristiphora opaca Lindqvist, 1955
Figs 22, 40, 197, 270

Pristiphora opaca Lindqvist, 1955b: 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 (Fig. 270). Unfortunately, it is rather difficult to distinguish females from *P. subopaca* as the differences in the lancets are small (Figs 197–198). The best character might be the structure of the tangium: on its basal part, *P. opaca* appears to have a fold (Fig. 197) that is absent in other species of the *ruficornis* group. There are also slight differences in external morphology between *P. opaca* and *P. subopaca*. In *P. opaca* (Fig. 40), the pterostigma is apically brown and basally dark brown (uniformly yellow in *P. subopaca*; Fig. 39), antennae are slightly paler ventrally (uniformly black in *P. subopaca*), and claws seem to have a somewhat smaller subapical tooth (Fig. 22) than in *P. subopaca* (Fig. 23).

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. 4). Maximum distance within the BIN is 3.33% and minimum between species distance is 0.00%. The nearest neighbour to BOLD:AAG3568, diverging by a minimum of 2.76%, is BOLD:AAQ2302 (*P. armata* and *P. leucopus*). Based on nuclear data (one specimen and both genes combined), the nearest neighbour is 0.4% different (*P. luteipes* or *P. pusilla*).

Host plants. Unknown.

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

Pristiphora pusilla Malaise, 1921
Figs 18, 32, 201, 271

Pristiphora pusilla Malaise, 1921: 11–12. Lectotype ♂ (NHRS-HEVA000004942; designated by Prous et al. 2016) in NHRS, examined. Type locality: Torne Träsk, Torne Lappmark, Sweden.

Pristiphora amaura Lindqvist, 1955b: 43–45. Holotype ♀ (http://id.luomus.fi/ GL.5205) in MZH, examined. Type locality: Kangasala, South Häme, Finland.

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 271) and female lancet (Fig. 201). In females, the lack of small spiny pectines (or dentes semicirculares) on the inner surface of the lancet, and weakly developed setae, distinguish it from other similar species. Male penis valves are asymmetric, the left one (Fig. 271) having a noticeably stronger dorsal depression in the middle of pseudoceps and a more strongly bent valvispina than the right one (Fig. 94 in Prous et al. 2016). The most similar penis valves are those of *P. subopaca* (Fig. 269), which have a less distinct dorsal depression in the middle of pseudoceps and a less strongly bent valvispina, but this difference is clear only when compared to the left penis valve of *P. pusilla*. Externally, *P. pusilla* can usually be distinguished from *P. subopaca* by having ventrally paler antennae (uniformly black in *P. subopaca*; Fig. 15), which is more evident in males (Fig. 18).

   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. 4). Maximum distance within the BIN is 3.33% and minimum between species distance is 0.00%. The nearest neighbour to BOLD:AAG3568, diverging by a minimum of 2.76%, is BOLD:AAQ2302 (*P. armata* and *P. leucopus*). Based on nuclear data, maximum within species divergence is 0.2% (based on seven specimens and TPI or both genes combined) and the nearest neighbour is 0.1% different (*P. confusa* or *P. subopaca*, only TPI).

   Host plants. Unknown.

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

Pristiphora ruficornis (Olivier, 1811)
Figs 15, 42, 266

Nematus ruficornis Olivier in Olivier and Manuel, 1811: 167. No unambiguous type specimens were found in MNHN. Type locality: near Paris, France. Note. Two male specimens in Lepeletier's type collection in MNHN (which we identified as *P. armata*, but could also be *P. leucopus*) were under the name *N. ruficornis*, but only one of them had a label "N. ruficornis 216 ♂". The number "216" apparently refers to Olivier's *Nematus ruficornis* in Lepeletier de Saint-Fargeau (1823: 71) ("216. NEMATUS RUFICORNIS. Oliv. Enc., n°9."). However, Lepeletier de Saint-Fargeau (1823: 71) mentions females, not males. In an old box of uncertain origin in MNHN there is also a female (we identified it as *P. armata*?) labelled ""N. ruficornis" Lp. 216 N. crassicornis H. 37.", but this seems to be of later origin

than the publication of Lepeletier de Saint-Fargeau (1823), because the specimen is identified as Hartig's *crassicornis* (Hartig 1837). In order to reserve the name *ruficornis* Olivier for the species concept used in the widely known identification key by Benson (1958) and recently reviewed by Prous et al. (2016), i.e. for the species feeding on *Betula* not on *Crataegus*, designation of a neotype would be desirable. However, we refrain doing so at this point, as no fresh specimens of *ruficornis* are available from or near the type locality (near Paris). The neotype specimen should be fresh enough to enable extraction of good quality DNA, that could greatly facilitate solving the problem of separating *ruficornis* from *melanocarpa* (if they indeed are different species).

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 ruficornis* (Olivier, 1811)]. Syntype(s) ♂ not found in MNHN (Lacourt 2000). Type locality: Paris, France. Synonymised with *P. ruficornis* by André (1882).

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

Nematus fraxini Hartig, 1837: 204. Lectotype ♀ (GBIF-GISHym3285; designated by Prous et al. 2016) 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. Synonymised with *P. ruficornis* by Konow (1902).

Nematus (*Pristiphora*) *ruficornis* var. *integer* Hellén, 1948b: 116. 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 usually have a distinctly paler ventral side of antennae (Fig. 15), while the antennae in *P. melanocarpa* are uniformly black (Fig. 14) or have only a slightly paler ventral side. Males of *P. ruficornis* also have generally paler antennae than in *P. melanocarpa* (Fig. 18), but penis valves should be studied to distinguish them from *P. melanocarpa* specimens having conspicuously pale antennae. The valvispina of penis valve (Fig. 266) bends more gradually (forming a half circle) and is usually broader than in *P. melanocarpa* (Fig. 264).

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 in Prous et al. 2016). Minimal distance between the two clusters is only 1.13%. Based on nuclear data, within species divergence is 0.3% (based on two specimens and TPI) and the nearest neighbour is 0.0% different (*P. melanocarpa*, only TPI including introns).

Host plants. *Betula pubescens* Ehrh. (Prous et al. 2016).

Distribution and material examined. Palaearctic. Specimens studied are from Finland, France, Germany, Portugal, Russia (Republic of Bashkortostan, Republic of Buryatia), Sweden, and Ukraine.

Pristiphora sootryeni **Lindqvist, 1955**

Figs 190; http://dx.doi.org/10.6084/m9.figshare.4690174

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

Pristiphora listoni Lacourt, 1998: 129–130, **syn. n.** Holotype ♂ (DEI-GISHym31733) in CTN, examined. Type locality: Saint-Véran, Provence-Alpes-Côte d'Azur, France.

Similar species. Most similar species are *P. albitibia* and *P. astragali*. Females of *P. sootryeni* are best distinguished by the structure of the lancet (Fig. 190), which has long apical serrulae (shorter in *P. albitibia* and *P. astragali*) and numerous setae (fewer in *P. astragali*). Externally, males and females tend to have a paler pterostigma (uniformly yellow or brown) than *P. albitibia* (basally dark brown and apically brown) and smoother mesepisternum than *P. astragali* (usually strongly matt). Males of *P. sootryeni* (only the holotype of *P. listoni* Lacourt is known) seem to have a somewhat more elongate pseudoceps (http://dx.doi.org/10.6084/m9.figshare.4690174) of penis valve than in *P. albitibia* (Fig. 273). The single paratype female of *listoni* Lacourt that was collected at the same time and place (Lacourt 1998) as the holotype male has the same lancet as *P. sootryeni* (Fig. 190) and externally seems to have only smoother mesepisternum (almost completely smooth) than specimens studied from Finland. Because the sculpture of mesepisternum commonly varies within species, it is not sufficient to separate *listoni* Lacourt from *sootryeni* Lindqvist and therefore we synonymise the former with the latter.

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 in Prous et al. 2016). Maximum distance within the BIN is 1.01% and minimum between species distance is possibly 0.00%. The nearest neighbour to BOLD:AAL8292, diverging by minimum of 2.40%, is BOLD:AAL8277 (*P. astragali*). No nuclear DNA data available.

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

Rearing notes. See Vikberg (2006).

Distribution and material examined. West Palaearctic. Specimens studied are from Finland and France.

Pristiphora staudingeri **(Ruthe, 1859)**

Figs 202, 272

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. Synonymised with *P. staudingeri* by Smith (1979).

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. Synonymised with *P. staudingeri* by Lindqvist (1953).

Similar species. The most similar species is *P. luteipes*, which can sometimes be difficult to distinguish from *P. staudingeri*: occasional specimens from arctic habitats have intermediate coloration of metafemur (between completely black and completely pale, e.g. specimen DEI-GISHym80238 has a nearly completely pale metafemur). See Vikberg (2006) and Prous et al. (2016) for more detailed discussion.

Genetic data. Based on COI barcode sequences, *P. staudingeri* belongs to the same BIN cluster (BOLD:AAG3568) as *P. aphantoneura*, *P. bifida*, *P. confusa*, *P. opaca*, *P. pusilla*, and *P. subopaca* (Fig. 4). Maximum distance within the BIN is 3.33% and minimum between species distance is 0.00%. The nearest neighbour to BOLD:AAG3568, diverging by a minimum of 2.76%, is BOLD:AAQ2302 (*P. armata* and *P. leucopus*). Based on nuclear data, maximum within species divergence is 0.7% (based on four specimens and TPI or both genes combined) and the nearest neighbour is 0.1% different (*P. bifida*, *P. confusa*, *P. luteipes*, or *P. subopaca*, only TPI).

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

Rearing notes. Ovipositing experiment no. 11/1974 as *P. hyperborea*: Finland, Enontekiö Lapland, Saana. On 21–22.VI.1974 one captured female laid 11 eggs into leaf-edge teeth of *Salix phylicifolia*. No eggs were laid on *Salix reticulata*, *Betula pubescens* var. *pumila*, *Astragalus alpinus* and *A. frigidus*. Larvae hatched on 25–26.VI.1974. They feed on the leaf margin. Four larval instars were observed. Their development was rapid and on 6.VII.1974 prepupae were found. No extra moult after feeding.

Distribution and material examined. West Palaearctic, Nearctic. Specimens studied are from Finland, France, Iceland, Norway, Sweden, Switzerland, and United Kingdom.

Pristiphora subopaca Lindqvist, 1955
Figs 39, 55, 198, 269

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

Pristiphora coniceps Lindqvist, 1955b: 39–40. Holotype ♀ (http://id.luomus.fi/GL.5207) in MZH, examined. Type locality: Pihtipudas, Central Finland, Finland.

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

Similar species. 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 (Fig. 269). Unfortunately, it is rather difficult to separate females of *P. subopaca* from *P. confusa* and *P. opaca* as the differences in the lancets are small (Figs 196–198). Apical serrulae are perhaps less protruding and longer (Fig. 198) than in *P. confusa* (Fig. 196) and the basal part of the tangium lacks a fold that is present in *P. opaca* (Fig. 197). Externally, the pterostigma is usually uniformly yellow (Fig. 39) unlike in *P. confusa* and *P. opaca*, in which the pterostigma is basally dark brown and apically brown (Fig. 40). In addition, the claws of *P. subopaca* tend to have a larger subapical tooth (Fig. 23) than in *P. opaca* (Fig. 22). Among the males, the most similar penis valves are of *P. confusa* and *P. pusilla*. The valvispina is bent more strongly and the pseudoceps is broader (Fig. 269) than in *P. confusa* (Fig. 268). Compared to *P. pusilla* (Fig. 271), the valvispina 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*.

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. 4). Maximum distance within the BIN is 3.33% and minimum between species distance is 0.00%. The nearest neighbour to BOLD:AAG3568, diverging by a minimum of 2.76%, is BOLD:AAQ2302 (*P. armata* and *P. leucopus*). Based on nuclear data, maximum within species divergence is 0.3% (based on four specimens and both genes combined) and the nearest neighbour is 0.0% (*P. luteipes*, only TPI) or 0.3% different (*P. pusilla*, both genes combined). When including TPI introns, the nearest neighbour is 0.1% different (*P. bifida* or *P. confusa*).

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

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

Pristiphora rufipes group

Pristiphora brevis (Hartig, 1837)
Figs 219, 245

Nematus brevis Hartig, 1837: 205. Lectotype ♀ (GBIF-GISHym3209; here designated) in ZSM, examined. Type locality: Germany.

Nematus fumipennis Thomson, 1871: 112. Primary homonym of *Nematus fumipennis* Stephens, 1835 [= *Nematinus fuscipennis* (Serville, 1823)]. Syntype ♀ (DEI-GISHym20852) in MZLU, examined. Type locality: Gotland, Sweden.

Pristiphora fuscata Benson, 1943: 181. Replacement name for *Nematus fumipennis* Thomson, 1871.

Similar species. Species limits in the *rufipes* group are still unclear.

Genetic data. Based on COI barcode sequences, specimens of the *rufipes* group are divided between five BIN clusters (BOLD:AAI2590, BOLD:AAU8834,

BOLD:ABU9175, BOLD:ABV4437, and BOLD:ACW1774), four of which are found in Europe (BOLD:AAU8834 is so far known only from Canada) (Fig. 5). Minimal distances between these clusters are 3.06–4.35%. Because of unresolved taxonomy, it is not yet clear how different species are divided among these BIN clusters. Based on nuclear data, maximum divergence within the group is 1.4% (based on eight specimens and TPI) and the nearest neighbour is 1.0% (*P. cincta*, both genes combined) or 0.4% different (*P. cincta*, only NaK).

Host plants. *Thalictrum flavum* L. (Chambers 1953, as *P. fuscata*).

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

Pristiphora dochmocera (Thomson, 1871)
Fig. 220

Tenthredo flavipes Zetterstedt, 1838: 350–351, **syn. n.** Primary homonym of *Tenthredo flavipes* O.F. Müller, 1776 [= Hymenoptera non-Symphyta, 1758]. Holotype ♀ (DEI-GISHym20851) in MZLU, examined. Type locality: Senja Island, Troms, Norway.

Nematus dochmocerus Thomson, 1871: 93. Lectotype ♀ (NHRS-HEVA000003757; here designated) in NHRS, examined. Type locality: Dalarna, Sweden.

Nematus congener W.F. Kirby, 1882: 394, **syn. n.** Replacement name for *Tenthredo flavipes* Zetterstedt, 1838.

Pristiphora thomsoni Lindqvist, 1953: 223–224, **syn. n.** Holotype ♀ (MZLU2015172) in MZLU, examined. Type locality: Norrland, Sweden.

Similar species. The small differences in the length of antennae and coloration of the legs among the primary types of *flavipes* Zetterstedt, *dochmocerus* Thomson, and *thomsoni* Lindqvist do not allow clear separation of these taxa. The legs are darkest in *thomsoni* (trochanters, trochantelli, and metafemur are more or less completely black), palest in *flavipes* Zetterstedt (trochanters, trochantelli, and metafemur are more or less completely pale), and *dochmocerus* Thomson differs from *flavipes* only by having a slightly darker metafemur (black in basal 1/3). The lancets of the types are very similar (Fig. 220) and therefore we treat these taxa as a single species. The only difference from *P. thalictrivora* is the black tegula (extensively pale in *P. thalictrivora*).

Genetic data. Based on COI barcode sequences, specimens of the *rufipes* group are divided between five BIN clusters (BOLD:AAI2590, BOLD:AAU8834, BOLD:ABU9175, BOLD:ABV4437, and BOLD:ACW1774), four of which are found in Europe (BOLD:AAU8834 is so far known only from Canada) (Fig. 5). Minimal distances between these clusters are 3.06–4.35%. Because of unresolved taxonomy, it is not yet clear how different species are divided among these BIN clusters. Based on nuclear data, maximum divergence within the group is 1.4% (based on eight specimens and TPI) and the nearest neighbour is 1.0% (*P. cincta*, both genes combined) or 0.4% different (*P. cincta*, only NaK).

Host plants. Unknown. Based on the structure of the lancet (Fig. 220), the host is probably *Thalictrum*, as the other closely related species feeding on *Thalictrum* have similar or identical lancets.

Distribution and material examined. West Palaearctic. Specimens studied are from Norway and Sweden.

Pristiphora rufipes Serville, 1823
Figs 222, 250

Pristiphora rufipes Serville, 1823: 75. Lectotype ♀ (designated by Lacourt 2000) in MNHN, not examined. Type locality: North of France.

Pristiphora fusca Serville, 1823: 75–76. Possible syntype(s) ♂ were not confidently identified in MNHN (Lacourt 2000). Type locality: Paris, France. Synonymised with *P. rufipes* by Lacourt (1999).

Nematus suessionensis Serville, 1823: 68. Lectotype ♂ (designated by Lacourt 2000) in MNHN, not examined. Type locality: near Paris (Île-de-France) or Soissons (Hauts-de-France), France. Synonymised with *P. rufipes* by Lacourt (1999).

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

Pristiphora fusca Lepeletier, 1823: 60. Primary homonym of *Pristiphora fusca* Serville, 1823 [= *Pristiphora rufipes* Serville, 1823]. Possible syntype(s) ♂ were not confidently identified in MNHN (Lacourt 2000). Type locality: Paris, France.

Nematus Suessionensis [sic!] Lepeletier, 1823: 66. Primary homonym of *Nematus suessionensis* Serville, 1823 [= *Pristiphora rufipes* Serville, 1823]. Lectotype ♂ (designated by Lacourt 2000) in MNHN, not examined. Type locality: near Paris (Île-de-France) or Soissons (Hauts-de-France), France.

Nematus selandrioides Costa, 1859: 21–22. Syntype(s) ♀ possibly in MZUN, not examined. Type locality: Sile, Italy. Synonymised with *P. alnivora* auct. by Konow (1905).

Nematus aquilegiae Snellen van Vollenhoven, 1866: 202–205 (Sep. 14–17), pl. 9. Lectotype ♀ in RMNH (designated by Thomas 1987), not examined. Type locality: Renkum, Gelderland, Netherlands. Synonymised with *P. rufipes* by Lacourt (1999).

Similar species. Species limits in the *rufipes* group are still unclear

Genetic data. Based on COI barcode sequences from larvae collected from *Aquilegia* sp. (DEI-GISHym20983 and DEI-GISHym21482), *P. rufipes* belongs to the same BIN cluster (BOLD:AAI2590) as *P. brevis* and *P. thalictri* (Fig. 5). Maximum distance within the BIN is 1.74% and minimum between species distance is 0.00%. The nearest neighbour to BOLD:AAI2590, diverging by minimum of 3.58%, is BOLD:AAU8834 (specimens are from Canada, which externally look like *P. cincta*). It is possible that specimens of *P. rufipes* belong also to other closely related BINs (BOLD:ABV4437, BOLD:ABU9175, and BOLD:ACW1774). Based on nuclear data, maximum within species divergence is

0.4% (based on three specimens and both genes combined) and the nearest neighbour (*P. brevis*) is 0.2% (only NaK) or 0.5% (both genes combined) different.

Host plants. *Aquilegia vulgaris* L. (Macek 2016), *A. chrysantha* A.Gray (Chevin 1994, as *P. aquilegiae*), *A. caerulea* E.James (Chevin 1994, Hellrigl 2007), *A. canadensis* L. (Chevin 1994), *A. flabellata* Siebold & Zucc. (Hellrigl 2007), *A. olympica* Boiss. (Liston 2011).

Distribution and material examined. West Palaearctic, (Nearctic). Specimens studied are from Canada, Estonia, Finland, and Germany.

Pristiphora thalictri (Kriechbaumer, 1884)
Fig. 249

Nematus Thalictri [sic!] Kriechbaumer, 1884: 105–106. Lectotype ♀ (GBIF-GISHym3448; here designated) in ZSM, examined. Type locality: between Hessellohe and Pullach near München, Germany.

Pristiphora Henschi [sic!] Konow, 1902: 162, 168–169. Lectotype ♀ (GBIF-GISHym3884; here designated) in SDEI, examined. Type locality: Krapina, Croatia.

Diphadnus thalictri Takeuchi, 1922: 290–294. Note. Described as "*Diphadnus* ? *thalictri*". Holotype ♀ in NSMT, not examined. Type locality: Gifu, Honshu, Japan. Synonymised with *P. thalictri* (Kriechbaumer) by Takeuchi (1952).

Similar species. Species limits in the *rufipes* group are still unclear.

Genetic data. Based on COI barcode sequences, specimens of the *rufipes* group are divided between five BIN clusters (BOLD:AAI2590, BOLD:AAU8834, BOLD:ABU9175, BOLD:ABV4437, and BOLD:ACW1774), four of which are found in Europe (BOLD:AAU8834 is so far known only from Canada) (Fig. 5). Minimal distances between these clusters are 3.06–4.35%. Because of unresolved taxonomy, it is not yet clear how different species are divided among these BIN clusters. Based on nuclear data, maximum divergence within the group is 1.4% (based on eight specimens and TPI) and the nearest neighbour is 1.0% (*P. cincta*, both genes combined) or 0.4% different (*P. cincta*, only NaK).

Host plants. *Thalictrum aquilegiifolium* L. (Pschorn-Walcher and Altenhofer 2006, Macek 2016), *T. minus* L. (Takeuchi 1949, Okutani 1967).

Distribution and material examined. Palaearctic. Specimens studied are from Austria, Germany, and United Kingdom.

Pristiphora thalictrivora Lindqvist, 1962
Figs 218, 221, 247

Pristiphora thalictrivora Lindqvist, 1962: 110–111. Holotype ♀ (DEI-GISHym20905) in MZH, examined. Type locality: Helsinki, Finland.

Pristiphora rufiventris Lindqvist, 1974a: 118–119. Holotype ♂ (DEI-GISHym20909) in MZH, examined. Type locality: Kuusamo, Finland.

Pristiphora thalictricola Lindqvist, 1974a: 117–118. Holotype ♀ (DEI-GISHym20850) in MZH, examined. Type locality: Oulanka, Kuusamo, Koillismaa, Finland.

Similar species. Species limits in the *rufipes* group are still unclear.

Genetic data. Based on COI barcode sequences, specimens of the *rufipes* group are divided between five BIN clusters (BOLD:AAI2590, BOLD:AAU8834, BOLD:ABU9175, BOLD:ABV4437, and BOLD:ACW1774), four of which are found in Europe (BOLD:AAU8834 is so far known only from Canada) (Fig. 5). Minimal distances between these clusters are 3.06–4.35%. Because of unresolved taxonomy, it is not yet clear how different species are divided among these BIN clusters. Based on nuclear data, maximum divergence within the group is 1.4% (based on eight specimens and TPI) and the nearest neighbour is 1.0% (*P. cincta*, both genes combined) or 0.4% different (*P. cincta*, only NaK).

Host plants. *Thalictrum flavum* L. (Lindqvist 1962, *ex ovo* rearing experiments by VV), *Thalictrum simplex* L. (Lindqvist 1974a, as *P. thalictricola*).

Rearing notes. Ovipositing experiment 52/1987: Finland, South Häme, Janakkala (uniform grid reference 6760:3370). On 18–19.VI.1987 one captured female laid eggs on leaf margin of *Thalictrum flavum*. Larvae hatched on 22.VI.1987. There were four larval instars, larvae grew rapidly and on 2.VII.1987 prepupae were seen. No extra moult after feeding.

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

Species not placed in groups

Pristiphora abbreviata (Hartig, 1837)
Figs 66–67, 128, 252

Nematus abbreviatus Hartig, 1837: 205. Lectotype ♀ (GBIF-GISHym3181; here designated) in ZSM, examined. Type locality: Germany.

Gymnonychus californicus Marlatt, 1896: 122–123. 11 possible ♀ syntypes (USNMENT00778445) in USNM, not examined. Type locality: Brockport, New York and Sacramento, California, United States. Synonymised with *P. abbreviata* by Benson (1958).

Similar species. Most easily confused with *P. monogyniae*, from which it differs by having pale pronotal angles (black in *P. monogyniae*), black clypeus (pale in *P. monogyniae*), and the valvula 3 with a distinct dorsoapical projection (absent in *P. monogyniae*) (Figs 66–67, 71–72). Males, which are extremely rare (we have seen one), are best recognised by examining penis valves (Figs 252, 256). See the Key for more details.

Genetic data. Based on COI barcode sequences (only one specimen in BOLD), it forms its own BIN cluster (BOLD:ACV9937). The nearest neighbour (BOLD:AAG3540, *P. melanocarpa*) is 8.43% different. Based on nuclear data (one specimen; NaK), the nearest neighbour is 4.2% different (unidentified specimen DEI-GISHym84983 belonging to the *ruficornis* group).

Host plants. *Pyrus communis* L. (Zocchi 1949, as *Micronematus abbreviatus*) and *Pyrus spinosa* Forsk. (Schedl and Ritzau 1995).

Distribution and material examined. West Palaearctic, (Nearctic). Specimens studied are from Germany and Greece.

Pristiphora angulata Lindqvist, 1974
Figs 68–70, 132, 228

Pristiphora angulata Lindqvist, 1974b: 21–22. Holotype ♀ (GBIF-GISHym20805) in MZH, examined. Type locality: Luopioinen, Finland.

Similar species. Because of the rather distinct shape of valvula 3 (see the Key), it should be possible to distinguish the females relatively easily. Males are best recognised by examining penis valves (see the Key), which are most similar to *P. bohemica* Macek, 2012a, a species not treated here (see Macek 2012a).

Genetic data. Based on COI barcode sequences, *P. angulata* forms its own BIN cluster (BOLD:ACB1782) (Fig. 5). Maximum distance within the BIN is 0.32%. The nearest neighbour to BOLD:ACB1782, diverging by minimum of 7.54%, is BOLD:ABV9415 (*P. parva*). Based on nuclear data (two specimens; NaK), maximum within species divergence is 0.0% and the nearest neighbour is 0.9% different (*P. cincta*).

