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

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Abstract

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

Keywords

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

Introduction

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

The host plant associations, details of larval morphology, and bionomy of only a few species of the *ruficornis* group have been recorded in detail. Because its larvae sometimes defoliate cultivated *Ribes*, particularly *R. uva-crispa* (gooseberry), biological observations on *P. appendiculata* are included in numerous publications, including many general and popular works on plant "pests" (e.g. Meitzner 1985; Alford 2014). As a result of its status as a "pest", this is the only species in the *ruficornis* group that has vernacular names in several languages, such as "small gooseberry sawfly" in English, and "Schwarzen Stachelbeerblattwespe" in German. This species is normally thelytokous, with very rare males (Comrie 1938). Males of several other species of the *ruficornis* group are unknown or very rare (*P. aphantoneura*, *P. astragali*, populations of *P. luteipes* in northern and middle Europe, and *P. sootryeni*: Vikberg 1978; 2006), or occur at a low ratio (e.g. *P. leucopus*: Grearson and Liston 2012), whereas the sex ratio of others appears to be about normal. Voltinism differs between species, and probably also according to climate. The group shows a broad spectrum of phenological patterns: particularly the boreo-alpine species, e.g. *P. staudingeri*, are probably univoltine, based on collection dates of adults, while others are apparently bivoltine (e.g. *P. bifida*: Liston and Burger 2009), or plurivoltine, with four generations per year, or even more in optimal conditions (e.g. *P. appendiculata*, *P. leucopus*: Miles 1932, Grearson and Liston 2012). So far unique in the species group, and a rare phenomenon in the Tenthredinidae, is the seasonal dimorphism detected in adult *P. leucopus* (Grearson and Liston 2012). In all species, as far as observations have been made: oviposition is in the leaf-blade margin (Vikberg 2006, Grearson and Liston 2012), in *P. appendiculata* also infrequently in the interior, near a vein (Miles 1932); only one egg is laid per leaf, and the larvae are normally solitary, feeding from the leaf-edge (Grearson and Liston 2012, Meitzner 1985, personal observations on *P. bifida*). Exceptionally, more eggs are

laid per leaf at high population levels in *P. appendiculata*, but density of larvae is probably regulated by egg cannabilism: Rahoo and Luff 1988). There are four or five larval instars and no prepupal ecdysis ("extra moult") (Miles 1932, Vikberg 2006). Cocoons of the overwintering generation are made in the soil, but those of some the summer generations may be made above ground, often between leaves or on the underside of leaves (Miles 1932, Grearson and Liston 2012).

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

Material and methods

Specimens examined or mentioned are deposited in the following collections:

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

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

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

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

Morphological methods

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

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

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

Molecular methods

DNA was extracted and purified with an EZNA Tissue DNA Kit (Omega Bio-tek) according to the manufacturer's protocol and stored at -20 °C for later use. Typically,

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

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

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

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

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

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

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

Sequence data were analysed using the maximum likelihood method (ML) with PhyML 3.0.1 (http://www.atgc-montpellier.fr/phyml/; Guindon and Gascuel 2003). In PhyML nearest neighbor interchanges (NNI) and subtree pruning and regrafting (SPR) were always used to estimate tree topologies (i.e. using the extensive tree search option). Robustness of reconstructed trees was estimated with 1000 bootstrap rep-

licates and approximate likelihood-ratio test (aLRT) implemented in PhyML (Anisimova and Gascuel 2006). Prior to analyses using maximum likelihood, duplicate sequences were removed to save computation time. General Time Reversible model of nucleotide substitution under discrete Gamma model of rate heterogeneity among sites with four rate categories (GTR+G4) was used to calculate maximum likelihood trees. Estimation of proportion of invariable sites as commonly used in phylogenetic likelihood analyses was not applied, because the Gamma model already allows for sites that evolve very slowly (i.e. are effectively invariable). As described in the RAxML manual, combining Gamma model and proportion of invariable sites (G+I) is problematic for parameter estimation as they are interdependent (http://sco.h-its.org/exelixis/resource/download/NewManual.pdf). Alignment files and tree files from the PhyML analyses are available at Dryad Digital Repository (http://dx.doi.org/10.5061/dryad.tj4t0).

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

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

Preparation of the keys

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

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

Results

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

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

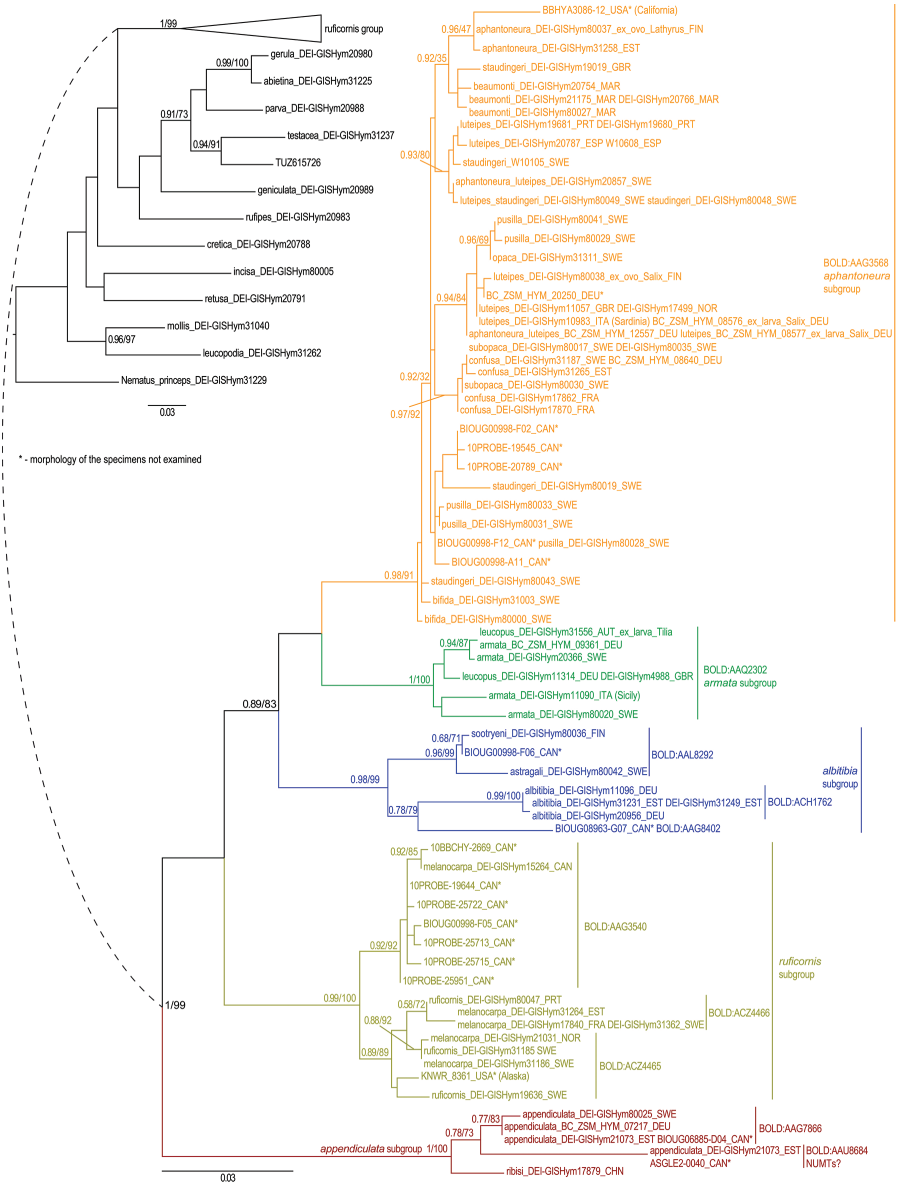


Figure 1. Maximum likelihood tree of *Pristiphora ruficornis* group based on cytochrome oxidase subunit I (COI) sequences (1078 bp). Specimens that had at least the full barcode sequence (658 bp) were included in the analysis. Branches with multiple specimen identification labels represent identical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