Host plants. *Spiraea chamaedryfolia* L. (Kangas 1985, Liston 2015, *ex ovo* rearing experiments by VV), *Spiraea salicifolia* L. (Kangas 1985).

Rearing notes. Ovipositing experiment no. 2/1975: Finland, South Häme, Koski, H. l. (Uniform grid reference 676:339). One captured female laid eggs on 25–26.V.1975 on *Spiraea chamaedryfolia*. The eggs are laid into pockets on outer surface of the calyces (green leaves at the base of flowers). Larvae eat flowers first, later also leaves. There are four or five instars, the development of larvae is rapid and on 9.VI.1975 prepupae were seen. No extra moult after feeding.

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

Pristiphora biscalis (Förster, 1854)
Figs 27, 52, 76–77, 129, 253

Nematus biscalis Förster, 1854b: 326–327. Lectotype ♀ (GBIF-GISHym3698; here designated) in ZSM, examined. Type locality: Aachen, North Rhine-Westphalia, Germany.

Nematus conspersus Zaddach in Brischke, 1883b: 186. Syntype(s) possibly destroyed (Blank and Taeger 1998). Type locality: not stated. Synonymised with *Lygaeonematus biscalis* by Konow (1905).

Nematus pruni Brischke, 1883: pl. I, 2. Holotype (sex not stated, see Brischke 1884) possibly destroyed (Blank and Taeger 1998). Type locality: Oliwa (Oliva), Gdańsk, Poland. Listed as a synonym of *P. biscalis* by Taeger et al. (2010), but see commentary by Blank & Taeger (1998).

Nematus lateralis Brischke, 1885: 246. Primary homonym of *Nematus lateralis* Norton, 1867. Holotype ♀ possibly destroyed (Blank and Taeger 1998). Type locality: Matemblewo, Gdańsk, Poland. Synonymised with *Lygaeonematus biscalis* by Konow (1898).

Nematus postumus Dalla Torre, 1894: 251. Replacement name for *Nematus lateralis* Brischke, 1885.

Similar species. Females are perhaps most similar to *P. maesta*, from which *P. biscalis* differs by having black cercus (usually pale in *P. maesta*) and at least partly pale clypeus (black in *P. maesta*). Males are best recognised by examining penis valves (see the Key). A female specimen DEI-GISHym11094 (GenBank accession KC975746) from Brandenburg, Germany, is morphologically almost indistinguishable from *P. biscalis*, but might represent a different species based on rather divergent COI barcode sequence. Additional specimens are needed to evaluate if there are reliable morphological differences between these two forms and to check if nuclear sequences support the divergence found in COI.

Genetic data. Based on COI barcode sequences, *P. biscalis* forms its own BIN cluster (BOLD:AAM9740) (Fig. 3). Maximum distance within the BIN is 0.16%. The nearest neighbour to BOLD:AAM9740, diverging by minimum of 7.43%, is BOLD:ABX2630 (specimen DEI-GISHym11094, which we have identified as *P. biscalis*, but might be a different species). Based on nuclear data (one specimen and NaK), the nearest neighbour is 2.5% different (*P. dedeara*).

Host plants. *Prunus spinosa* L. (Weiffenbach 1985).

Distribution and material examined. West Palaearctic. Specimens studied are from Germany and Sweden.

Pristiphora bufo (Brischke, 1883)
Figs 108–110, 168, 275

Nematus bufo Brischke, 1883a: pl. I, 1f. Nomen protectum. See Blank et al. (2009). Syntype(s) ♀ possibly destroyed (Blank and Taeger 1998). Type locality: Sopot (Zoppot), Poland.

Pristiphora pallidula Konow, 1902: 178–179. Lectotype ♀ (GBIF-GISHym3904, designated by Vikberg 1975) in SDEI, examined. Type locality: Bohemia, Czech Republic.

Pachynematus crassicauda Lindqvist, 1964: 129–130. Holotype ♀ in MZH, examined. Type locality: Pälkäne, South Häme, Finland.

Pristiphora laricicola Verzhutskii, 1966: 126–127, 21. Syntypes ♀♂ possibly in ZMUM, not examined. Type locality: Irkutsk Oblast and Republic of Buryatia, Russia. Synonymised with *Nematus bufo* by Zhelochovtsev and Zinovjev (1988).

Similar species. Females are most similar to *P. paralella*. In *P. bufo*, valvula 3 is clearly not truncate (Fig. 109) in lateral view (slightly truncate in *P. paralella*; Fig. 113) and anterior protibial spur is with velum (Fig. 34) (without velum in *P. paralella*; Fig. 33). Males are best recognised by examining penis valves (see the Key).

Genetic data. Based on COI barcode sequences, *P. bufo* belongs to its own BIN cluster (BOLD:AAU4835). Maximum distance within the BIN is 0.2%. The nearest neighbour to BOLD:AAU4835, diverging by minimum of 6.15%, is BOLD:ABV9415 (*P. parva*). Based on nuclear data (one specimen and NaK), the nearest neighbour is 1.4% different (*P. siskiyouensis*).

Host plants. *Larix* species: *L. decidua* Mill. (Kangas 1985, Huflejt and Sawoniewicz 1999, Pschorn-Walcher and Altenhofer 2000), *L. kaempferi* (Lamb.) Carrière (Huflejt and Sawoniewicz 1999; Pschorn-Walcher and Altenhofer 2000), *L. sibirica* Ledeb. (Vikberg 1975; Kangas 1985), *L. gmelinii* (Rupr.) Kuzen., *L. laricina* (Du Roi) K. Koch, *Larix×eurolepis* A.Henry (Huflejt and Sawoniewicz 1999).

Distribution and material examined. West Palaearctic. Specimens studied are from Czech Republic, Finland, Germany, and Switzerland.

Pristiphora cadma Wong & Ross, 1960
Figs 51, 331–337

Pristiphora cadma Wong & Ross, 1960: 198. Holotype ♀ was not found in CNC. Type locality: Meadow Lake, Saskatchewan, Canada.

Similar species. Females of *P. cadma* could most likely be confused with *P. bufo* or *P. conjugata*. Completely or nearly completely pale mesepisternum (Fig. 336) and sometimes extensively pale dorsal part of thorax (Fig. 51) distinguish *cadma* from *conjugata*. Claws with large subapical tooth (Fig. 335) can be used to distinguish *cadma* from *bufo* (which has a small subapical tooth, Fig. 22). Additionally, the serrulae of lancet of *cadma* are more protruding than in *bufo* and *conjugata*. Penis valves of *cadma* (Fig. 337) are most similar to *P. nigricans* and *P. pallidiventris*, but completely or nearly completely pale mesepisternum (Fig. 336) of *cadma* distinguishes it from the two species (mesepisternum is at most partly pale in some *P. pallidiventris*). The head and dorsal part of thorax of two studied European females (Estonia and Sweden) are distinctly paler than three studied Canadian females (which fit the original description). However, it is quite likely that these characters vary continuously, as for example in *P. bufo* and *P. paralella*. Small differences in the lancet (Figs 331, 333)

(shape of the basal sutures of the annuli and tip of the lancet) are probably not reliable either. According to the original description, the holotype female is 8 mm long, but the studied females from Canada (5.9–6.5 mm) are in the same size range as the European specimens (6.1–6.5 mm).

Genetic data. Based on a single COI barcode sequence (TUZ615726), *P. cadma* forms its own cluster (no BIN number has been assigned yet) (Fig. 5). Based on nuclear data (one specimen and both genes combined), the nearest neighbour is 1.0% different (*P. testacea*).

Host plants. *Betula papyrifera* Marshall (based on label data of five reared specimens from Canada) and probably some other *Betula* species (*B. papyrifera* occurs naturally only in northern North America).

Distribution and material examined. West Palaearctic, Nearctic. Specimens studied are from Canada, Estonia and Sweden.

Pristiphora cincta Newman, 1837
Figs 47, 104, 145–146, 244, 246

Nematus (*Nematus*) *Friesi* [sic!] Dahlbom, 1835: 10. Not available. Nomen nudum.

Pristophora [sic!] *cincta* Newman, 1837: 259. Holotype (sex unknown) possibly lost. Type locality: Herefordshire, United Kingdom.

Nematus quercus Hartig, 1837: 188–189. Syntype ♀ (GBIF-GISHym3403) in ZSM, examined. Type locality: Berlin, Germany. Note. Abdomen is missing in the single known syntype specimen.

Tenthredo borealis Zetterstedt, 1838: 353. Lectotype ♀ (MZLU2014479; here designated) in MZLU, examined. Type locality: Lyngen, Troms, Norway.

Pristiphora identidem Norton, 1867a: 77. Lectotype ♀ in ANSP (designated by Cresson 1928), not examined. Type locality: Illinois and Maine, USA. Synonymised with *P. cincta* by Smith (1979).

Pristiphora idiota Norton, 1867a: 77. Lectotype ♂ in ANSP (designated by Cresson 1928), not examined. Type locality: Illinois, USA. Synonymised with *P. quercus* by Benson (1962).

Pristiphora coloradensis Marlatt, 1896: 113–114 (key), 121–122. Note. Synonymy with *P. cincta* questionable (Smith 1979). Holotype ♂ in ANSP (Cresson 1928), not examined. Type locality: Colorado, USA.

Pristiphora hoodi Marlatt, 1896: 113–114 (key), 119. Note. Synonymy with *P. cincta* questionable (Smith 1979). Holotype ♀ in ANSP (Cresson 1928), not examined. Type locality: Mount Hood, Oregon, USA.

Pristiphora seorsa Konow, 1897a: 180. 3 ♀♀ syntypes in SDEI, examined. Type locality: Mauken (Norway) and Irkutsk (Russia). Note. We refrain from designating a lectotype, because the syntype series may not be homogenous: the lancet of one of the specimens from Irkutsk has bands of setae on the annuli, unlike the studied European specimen.

Pristiphora idiotiformis Rohwer, 1910b: 199–200. Holotype ♀ (Cat. No. 12923; US-NMENT00779081) in USNM, not examined. Type locality: Nerepis, New Brunswick, Canada. Synonymised with *P. cincta* by Smith (1979).

Pristiphora cincta ab. *nigriventris* Hellén, 1943: 71. Not available. Infrasubspecific name.

Pristiphora cincta ab. *maukeniensis* Hellén, 1943: 71. Not available. Infrasubspecific name. Note. Published as "maukeniensis Conde".

Pristiphora nigrogroenblomi Haris, 2002: 74–75, **syn. n.** Holotype ♂ (DEI-GISHym80334; http://dx.doi.org/10.6084/m9.figshare.5100994) in HNHM, examined. Type locality: Ulaanbaatar 10 km N, Mongolia.

Similar species. The most similar species is *P. condei*, which has a pale supraclypeal area (usually black in *P. cincta*) and darker metatibia (half or more is black in *P. condei*, usually less than half in *P. cincta*). The shorter postocellar area in *P. cincta* (1.0–1.5 times longer than diameter of lateral ocellus) can also distinguish it from at least females of *P. condei* (1.5–2.5 times longer). Because males of *P. cincta* frequently lack a red band on the abdomen, penis valves (which are very similar to species in the *rufipes* group) should be studied to distinguish them from many other species (see the Key). It is possible that more than one species is involved under *P. cincta*, but this requires additional research (names are possibly already available among current synonyms).

Genetic data. Based on COI barcode sequences, *P. cincta* belongs to its own BIN cluster (BOLD:AAG3565) (Fig. 5). Maximum distance within the BIN is 3.21%. The nearest neighbour to BOLD:AAG3565, diverging by minimum of 6.26%, is BOLD:AAU8834 (specimens from Canada, which externally look like *P. cincta*, but apparently belong to the *rufipes* group; Fig. 5). Based on nuclear data, maximum within species divergence is 0.7% (based on four specimens and both genes combined) and the nearest neighbour is 1.0% (both genes combined) or 0.4% (only NaK) different (*P. brevis*).

Host plants. *Betula pubescens* Ehrh. (Conde 1938, Stritt 1952, as *P. quercus*), *Salix* sp. (Lindqvist 1955b), *Vaccinium myrtillus* L. (Loth 1913, Stritt 1952, as *P. quercus*, *ex ovo* rearing experiments by VV), *Vaccinium uliginosum* L. (Weiffenbach 1962, as *P. quercus*), *Vaccinium myrtilloides* Michx. (Neilson 1955, 1958, as *P. idiota*), *Vaccinium angustifolium* Ait. (Neilson 1955), *Vaccinium macrocarpon* Ait. (Neilson 1955, Bardwell and Averill 1996, as *P. idiota*). It is possible, that three species (each on *Betula*, *Salix*, and *Vaccinium*) are involved. *Spiraea* sp. (Verzhutskii 1966, Verzhutskii 1981, as *P. quercus*) as a host is doubtful, because similar species might be involved, perhaps *P. pallidiventris*, *P. nigricans* (which feed on Rosaceae), or something else.

Rearing notes. Ovipositing experiment no. 5/1971: Finland, North Karelia, Ilomantsi, Heinävaara. One captured female laid eggs on 31.V.1971 in pockets through margins of the leaves of *Vaccinium myrtillus*. Larvae hatched on 5.VI.1971; four larval instars were observed. The development was rapid, the larvae were fully grown on 14.VI.1971. No "extra" moult after feeding. Also leaves of *Betula pubescens* were offered, but the female did not lay any eggs on them.

Distribution and material examined. Palaearctic, Nearctic. Specimens studied are from Canada, Estonia, Finland, Germany, Norway, Mongolia, Russia (Irkutsk Oblast, Primorsky Krai), Slovakia, Sweden, and Ukraine.

Pristiphora condei **Lindqvist, 1955**
Figs 48, 149, 232

Pristiphora condei Lindqvist, 1955b: 48–49. Holotype ♀ (DEI-GISHym20900) in
     MZH, examined. Type locality: Juupajoki, South Häme, Finland.

Similar species. The most similar species is *P. cincta*, which nearly always has a black
supraclypeal area (pale in *P. condei*) and paler metatibia (usually more than half is pale
in *P. cincta*, half or less in *P. condei*). Longer postocellar area in *P. condei* (1.5–2.5 times
longer than diameter of lateral ocellus) can also distinguish it from at least females of
P. cincta (1.0–1.5 times longer).

    Genetic data. Based on COI barcode sequences, *P. condei* forms its own cluster
(no BIN number has been assigned yet) (Fig. 5). When considering only the barcod-
ing region (658 bp), the distance between Estonian and Far Eastern (Primorsky Krai)
specimens is 3.2%. A short sequence (380 bp; FISYN019-15) from a Finnish specimen
(MHV00070) available in BOLD is identical to the Estonian. The nearest neighbour to
P. condei, diverging by a minimum of 8.44%, is BOLD:ACO1401 (*P. euxantha*). Based
on nuclear data, within species divergence is 0.1% (based on two specimens and both
genes combined) and the nearest neighbour is 1.4% different (*P. wesmaeli*, only NaK).

    Host plants. *Sorbus aucuparia* L. (Lindqvist 1955b, Vikberg and Kangas 1980)
and *Amelanchier spicata* (Lam.) K. Koch (Vikberg and Kangas 1980).

    Rearing notes. See Vikberg and Kangas (1980).

    Distribution and material examined. Palaearctic. Specimens studied are from
Estonia, Finland, Russia (Primorsky Krai), and Ukraine.

Pristiphora conjugata **(Dahlbom, 1835)**
Figs 43, 49, 153–155, 255, 257, 259

Nematus gonymelas Stephens, 1829: 329. Not available. Nomen nudum.
Nematus conjugatus Dahlbom, 1835a: 21–22, 40. Lectotype ♂ (MZLU2014464; here
     designated) in MZLU, examined. Type locality: Vallkärra, Skåne, Sweden.
Nematus gonymelas Stephens, 1835: 34. Syntype(s) possibly in BMNH, not examined. Type
     locality: Britain (Kirby 1882). Synonymised with *P. conjugata* by Konow (1897b).
Nematus (*Nematus*) *conjugatus* Dahlbom, 1835b: 8. Not available. Nomen nudum.
Nematus discipennis Herrich-Schäffer, 1840: 176. Note. Replacement name for "Pris-
     toph. myosotidis Lep. Pz. 98. 13. Tenthr.".
Nematus discoidalis Thomson, 1888: 1209–1210. Syntype ♀ in MZLU, not examined. Type
     locality: Örtofta, Skåne, Sweden. Synonymised with *P. conjugata* by Vikberg (1982).
Pristiphora conjugata var. *forsiusi* Enslin, 1916: 534. Lectotype ♀ (GBIF-GISHym3282;
     here designated) in ZSM, examined. Type locality: Karislojo, Uusimaa, Finland.
Pristiphora conjugata var. *ulbrichti* Enslin, 1916: 534. Lectotype ♀ (GBIF-
     GISHym3450; here designated) in ZSM, examined. Type locality: Krefeld (Cre-
     feld), North Rhine-Westphalia, Germany.

Similar species. The most similar species in Europe are *P. testacea*, *P. pallidiventris*, and *P. nigricans*, which have a unicoloured (dark or pale) pterostigma (bicoloured in *P. conjugata*, but this is less clear in males). Lancets and penis valves can also be distinguished from other species (see the Key). Darker specimens of *P. conjugata* (e.g. females with black mesepisternum and dorsally black abdomen) feeding on *Salix* have been treated as a separate species, *P. forsiusi* Enslin (Lindqvist 1964, Kangas 1985), although according to Zhelochovtsev and Zinovjev (1988) both *conjugata* and *forsiusi* feed on *Populus* and *Salix*. There is no gap in colour variation between paler and darker forms (two females reared from *Salix fragilis* by Ewald Altenhofer have a partly pale mesepisternum). There are no reliable differences in the structure of the lancets or penis valves either and the slight differences do not appear to correlate with the host plant. The only indication that there might be two species involved, is that the males reared from *Salix* have a completely or nearly completely black propleuron, which is extensively pale in males reared from *Populus*. More specimens should be reared to test this weak correlation. If there are two species, one feeding on *Salix*, the other on *Populus*, the name *conjugata* Dahlbom should be applied to the one feeding on *Salix*, as the only available type specimen (designated here as the lectotype) was reared from *Salix fragilis* (Dahlbom 1835a), which is a male with an almost completely black propleuron.

Genetic data. Based on a COI barcode sequences, *P. conjugata* forms its own BIN cluster (BOLD:ABV4426) (Fig. 5). Maximum distance within the BIN is 1.68%. The nearest neighbour to BOLD:ABV4426, diverging by minimum of 3.69%, is BOLD:ACG2245 (*P. beijingensis*?). Based on nuclear data, maximum within species divergence is 0.4% (based on two specimens and NaK) and the nearest neighbour is 1.2% different (*P. wesmaeli*, only NaK).

Host plants. *Populus nigra* L. (Pesarini and Turrisi 2001, Okutani 1970), *P. tremula* L. (Okutani 1970, Boevé 1990, Pschorn-Walcher and Altenhofer 2000), *Populus×canadensis* Moench (Martelli 1954), *Salix alba* L. (Delmas 1926), *S. caprea* L. (Weiffenbach 1985), *S. cinerea* L. (Benander 1966), *S. fragilis* L. (Dahlbom 1835a, Boevé 1990, Pschorn-Walcher and Altenhofer 2006, and based on the adults reared from larvae by Ewald Altenhofer), *S. pentandra* L. (Benander 1966, Kangas 1985).

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

Pristiphora dedeara Liston & Prous, sp. n.

http://zoobank.org/8E1B8854-DDF2-4187-ADE8-6CF44BEE379D
Figs 320–330

Description. Female holotype (DEI-GISHym80053), Figs 320, 322–326, 330. Body 4.7 mm. Colour mostly black. Labrum pale; labial and maxillary palps brown; mandibles reddish-brown at apex; apex of pro- and mesofemur pale; metatibia in basal 1/3 pale; trochanters and trochantelli mainly pale; pronotum and tegula extensively pale;

valvifer 2 slightly pale; terga 5–10 laterally and sterna 5–7 slightly pale. Labrum more or less symmetrical; clypeus truncate; postocellar area about 1.4 times as long as diameter of lateral ocellus; flagellum length 3.0 mm, 2.1 times as long as width of head. Mesopostnotum matt; mesepisternum smooth; claws without subapical tooth; anterior protibial spur with velum. Hypopygium posteriorly not excised. Sawsheath (valvula 3 + valvifer 2) simple, without scopa, in dorsal view gradually narrowing toward apex and about as long as cerci, in lateral view ventral margin gradually narrowing toward apex. Lancet (valvula 1) with numerous setae on annuli; serrulae flat with numerous denticles on ventro-apical surface; small spiny pectines on the inner surface (dentes semicirculares) that reach sclerora absent; tangium without lobe.

Male paratypes (DEI-GISHym80258, 80266), Figs 321, 327–329. Body 4.5 mm. Colour mostly black, similar to female. Labrum dark brown; labial and maxillary palps brown; mandibles reddish-brown at apex; apex of pro- and mesofemur pale; metatibia in basal 1/3 pale, trochanters and trochantelli partly pale; pronotum and tegula extensively pale. Labrum more or less symmetrical; clypeus truncate; postocellar area about 1.3 times as long as diameter of lateral ocellus; flagellomeres without or apparently without stout black setae among finer paler ones; flagellum length 3.7–3.9 mm, 2.7–2.9 times as long as width of head. Mesopostnotum matt; mesepisternum smooth; claws without subapical tooth; anterior protibial spur with velum. Tergum 8 with indistinct apical projection; sternum 9 without notch. Valvispina of penis valve medium sized, more or less straight, narrow, unmodified, sharp at apex, and position at ventral margin of paravalva; angle between dorsal part of valvispina and paravalva, as well as between ventral part, obtuse; ventral margin of paravalva convex or slightly protruding, dorsoapical part abruptly narrowing before valvispina and more or less entirely convex; valvar strut not clearly evident at anterior margin of paravalva; pseudoceps relatively long and narrow, dorsally without depression, distinct spines, hair, and membranous regions or folds.

Etymology. The species name is an arbitrary combination of letters, to be treated as a noun.

Similar species. Black thorax, head, and mostly abdomen, dark pterostigma, smooth mesepisternum, claw without subapical tooth, and simple valvula 3 (Figs 320, 322–326) distinguish females of this species from the others (see the Key). Males are externally most similar to *P. abbreviata*, but penis valves clearly separate them (Figs 252, 321; see also the Key).

Genetic data. Based on two identical COI barcode sequences, *P. dedeara* forms its own cluster (no BIN number has been assigned yet) (Fig. 3). Based on nuclear data (two specimens and both genes combined), within species divergence is 0.0% and the nearest neighbour is 2.4% different (*P. monogyniae*, only NaK).

Host plants. Unknown.

Distribution and material examined. West Palaearctic. Germany.

Holotype. Female. Germany, Brandenburg, Ruhlsdorf bei Strausberg, 52.57070°N 13.99780°E, 30.IV.2016, leg. A. Liston (SDEI). Paratypes. 2♂, same locality as holotype, but 09.IV.2017, leg. A. Liston & M. Prous (SDEI).

Pristiphora fausta (Hartig, 1837)
Figs 152, 299

Nematus faustus Hartig, 1837: 189. Holotype ♀ (GBIF-GISHym3273) not found in ZSM. Type locality: Berlin, Germany.

Similar species. The combination of nearly completely red head and completely black hind legs enables quite easy identification of this species (see also the Key).

Genetic data. Based on COI barcode sequences (only one specimen in BOLD), *P. fausta* belongs to its own BIN cluster (BOLD:ABU7035). The nearest neighbour to BOLD:ABU7035, diverging by minimum of 5.45%, is BOLD:ABA3518 (*P. parnasia* Konow, 1902, a species not treated here). Based on nuclear data (one specimen and TPI), the nearest neighbour is 1.3% different (*P. calliprina* Liston & Jacobs, 2012, a species closely related to *P. parnasia*, that is not treated here).

Host plants. *Quercus robur* L. (Macek and Kula 2014).

Distribution and material examined. West Palaearctic. Specimens studied are from Germany, Greece, and Italy.

Pristiphora geniculata (Hartig, 1840)
Figs 23, 150, 229

Nematus geniculatus Hartig, 1840: 26. Lectotype ♀ (GBIF-GISHym3290; here designated) in ZSM, examined. Type locality: not stated.
Nematus cheilon Zaddach, 1876: 41. Syntypes possibly destroyed (Blank and Taeger 1998). Type locality: Danzig (Poland), Sonderburg (Denmark), Silesia (Central Europe) (Brischke 1884). Synonymised with *P. geniculata* by Konow (1890).

Similar species. The most similar species is *P. pseudogeniculata*. Both, females and males of *P. pseudogeniculata* have shorter antenna (1.9–2.1 times as long as head width compared to 2.4–2.5 in *P. geniculata*) and a paler metatarsomere 1 (completely or nearly completely pale, compared to largely black in *P. geniculata*). Lancets are also different (see the Key and Figs 150–151), but there appear to be no clear differences in penis valves (Figs 229–230).

Genetic data. Based on COI barcode sequences, *P. geniculata* belongs to its own BIN cluster (BOLD:AAK9465) (Fig. 5). Maximum distance within the BIN is 0.18%. The nearest neighbour to BOLD:AAK9465, diverging by minimum of 7.02%, is BOLD:ACO1401 (*P. euxantha*). Even closer might be *P. pseudogeniculata*, but no sufficiently fresh specimens were available for sequencing. Based on nuclear data (two specimens and NaK), maximum within species divergence is 0.0% and the nearest neighbour is 0.7% different (*P. maesta*).

Host plants. *Sorbus aucuparia* L. (Forbes and Daviault 1964, Adam 1973, Pschorn-Walcher and Altenhofer 2000), *S. americana* Marshall (Forbes and Daviault 1964),

S. decora (Sarg.) C.K.Schneid. (Forbes and Daviault 1964), ×*Sorbaronia hybrida* (Moench) Schneider (an intergeneric hybrid between *S. aucuparia* and *Aronia arbutifolia* (L.) Pers.) (Forbes and Daviault 1964).

Distribution and material examined. Palaearctic, (Nearctic). Specimens studied are from Austria, Estonia, Finland, and Germany.

Pristiphora insularis Rohwer, 1910
Figs 86–87, 135, 254

Pristiphora insularis Rohwer, 1910a: 106. Holotype ♀ (USNMENT00779086) in USNM, not examined. Type locality: Japan.
Amauronematus amelanchieris Takeuchi, 1922: 289–293. Holotype ♀ in NSMT, not examined. Type locality: Gifu, Japan. Synonymised with *P. insularis* by Haris (2006b).
Pristiphora kamtchatica Malaise, 1931: 56–57. Lectotype ♀ in NHRS (designated by Koch 1989), examined. Type locality: Kamchatka Krai, Russia.
Pristiphora luteiventris Koch, 1989: 145–148. Holotype ♀ (GBIF-GISHym2821) in ZMHB, not examined. Type locality: Niederlahnstein, Lahnstein, Rhineland-Palatinate, Germany. Synonymised with *P. kamtchatica* by Liston (1995).

Similar species. Because of the shape of valvula 3, females might be confused most often with the *P. leucopodia* group. In addition to small differences in the valvula 3 (see the Key and Figs 84–87), species in the *P. leucopodia* group lack a velum (Figs 33), which is present in *P. insularis* (Fig. 34). Males are best recognised by examining penis valves (see the Key).

Genetic data. Based on COI barcode sequences, specimens are divided between two BIN clusters (BOLD:AAU3333 and BOLD:AAX8162), which are the closest neighbours of each other, with 3.79% difference (Fig. 5). Based on nuclear data (one specimen and TPI), the nearest neighbour is 4.3% different (*P. pallidiventris*).

Host plants. *Amelanchier asiatica* (Siebold & Zucc.) Endl. ex Walp., *Chaenomeles japonica* (Thunb.) Lindl. ex Spach (Takeuchi 1922, as *Amauronematus amelanchieris*), *Rosa* sp. (Chambers 1961, as *P. paedida*), *R. majalis* J. Herrm. (Kangas 1985, as *P. paedida*, *ex ovo* rearing experiments by VV), *R. pimpinellifolia* L. (Dvorak et al. 2008), *Rosa onoei* Makino (Okutani 1970, as *P. paedidius* [sic!]).

Rearing notes. Ovipositing experiment no. 12/1977: Finland, South Häme, Hämeenlinna, Aulanko. On 6–7.VI.1977 one captured female laid eggs into teeth (leaf edges) of unopened leaves of *Rosa majalis*. Larvae hatched on 9–10.VI.1977, four larval instars were observed. Their development was rapid and on 22.VI.1977 prepupae were seen. No extra moult after feeding.

Distribution and material examined. Palaearctic, Nearctic. Specimens studied are from Finland, France, Germany, Greece, Spain, and Sweden.

Pristiphora maesta (Zaddach, 1876)
Figs 78, 130, 227

Nematus brevicornis Thomson, 1863: 622–623. Primary homonym of *Nematus brevicornis* Förster, 1854b [= *Euura brevicornis* (Förster, 1854b)]. Syntype ♀ (MZLU2014457) in MZLU, examined. Type locality: Småland and Skåne, Sweden.

Nematus maestus Zaddach, 1876: 85–86. Syntypes ♀ and ♂ possibly destroyed (Blank and Taeger 1998). Type locality: Danzig, Poland.

Nematus parvicornis W.F. Kirby, 1882: 118. Replacement name for *Nematus brevicornis* Thomson, 1863.

Pachynematus insularis Malaise, 1921: 7–8. Syntype(s) ♀ in MZLU, not examined. Type locality: Resarö Island, Sweden. Synonymised with *P. brevicornis* by Lindqvist (1955a).

Similar species. Females are perhaps most similar to *P. biscalis*, from which *P. maesta* differs by having pale cercus (black in *P. biscalis*) and black clypeus (at least partly pale in *P. biscalis*). Males are best recognised by examining penis valves.

Genetic data. Based on COI barcode sequences, *P. maesta* forms its own cluster (no BIN number has been assigned yet) (Fig. 5). The nearest neighbour to *P. maesta*, diverging by a minimum of 5.95%, is BOLD:AAF5120 (*P. nigella* and *P. amphibola*). Based on nuclear data (one specimen and NaK), the nearest neighbour is 0.7% different (*P. geniculata*).

Host plants. *Malus sylvestris* (L.) Mill. and *M. domestica* Borkh. (Pschorn-Walcher and Altenhofer 2000).

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

Pristiphora mollis (Hartig, 1837)
Figs 156, 300

Tenthredo bipunctata Gmelin, 1790: 2670. Primary homonym of *Tenthredo bipunctata* O.F. Müller, 1776 [= *Tenthredo* (*Tenthredella*) *livida* Linné, 1758]. Type specimens probably lost (Blank et al. 2009: 13). Type locality: Lusatia [Lausitz], Brandenburg or Saxony, Germany.

Nematus mollis Hartig, 1837: 201. Lectotype ♀ (GBIF-GISHym3355; here designated) in ZSM, examined. Type locality: Harz or Berlin [from original description, no locality label on the lectotype], Germany.

Tenthredo lapponica Zetterstedt, 1838: 350. Lectotype ♀ (MZLU2014469; here designated) in MZLU, examined. Type locality: Karungi, Norrbotten, Sweden. Note. Konow (1905) proposed synonymy with *Tenthredo* (*Emphytus*) *grossulariae* Klug, 1818 [= *Ametastegia pallipes* (Spinola, 1808)], which was accepted by Taeger et

al. (2010). The synonymy with *mollis*, first proposed by Thomson (1863), is here confirmed.

Nematus whitei Cameron, 1878b: 35–36. Syntype(s) ♂ possibly in BMNH, not examined. Type locality: Braemar, Aberdeenshire, Scotland, United Kingdom. Synonymised with *P. mollis* by Konow (1904b).

Pachynematus orarius Kincaid, 1900: 348. Syntype ♀ (USNMENT00778196) in USNM, not examined. Type locality: Kukak Bay and Sitka, Alaska, USA. Synonymised with *P. mollis* by Ross (1951).

Lygaeonematus mollis ab. *albipes* Lindqvist, 1943: 107. Not available. Infrasubspecific name.

Lygaeonematus mollis ab. *rufonotata* Lindqvist, 1943: 107. Not available. Infrasubspecific name.

Pachynematus kontkaneni Lindqvist, 1960a: 35–36. Holotype ♀ in MZH, examined. Type locality: Kuusamo, Koillismaa, Finland.

Similar species. The most similar species belong to the *carinata* group. Externally, both females and males of *P. mollis* generally have a more depressed frontal field (area anterior to median ocellus) and it is often rather smooth compared to *carinata* group specimens, but the difference is rather small and difficult to quantify. Females of *P. mollis* can often be distinguished from *carinata* group specimens by the combination of darker coloration of the head and abdomen (black clypeus and valvifer 2, and usually black tergum 10), the paler metatarsus (usually mainly pale), and longer cerci. Lancet (Fig. 156) and penis valve (Fig. 300) of *P. mollis* are clearly different from those in the *carinata* group (Figs 210–217, 238–242).

Genetic data. Based on COI barcode sequences, *P. mollis* forms its own BIN cluster (BOLD:AAF5097) (Fig. 3). Maximum distance within the BIN is 1.51%. The nearest neighbour to BOLD:AAF5097, diverging by a minimum of 6.2%, is BOLD:AAH7553 (*P. leucopodia*). Based on nuclear data, the nearest neighbour is 2.8% (*P. nigriceps*, only NaK) or 4.2% different (*P. laricis*, both genes combined).

Host plants. *Vaccinium myrtillus* L. (Savina et al. 2014, *ex ovo* rearing experiments by VV), *V. uliginosum* L. (Verzhutskii 1981, Kangas 1985).

Rearing notes. Ovipositing experiment no. 4/1986: Finland, South Häme, Janakkala, Kalpalinna. One captured female laid several eggs on 23.V.1986 in pockets on undersides of young leaves of *Vaccinium myrtillus*. Eggs were situated very close to the leaf margin at the base of teeth (leaf edges) of the plant. 5 larval instars were observed, the development of larvae was rapid and on 6.VI.1986 first cocoon was observed. No extra moult after feeding. Larva can be green or red. On both sides of the dark dorsal vessel, there are longitudinal white subcutaneous fat stripes on the thorax and abdominal segments 1–9.

Distribution and material examined. West Palaearctic, Nearctic. Specimens studied are from Estonia, Finland, France, Germany, Norway, Sweden, Switzerland, and Ukraine.

Pristiphora monogyniae (Hartig, 1840)
Figs 71–72, 131, 256

Nematus Monogyniae [sic!] Hartig, 1840: 27. Lectotype ♀ (GBIF-GISHym3358; here designated) in ZSM, examined. Type locality: not stated.

Nematus pullus Förster, 1854a: 330–331. Lectotype ♀ (GBIF-GISHym3391; here designated) in ZSM, examined. Type locality: Aachen, North Rhine-Westphalia, Germany.

Nematus filicornis Thomson, 1863: 625. Syntype(s) ♀ in MZLU, not examined. Type locality: Bohus Län [Bohuslän] and Skåne, Sweden. Synonymised with *Micronematus pullus* by Konow (1890).

Nematus hibernicus Cameron, 1878a: 225. Syntype(s) possibly in BMNH, not examined. Type locality: near Dublin, Ireland. Synonymised with *Micronematus monogyniae* by Konow (1905).

Nematus nanus Zaddach in Brischke, 1884: 137. 3 ♂♂ and 2 ♀♀ syntypes possibly destroyed (Blank and Taeger 1998). Type locality: not stated, but probably in former East Prussia (now Kaliningrad Oblast of Russia, or Poland). Synonymised with *Micronematus monogyniae* by Konow (1905).

Nematus serotinus Zaddach in Brischke, 1884: 137–138. Holotype ♀ possibly destroyed (Blank and Taeger 1998). Type locality: not stated, but probably in former East Prussia (now Kaliningrad Oblast of Russia, or Poland). Synonymised with *Micronematus monogyniae* by Konow (1905).

Nematus catulus Zaddach in Brischke, 1884: 142–143. Syntype(s) ♂ possibly destroyed (Blank and Taeger 1998). Type locality: Gdańsk [Danzig], Poland. Synonymised with *Micronematus monogyniae* by Konow (1905).

Nematus ludens Costa, 1894: 72. 2 ♀ syntypes possibly in MZUN, not examined. Type locality: Emilia [part of Emilia-Romagna], Italy. Synonymised with *Micronematus monogyniae* by Konow (1905).

Similar species. Most easily mixed up with *P. abbreviata*, from which it differs by having black pronotal angles (pale in *P. abbreviata*), at least partly pale clypeus (black in *P. abbreviata*), and valvula 3 without distinct dorsoapical projection (present in *P. abbreviata*). Males are best recognised by examining penis valves (see the Key).

Genetic data. Based on COI barcode sequences, specimens of this species are divided between two BIN clusters (BOLD:AAX8166 and BOLD:ACG5295) (Fig. 3). Minimal distance between the two clusters is 3.07%. Based on nuclear data, the nearest neighbour is 2.4% different (*P. dedeara*, only NaK).

Host plants. *Prunus spinosa* L. (Lorenz and Kraus 1957, Pschorn-Walcher and Altenhofer 2006), *P. domestica* L. (Lindqvist 1966).

Distribution and material examined. West Palaearctic. Specimens studied are from Germany, Greece, and Sweden.

Pristiphora paralella (Hartig, 1840), comb. n.
Figs 36, 112–114, 169, 296

Nematus paralellus Hartig, 1840: 25. Lectotype ♀ (GBIF-GISHym3375; here designated) in ZSM, examined. Type locality: not stated.

Lygaeonematus tenuicornis Lindqvist, 1955a: 142–143, **syn. n.** Holotype ♀ (NHRS-HEVA000003769) in NHRS, examined. Type locality: Freskati, Stockholm, Sweden. Note. The name *tenuicornis* has apparently not been used as valid more than 25 times during the last 50 years (we found 19 publications) and therefore Article 23.9.1 (ICZN 1999) cannot be applied in this case.

Similar species. Females are most similar to *P. bufo*. In *P. paralella*, valvula 3 is slightly truncate (clearly not truncate in *P. bufo*) in lateral view, and the anterior protibial spur is without velum (with velum in *P. bufo*). Males are best recognised by examining penis valves (see the Key).

Genetic data. Based on COI barcode sequences, *P. paralella* belongs to its own BIN cluster (BOLD:AAX8164) (Fig. 5). Maximum distance within the BIN is 1.29%. The nearest neighbour to BOLD:AAX8164, diverging by minimum of 6.16%, is BOLD:ACO1401 (*P. euxantha*). No nuclear data are available.

Host plants. *Picea* sp. (Kajmuk 1988, as *P. tenuicornis*).

Distribution and material examined. Palaearctic. Specimens studied are from Germany, Poland, Russia (Primorsky Krai), and Sweden.

Pristiphora pseudogeniculata Lindqvist, 1969
Figs 31, 100, 151, 230

Pristiphora pseudogeniculata Lindqvist, 1969: 246. Holotype ♀ (http://id.luomus.fi/GL.5215) in MZH, examined. Type locality: Helsinki, Finland.

Similar species. The most similar species is *P. geniculata*. Both females and males of *P. geniculata* have longer antenna (2.4–2.5 times as long as head width compared to 1.9–2.1 in *P. pseudogeniculata*) and a darker metatarsomere 1 (largely black compared to completely or nearly completely pale in *P. pseudogeniculata*). The female of *P. geniculata* also has a different lancet (see the Key).

Genetic data. No data.

Host plants. *Prunus padus* L. (*ex ovo* rearing experiments by VV).

Rearing notes. Ovipositing experiment no. 3/1979: Finland, South Häme, Hämeenlinna, Katinen. One female was captured on 4.VI.1979 and leaves of *Malus* sp., *Sorbus aucuparia* and *Prunus padus* were offered her. On 4–5.VI.1979 she laid several eggs only in teeth of leaves of *Prunus padus*. Four larval instars were observed. Larvae

feed gregariously on the leaf margin, like larvae of *P. geniculata* on *Sorbus aucuparia*. Prepupae were seen on 19.VI.1979. No extra moult after feeding.

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

Pristiphora punctifrons (Thomson, 1871)
Figs 107, 138–140, 231

Nematus punctifrons Thomson, 1871: 111. Holotype ♀ (MZLU2014459) in MZLU, examined. Type locality: Fogelsång near Lund, Sweden.

Nematus platyceros Zaddach in Brischke, 1884: 135–136. Syntypes ♀♂ possibly destroyed (Blank and Taeger 1998). Type locality: Gdańsk (=Danzig), Poland; East Prussia (now divided between Russia, Poland, and Lithuania); Scotland, United Kingdom, Sweden; Vienna, Austria. Synonymised with *P. punctifrons* by Konow (1902).

Pristiphora viridana Konow, 1902: 164 (key), 176–177. Lectotype ♀ (GBIF-GISHym3896; designated by Liston et al. 2006) in SDEI, examined. Type locality: Teschendorf, Mecklenburg-Vorpommern, Germany.

Micronematus camtschatcalis Enslin, 1927: 376–377. Holotype ♀ (DEI-GISHym30136) in ZIN, examined. Type locality: Klyuchevskoye, Kamchatka Krai, Russia. Note. Synonymy by Conde (1934) is here accepted.

Nematus (*Pristiphora*) *punctifrons* ab. *maculipleura* Hellén, 1948a: 45. Not available. Infrasubspecific name.

Pristiphora aspericeps Lindqvist, 1960a: 37. Holotype ♀ (http://id.luomus.fi/GL.5216) in MZH, examined. Type locality: Tyrväntö, Kanta-Häme, Finland.

Pristiphora flavipicta Lindqvist, 1975: 14, **syn. n.** Holotype ♀ (DEI-GISHym20895) in MZH, examined. Type locality: near Murino, Tunkinsky District, Republic of Buryatia, Russia.

Pristiphora mongoloexigua Haris, 2002: 76–77, **syn. n.** Holotype ♂ (DEI-GISHym80346; http://dx.doi.org/10.6084/m9.figshare.5101081) in HNHM, examined. Type locality: Zaisan, Bogd Khan Mountain, Ulaanbaatar, Mongolia.

Pristiphora flavopleura Haris, 2002: 81, **syn. n.** Holotype ♀ (DEI-GISHym80355; http://dx.doi.org/10.6084/m9.figshare.5101099) in HNHM, examined. Type locality: Nukht, Bogd Khan Mountain, Ulaanbaatar, Mongolia.

Pristiphora mongolofausta Haris, 2003: 116–118, **syn. n.** Holotype ♀ (DEI-GISHym80354; http://dx.doi.org/10.6084/m9.figshare.5101090) in HNHM, examined. Type locality: Üyench District, Khovd Province, Mongolia.

Similar species. Females of *P. punctifrons* can be distinguished from other species by having a very deep scopa of valvula 3 (Fig. 107), at least dorsally black coloration (except terga 9–10, which are usually pale), and minute subapical tooth of claws. Males, which seem to be very rare (we have seen only two), are best recognised by examining penis valves (see the Key). We do not treat *viridana* Konow (pale form) as a separate species from *punctifrons* Thomson (dark form), as the variation in the characters mentioned by Liston et al. (2006)

is continuous. Holotypes of *flavipicta* Lindqvist and *flavopleura* Haris differ from pale forms of *punctifrons* only by having a largely pale mesepisternum (which is only slightly pale in one other studied specimen from Kazakhstan). This kind of variation can be considered intra-specific, as it is common in many other species of *Pristiphora*.

Genetic data. Based on COI barcode sequences, specimens of this species are divided between three BIN clusters (BOLD:AAU9246, BOLD:ACW2731, BOLD:ACB0668), which form a monophyletic group (Fig. 3). Minimal distances between these clusters are 1.68–2.57%. Based on nuclear data, maximum within species divergence is 0.9% (based on three specimens and NaK) and the nearest neighbour is 3.2% different (*P. geniculata*, only NaK).

Host plants. *Rosa canina* L. s. l. (Lorenz and Kraus 1957, Savina and Chevin 2012), *Rosa majalis* Herrm. (Kangas 1985, *ex ovo* rearing experiments by VV). Records from *Betula* (Enslin 1918, 1919, Stritt 1952) (as *P. viridana*) probably refer to *P. alpestris* (Conde 1934) or *P. albilabris*.

Rearing notes. Ovipositing experiment no. 9/1976: Finland, South Häme, Hämeenlinna, Aulanko. On 14.VI.1976 one captured female laid 3 eggs into teeth of unopened leaves of *Rosa majalis*. Larvae hatched on 18.VI.1976, four larval instars were observed. Their development was rapid and on 29.VI.1976 prepupae were seen. No extra moult after feeding.

Distribution and material examined. Palaearctic, Nearctic. Specimens studied are from Canada, Finland, France, Germany, Kazakhstan, Mongolia, Russia (Kamchatka Krai and Republic of Buryatia), Sweden, and USA.

Pristiphora tenuiserra (Lindqvist, 1959)
Figs 119, 123, 173, 302

Micronematus tenuiserra Lindqvist, 1959: 72. Holotype ♀ in MZLU (DEI-GISHym31572), examined. Type locality: Knivsta, Uppland, Sweden.

Similar species. Females can be distinguished from other species by the combination of the structure of valvula 3 (long and narrow and practically without scopa; Figs 119, 123) and (at least usually) relatively dark coloration (head dorsally black or with small pale spots, thorax black, abdomen at least dorsally black). Males are best recognised by examining penis valves (see the Key).

Genetic data. Based on COI barcode sequences (only one specimen in BOLD), *P. tenuiserra* forms its own BIN cluster (BOLD:ADD2616) (Fig. 5). The nearest neighbour to BOLD:ADD2616, diverging by a minimum of 5.22%, is BOLD:ACO1401 (*P. euxantha*). No nuclear data are available.

Host plants. Unknown, but the structure of valvula 3 suggests that the species is probably a conifer-feeder.

Distribution and material examined. West Palaearctic. Specimens studied are from Finland, Germany, Poland, and Sweden.

Pristiphora testacea (Jurine, 1807)
Figs 7, 50, 59, 147–148, 261

Tenthredo Betulae [sic!] Retzius, 1783: 72–73, by indication to Degeer (1771: 994, Pl. 37. Fig. 23). Primary homonym of *Tenthredo betulae* Linné, 1758 [= *Pamphilius betulae* (Linné, 1758)]. Syntype(s) possibly in NHRS. Type locality: possibly Lövstabruk, Uppland, Sweden (place of residence of Degeer; see Taeger and Blank 1998).

Tenthredo betulae Christ, 1791: 453, by indication to Degeer (1771: 994, Pl. 37. Fig. 23). Primary homonym of *Tenthredo betulae* Linné, 1758 [= *Pamphilius betulae* (Linné, 1758)]. Syntype(s) possibly in NHRS. Type locality: possibly Lövstabruk, Uppland, Sweden (place of residence of Degeer; see Taeger and Blank 1998).

Pteronus testaceus Jurine, 1807: pl. 13 fig. 8. Syntype(s) probably lost (Zinovjev and Vikberg 2006). Type locality: not stated.

Nematus (*Nematus*) *betulinus* Dahlbom, 1835b: 8. Note. Replacement name for "(an. *Tenthr. Betulae* De Geer)". Syntype(s) possibly in NHRS. Type locality: possibly Lövstabruk, Uppland, Sweden (place of residence of Degeer; see Taeger and Blank 1998).

Nematus betularius Hartig, 1837: 192–193. Holotype ♀ (GBIF-GISHym4688) in NFVG, examined. Type locality: Harz, Germany.

Nematus betulae Hartig, 1837: 219–220, by indication to Degeer (1771: 994, Pl. 37. Fig. 23). Syntype(s) possibly in NHRS. Type locality: possibly Lövstabruk, Uppland, Sweden (place of residence of Degeer; see Taeger and Blank 1998).

Nematus melanurus Hartig, 1840: 24. Syntype ♀ (GBIF-GISHym3347) in ZSM, not examined. Type locality: not stated. Synonymised with *Nematus betulae* by Kriechbaumer (1885).

Nematus erythrogaster Thomson, 1871: 103–104. Primary homonym of *Nematus erythrogaster* Norton, 1864. Syntype(s) ♀ in MZLU, not examined. Type locality: Torekov, Skåne and North-Western Skåne, Sweden. Synonymised as *P. erythrogastra* with *P. betulae* by Konow (1890).

Nematus crassiventris Cameron, 1878c: 267. Replacement name for *Nematus erythrogaster* Thomson, 1871.

Nematus hartigii W.F. Kirby, 1882: 127. Replacement name for *Nematus betulae* Hartig, 1837.

Nematus luteogaster W.F. Kirby, 1882: 132. Replacement name for *Nematus erythrogaster* Thomson, 1871.

Pristiphora gaunitzi Lindqvist, 1968b: 196, **syn. n.** Holotype ♀ (NHRS-HEVA000003644) in NHRS, examined. Type locality: Vännäs, Sorsele Lycksele Lappmark, Sweden.

Similar species. The most similar are pale specimens (with completely yellow abdomen) of *P. pallidiventris* and *P. conjugata*. *Pristiphora pallidiventris* is best distinguished from *P. testacea* by having valvula 3 with long medial projection (short in *P. testacea*)

and short postocellar area (1.0–1.5 times longer than diameter of lateral ocellus, about 2.0 times in *P. testacea*). The bicoloured pterostigma (Fig. 43) of *P. conjugata* is useful for distinguishing this species from *P. testacea*.

We treat *gaunitzi* Lindqvist as a rare colour form (abdomen dorsally black) of *testacea*. We have seen one additional female with this coloration, from Pallastunturi in Finnish Lapland, that was reared from *Betula*, the host plant of *testacea*. The penis valve of what Lindqvist (1972) thought to be *gaunitzi*, is not distinguishable from *testacea* (Fig. 261).

Genetic data. Based on COI barcode sequences, *P. testacea* forms its own BIN cluster (BOLD:AAX8158) (Fig. 5). Maximum distance within the BIN is 0%. The nearest neighbour to BOLD:AAX8158, diverging by minimum of 6.17%, is BOLD:AAX8150 (*P. pallida*). Based on nuclear data, maximum within species divergence is 0.0% (based on three specimens and TPI or NaK) and the nearest neighbour is 1.0% (*P. cadma*, both genes combined) or 0.9% (*P. parva*, only NaK) different.

Host plants. *Betula humilis* Schrank, *B. pendula* Roth, and *B. pubescens* Ehrh. (Adam 1973).