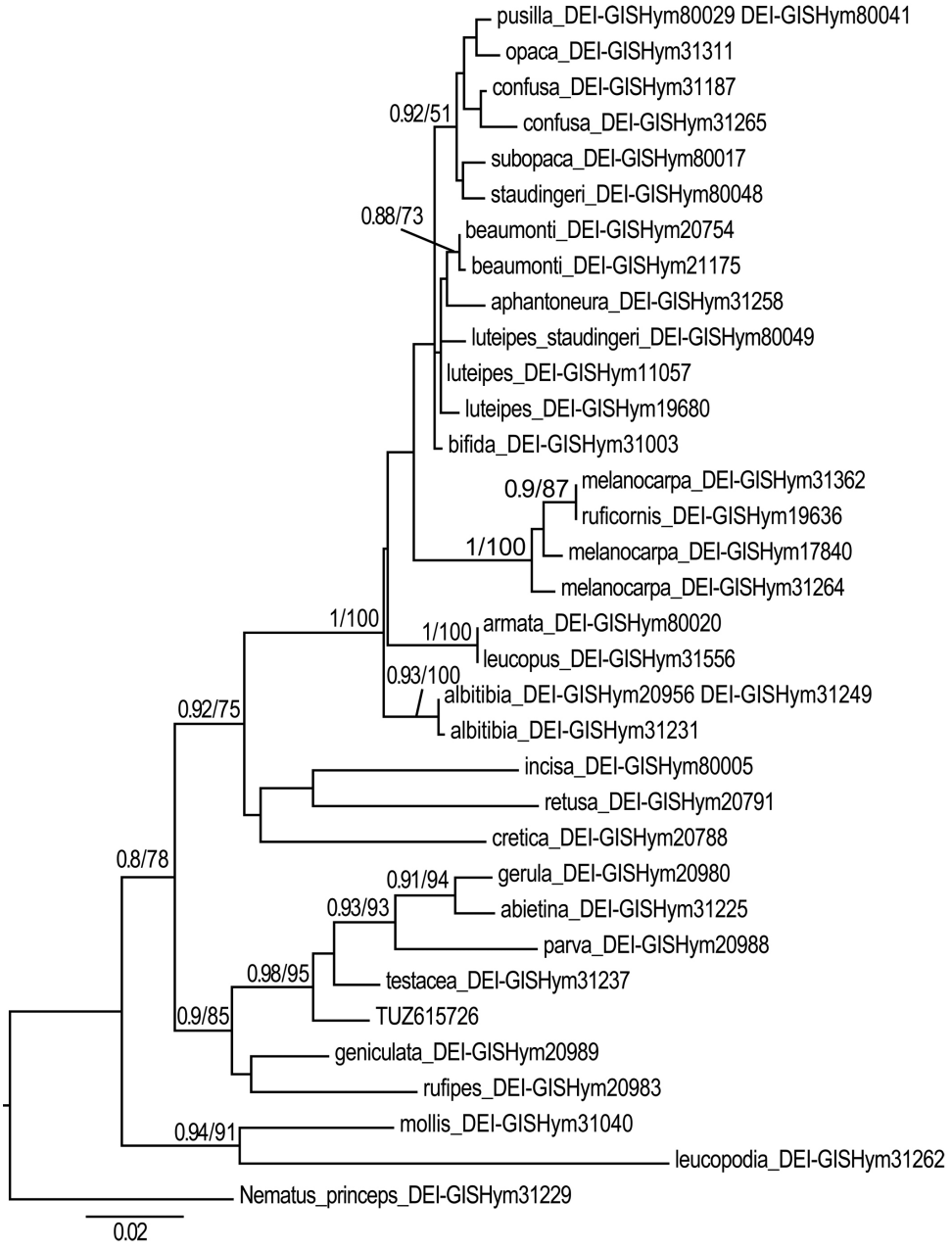


Figure 2. Maximum likelihood tree of *Pristiphora ruficornis* group based on triose-phosphate isomerase (TPI) sequences (alignment length 842 bp). Branches with multiple specimen identification labels represent identical sequences, only one of which was used in the analysis. Numbers on the nodes show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

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

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

Assessment of morphological characters of the adults

Because of the high similarity of the species in *ruficornis* group, the number of external characters that can be used for species identification is rather small. These include colour of trochanters, trochantelli, metafemur (Figs 21–23), flagellum (Figs 24–26, 35–36), and pterostigma (Figs 27–29); sculpture of mesopostnotum (Figs 7–8) and mesepisternum (Figs 18–29); size of the subapical tooth (Figs 30–34); and shape of tergum 8 in males (Figs 16, 18). Shape of frontal area as used by Lindqvist (1955) and followed by Benson (1958) was found not to be a reliable character for species identification. Most of these characters vary continuously within the group and sometimes there is a large degree of variation also within species. Nevertheless, these characters can be useful to recognise species, because usually there are different tendencies in differ-

ent species. The shape of tergum 8 in males of *P. armata* and *P. leucopus* (with distinct apical projection; Fig. 16) is the clearest character to distinguish the males of these species from all other *Pristiphora* (Fig. 17). Sculpture of mesopostnotum and the presence or absence of a subapical tooth on the claws are also good characters to recognise *P. appendiculata* (smooth mesopostnotum and simple claws; Figs 7, 30) from other European species (matt mesopostnotum and claws with at least a small subapical tooth; Figs 8, 31–34) in the group. Size or the shape of the subapical tooth is also a relatively stable character. Two species (*P. bifida*, *P. frigida*) have a long subapical tooth close to the apical one (bifid; Fig. 34), while others have a large or small subapical tooth clearly separated from apical one (Figs 31–33), although this difference can be rather small when compared to large subapical tooth of *P. armata* and *P. leucopus*. Antennae vary from completely black to completely yellow, depending on the species, being either always black (Figs 24, 35), black or ventrally pale (Fig. 25, 36), or always at least ventrally pale (Figs 25–26, 36). Trochanters, trochantelli, and pterostigma show a similar pattern of variation. The metafemur is completely black in most species, but in a few species it is often or always partly or completely pale (Figs 21–23). If the metafemur is pale, it can be either whitish (as in *P. appendiculata* and *P. leucopus*; Fig. 22) or yellowish (*P. aphantoneura* and *P. luteipes*; Fig. 23), although this distinction is not particularly clear. Sculpture of mesepisternum varies from completely smooth to strongly matt, depending on the species, being either always smooth (Fig. 18), smooth or slightly matt (Fig. 19), or usually strongly matt (Fig. 20).

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

The clearest differences between species in the *ruficornis* group are found in the penis valves. Shape of the ventro-apical spine and pseudoceps usually show distinct and stable differences between most species. In *P. frigida* (Fig. 88), *P. melanocarpa* (Figs 80, 82), and *P. ruficornis* (Figs 79, 81) there is also a membranous fold near to or covering the tip of the ventro-apical spine that is missing in other species. Interestingly, we discovered that left and right penis valves differ consistently and distinctly in shape

in *P. pusilla*. The left penis valve (Fig. 93) has a noticeably stronger dorsal depression in the middle of the pseudoceps and a more strongly bent ventro-apical spine than the right one (Fig. 94). Among sawflies, asymmetrical penis valves have been observed also for *Cladius compressicornis* (Fabricius, 1804) (Benson 1958; as *Priophorus pallipes*). Asymmetrical genitalia are apparently very rare in Hymenoptera, as Huber et al. (2007) did not mention any cases for this group in their review.

Dichotomous key to *Pristiphora ruficornis* group adults

1 a Mesopostnotum smooth (Fig. 7)
b Claws without subapical tooth (Fig. 30)
c Mesepisternum smooth (Fig. 18)
d Antenna *usually* ventrally paler than dorsally (Fig. 25) ... ***P. appendiculata***

– aa Mesopostnotum matt (Fig. 8)
bb Claws with subapical tooth (Figs 31–34)
cc Mesepisternum smooth or matt (Figs 18–20)
dd Antenna uniformly black or ventrally paler than dorsally (Figs 24–26, 36) **2**

2(1) a Metafemur pale in most part (Figs 22–23) **3**

– aa Metafemur black in most part (Fig. 21) **4**

3(2) a Claws with large subapical tooth (Fig. 33)
b Antenna ventrally paler than dorsally (Figs 25, 36) or uniformly yellow (Fig. 26)
c Metafemur whitish (Fig. 22) ..... ***P. leucopus*** in part

– aa Claws with small subapical tooth (Fig. 31)
bb Antenna uniformly black (Fig. 24)
cc Metafemur yellowish (Fig. 23).....
..... **females of *P. aphantoneura* (on *Lathyrus*) and *P. luteipes* (on *Salix*)** (see Vikberg 2006 for minor characters for separating these species)

4(2) a Claws with long subapical tooth close to apical one (bifid) (Fig. 34) **5**

– aa Claws with small or large subapical tooth clearly separated from apical one (Figs 31–33) **6**

5(4) a Hind trochanters, trochantelli, and tibia partly pale
b Antenna (usually?) ventrally at least slightly paler than dorsally (Figs 25, 36)
c In males, antennae with numerous and clearly visible stout black setae among finer paler ones (Fig. 36)
d Apical serrulae of lancet short and protruding, and tangium long and narrow (Fig. 70)
e Penis valve without membranous fold near tip of ventro-apical spine and pseudoceps with distinct dorsal depression in middle or basal part (Fig. 87) ...
..... ***P. bifida***

–	aa	Hind trochanters, trochantelli, and tibia uniformly black or brown
	bb	Antenna uniformly black (Fig. 24)
	cc	In males, antennae with only some barely visible stout black setae among finer paler ones (Fig. 35)
	dd	Apical serrulae of lancet long and flat, and tangium short and broad (Fig. 71)
	ee	Penis valve with membranous fold near tip of ventro-apical spine and pseudoceps without dorsal depression in middle or basal part (Fig. 88) ..... ***P. frigida***
6(4)	a	♀ **7**
–	aa	♂ **17**
7(6)	a	Tangium of lancet with distinct lobe (Figs 14, 46–53)
	b	Mesepisternum smooth (Fig. 18)
	c	Claws with small subapical tooth (rarely with large) (Fig. 31) **8**
–	aa	Tangium of lancet without distinct lobe (Figs 41–45, 54–57, 62–69, 72–76)
	bb	Mesepisternum smooth or matt (Figs 18–20)
	cc	Claws with small or large subapical tooth (Figs 31–33) **9**
8(7)	a	Antenna ventrally distinctly paler than dorsally (Fig. 25) .... ***P. ruficornis***
–	aa	Antenna *usually* uniformly black (Fig. 24), but sometimes ventrally slightly paler than dorsally..... ***P. melanocarpa***
9(7)	a	Inner surface of lancet with small spiny pectines (or dentes semicirculares) that reach sclerora (Figs 41–45) (visible only by examining slide preparations of the lancet with high magnification) **10**
–	aa	Inner surface of lancet without small spiny pectines (Figs 54–57, 62–69, 72–76)..... **12**
10(9)	a	Mesepisternum smooth (Fig. 18)
	b	Lancet with numerous ctenidia (Figs 41–42)
	c	Apical serrulae of lancet short (Figs 41–42)
	d	Pterostigma basally dark brown and apically brown (Fig. 28) ..... ***P. albitibia***
–	aa	Mesepisternum at least slightly matt (Figs 19–20)
	bb	Lancet with numerous or few ctenidia (Figs 43–45)
	cc	Apical serrulae of lancet short or long (Figs 43–45)
	dd	Pterostigma uniformly yellow or brown (Fig. 27) **11**
11(10)	a	Lancet with numerous ctenidia (Fig. 45)
	b	Apical serrulae of lancet long (Fig. 45) ..... ***P. sootryeni***
–	aa	Lancet with few ctenidia (Figs 43–44)
	bb	Apical serrulae of lancet short (Figs 43–44)..... ***P. astragali***
12(9)	a	Lancet with few ctenidia (Fig. 72)
	b	Serrulae of lancet flat (Fig. 72)
	c	Antenna (usually?) ventrally slightly paler than dorsally (Fig. 25) ..... ***P. pusilla***
–	aa	Lancet with numerous ctenidia (Figs 54–57, 62–69, 73–76)

bb Serrulae of lancet flat or protruding (Figs 54–57, 62–69, 73–76)
cc Antenna uniformly black or ventrally paler than dorsally (Figs 24–25) ... **13**

13(12) a Mesepisternum (usually?) strongly matt (Fig. 20)
b Antenna uniformly black (Fig. 24)
c Pterostigma (usually?) uniformly yellow or brown (Fig. 27)
d Arctic habitats..... ***P. staudingeri***

– aa Mesepisternum (usually?) smooth or slightly matt (Figs 18–19)
bb Antenna uniformly black or ventrally paler than dorsally (Figs 24–25)
cc Pterostigma uniformly yellow to dark brown, or basally dark brown and apically brown (Figs 27–29)
dd *Usually* non-arctic habitats..... **14**

14(13) a Apical serrulae protruding (Figs 54–57, 62–63)
b Antenna *often* ventrally paler than dorsally (Fig. 25) **15**

– aa Apical serrulae flat (Figs 64–69)
bb Antenna uniformly black or ventrally paler than dorsally (Figs 24–25).... **16**

15(14) a Pterostigma *usually* basally dark brown and apically brown (Fig. 28)
b Ctenidia of lancet more distinct (Figs 62–63) ..... ***P. confusa***

– aa Pterostigma *usually* uniformly dark brown (Fig. 29)
bb Ctenidia of lancet less distinct (Figs 54–57) .....
..***P. armata* (on *Crataegus*) and *P. leucopus* (on *Tilia*)** in part (see the main text and Grearson and Liston 2012 for discussion separating these species)

16(14) a Tangium of lancet without fold (Figs 66–69)
b Antenna uniformly black (Fig. 24)
c Pterostigma uniformly yellow (Fig. 27) ..... ***P. subopaca***

– aa Tangium of lancet with fold (Figs 64–65)
bb Antenna ventrally slightly paler than dorsally (Fig. 25)
cc Pterostigma (usually?) basally dark brown and apically brown (Fig. 28)....
..... ***P. opaca***

17(6) a Tergum 8 with apical projection (Fig. 16)
b Antennae ventrally distinctly paler than dorsally or uniformly yellow (Figs 26, 36)
c Claws with large subapical tooth (Fig. 33)
d Mesepisternum smooth (Fig. 18) .....
..... ***P. armata* (on Crataegus) and *P. leucopus* (on Tilia)** (see the main text and Grearson and Liston 2012 for discussion separating these species)

– aa Tergum 8 without apical projection (Fig. 17)
bb Antennae uniformly black to uniformly yellow (Figs 24–26, 36)
cc Claws with small or large subapical tooth (Figs 31–33)
dd Mesepisternum smooth or matt (Figs 18–20) **18**

18(17) a Penis valve with membranous fold near or covering tip of ventro-apical spine (Figs 79–82)

b Claws with small subapical tooth (Fig. 31)
c Mesepisternum smooth (Fig. 18) **19**

– aa Penis valve without membranous fold (Figs 78, 89–103)
bb Claws with small or large subapical tooth (Figs 31–33)
cc Mesepisternum smooth or matt (Figs 18–20) **20**

19(18) a Ventro-apical spine of penis valve less sharply bent (forming half circle) (Figs 79, 81) ..... ***P. ruficornis***

– aa Ventro-apical spine of penis valve more sharply bent (being almost L-shaped) (Figs 80, 82) ..... ***P. melanocarpa***

20(18) a Pseudoceps of penis valve short and broad (Fig. 78)
b Mesepisternum smooth (Fig. 18)
c Antennae uniformly black (Fig. 24)
d Pterostigma (usually?) basally dark brown and apically brown (Fig. 28)....
..... ***P. albitibia***

– aa Pseudoceps of penis valve longer and narrower (Figs 89–103)
bb Mesepisternum smooth or matt (Figs 18–20)
cc Antennae uniformly black (Fig. 24) or ventrally paler than dorsally (Fig. 36)
dd Pterostigma uniformly yellow to uniformly dark brown (Figs 27–29) ... **21**

21(20) a Penis valve with weakly bent and broad ventro-apical spine, and with narrow pseudoceps without distinct dorsal depression in middle part (Figs 89–90) ..... ***P. confusa***

– aa Penis valve with different combination of characters (Figs 91–103) ... **22**

22(21) a Ventro-apical spine of penis valve narrow and with blunt tip (Figs 95–96)
b Antennae ventrally paler than dorsally (Fig. 36) ..... ***P. opaca***

– aa Ventro-apical spine of penis valve broad or narrow and with sharp tip (Figs 91–94, 97–103)
bb Antennae uniformly black (Fig. 24) or ventrally paler than dorsally (Fig. 36) **23**

23(22) a Ventro-apical spine of penis valve narrow (Figs 97–103)
b Antennae uniformly black (Fig. 24) **24**

– aa Ventro-apical spine of penis valve broad (Figs 91–94)
bb Antennae uniformly black (Fig. 24) or ventrally paler than dorsally (Fig. 36) **25**

24(23) a Mesepisternum smooth to slightly matt (Figs 18–19)
b *Usually* non-arctic habitats ..... ***P. luteipes***

– aa Mesepisternum *usually* strongly matt (Fig. 20)
bb Arctic habitats ..... ***P. staudingeri***

25(23) a Pseudoceps of left and right penis valve without distinct dorsal depression in middle part and with weakly bent ventro-apical spine (Figs 91–92)
b Antennae uniformly black (Fig. 24) ..... ***P. subopaca***

– aa Pseudoceps of left penis valve with distinct dorsal depression in middle part and with strongly bent ventro-apical spine (Fig. 93)
bb Antenna ventrally paler than dorsally (Fig. 36) ..... ***P. pusilla***

Taxonomy

Pristiphora albitibia (Costa, 1859)

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

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

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

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

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

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

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

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

Pristiphora aphantoneura (Förster, 1854)

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

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

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

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

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

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

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

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

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

Pristiphora appendiculata (Hartig, 1837)

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

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

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

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

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

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

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

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

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

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

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

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

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

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

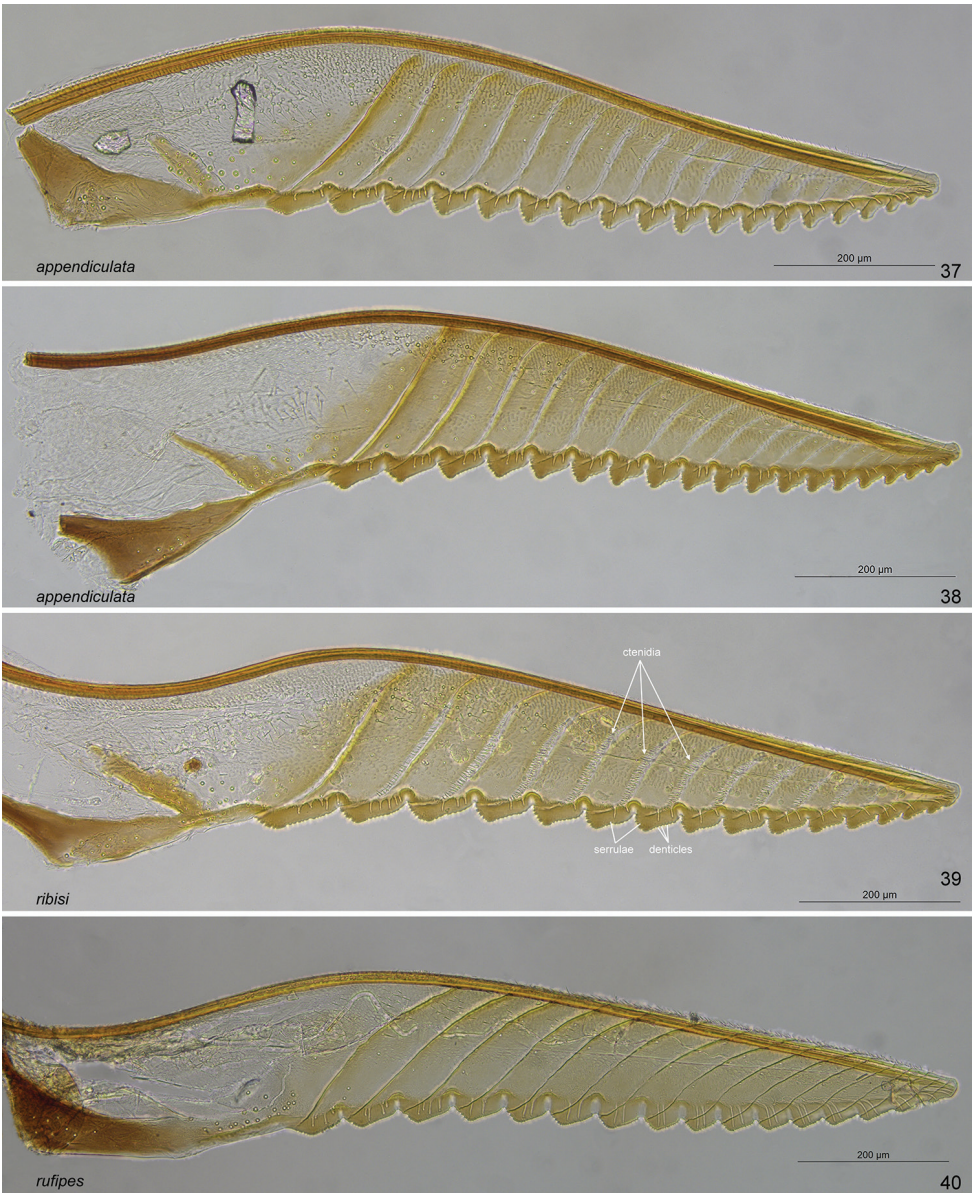
Nematus hypobalius Zaddach in Brischke, 1884: 154. Holotype ♀ possibly destroyed (Blank and Taeger 1998). Type locality: Hungary.