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

Taxa no longer placed in *Pristiphora*, unplaced, or from outside North-Western Palaearctic

Pristiphora lanifica (Zaddach, 1883)

Nematus lanificus Zaddach in Brischke, 1883b: 192–193. 3 syntypes possibly destroyed (Blank and Taeger 1998). Type locality: environment of Kaliningrad [Königsberg]. Note. Unplaced taxon. Konow (1905), who however may never have examined the type specimens, treated *N. lanificus* as a junior synonym of *Pristiphora pallidiventris*. Conde (1938), following the examination of what he held to be a type specimen in Zaddach's collection, interpreted *lanificus* as a member of what we here call the *P. micronematica* group. Conde's interpretation is however considered to be unlikely, because we have not seen specimens belonging to the *micronematica* group with the combination of characters given in Zaddach's description: body length 5.7–7.3 mm (in the *micronematica* group not more than 6.0 mm), sawsheath black (in *micronematica* group specimens with pale colour pattern resembling *lanificus*, the sawsheath is pale brown), and femora black-lined (entirely pale). Furthermore, pale coloured females of the *micronematica* group usually have the upper mesepisternum pale, whereas this is described as completely black in *lanificus*. Based only on the original description, the only evidence now available which can be used to identify the species, the synonymy with *P. pallidiventris* proposed by Konow is more likely.

Pristiphora mesatlantica Lacourt, 1976

Pristiphora mesatlantica Lacourt, 1976: 314. Holotype ♀ possibly in MNHN, not examined. Type locality: Ifrane, Meknès-Tafilalet, Morocco. Note. Examination of five paratype females confirmed that *mesatlantica* Lacourt is not a synonym of *insularis* Rohwer (synonymised by Haris 2006b). This is already evident from the original description (Lacourt 1976). *Pristiphora mesatlantica* belongs to the *micronematica* group and might be synonymous with *sermola* Liston, although distinguishing females in this group is problematic.

Euura melanocephalus (Hartig, 1837)

Nematus breviusculus Eversmann, 1847: 17, **syn. n.** Syntype gynandromorph (DEI-GISHym30032) in ZIN, examined. Type locality: Casan [Republic of Tatarstan], Russia. Note. Removed from synonymy with *P. pallidiventris*.

Euura caudalis (Eversmann, 1847), comb. n.

Nematus caudalis Eversmann, 1847: 16. Syntype ♂ (DEI-GISHym30028) in ZIN, examined. Type locality: Casan [Republic of Tatarstan], Russia. Note. Removed from synonymy with *P. pallidiventris*. Belongs to the *Euura ribesii* group and could be a synonym of *Euura vastatrix* (Zhelochovtsev, 1935), **comb. n.** Consequently, the valid name for *Pteronidea caudalis* Lindqvist, 1968 (secondary homonym of *Nematus caudalis* Eversmann, 1847) is *E. squamicauda* (Vikberg, 1982), **comb. n.**

Nematinus carpathiensis (Haris, 2001), comb. n.

Pachynematus (Pikonema) carpathiensis Haris, 2001: 80–81. Holotype ♂ (DEI-GISHym80338; http://dx.doi.org/10.6084/m9.figshare.5100877) in HNHM, examined. Type locality: Menchul, Zakarpattia Oblast, Ukraine. Note. The species is similar in colouration to *Nematinus bilineatus* (Klug, 1819), but the penis valve has much shorter apical filament.

Discussion

The lack of modern keys or revisions for the large nematine genus *Pristiphora* seriously hampers its study. High species diversity coupled to the small number of reliable morphological characters are probably the main reasons for this neglect. Here, we have revised the North-Western Palaearctic species, but three species groups (*carinata*, *micronematica*, and *rufipes* groups) still await more thorough revision. About 13 additional West Palaearctic species, not belonging to the three problematic groups, would have to be considered when identifying species outside of North-Western Europe: *P. beaumonti* Zirngiebl, 1957, *P. bensoni* Lindqvist, 1953, *P. murielae* Lacourt, 1995 (all three in the *ruficornis* group), *P. bohemica* Macek, 2012a, *P. calliprina* Liston & Jacobs, 2012, *P. parnasia* Konow, 1902 (the last two were keyed by Liston and Jacobs 2012), *P. cretica* Schedl, 1981, *P. ifranensis* Lacourt, 1973, *P. schedli* Liston and Späth, 2008 (the last three belonging to the *depressa* group, see Liston and Späth 2008), *P. euxantha* Huflejt, 2006, *P. weii* Liston, 2012 (possibly a synonym of *P. euxantha*), *P. helvetica* (Benson, 1960), and *Dinematus krausi* Lacourt, 2006 (possibly belonging to *Pristiphora* and morphologically similar to the *P. depressa* group).

For animals, mitochondrial COI is widely used for species identification (http://www.boldsystems.org/), but our results show that about 48% of the species of *Pristiphora* (out of 60 where it was possible to give an assessment) cannot be reliably identified based on COI barcodes. This increases to 62% (out of 81) when the *carinata*, *micronematica*, and *rufipes* groups (unresolved taxonomy, but with indications of barcoding failure) are included. Therefore we caution against using COI barcodes to identify species in *Pristiphora*, even if the match is 100% (identical barcodes for different species are common). Still, barcodes can be used at least to identify species groups, which would need more thorough investigation based on morphology or nuclear genes. Problems in using COI barcodes for species identification are known in many other groups of sawflies, but appear to be most frequent within Nematinae (Schmidt et al. 2017). Theoretical considerations (Patten et al. 2015) also suggest that when interspecific hybridisation takes place in haplodiploid groups, such as Hymenoptera, mitochondrial DNA crosses species boundaries more readily than nuclear DNA. In such groups, nuclear DNA might be more reliable for species identifications, which seems to be the case in *Pristiphora*, although data is still limited. About 21% of the species (out of 47 where it was possible to give an assessment) appear not to be clearly identifiable based on nuclear data, but morphological separation of most of these ten or so species is also problematic (*P. glauca* and *P. wesmaeli*, *ruficornis* subgroup, *armata* subgroup, *P. staudingeri* and *P. luteipes*).

Roux et al. (2016) found in a recent study based on genome-scale data for 61 animal species/population pairs, that an intermediate "grey zone" of speciation exists. This zone, where taxonomy is often controversial, spanned from 0.5% to 2% of net synonymous divergence. Net synonymous divergence is a genetic distance (proportion of differences) based on synonymous positions (codon positons that do not affect protein

sequence) that are fixed between populations (i.e. excluding within population diversity). Among the 61 species/population pairs that Roux et al. (2016) studied, gene flow between populations was always found to be prevalent when net synonymous divergence was below 0.5% and always absent when net synonymous divergence exceeded 2%. In the intermediate zone (net synonymous divergence 0.5%–2.0%), all degrees of reproductive isolation, from complete to none at all, were found (Roux et al. 2016). Although general applicability of the results for animals found by Roux et al. (2016) is uncertain due to limited taxonomic sampling, our results based on a limited dataset of two nuclear genes (2330 bp) and 25 species (for which at least two specimens and both genes were sampled) agree well with those of Roux et al. (2016). Most of the species among the 25 are distantly related to each other, as also suggested by net synonymous divergence, being 5.8–31.5% for the distantly related pairs. *Pristiphora cincta* and *rufipes* group species have very similar penis valves and are phylogenetically closely related (Figs 2, 5), but fall outside the grey zone too (net synonymous divergence 3.2–3.3% between *P. cincta* and the *rufipes* group). The situation is similar for closely related *P. albitibia* and *P. caraganae* with 3.3% divergence. However, divergences among species within the *aphantoneura* subgroup (based on *P. bifida, P. confusa, P. luteipes, P. staudingeri, P. pusilla*, and *P. subopaca*) and *rufipes* group (based on *P. brevis* and *P. rufipes*) fall mostly within the grey zone (0.1–2.8% or 0.6–2.8% without *P. luteipes*) and these groups are indeed taxonomically problematic. A very small divergence of 0.1% is found between *P. luteipes* and *P. confusa*, and *P. luteipes* and *P. staudingeri*. While separation of *P. luteipes* and *P. staudingeri* is also problematic using morphological characters, *P. confusa* is quite clearly a different species (Prous et al. 2016). Additional studies in the *aphantoneura* subgroup would be needed to see if other nuclear genes separate the species better, whether there really is gene flow between them, or if some taxonomic changes should be made.

Taken together, genetic results suggest that mitochondrial COI divergence within *Pristiphora* species usually remains within 3%, but could be as high as 5%. Divergences more than 5–6% probably indicate different species, although we cannot exclude that there are exceptions to this. Typical within species divergence for nuclear genes is less clear because of limited data, but seems to remain within 1%.

In summary, based on our results, the current number of West Palaearctic species of *Pristiphora* is reduced from 120 (Taeger et al. 2010) to 107, including the two newly described species and *Dinematus krausi* (possibly belonging to the *P. depressa* group). However, this number is not final, because we have not resolved all taxonomic questions and there are several probably undescribed species in the *depressa* group, mainly from the Mediterranean region.

Plates

Figures 6–28. External characters used to identify *Pristiphora* species. **6** *albitibia* DEI-GISHym31514 **7** *testacea* DEI-GISHym19770 **8** *pallida* DEI-GISHym20845 **9** *bifida* DEI-GISHym31512 **10** *groenblomi* DEI-GISHym31602 **11** *retusa* DEI-GISHym20965 **12** *abietina* DEI-GISHym31225 **13** *malaisei* DEI-GISHym19772 **14** *luteipes* DEI-GISHym80038, flagellum **15** *ruficornis* DEI-GISHym31185, flagellum **16** *armata* DEI-GISHym11092 **17** *frigida* NHRS-HEVA000005006, flagellum with barely visible stout black setae (arrows) **18** *pusilla* DEI-GISHym80050, flagellum with clearly visible stout black setae **19** *appendiculata* DEI-GISHym31500, smooth mesopostnotum (arrow) **20** *albitibia* DEI-GISHym31516, matt mesopostnotum (arrow) **21** *appendiculata* DEI-GISHym31500, claw **22** *opaca* holotype **23** *geniculata* DEI-GISHym20961 **24** *depressa* DEI-GISHym11043 **25** *bifida* DEI-GISHym31507 **26** *robusta* http://id.luomus.fi/GL.5197 **27** *biscalis* DEI-GISHym11088 **28** *subbifida* DEI-GISHym11332.
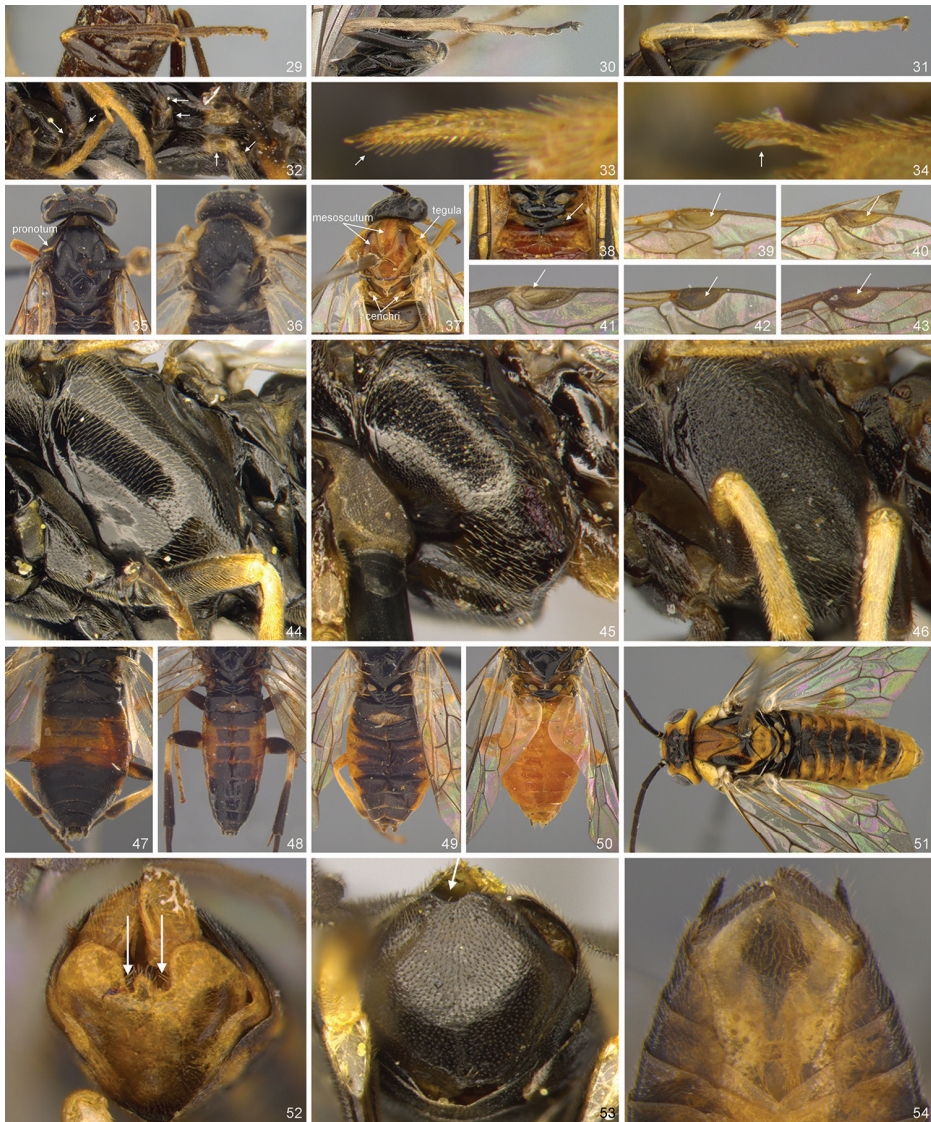
Figures 29–54. External characters used to identify *Pristiphora* species. **29** *atripes* holotype **30** *malaisei* DEI-GISHym10991 **31** *pseudogeniculata* DEI-GISHym20832 **32** *pusilla* DEI-GISHym80050 (arrows indicate trochanters and trochantelli) **33** *friesei* DEI-GISHym31524 (arrow indicates hair and the absence of velum on anterior protibial spur) **34** *nigella* DEI-GISHym31549 (arrow indicates the velum) **35** *erichsonii* DEI-GISHym20807 **36** *paralella* 15-255 **37** *nigriceps* DEI-GISHym31687 **38** *subbifida* DEI-GISHym11332 (arrow indicates partly pale metapostnotum) **39** *subopaca* holotype, pterostigma (arrow) **40** *opaca* holotype **41** *retusa* DEI-GISHym31584 **42** *ruficornis* DEI-GISHym31185 **43** *conjugata* DEI-GISHym20960 **44** *albitibia* DEI-GISHym31514, thorax in lateral view **45** *luteipes* DEI-GISHym80038 **46** *astragali* holotype **47** *cincta* DEI-GISHym31501 **48** *condei* DEI-GISHym20957 **49** *conjugata* DEI-GISHym20960 **50** *testacea* DEI-GISHym31237 **51** *cadma* TUZ615726 **52** *biscalis* DEI-GISHym80224 (arrows indicate a deep notch at the posterior margin of sternum 9) **53** *nigriceps* DEI-GISHym80059 (arrow indicates a notch at the posterior margin of sternum 9) **54** *pallidiventris* DEI-GISHym20971.
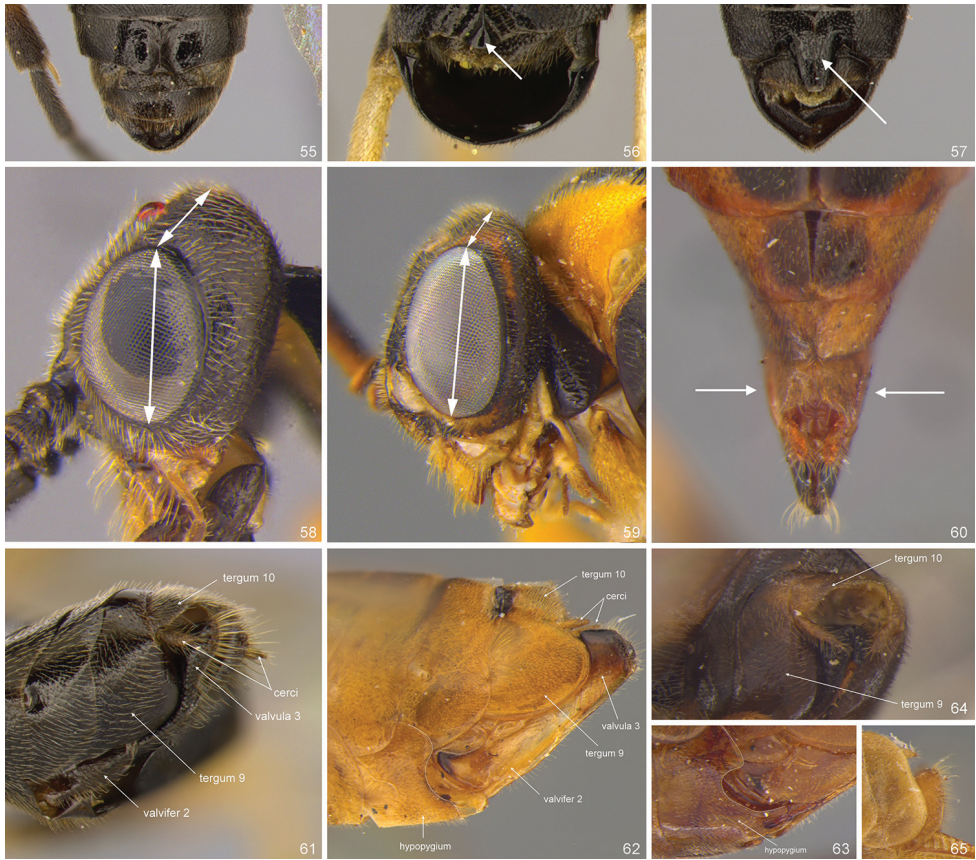
Figures 55–65. External characters used to identify *Pristiphora* species. **55** *subopaca* DEI-GISHym31560 **56** *leucopodia* DEI-GISHym80057 (arrow indicates an indistinct apical projection of the tergum 8) **57** *armata* DEI-GISHym11092 (arrow indicates a distinct apical projection) **58** *malaisei* DEI-GISHym10991 (arrows indicate small eyes relative to head length above eyes) **59** *testacea* DEI-GISHym19770 (arrows indicate large eyes relative to head length above eyes) **60** *saxesenii* DEI-GISHym20844 (arrows indicate lateral constriction of the apex of the abdomen) **61** *appendiculata* DEI-GISHym31500 **62** *pseudodecipiens* DEI-GISHym20999 **63** *decipiens* DEI-GISHym21256 **64** *laricis* DEI-GISHym31503 **65** *alpestris* lectotype.

Figures 66–87. Valvula 3 of *Pristiphora*. **66–67** *abbreviata* DEI-GISHym31505 **68–70** *angulata* DEI-GISHym31523 **71–72** *monogyniae* DEI-GISHym11352 **73–74** *dasiphorae* DEI-GISHym31598 **75** *malaisei* DEI-GISHym 15461 (arrows indicate small scopa) **76–77** *biscalis* DEI-GISHym11088 **78** *maesta* DEI-GISHym11381 **79–81** *friesei* DEI-GISHym31524 **82–83** *depressa* DEI-GISHym11043 **84–85** *nigriceps* DEI-GISHym21257 **86–87** *insularis* DEI-GISHym20966.

Figures 88–107. Valvula 3 of *Pristiphora*. **88** *alpestris* DEI-GISHym20881 **89–90** *pseudocoactula* DEI-GISHym19952 **91–92** *micronematica* group (DEI-GISHym20879) **93–94** *carinata* group (DEI-GISHym19835) **95–96** *lativentris* DEI-GISHym19838 **97** *carinata* group (DEI-GISHym19966) **98–99** *carinata* DEI-GISHym20847 **100** *pseudogeniculata* DEI-GISHym20832 **101–102** *exigua* DEI-GISHym31527 **103** *retusa* DEI-GISHym20965 **104** *cincta* DEI-GISHym31723 **105** *appendiculata* DEI-GISHym80025 (arrows indicate distinct scopa) **106** *pallidiventris* DEI-GISHym20964 **107** *punctifrons* DEI-GISHym21254.
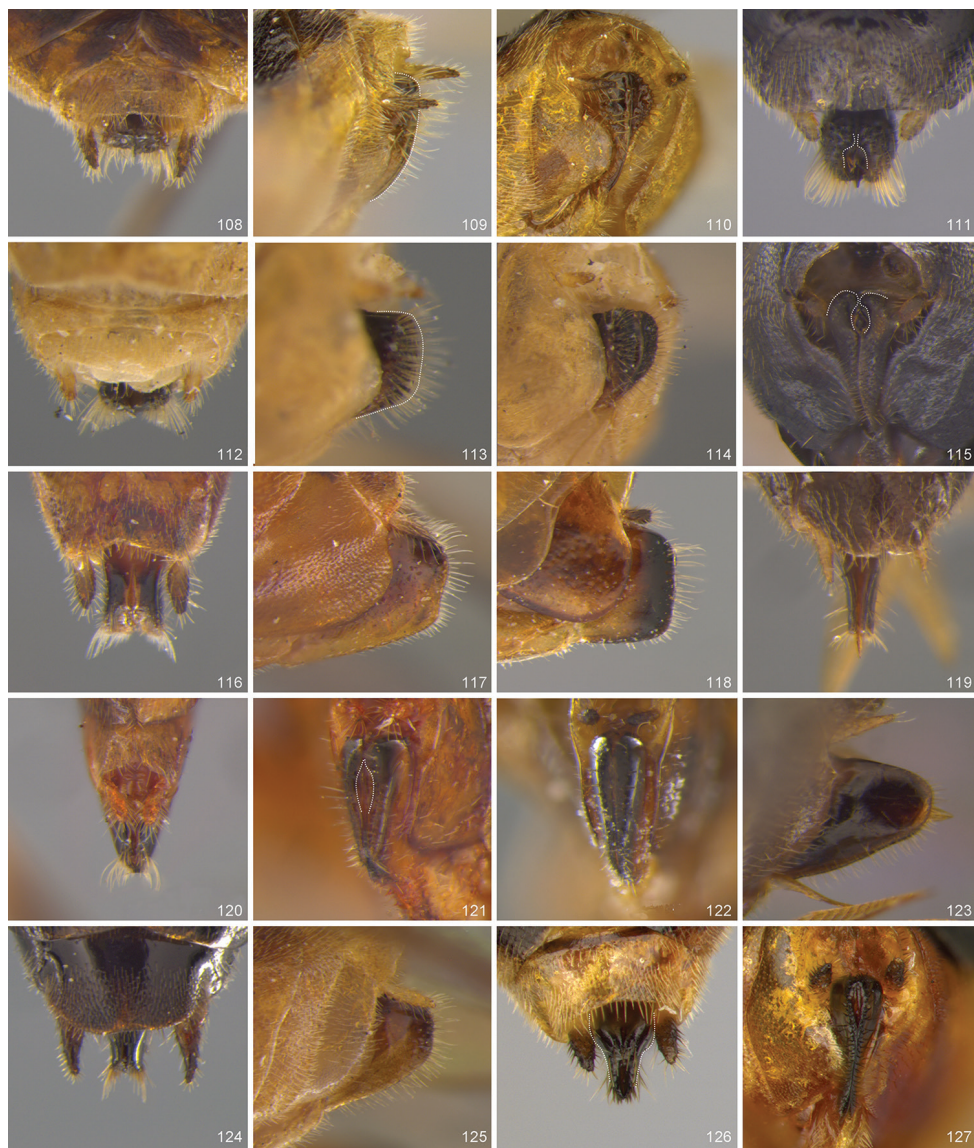
Figures 108–127. Valvula 3 of *Pristiphora*. **108–110** *bufo* DEI-GISHym17786 **111, 115** *nigella* DEI-GISHym20972 **112–114** *paralella* 15-255 **116–117** *decipiens* DEI-GISHym21256 **118, 122** *gerula* DEI-GISHym20843 **119, 123** *tenuiserra* DEI-GISHym20846 **120–121** *saxesenii* DEI-GISHym20844 **124** *erichsonii* DEI-GISHym20807 **125** *pallida* DEI-GISHym20845 **126–127** *glauca* DEI-GISHym31525.
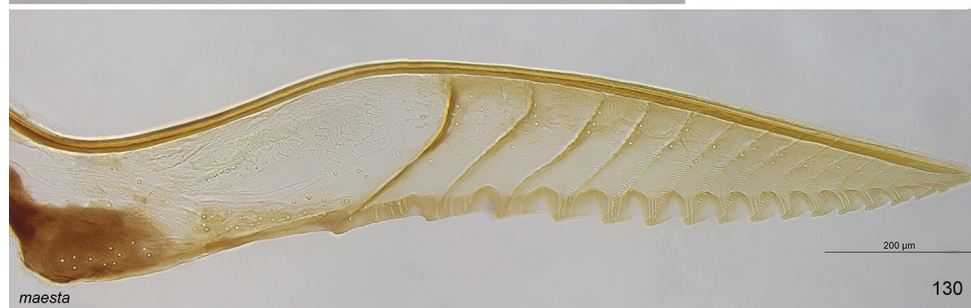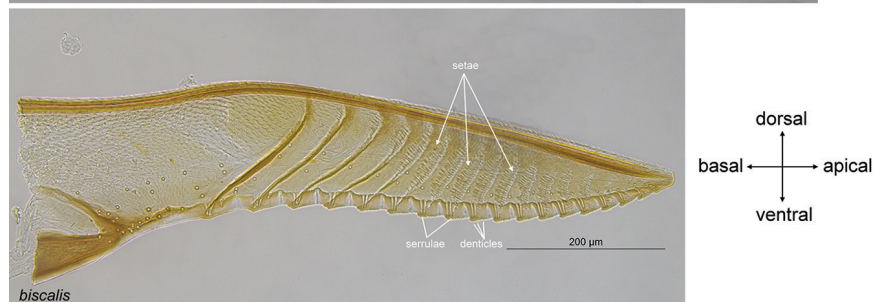
Figures 128–131. Lancets of *Pristiphora*. **128** *abbreviata* DEI-GISHym17687 **129** *biscalis* DEI-GISHym20953 **130** *maesta* PR.578VV_506 **131** *monogyniae* DEI-GISHym20954.