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

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

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

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



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

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

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

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

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

Pristiphora armata (Thomson, 1863)

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

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

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

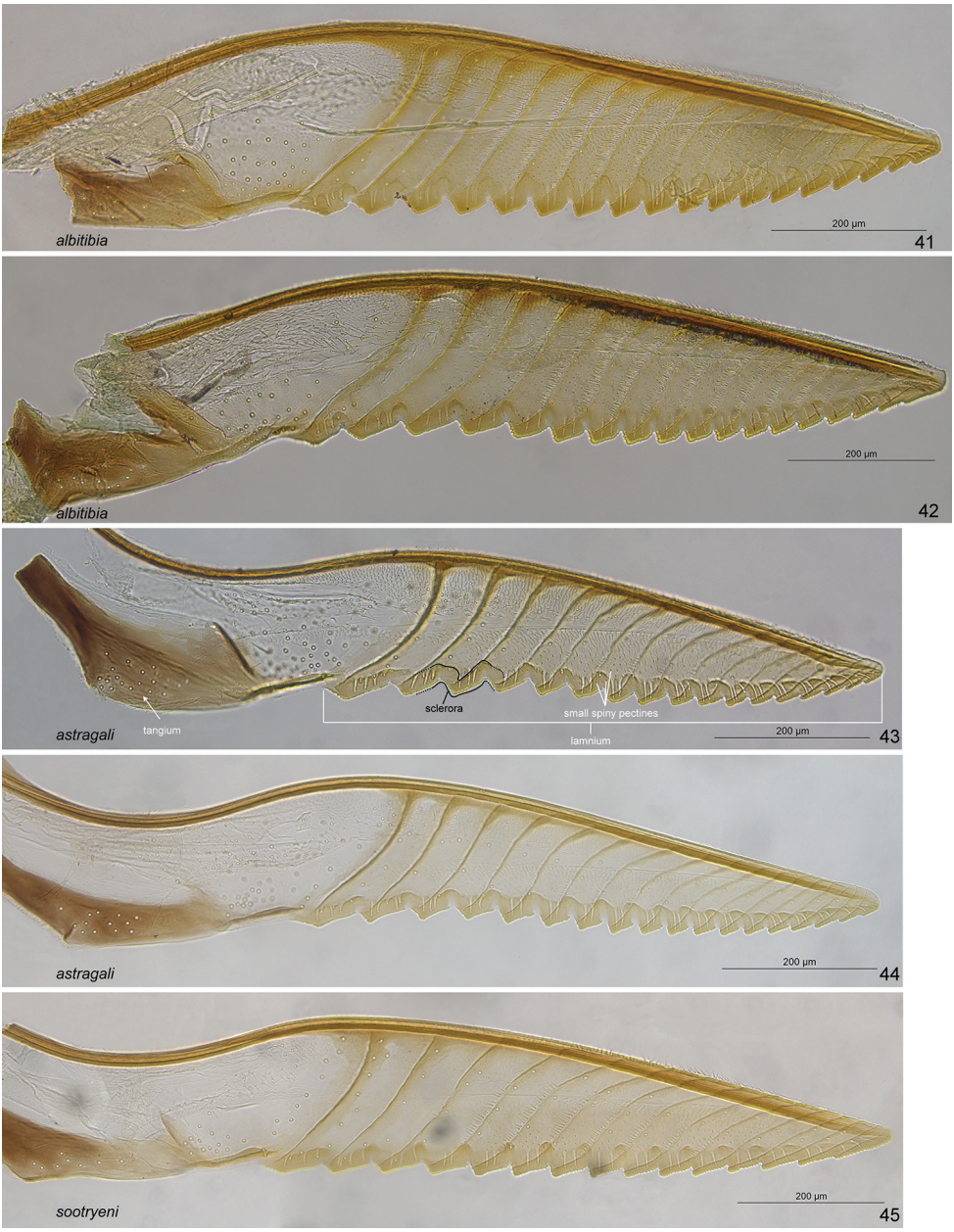
Nematus Fletcheri [sic!] Cameron, 1884: 26. Syntype(s) possibly in BMNH, not examined. Type locality: Worcester and Clydesdale, United Kingdom.

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

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

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

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



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

though serrulae are in this case somewhat weaker (Fig. 55). Males can perhaps be distinguished through small differences in penis valves (Figs 85–86 and Figs 9–10 in Grearson and Liston 2012), as described by Grearson and Liston (2012): "In *P. armata*, the outer edge of the spine has a short straight section near the apex, termi-

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

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

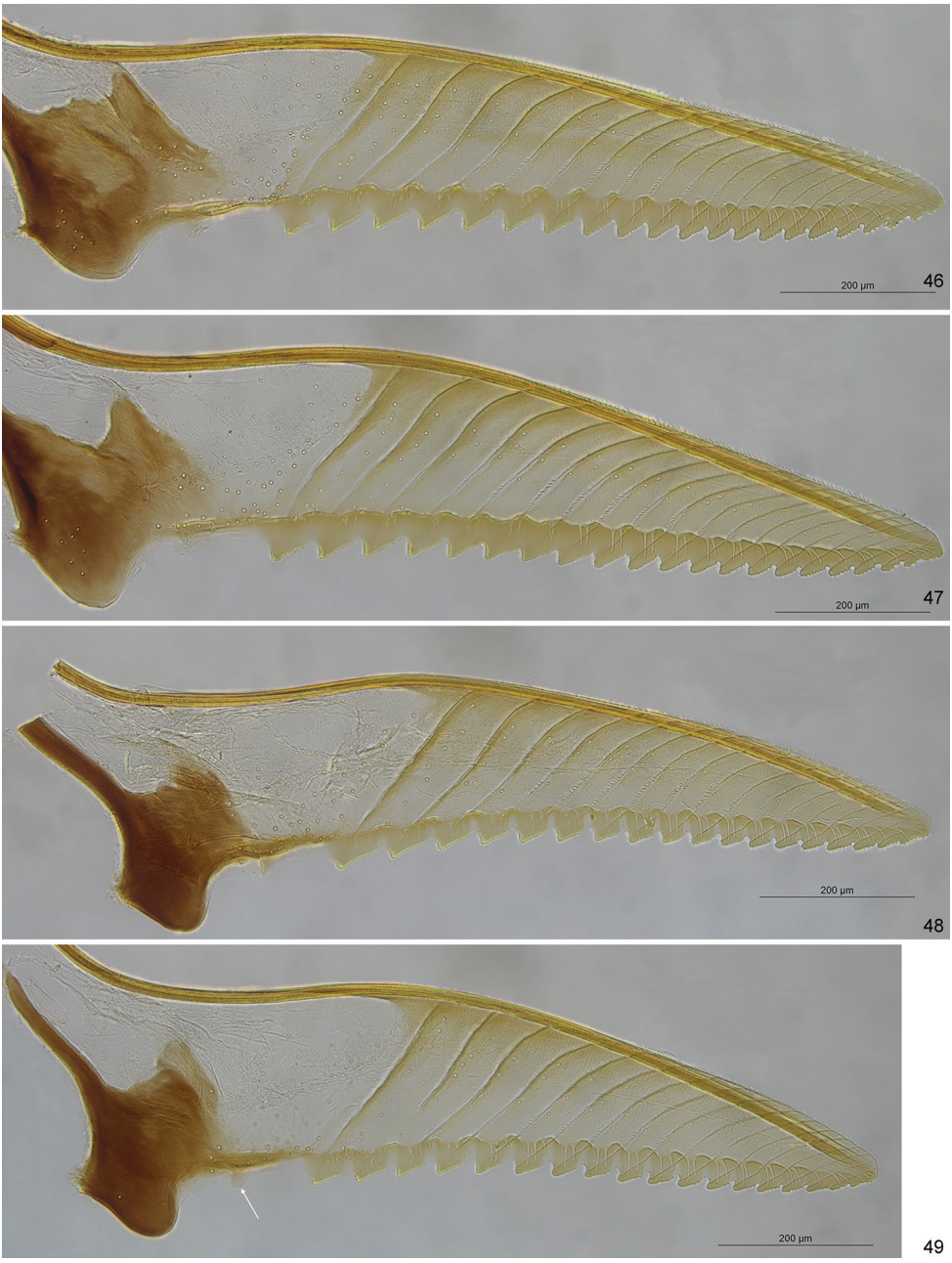
Host plants. *Crataegus* species (Brischke 1883; Grearson and Liston 2012).