Figures 132–135. Lancets of *Pristiphora*. **132** *angulata* DEI-GISHym31671 **133** *exigua* DEI-GISHym31527 **134** *retusa* DEI-GISHym20965 **135** *insularis* DEI-GISHym20966.
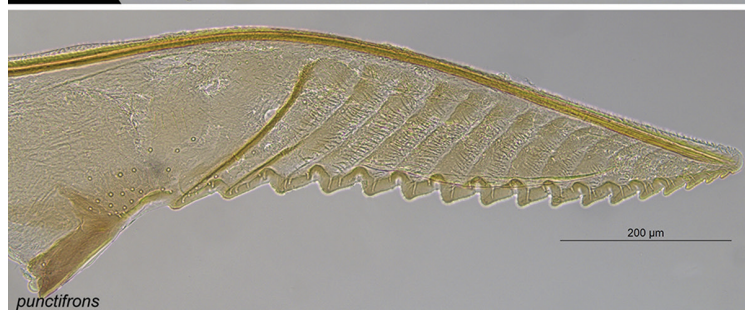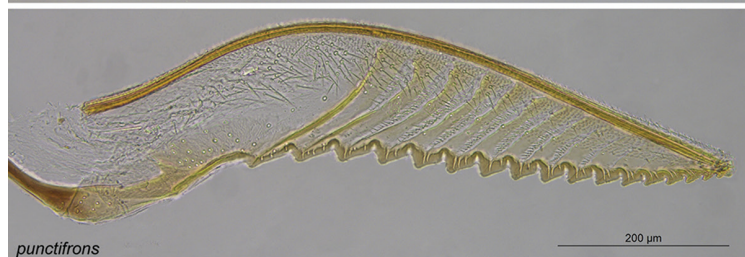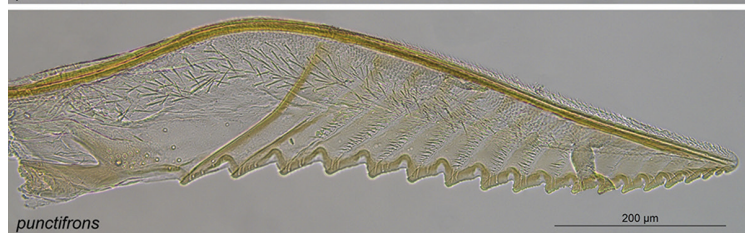
Figures 136–140. Lancets of *Pristiphora*. **136** *dasiphorae* DEI-GISHym31598 **137** *malaisei* PR.641VV **138** *punctifrons* DEI-GISHym20878 **139** *punctifrons* DEI-GISHym31578 **140** *punctifrons*, holotype of *flavipicta*.
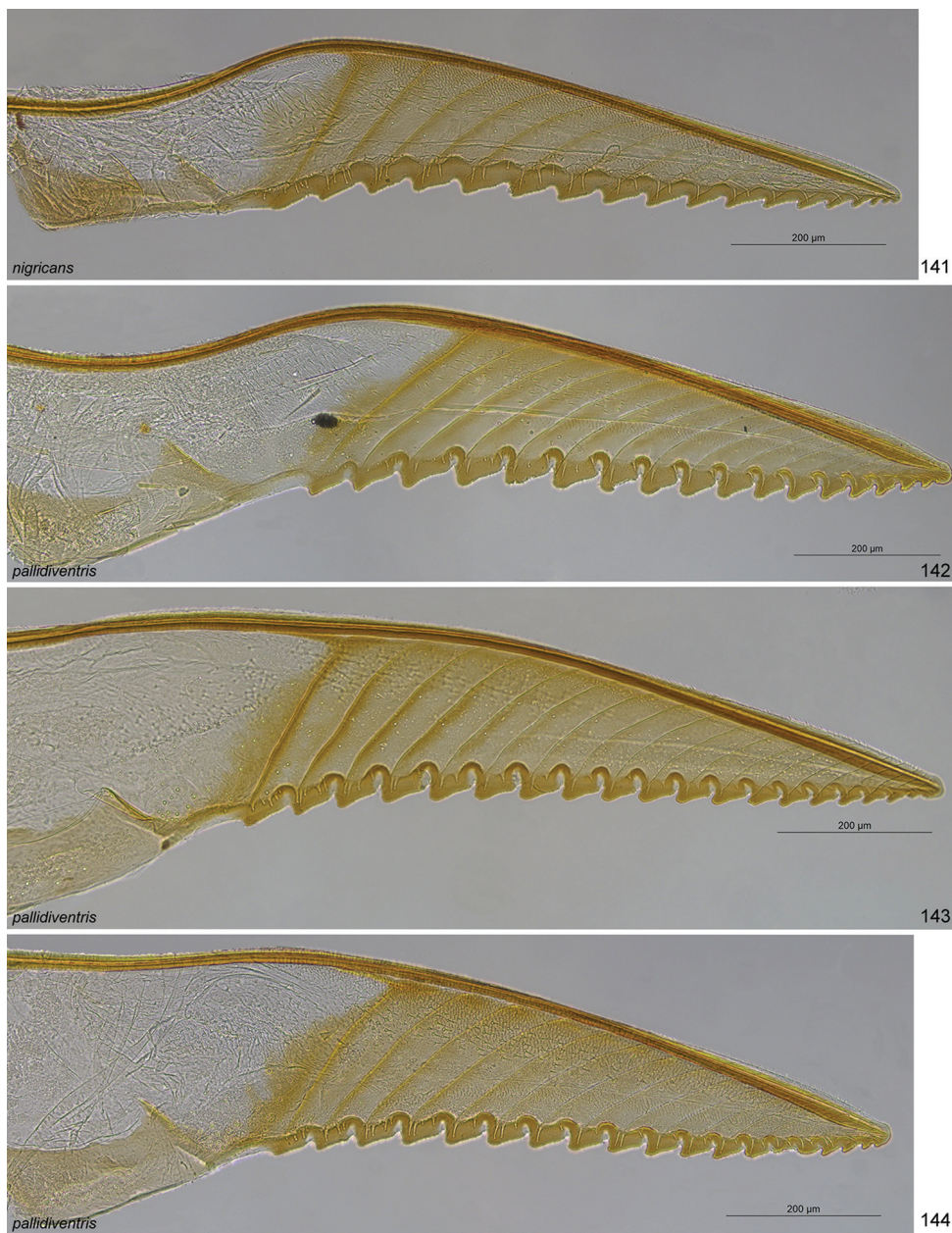
Figures 141–144. Lancets of *Pristiphora*. **141** *nigricans* DEI-GISHym20619 **142** *pallidiventris* DEI-GISHym20667 **143** *pallidiventris* W8473 **144** *pallidiventris* DEI-GISHym20864.
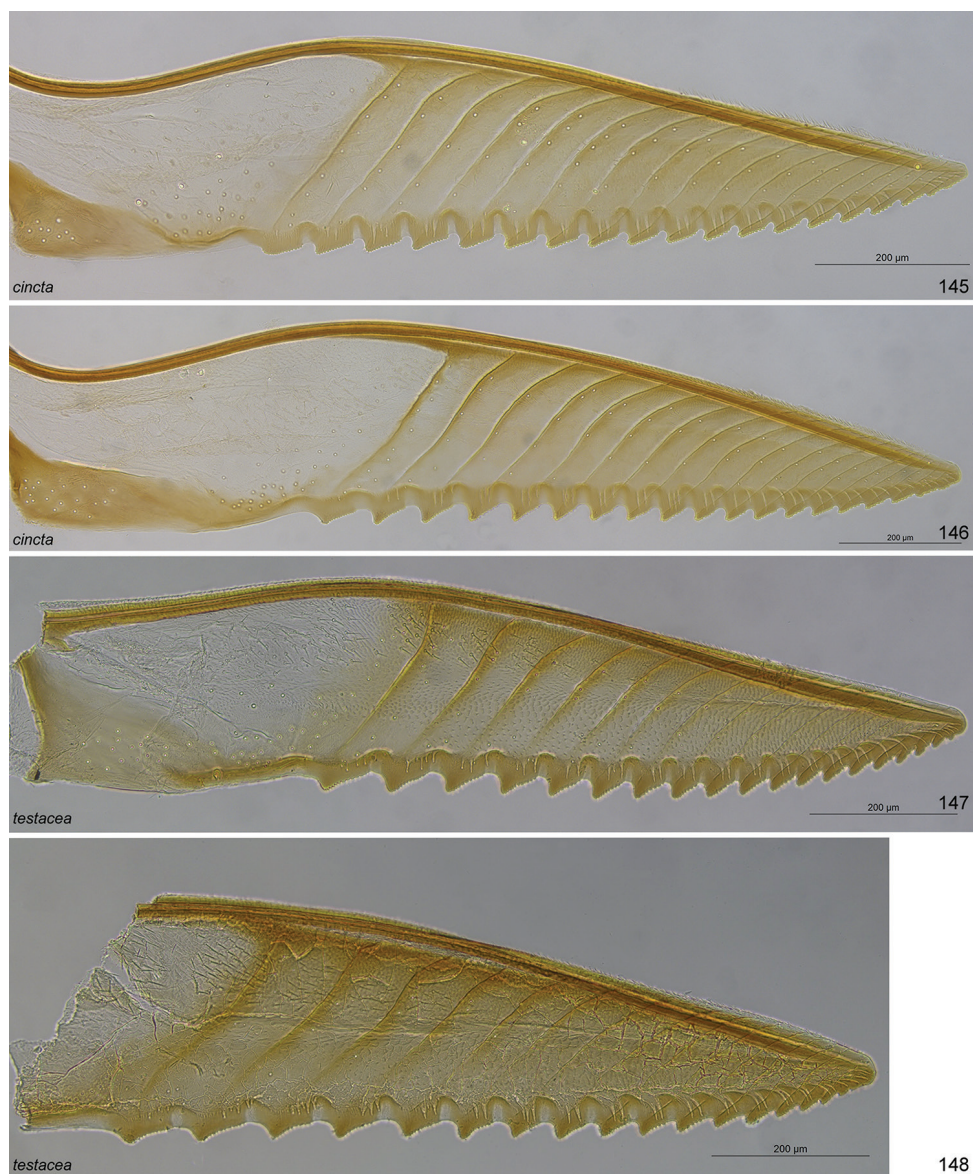
Figures 145–148. Lancets of *Pristiphora*. **145** *cincta* PR.581VV, oviposited in the leaves of *Vaccinium myrtillus* **146** *cincta* PR.582VV **147** *testacea* DEI-GISHym31638 **148** *testacea*, holotype of *gaunitzi*.
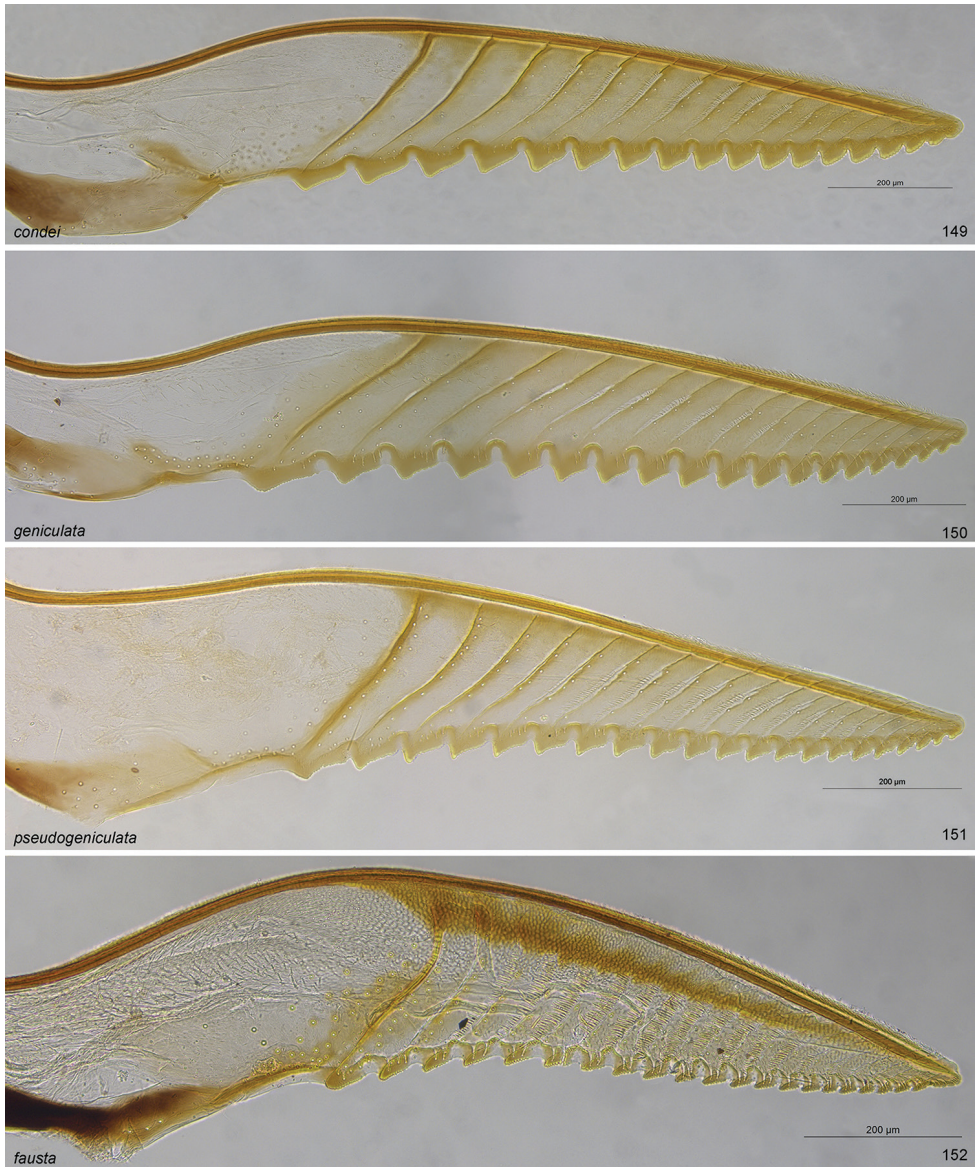
Figures 149–152. Lancets of *Pristiphora*. **149** *condei* PR.548VV **150** *geniculata* PR.550VV **151** *pseudogeniculata* holotype **152** *fausta* DEI-GISHym10986.
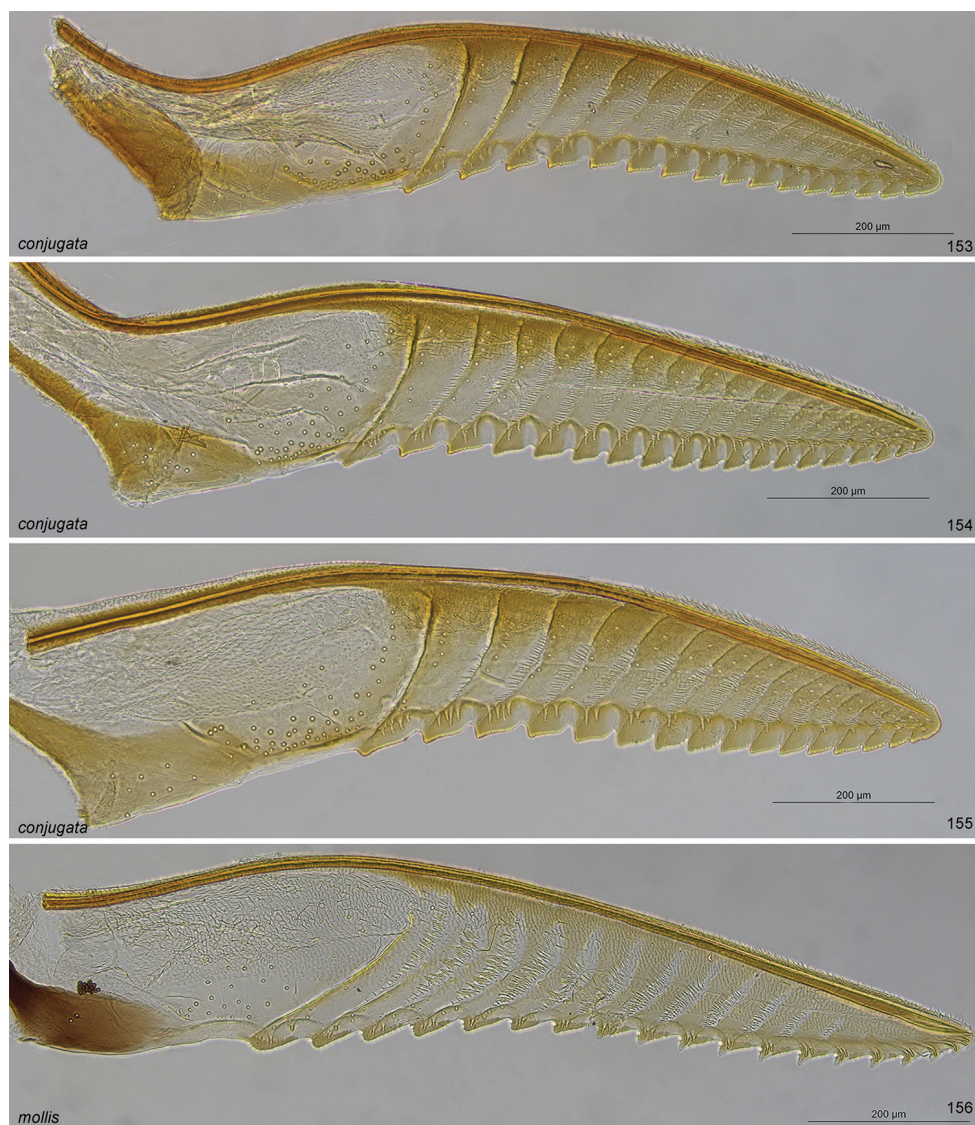
Figures 153–156. Lancets of *Pristiphora*. **153** *conjugata* DEI-GISHym31605, reared from *Populus tremula* **154** *conjugata* DEI-GISHym20960, reared from *Salix pentandra* **155** *conjugata* DEI-GISHym31546, reared from *Populus* sp. **156** *mollis* DEI-GISHym10982.
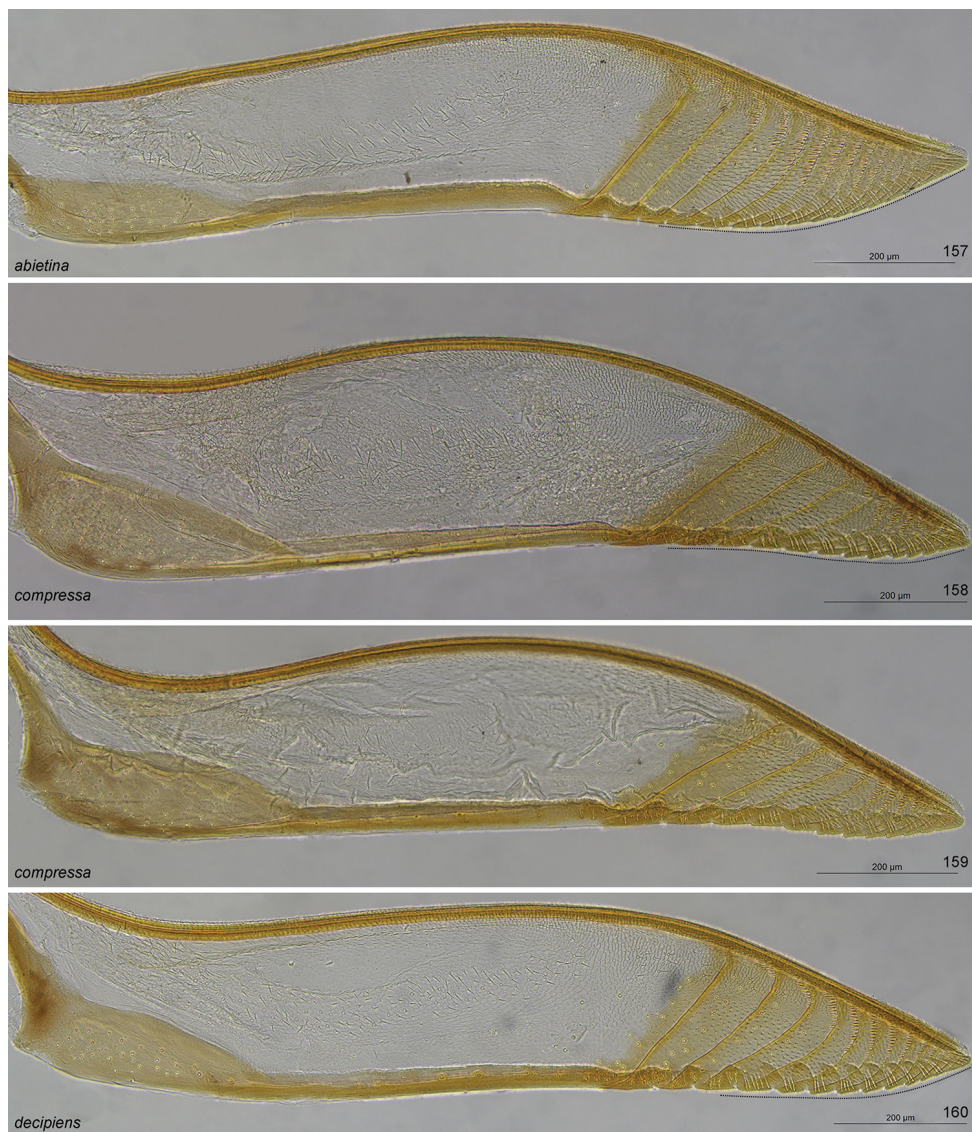
Figures 157–160. Lancets of *Pristiphora*. **157** *abietina* DEI-GISHym5174 **158** *compressa* DEI-GISHym31606 **159** *compressa* DEI-GISHym11922 **160** *decipiens* DEI-GISHym31604.
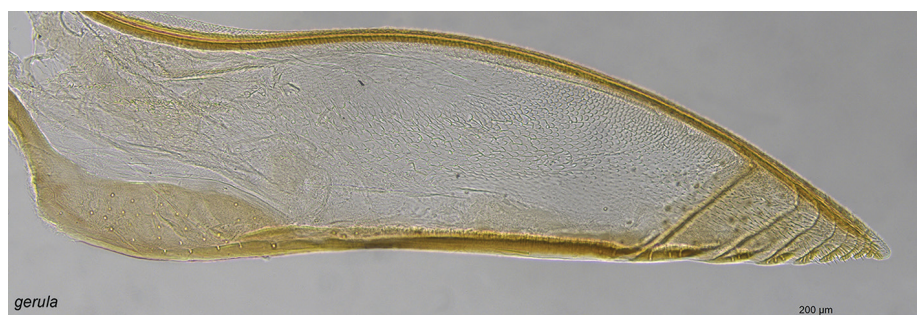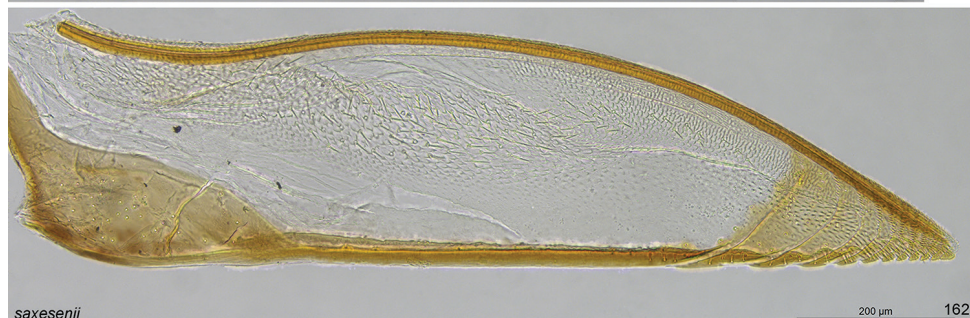
Figures 161–164. Lancets of *Pristiphora*. **161** *gerula* DEI-GISHym20980 **162** *saxesenii* DEI-GISHym20840 **163** *pseudodecipiens* DEI-GISHym31583 **164** *robusta* holotype.
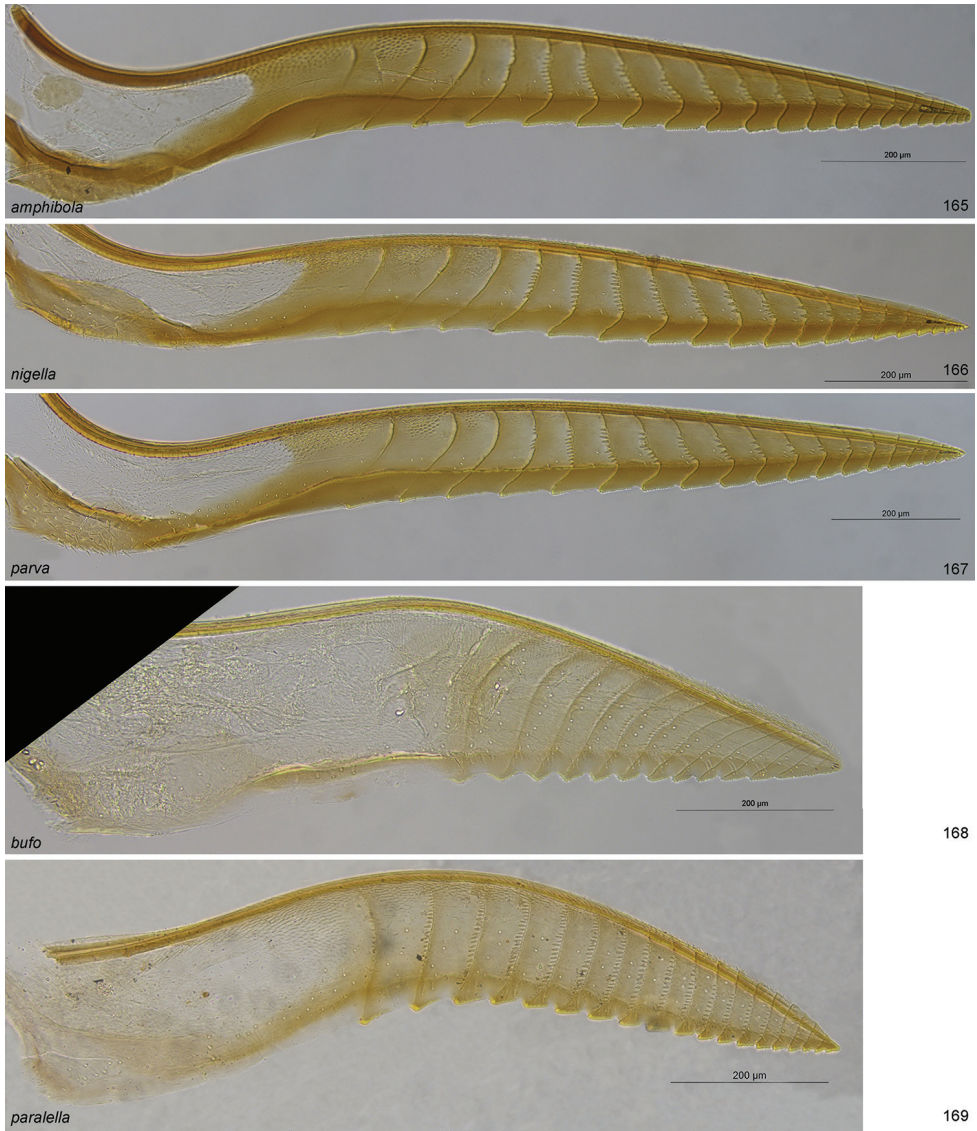
Figures 165–169. Lancets of *Pristiphora*. **165** *amphibola* PR.533VV **166** *nigella* PR.534VV **167** *parva* PR.539VV **168** *bufo* PR.422VV **169** *paralella* 15-255.