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

Pristiphora astragali Vikberg, 1978

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

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



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

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

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

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

Pristiphora bifida (Hellén, 1948)

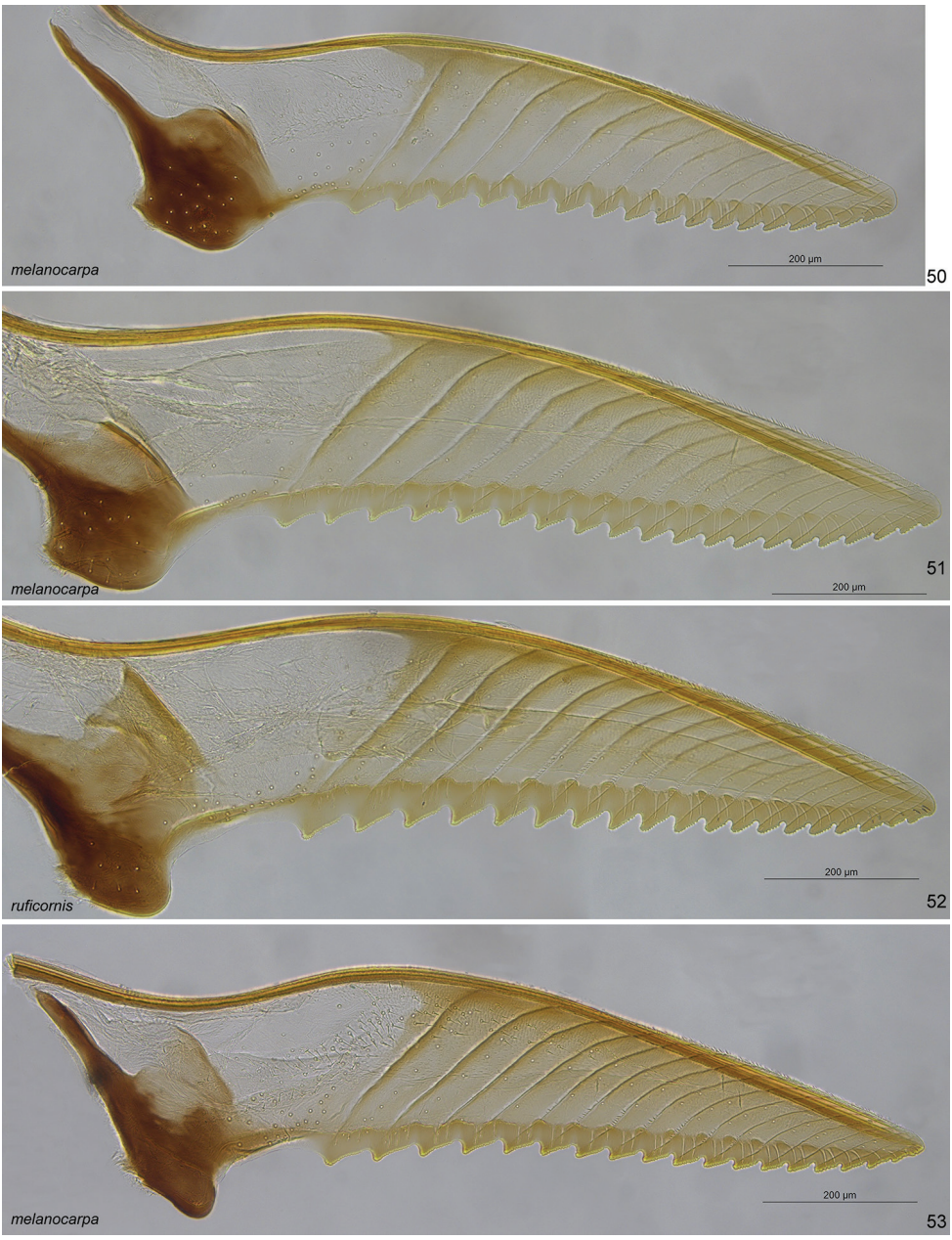
Nematus (*Pristiphora*) *bifidus* Hellén, 1948: 116–117. Lectotype ♀ (http://id.luomus.fi/GL.5214; here designated) in MZH, examined. Type locality: Malla, Kilpisjärvi, Enontekiö, Finland.

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

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

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

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



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

Pristiphora confusa Lindqvist, 1955

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

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

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

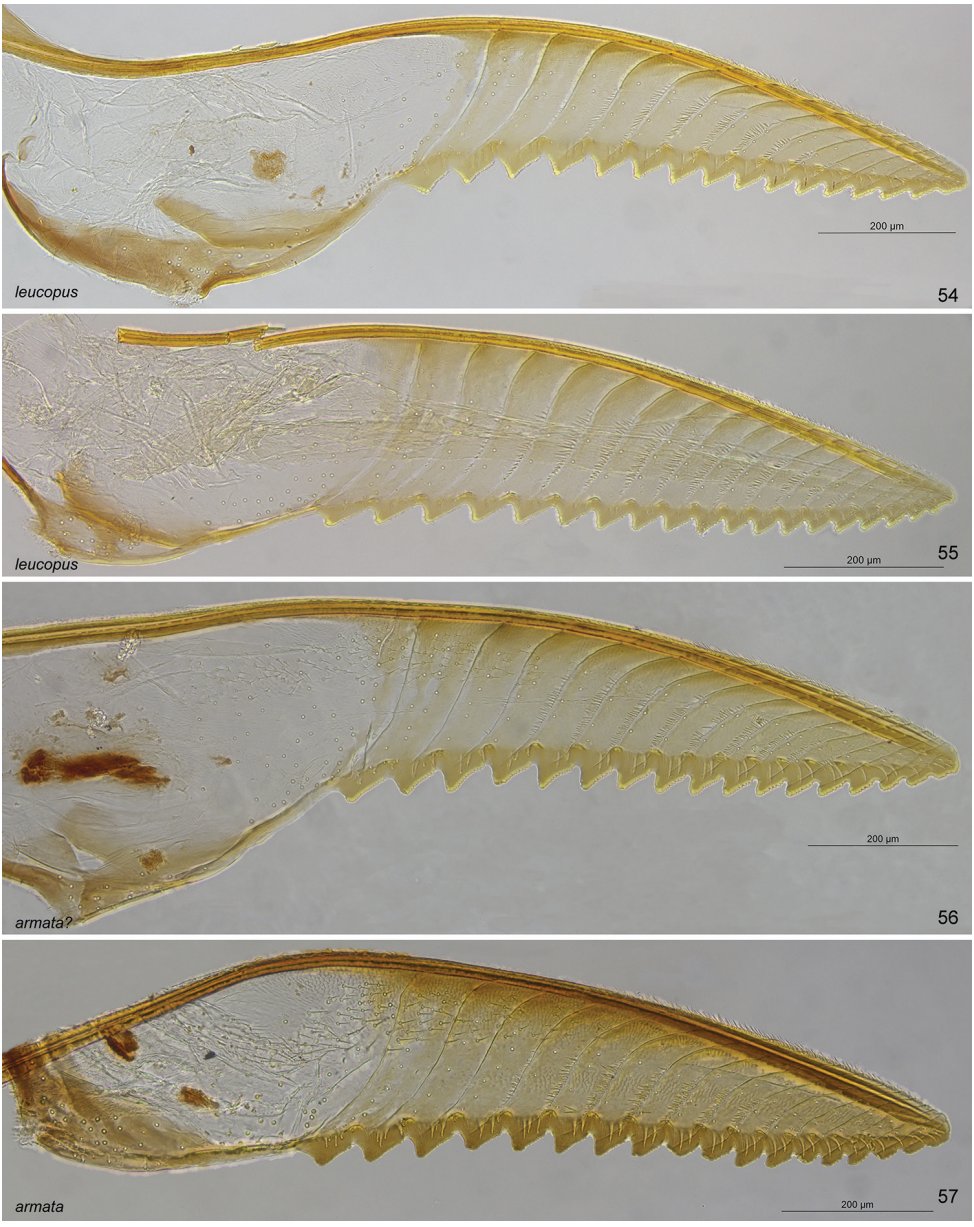
Host plants. *Salix caprea* L. (Kangas 1985), *Salix fragilis* L. (Benson 1958), *Salix phylicifolia* L. (Benson 1958).

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

Pristiphora frigida (Boheman, 1865)

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

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



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

Similar species. Externally, perhaps the most similar species is *P. bifida*, from which it can be distinguished by having black or brown hind trochanters, trochantelli, and tibiae (pale in *P. bifida*). In addition, antennae of males have only some barely visible stout black setae among finer paler ones (Fig. 35), while these are numerous and clearly

visible in *P. bifida* (Fig. 36). On the other hand, the penis valve (Fig. 88) might indicate a closer relationship to *P. melanocarpa* and *P. ruficornis* (Figs 79–82), because of a membranous fold near the tip of the ventro-apical spine that is missing in other species of *ruficornis* group. The tangium of the lancet (Fig. 71) also resembles more closely the *Betula* feeding *P. melanocarpa* and *P. ruficornis* (Figs 46–53) rather than *P. bifida* (Fig. 70): the dark sclerotized area is rather broader than long instead of longer than broad.

Genetic data. No data.

Host plants. Unknown.