Figures 170–173. Lancets of *Pristiphora*. **170** *erichsonii* DEI-GISHym20807 **171** *pallida* DEI-GISHym20845 **172** *subarctica*, holotype of *pseudosaxesenii* **173** *tenuiserra* 15-256.
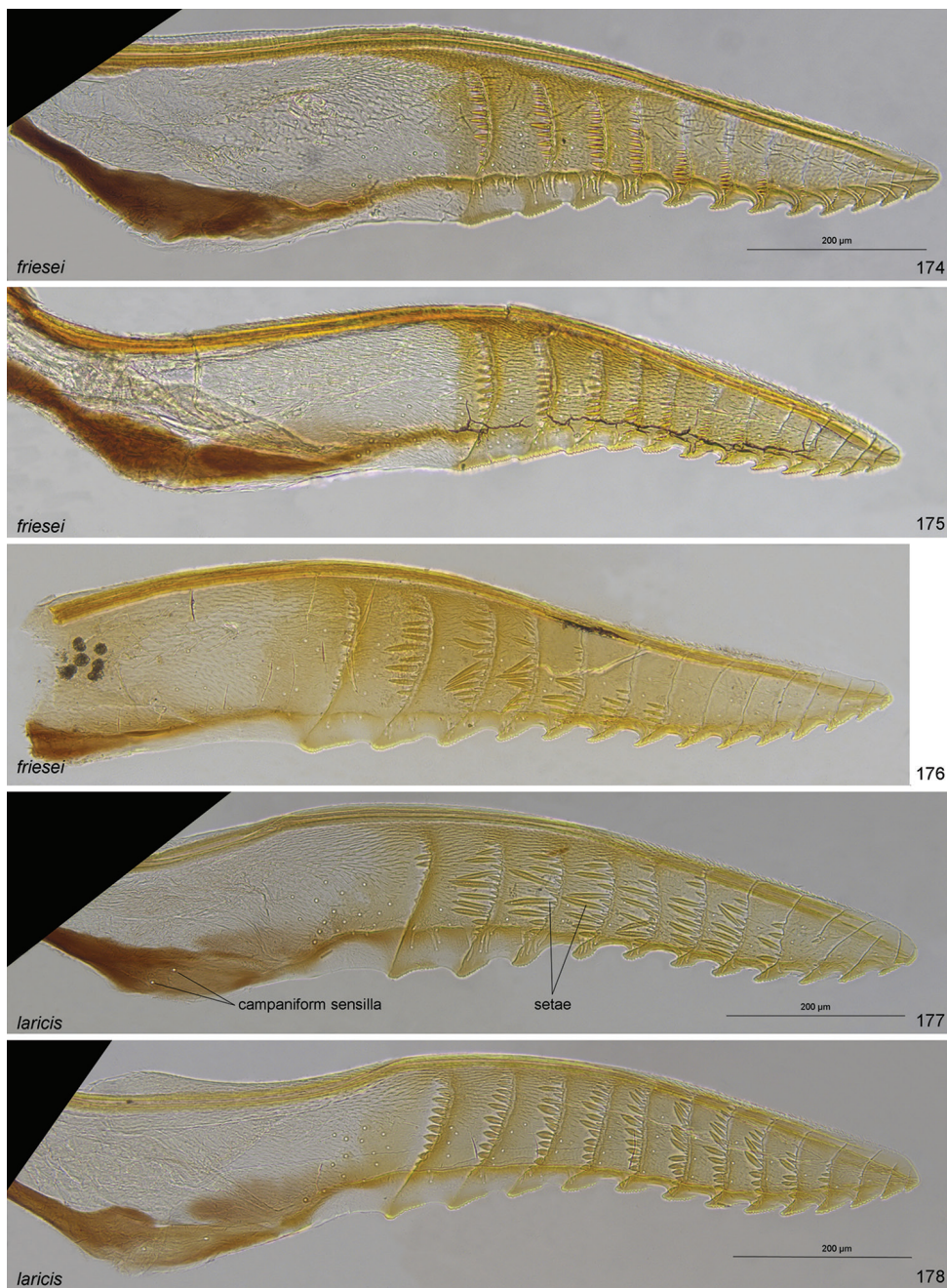
Figures 174–178. Lancets of *Pristiphora*. **174** *friesei* DEI-GISHym11557 **175** *friesei*, holotype of *atrata* **176** *friesei* lectotype **177** *laricis* PR.207VV **178** *laricis* PR.208VV.
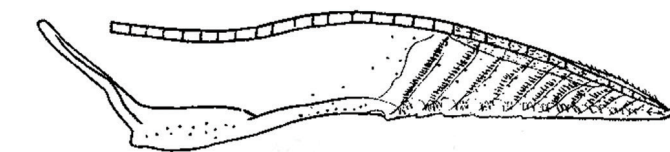
Figures 179–183. Lancets of *Pristiphora*. **179** *glauca* DEI-GISHym31573 **180** *wesmaeli* from Wong (1975) **181** *leucopodia* DEI-GISHym31262 **182** *leucopodia* DEI-GISHym20920 **183** *nigriceps* DEI-GISHym20922.
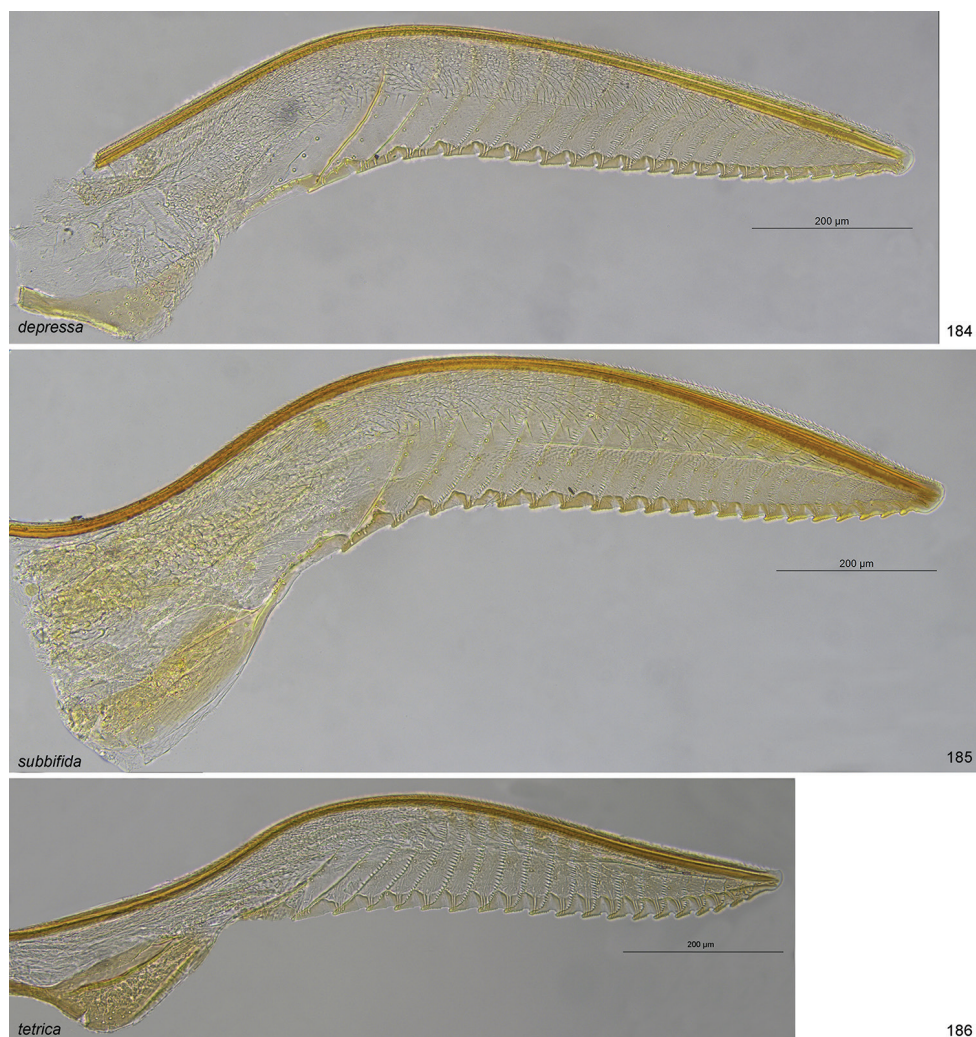
Figures 184–186. Lancets of *Pristiphora*. **184** *depressa* DEI-GISHym17704 **185** *subbifida* DEI-GISHym80062 **186** *tetrica* DEI-GISHym19843.

appendiculata

200 µm

187

albitibia

200 µm

188

astragali

small spiny pectines

200 µm

189

sootryeni

200 µm

190
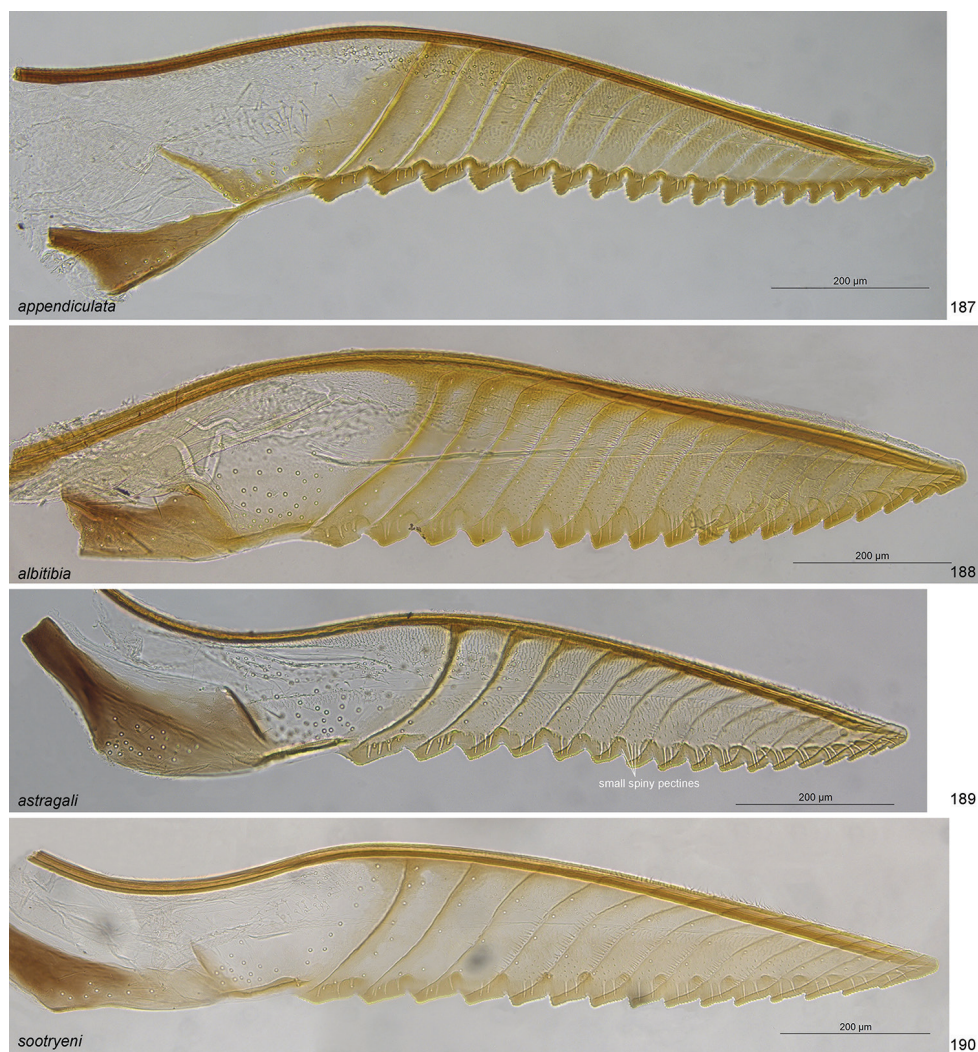
Figures 187–190. Lancets of *Pristiphora*. **187** *appendiculata* DEI-GISHym21073 **188** *albitibia* DEI-GISHym20944 **189** *astragali* DEI-GISHym80042 **190** *sootryeni* PR.366VV.
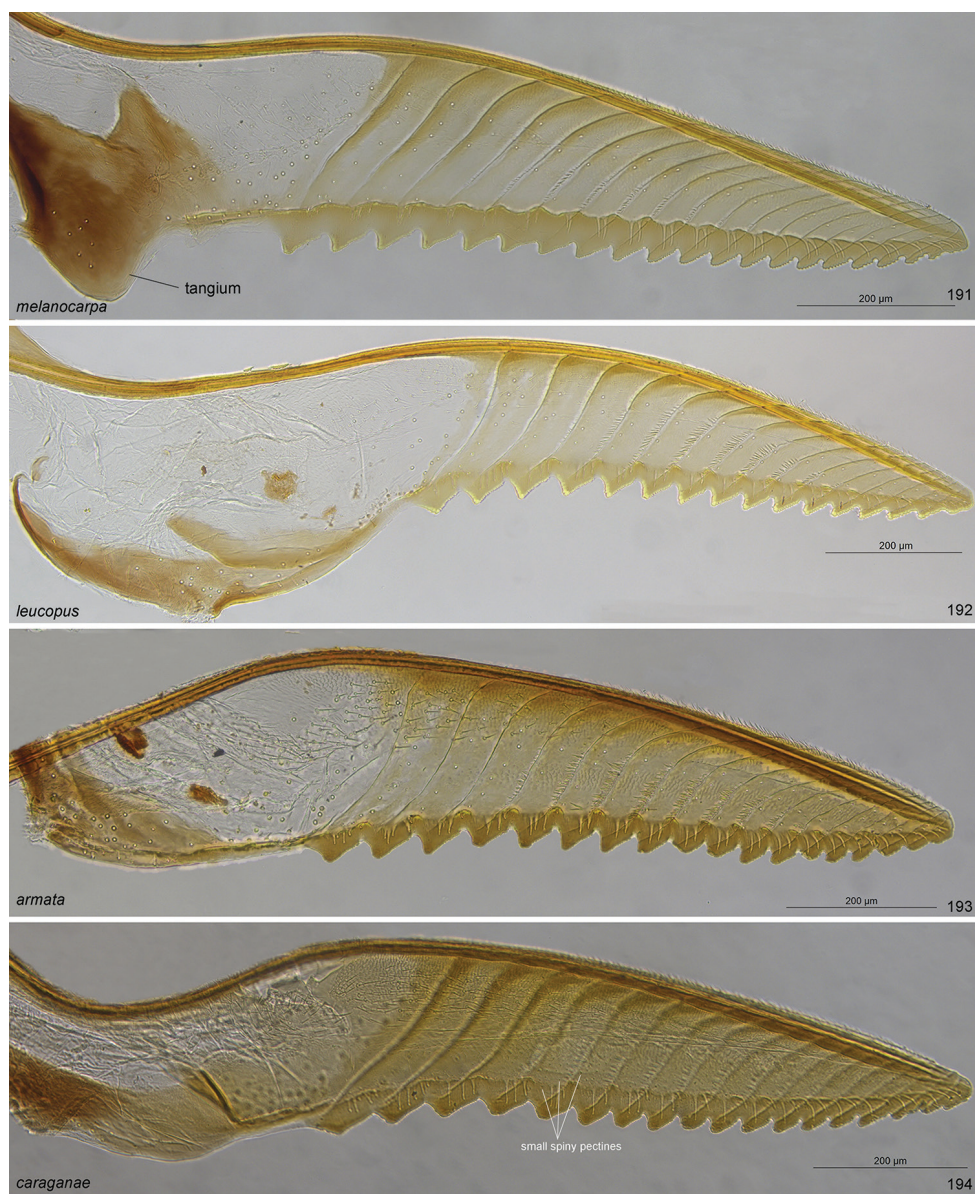
Figures 191–194. Lancets of *Pristiphora*. **191** *melanocarpa* PR.423VV **192** *leucopus* PR.393VV **193** *armata* DEI-GISHym20366 **194** *caraganae* DEI-GISHym80209.
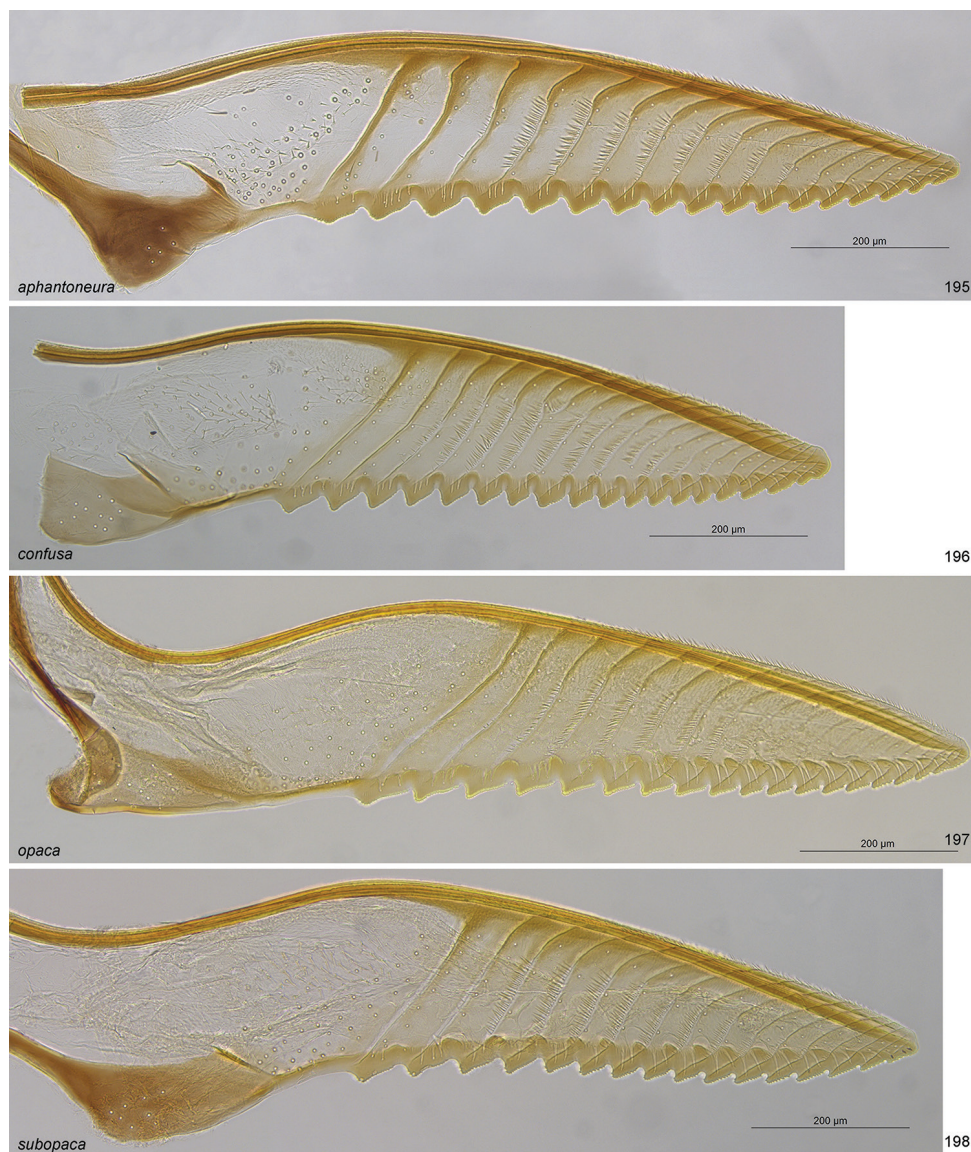
Figures 195–198. Lancets of *Pristiphora*. **195** *aphantoneura* PR.695VV, reared from *Lathyrus pratensis* **196** *confusa* PR.544VV **197** *opaca* PR.389VV **198** *subopaca* PR.403VV.

Figures 199–202. Lancets of *Pristiphora*. **199** *bifida* PR.408VV **200** *frigida* NHRS-HEVA000003873 **201** *pusilla* PR.369VV **202** *staudingeri* PR.373VV.