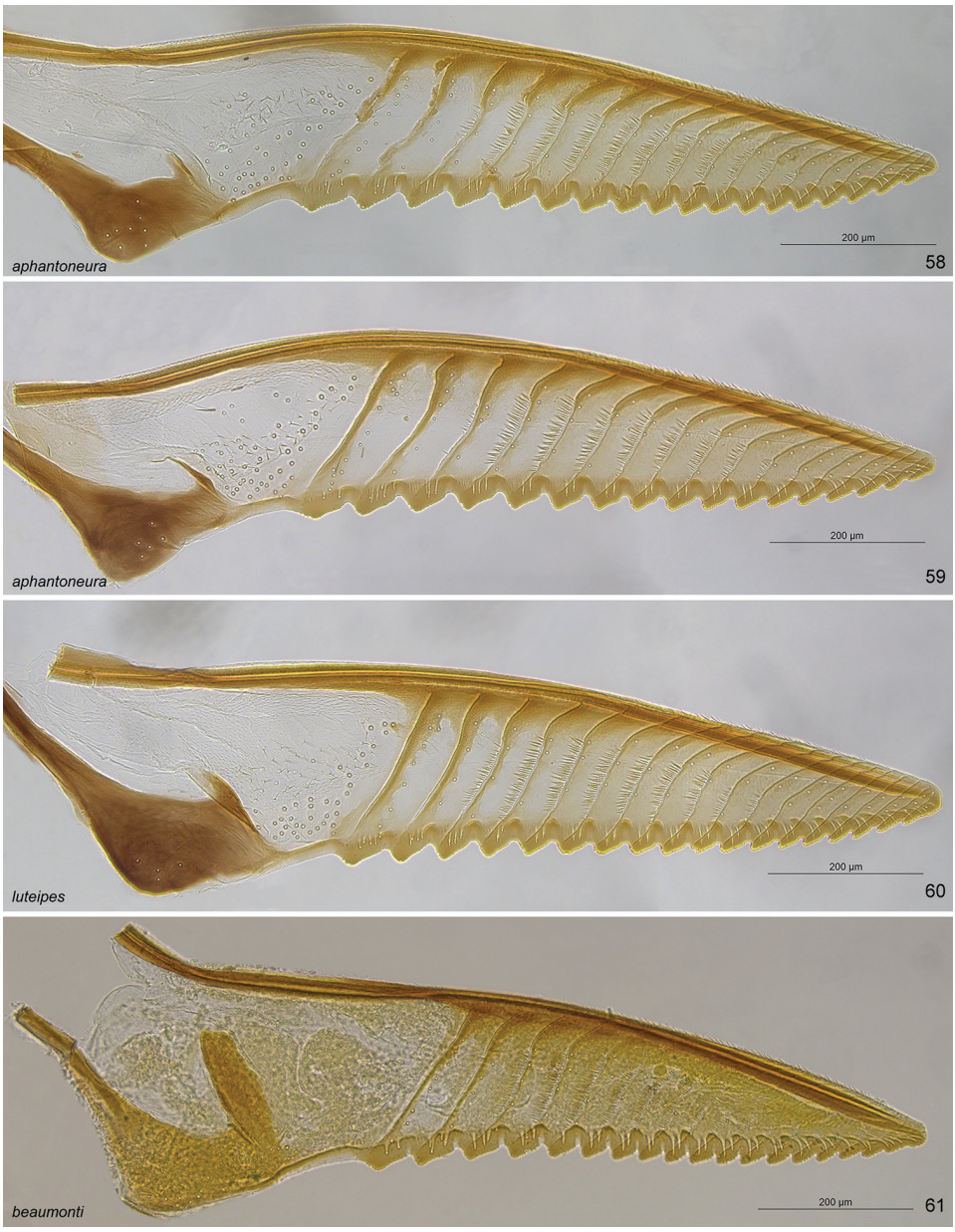
Distribution and material examined. Western Palaearctic. Specimens studied are from Norway (Svalbard).

Pristiphora leucopus (Hellén, 1948)

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

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

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



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

penis valves (Figs 85–86 and Figs 9–10 in Grearson and Liston 2012), as described by Grearson and Liston (2012) (see also under *P. armata*). Females with a black metafemur might also be confused with some specimens of *P. confusa* (if they have a com-

pletely smooth mesepisternum). Usually, *P. leucopus* (Fig. 29) has a uniformly dark brown pterostigma (usually basally dark brown and apically brown in *P. confusa*; Fig. 28), but the specimens with pterostigma apically paler than basally might not be externally distinguishable from *P. confusa*. However, small differences in the lancets can help distinguish these species, as ctenidia in *P. confusa* tend to be more distinct (Figs 62–63).

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

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

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

Pristiphora luteipes Lindqvist, 1955

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

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

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

ma in northern European specimens). However, the degree of coriaceous sculpture on the mesepisternum and the colour of pterostigma vary continuously and seem to correlate with latitude (specimens in the south tend to have a smoother mesepisternum and darker pterostigma). Lancets (Fig. 61) and penis valves (Fig. 101) of *P. beaumonti* are not distinguishable from *P. luteipes* (Figs 60, 103) or even from *P. staudingeri*

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

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

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

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

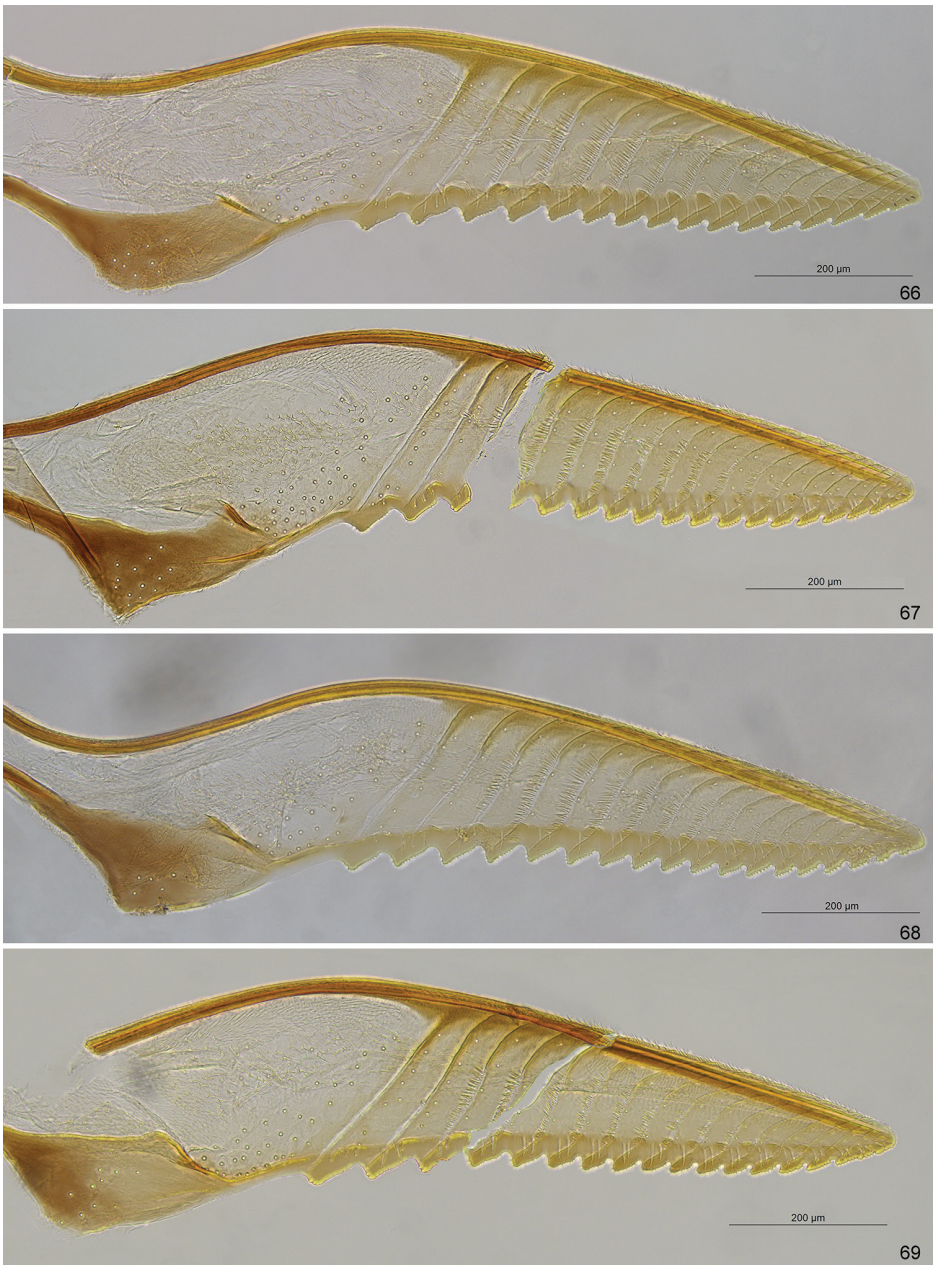
Pristiphora melanocarpa (Hartig, 1840)

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

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

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

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



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

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

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

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

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

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

Pristiphora opaca Lindqvist, 1955

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

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

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

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

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

Host plants. Unknown.