Figures 203–205. Lancets of *Pristiphora*. **203** *alpestris* DEI-GISHym20881 **204** *pseudocoactula* DEI-GISHym20883, paratype **205** *atripes* holotype.
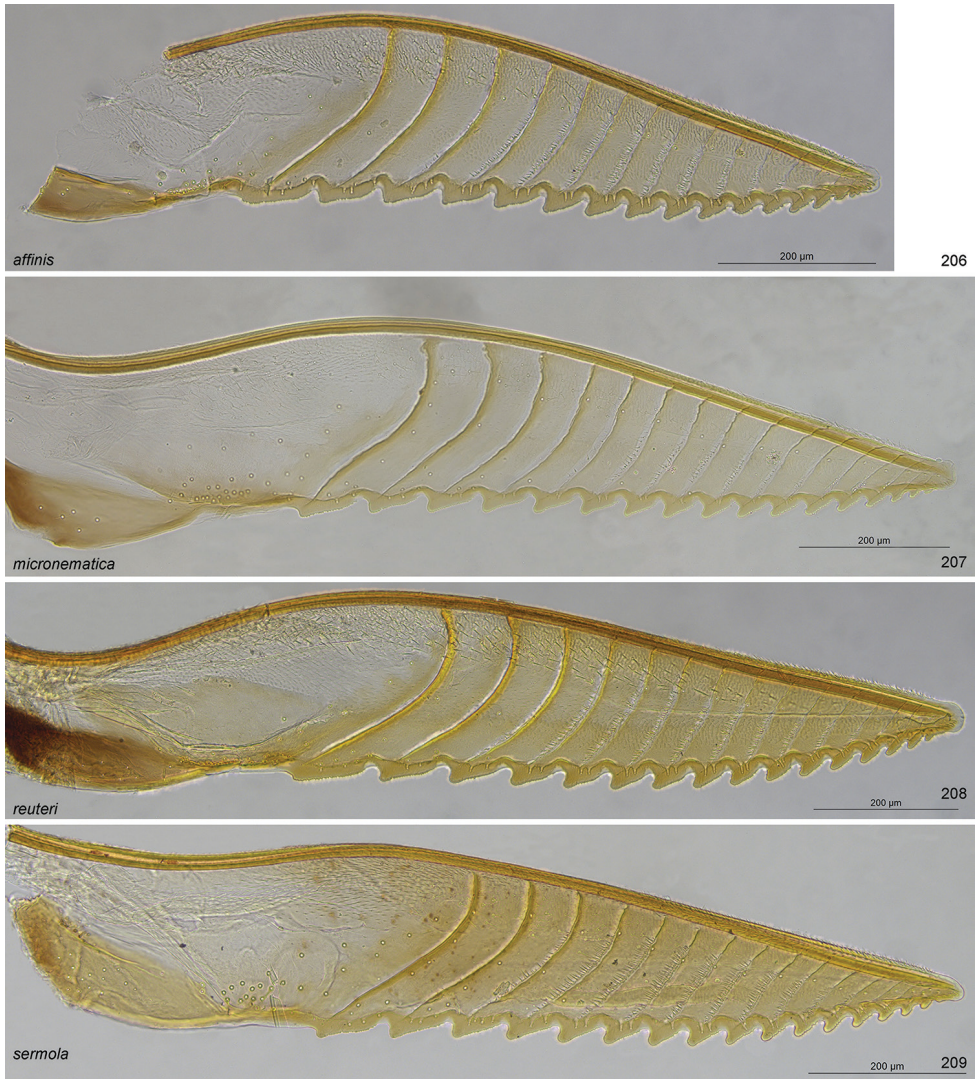
Figures 206–209. Lancets of *Pristiphora*. **206** *affinis* DEI-GISHym31626 **207** *micronematica* PR.258VV **208** *reuteri* DEI-GISHym31582 **209** *sermola* DEI-GISHym31579.
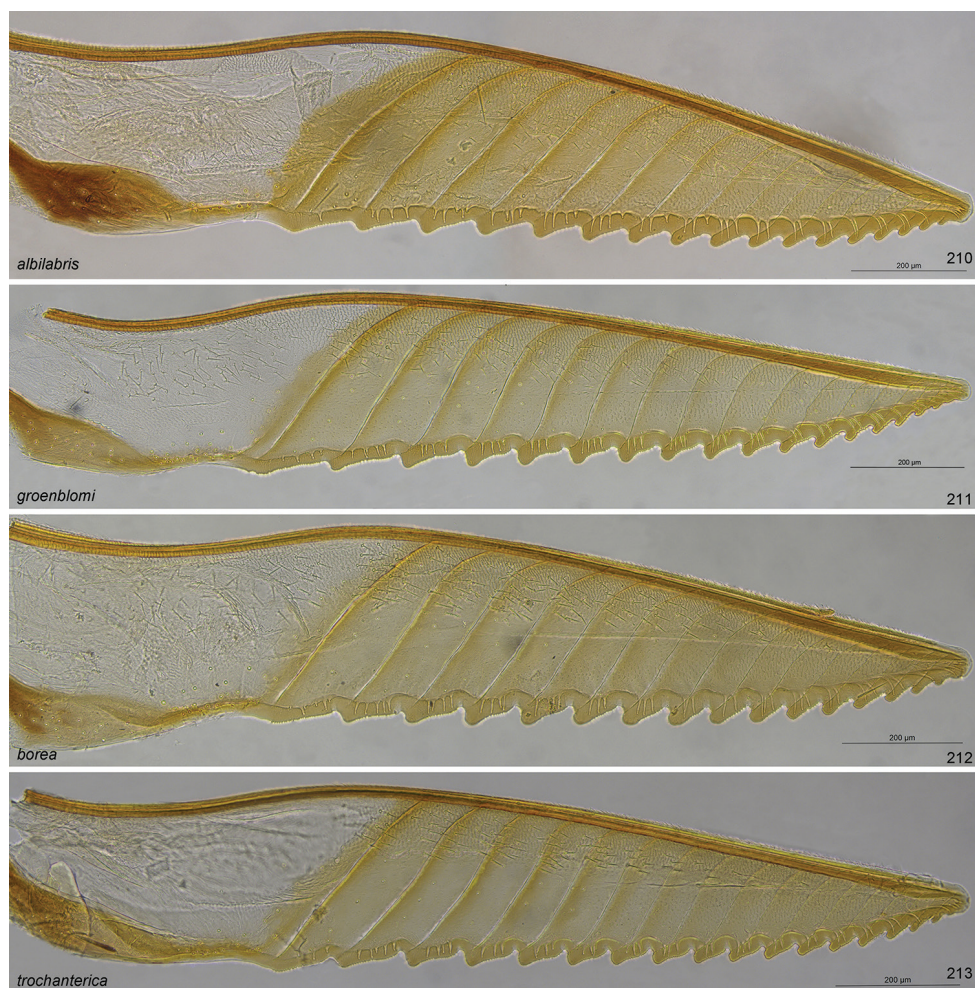
Figures 210–213. Lancets of *Pristiphora*. **210** *albilabris* DEI-GISHym20943 **211** *groenblomi* DEI-GISHym31597 **212** *borea* DEI-GISHym31609 **213** *trochanterica* DEI-GISHym31574.
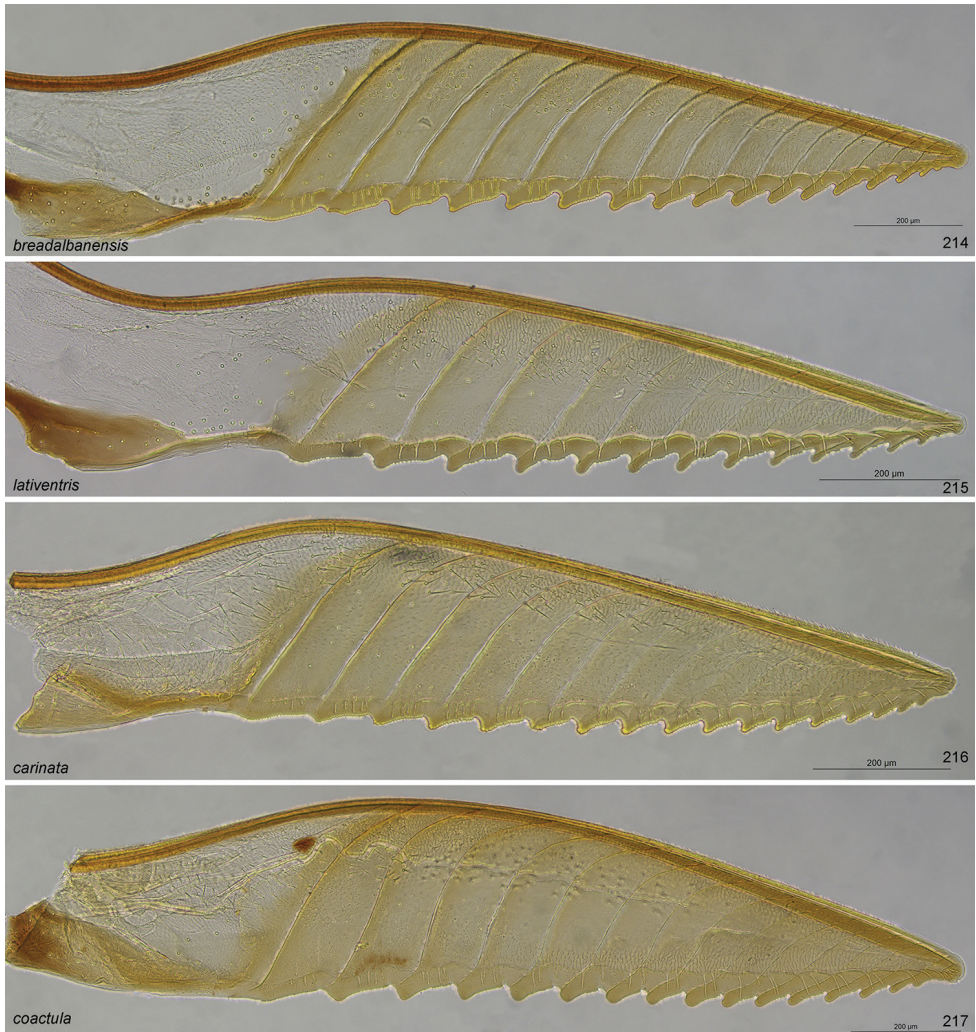
Figures 214–217. Lancets of *Pristiphora*. **214** *breadalbanensis* DEI-GISHym17784 **215** *lativentris* DEI-GISHym80240 **216** *carinata* DEI-GISHym20847 **217** *coactula* DEI-GISHym31608.
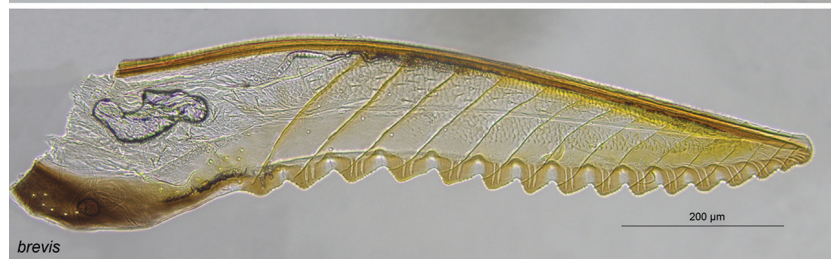
Figures 218–222. Lancets of *Pristiphora*. **218** *thalictrivora*, holotype of *thalictricola* **219** *brevis* DEI-GISHym31261 **220** *dochmocera* lectotype **221** *thalictrivora* DEI-GISHym20854 **222** *rufipes* DEI-GISHym31537.
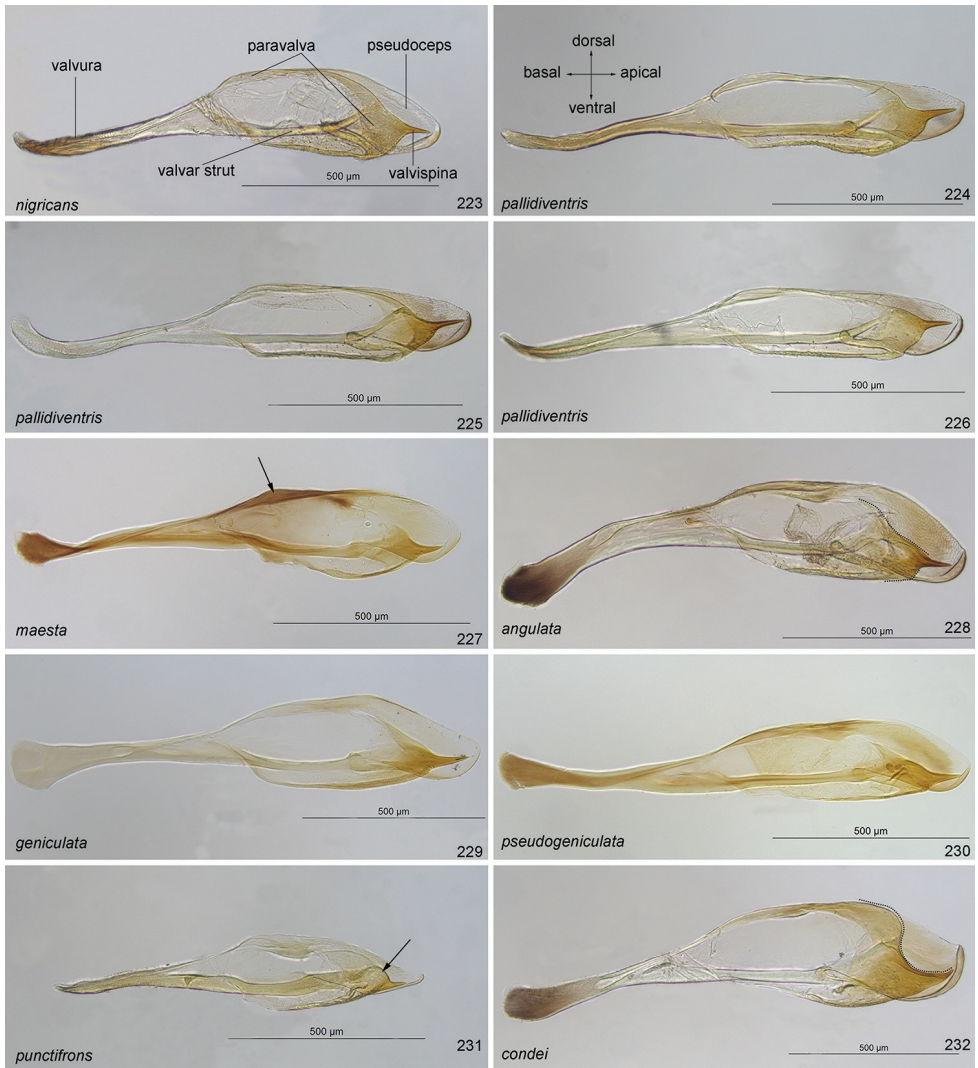
Figures 223–232. Penis valves of *Pristiphora*. **223** *nigricans* DEI-GISHym20869 **224** *pallidiventris* DEI-GISHym20866 **225** *pallidiventris* DEI-GISHym80143 **226** *pallidiventris* DEI- GISHym20976 **227** *maesta* PR.579VV (arrow indicates an angulate dark area) **228** *angulata* DEI-GISHym31030 **229** *geniculata* PR.549VV **230** *pseudogeniculata* PR.577VV **231** *punctifrons* DEI-GISHym31669 (arrow indicates a round hump) **232** *condei* DEI-GISHym80223.
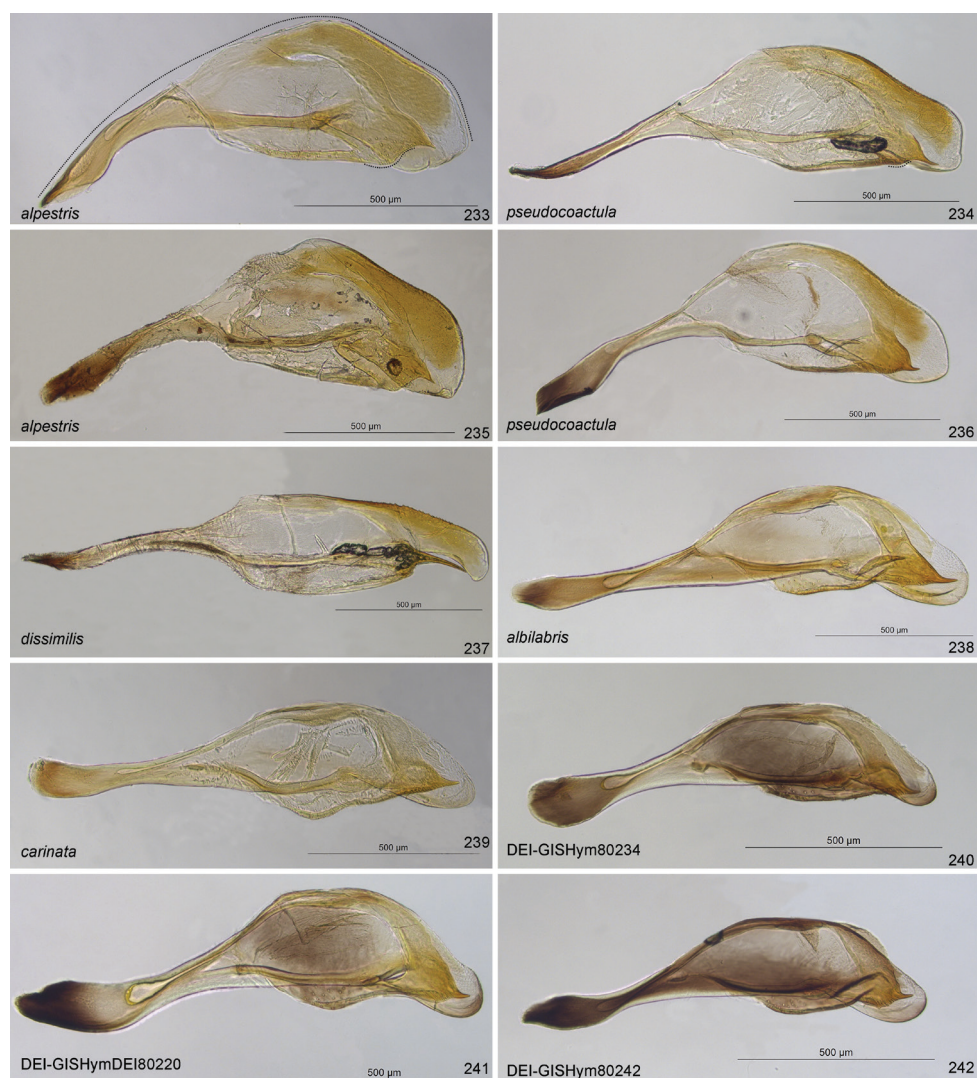
Figures 233–242. Penis valves of *Pristiphora*. **233** *alpestris* DEI-GISHym31711 **234** *pseudocoactula* DEI-GISHym19968 **235** *alpestris*, holotype of *karvoneni* **236** *pseudocoactula* DEI-GISHym80212 **237** *dissimilis* holotype **238** *albilabris* DEI-GISHym80210 **239** *carinata* syntype (GBIF-GISHym4689) **240** *carinata* group (DEI-GISHym80234) **241** *carinata* group (DEI-GISHym80220) **242** *carinata* group (DEI-GISHym80242).
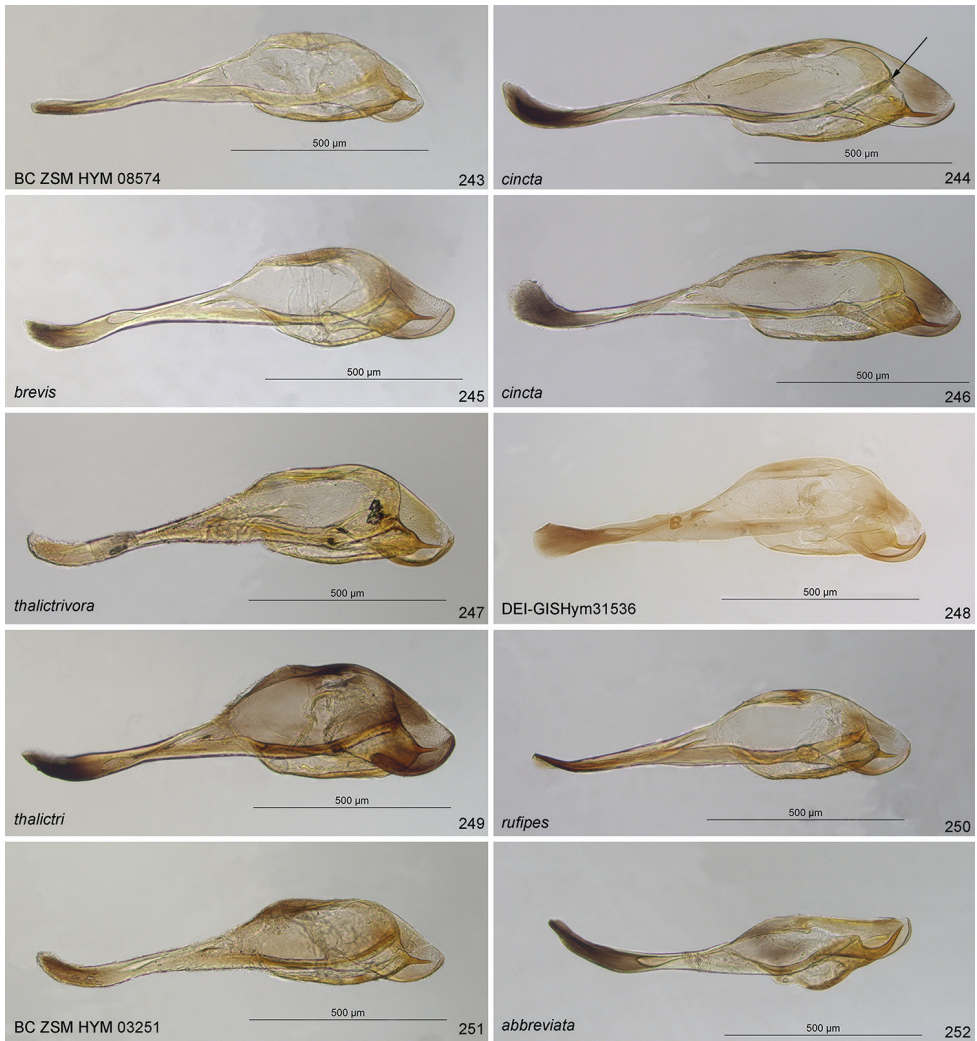
Figures 243–252. Penis valves of *Pristiphora*. **243** *rufipes* group (BC ZSM HYM 08574) **244** *cincta* DEI-GISHym80174 (arrow indicates clearly visible valvar strut at anterior margin of paravalva) **245** *brevis* DEI-GISHym20987 **246** *cincta* DEI-GISHym80158 **247** *thalictrivora* DEI-GISHym20908, paratype of *thalictricola*, reared from *Thalictrum simplex* **248** *rufipes* group (DEI-GISHym31536) **249** *thalictri* DEI-GISHym11428 **250** *rufipes* DEI-GISHym15263 **251** *rufipes* group (BC ZSM HYM 03251) **252** *abbreviata* DEI-GISHym80320.
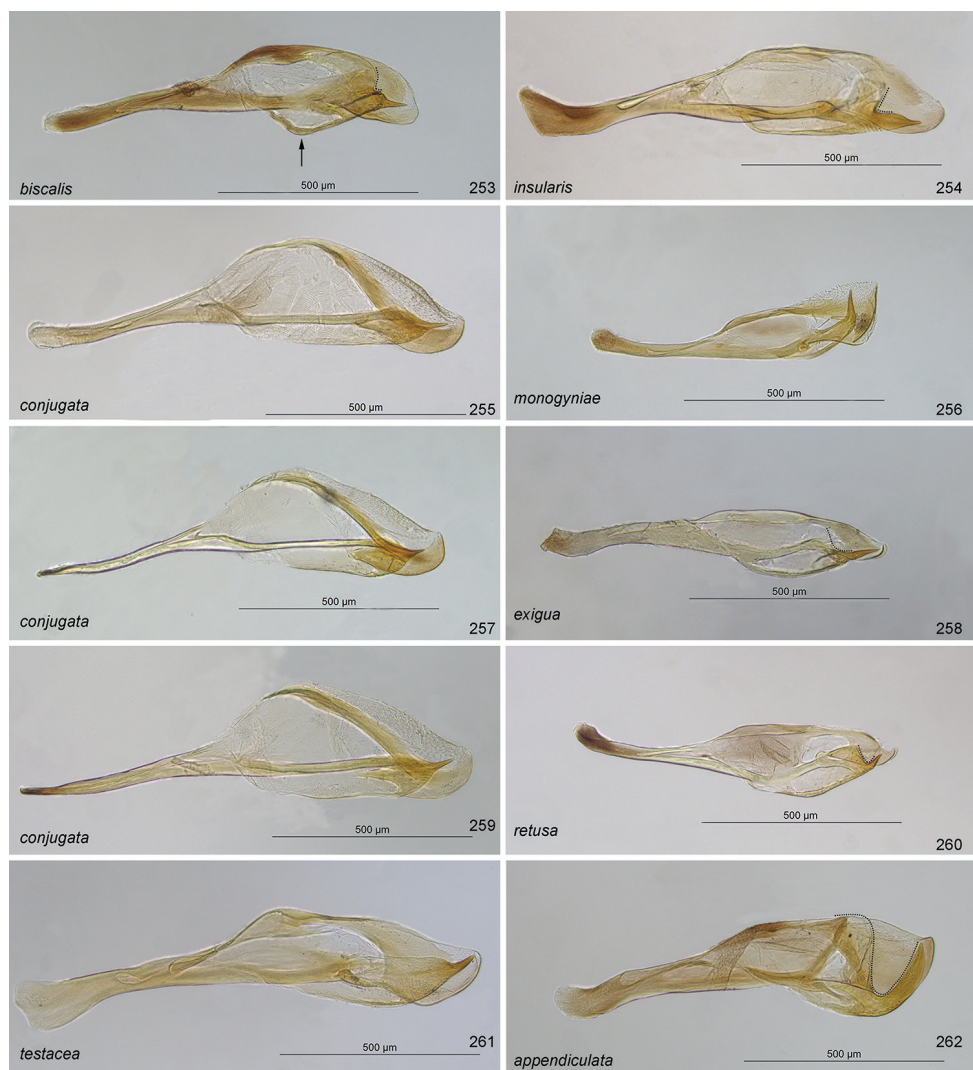
Figures 253–262. Penis valves of *Pristiphora*. **253** *biscalis* DEI-GISHym31533 (arrow indicates protruding ventral margin of paravalva) **254** *insularis* DEI-GISHym20941 **255** *conjugata* DEI-GISHym31542, reared from *Populus* sp. **256** *monogyniae* DEI-GISHym31590 **257** *conjugata* DEI-GISHym80024, reared from *Salix fragilis* **258** *exigua* holotype **259** *conjugata* DEI-GISHym31544, reared from *Salix pentandra* **260** *retusa* DEI-GISHym20791 **261** *testacea* DEI-GISHym31631 **262** *appendiculata* DEI-GISHym31555.
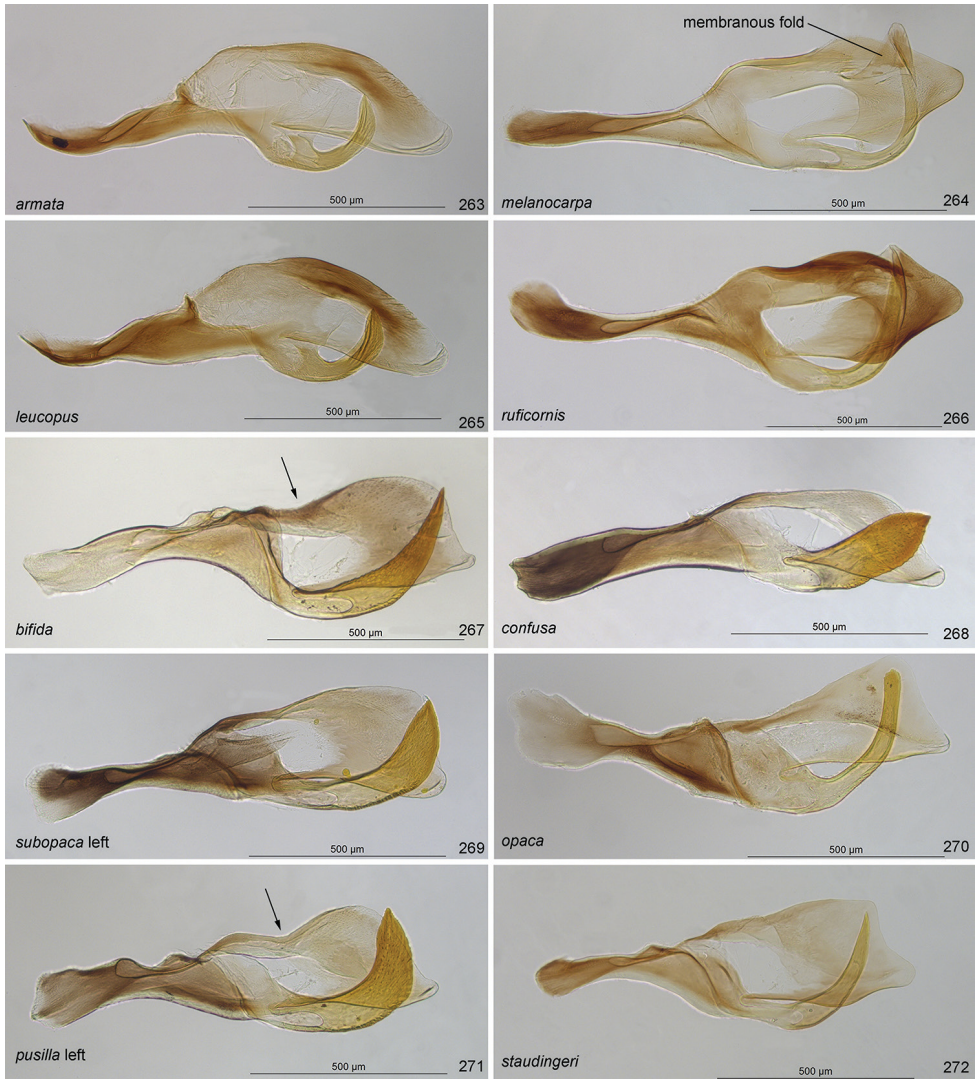
Figures 263–272. Penis valves of *Pristiphora*. **263** *armata* PR.465VV **264** *melanocarpa* PR.425VV **265** *leucopus* GBIF-GISHym3246, syntype of *Nematus crassicornis* Hartig **266** *ruficornis* PR.462VV **267** *bifida* DEI-GISHym80000 (arrow indicates a dorsal depression of the pseudoceps) **268** *confusa* DEI-GISHym31265 **269** *subopaca* DEI-GISHym80030, left penis valve **270** *opaca* PR.459VV **271** *pusilla* DEI-GISHym80029, left penis valve with strong dorsal depression of the pseudoceps (arrow) **272** *staudingeri* PR.352VV.
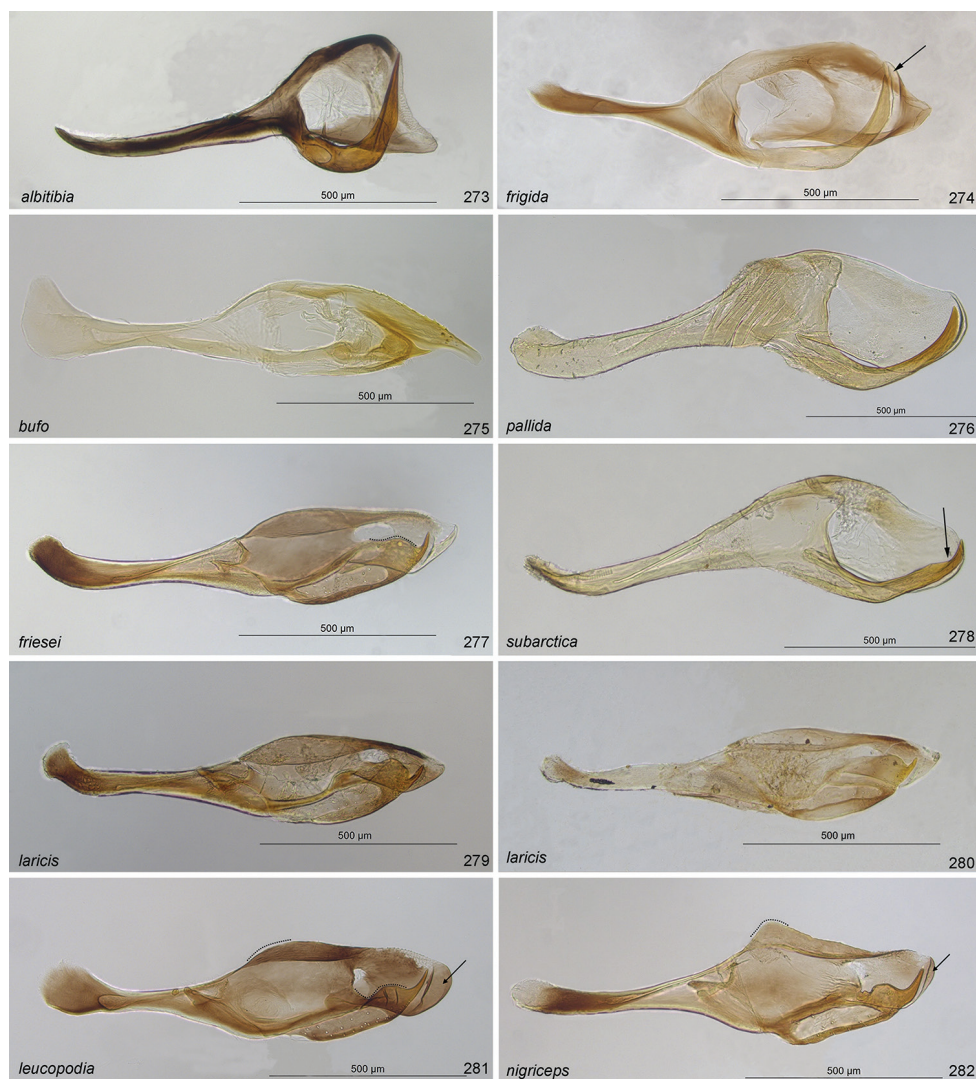
Figures 273–282. Penis valves of *Pristiphora*. **273** *albitibia* DEI-GISHym20956 **274** *frigida* NHRS-HEVA000003861 (arrow indicates a membranous fold near the tip of valvispina) **275** *bufo* PR.410VV **276** *pallida* DEI-GISHym31587 **277** *friesei* DEI-GISHym80003 **278** *subarctica* NHRS-HEVA000003752, paratype (arrow indicates a depression at the apical part of valvispina) **279** *laricis* DEI-GISHym20917 **280** *laricis* DEI-GISHym31553 **281** *leucopodia* 1f_PR.739VV (arrow indicates broad pseudocepal thickening) **282** *nigriceps* BC ZSM HYM 10976 (arrow indicates narrow pseudocepal thickening).
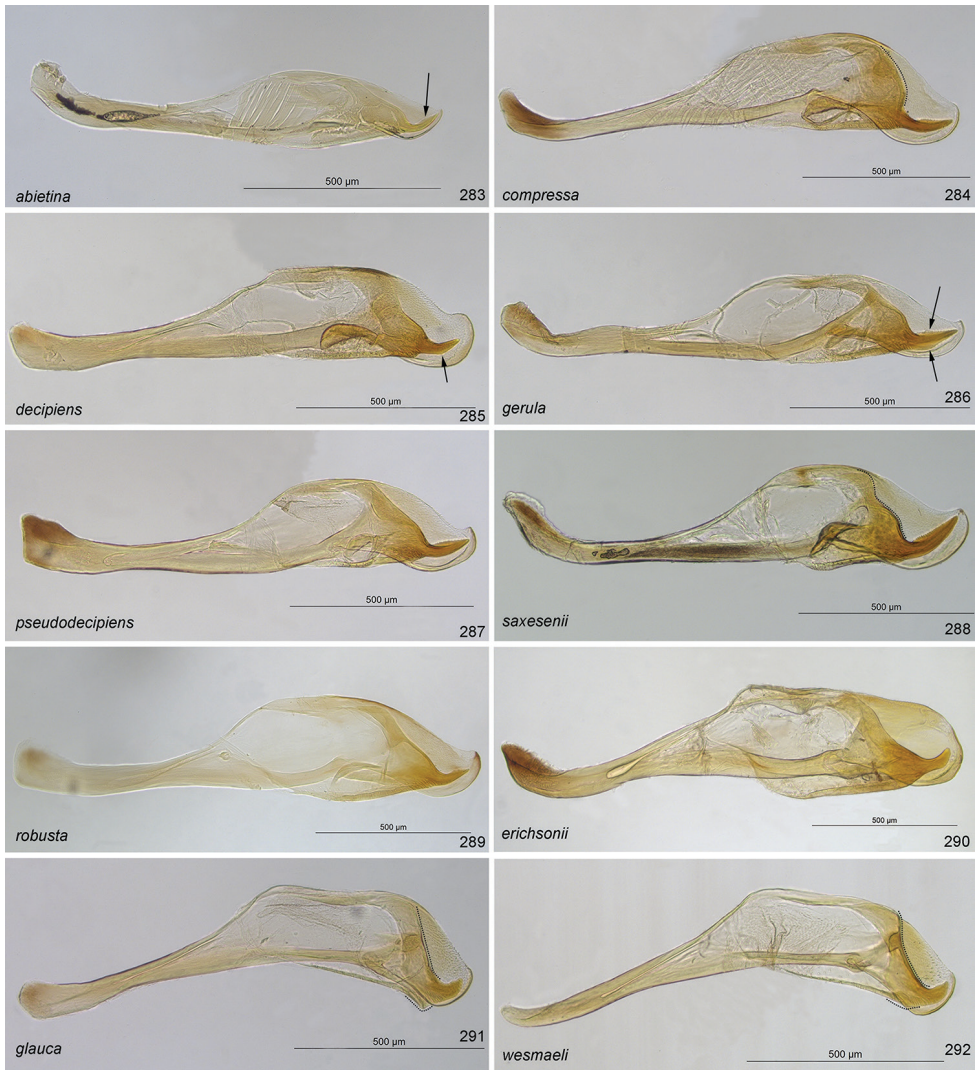
Figures 283–292. Penis valves of *Pristiphora*. **283** *abietina* PR.285VV (arrow indicates a thin non-serrate margin of valvispina) **284** *compressa* DEI-GISHym31607 **285** *decipiens* DEI-GISHym31585 (arrow indicates angled middle part of valvispina) **286** *gerula* DEI-GISHym31601 (arrows indicate dorsal and ventral thinned and serrate margins of valvispina) **287** *pseudodecipiens* DEI-GISHym31586 **288** *saxesenii* DEI-GISHym31547 **289** *robusta* PR.621VV **290** *erichsonii* DEI-GISHym80353 **291** *glauca* DEI-GISHym17724 **292** *wesmaeli* DEI-GISHym19512.
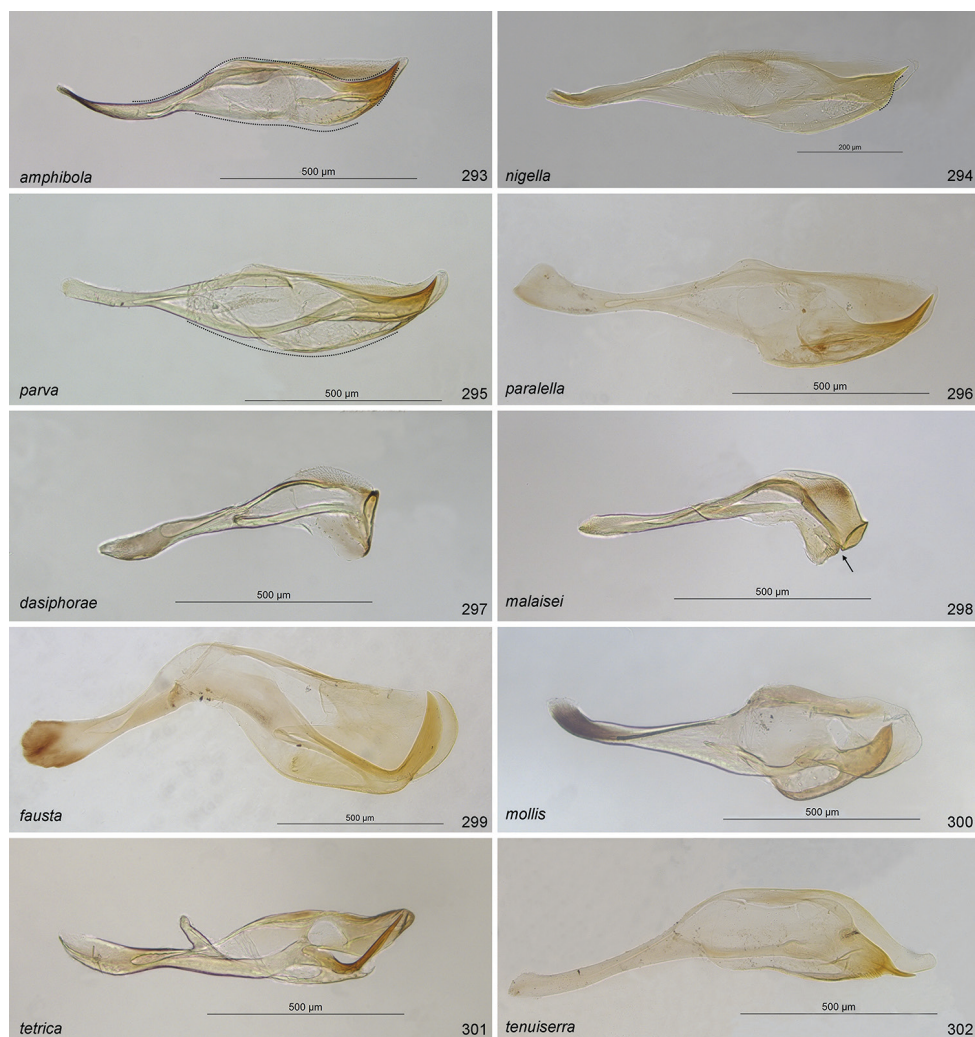
Figures 293–302. Penis valves of *Pristiphora*. **293** *amphibola* DEI-GISHym80051 **294** *nigella* PR.523VV **295** *parva* DEI-GISHym80061 **296** *paralella* 15-269 **297** *dasiphorae* DEI-GISHym20587 **298** *malaisei* DEI-GISHym80112 (arrow indicates a notch) **299** *fausta* DEI-GISHym31714 **300** *mollis* DEI-GISHym31040 **301** *tetrica* DEI-GISHym20946 **302** *tenuiserra* 15-300.
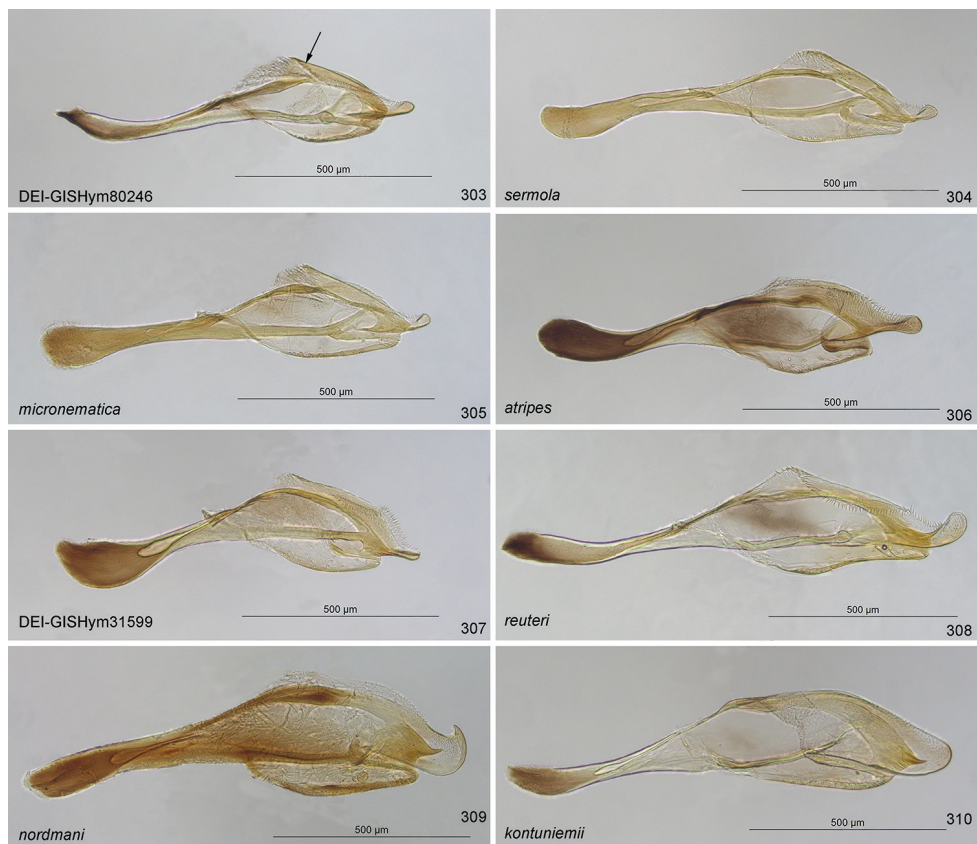
Figures 303–310. Penis valves of *Pristiphora micronematica* group. **303** DEI-GISHym80246 (arrow indicates a loose membranous region of pseudoceps) **304** *sermola* DEI-GISHym31580 **305** *micronematica* DEI-GISHym31592 **306** *atripes* DEI-GISHym80249 **307** DEI-GISHym31599 **308** *reuteri* DEI-GISHym80250 **309** *nordmani* paratype (DEI-GISHym31677) **310** *kontuniemii* DEI-GISHym31720, reared *ex ovo* from *Salix daphnoides*.
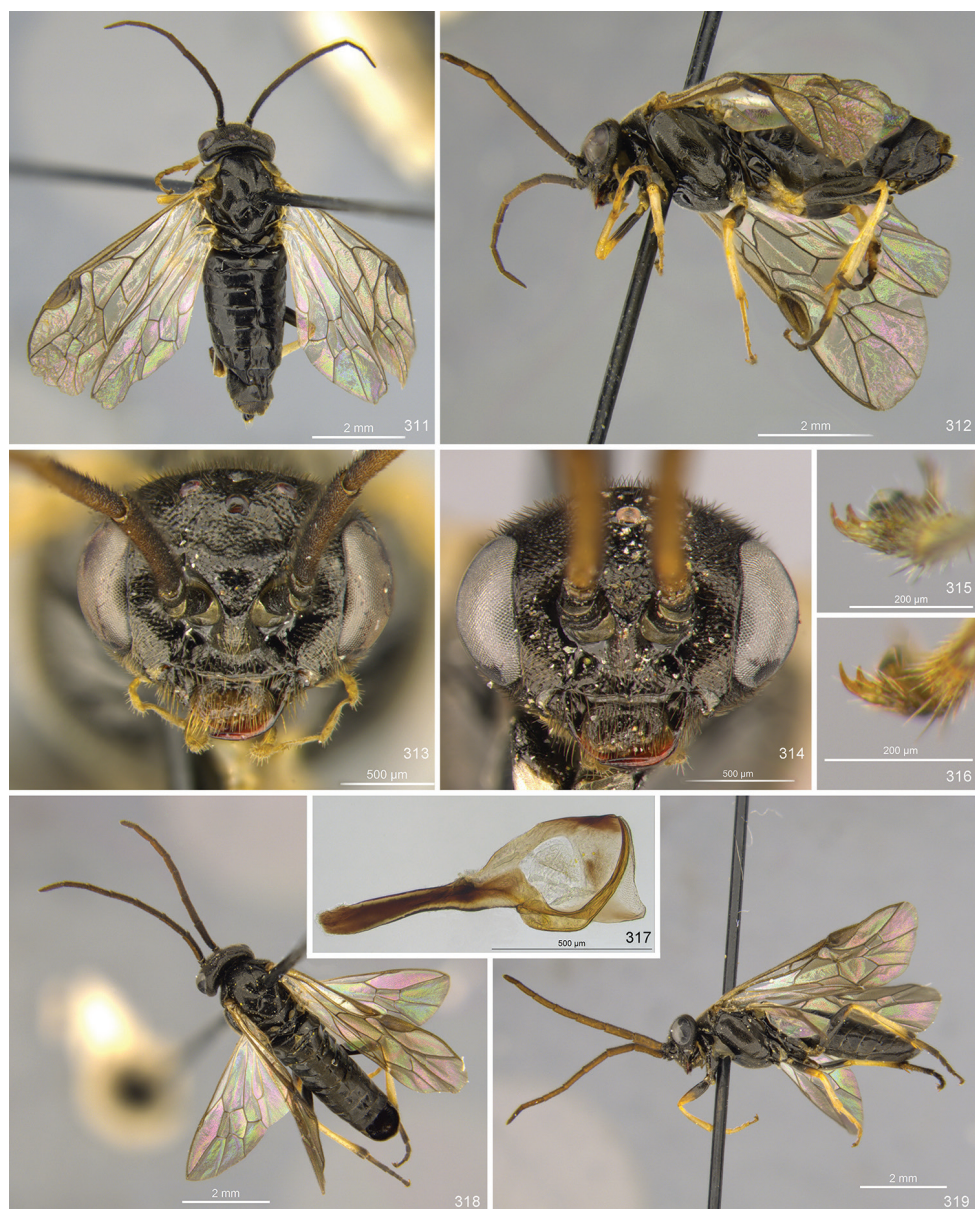
Figures 311–319. *Pristiphora caraganae* Vikberg & Prous, sp. n. **311–313, 315** female holotype DEI-GISHym80209 **314, 316–319** male paratype DEI-GISHym80356.

Figures 320–329. *Pristiphora dedeara* Liston & Prous, sp. n. **320, 322–326** female holotype DEI-GISHym80053 **321, 327–329** male paratype DEI-GISHym80258.
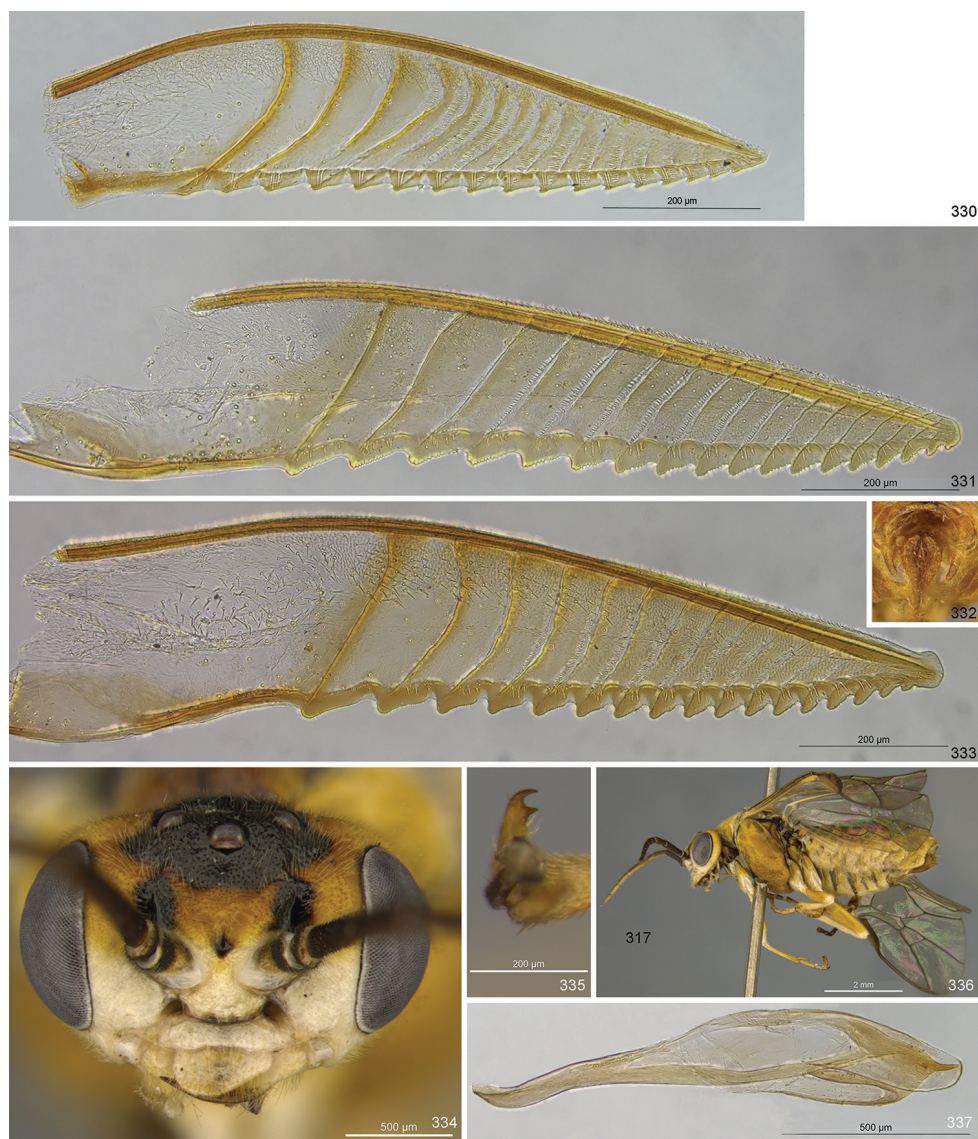
Figures 330–337. *Pristiphora dedeara* Liston & Prous, sp. n. and *P. cadma*. **330** lancet of *dedeara* holotype (DEI-GISHym80053) **331** lancet of *cadma* DEI-GISHym80406 (Canada) **332–333** valvula 3 (332) and lancet (333) of *cadma* NHRS-HEVA000003770 (Sweden) **334–336** *cadma* TUZ615726 (Estonia) **337** penis valve of *cadma* DEI-GISHym80409 (Canada).

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