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

Pristiphora pusilla Malaise, 1921

Pristiphora pusilla Malaise, 1921: 11–12. Lectotype ♂ (NHRS-HEVA000004942; here designated) in NHRS, examined. Type locality: Torne Träsk, Torne Lapp-

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

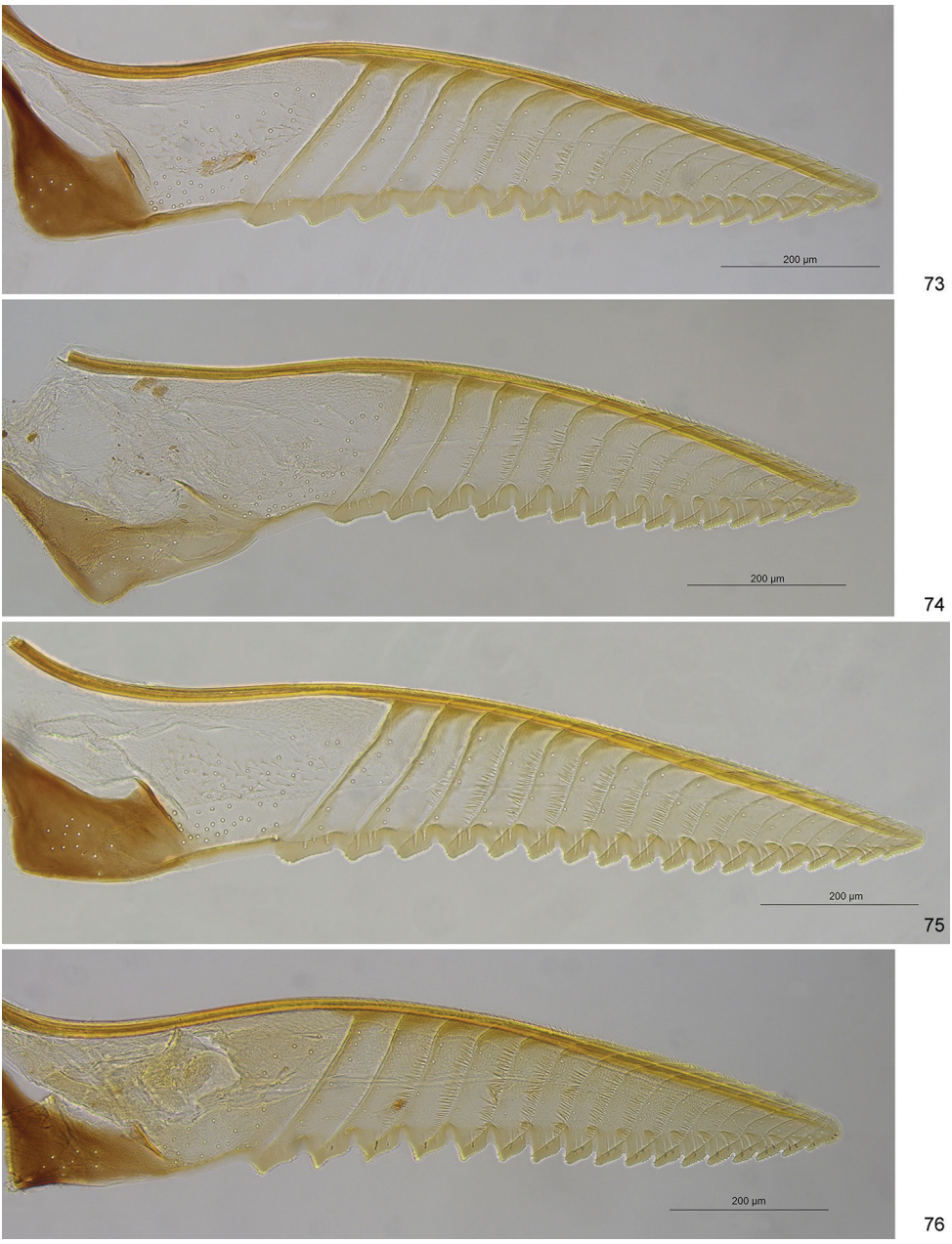
Pristiphora amaura Lindqvist, 1955: 43–45. Holotype ♀ (http://id.luomus.fi/GL.5205) in MZH, examined. Type locality: Kangasala, Pirkanmaa, Finland. Note. The male paratype of *P. amaura* (http://id.luomus.fi/GL.5206) (Fig. 96) was misidentified and belongs to *P. opaca* Lindqvist, 1955 instead.

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

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

Host plants. Unknown.

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



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

***Pristiphora ruficornis* (Olivier, 1811)**

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

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

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

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

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

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

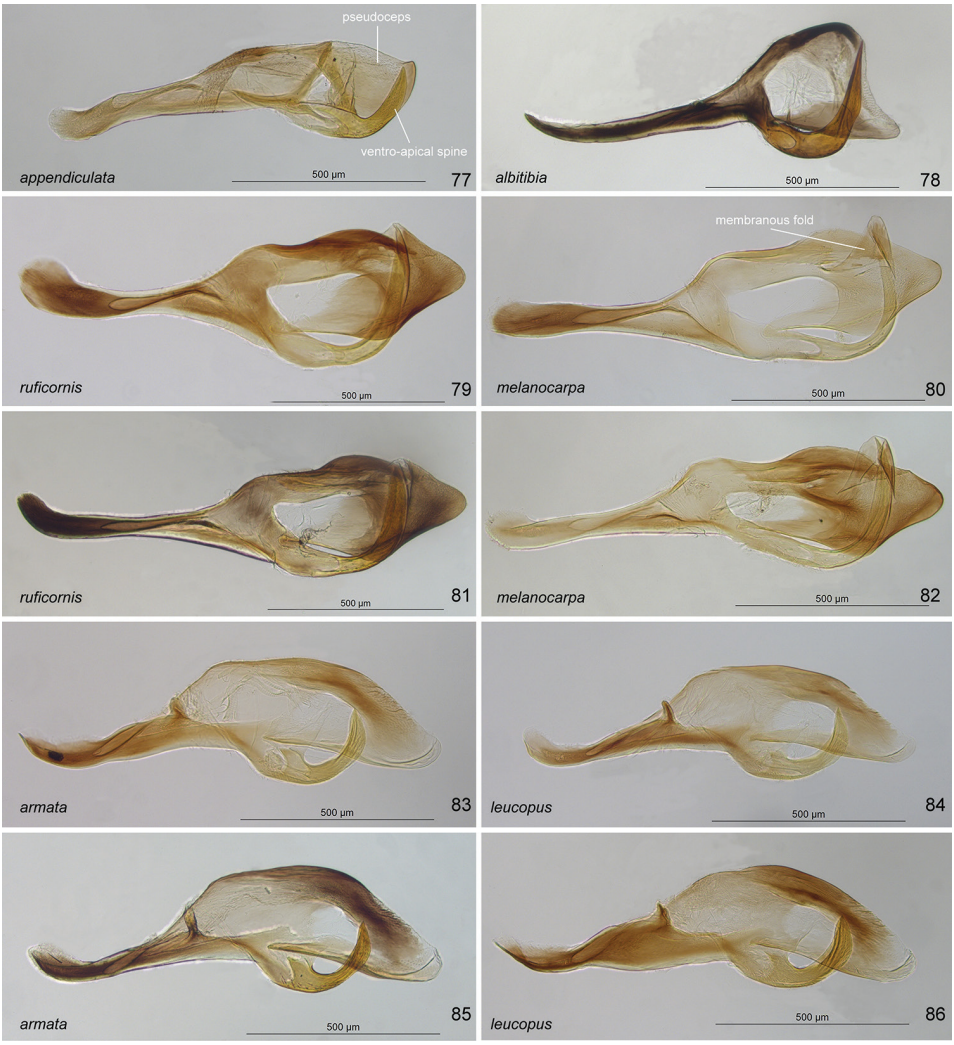
Nematus (*Pristiphora*) *ruficornis* var. *integer* Hellén, 1948: 116, **syn. n.** Primary homonym of *Nematus integer* Say, 1836. Holotype ♀ (http://id.luomus.fi/GL.5212) in MZH, examined. Type locality: Hammaslahti, North Karelia, Finland.

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

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

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

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



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

Pristiphora sootryeni Lindqvist, 1955

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

Similar species. Based on the external morphology, the most similar species are *P. astragali*, *P. confusa*, *P. opaca*, *P. pusilla*, *P. staudingeri*, and *P. subopaca*, from which it is

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

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

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

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

Pristiphora staudingeri (Ruthe, 1859)

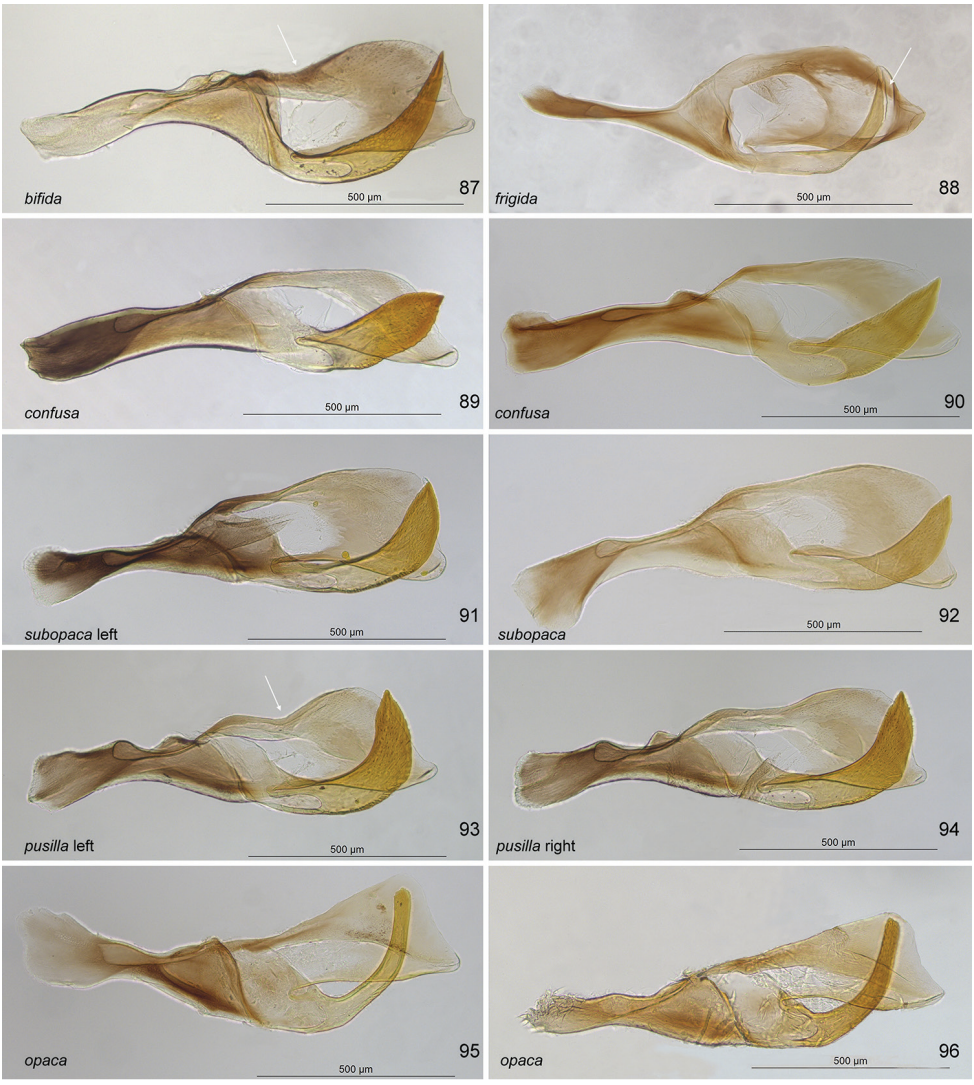
Nematus Staudingeri [sic!] Ruthe, 1859: 306–307. Lectotype ♀ (designated by Vikberg 1978) in NMW, examined. Type locality: Iceland.

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

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

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

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



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

beaumonti (see under *P. luteipes*) (Figs 60–61, 101, 103), which can have a completely smooth mesepisternum (Fig. 19) and can be extremely pale (Fig. 13). Because of the black metafemur, females of *P. staudingeri* can easily be distinguished from *P. luteipes*

(completely yellow metafemur; Fig. 23), but two studied Swedish specimens (Jämtland County at an altitude 900 m) had an apically slightly yellow (W10115) or even apically half yellow metafemur (W10105), weakening the distinction between these taxa.

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

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

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

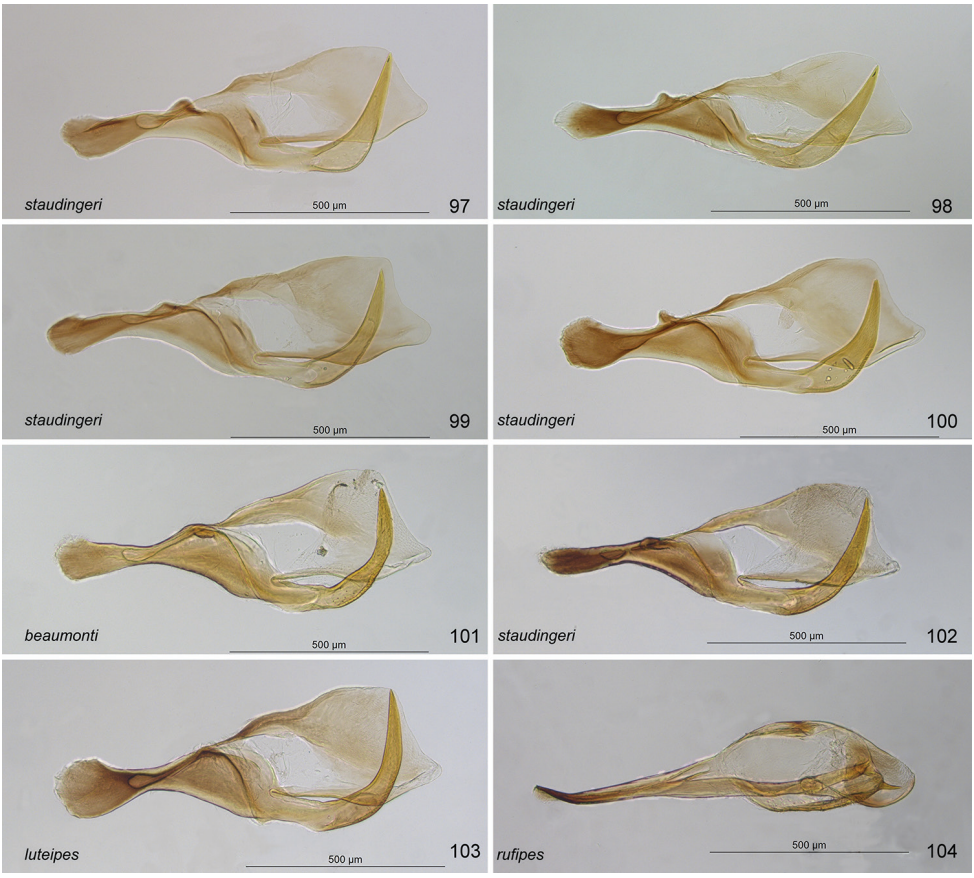
Pristiphora subopaca Lindqvist, 1955

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

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

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

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



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

dark brown and apically brown (Fig. 28). In addition, the claws of *P. subopaca* tend to have a larger subapical tooth (Fig. 32) than in *P. opaca* (Fig. 31). Among the males, the most similar penis valves are of *P. confusa* and *P. pusilla*. The ventro-apical spine is bent more strongly and the pseudoceps is broader (Figs 91–92) than in *P. confusa* (Figs 89–90). Compared to *P. pusilla* (Figs 93–94), the ventro-apical spine is bent less strongly and the dorsal depression in the middle of pseudoceps is less distinct, which is clear only when compared to the left penis valve of *P. pusilla* (Fig. 93). The holotype of *coniceps* Lindqvist does not differ in any significant way from the holotype of *subopaca* Lindqvist. The characters mentioned in the structure of the head and thorax for *coniceps* in the original description (Lindqvist 1955), that are supposed to differentiate this species from others in the *ruficornis* group, are minute and unreliable. The characters that help in species identifications in closely related species (colour of pterostigma and antennae, degree of coriaceous sculpture of mesepisternum, size of subapical tooth of

claws, and the structure of the lancet) are not different between the holotypes of *coniceps* and *subopaca*. The host (*Salix*) mentioned for *coniceps* in the original description (Lindqvist 1955) and by Kangas (1985) (as *Salix caprea* L.) also fits with the data recorded for *P. subopaca* (Lindqvist 1965; Kangas 1985). Consequently we treat *coniceps* as a synonym of *subopaca*. We also treat *brunniapex* Lindqvist as a rare colour form (only the holotype and one additional female are known to us) of *subopaca* Lindqvist, because the only difference is that *brunniapex* has a pale tip of the abdomen (terga 7–10 or 8–10; Figs 10, 12). Based on the second known specimen (DEI-GISHym20899, deposited in MZH) reared by J. Perkiömäki from *Salix* sp. (near Helsinki, Finland), we can say that the host is not different from *subopaca* either. Although the lancet of *brunniapex* cannot be distinguished from *P. aphantoneura*, *P. luteipes* and *P. staudingeri*, these species can be separated from *subopaca-brunniapex* by having different host (*Lathyrus pratensis* for *P. aphantoneura*), yellow metafemur (*P. aphantoneura* and *P. luteipes*), or as in *P. staudingeri* usually strongly coriaceous sculpture of mesepisternum and different habitat (arctic or subarctic).

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

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

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

Discussion

Taxonomy of the species belonging to the *ruficornis* group as defined here (Fig. 1) has hitherto been rather complicated, and there has not been a review of all the species involved. The main questions have been, how many species there are, how to identify them, and association of males and females. For northern Europe, we identified which species are well supported (most) and should be recognised and which ones require more detailed studies (e.g. host plant choice experiments and sequencing of more nuclear DNA data) to decide their validity. The species pairs that are not well supported are *P. aphantoneura-P. luteipes*, *P. armata-P. leucopus*, and *P. melanocarpa-P.ruficornis*, identification of which is difficult or not always possible. Although our limited genetic data is consistent with separation of *P. luteipes* from *P. aphantoneura* (Fig. 2), the limited sampling of specimens does not allow us to make any definite conclusions. There is no clear genetic support for separating *P. leucopus* from *P. armata*, nor *P. melanocarpa* from *P. ruficornis*. The separation of *P. leucopus* from *P. armata* is currently supported mainly by two biological differences: their different hosts, and the existence of seasonal morphs in the former, but not in the latter. Furthermore, the coloration of the larvae may be

different (see above, under Introduction). However, the larval morphology of both species needs more detailed study. *P. melanocarpa* is separated from *P. ruficornis* only on minor morphological differences in the adults. Here too, the larvae require further study. Another issue not entirely solved involves *P. luteipes*, *P. staudingeri*, and *P. beaumonti* (North African taxon not treated here), because morphological characters used to distinguish them (colouration and sculpture of the mesepisternum) might be influenced by environmental factors rather than genetic ones, though our limited nuclear data indicates several separate lineages (Fig. 2). The other taxa treated here can be considered to be distinct species, although the evidence for treating *P. astragali* and *P. sootryeni* as separate species is currently relatively weak (basically based only on the differences in the structure of the lancet), as the males are unknown and nuclear DNA data are lacking.

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

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

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

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