Zoological Journal of the Linnean Society, 2018, **XX**, 1–24. With 17 figures.

Hidden European diversity: a new monotypic hoverfly genus (Diptera: Syrphidae: Eristalinae: Rhingiini)

ANTE VUJIĆ[1], GUNILLA STÅHLS[2], AND SNEŽANA RADENKOVIĆ[1,*]

[1]*Department of Biology and Ecology, Faculty of Sciences, University of Novi Sad, Trg Dositeja Obradovića 2, 21000 Novi Sad, Serbia*
[2]*Zoology Unit, Finnish Museum of Natural History Luomus, PO Box 17, FI-00014 University of Helsinki, Finland*

Received 5 January 2018; revised 24 August 2018; accepted for publication 2 September 2018

For the first time in more than 30 years, a new European hoverfly genus has been discovered, ***Katara* gen. nov.** Its type species ***Katara connexa* sp. nov.** (Diptera: Syrphidae) is described from the Pindos Mountains (Greece), and the systematic position of the monotypic taxon within the tribe Rhingiini is analysed using morphological and molecular data. Phylogenetic analyses resolved ***Katara connexa* gen. et sp. nov.** as sister taxon to *Pelecocera latifrons*. We assert based on the molecular phylogenetic results and the morphological distinctness of *Pelecocera latifrons* that this taxon merits a generic rank, thus we erect the genus ***Pseudopelecocera* gen. nov.** and also place *Pelecocera persiana* in this new genus based on shared characteristics. Based on our results, we place *Chamaesyrphus* in subgeneric rank and as a sister group to the nominal subgenus *Pelecocera*. We provide an identification key to the Rhingiini genera. Our phylogenetic analyses recovered all speciose Rhingiini genera as monophyletic and support existence of three main lineages within the tribe: (1) genus *Rhingia* with two groups, Palaearctic+Neotropical and Afrotropical taxa, (2) genus *Cheilosia* with its subgenera, and (3) lineage with remaining genera (***Pseudopelecocera* gen. nov.**, ***Katara* gen. nov.**, *Ferdinandea*, *Psarochilosia*, *Psarus*, *Portevinia* and *Pelecocera*).

ADDITIONAL KEYWORDS: *Katara connexa* – new genus – new species – *Pelecocera latifrons* – Pindos Mountains – *Pseudopelecocera*.

INTRODUCTION

The tribe Rhingiini (formerly Cheilosiini) comprises the genera *Chamaesyrphus* Mik, 1895, *Cheilosia* Meigen, 1822, *Ferdinandea* Rondani, 1844, *Ischyroptera* Pokorny, 1887, *Macropelecocera* Stackelberg, 1952, *Pelecocera* Meigen, 1822, *Portevinia* Goffe, 1944, *Psarochilosia* Stackelberg, 1952, *Rhingia* Scopoli, 1763, and *Psarus* Latreille, 1804. Most of these genera are primarily distributed in the Holarctic region (Table 1). The Catalogue of Palaearctic Diptera (Peck, 1988) listed all mentioned genera in the tribe Cheilosiini, except for *Psarus* that was ascribed to Psarini. Different subtribal classification schemes of the taxa have previously been presented (e.g. Thompson, 1972; Shatalkin, 1975), but none has been generally adopted. Phylogenetic relationships of the Rhingiini taxa have been studied by several authors using morphological and/or molecular characters (Rotheray & Gilbert, 1999; Stuke, 2000; Ståhls *et al.*, 2004). The study by Ståhls *et al.* (2004) based on both morphological and molecular characters found that the monophyly of the highly speciose genus *Cheilosia*, comprising well over 400 species primarily distributed in the Holarctic region, was well-supported. Different authors have variously treated *Chamaesyrphus* as a subgenus of *Pelecocera* or recognized it as a separate genus (e.g. Thompson & Rotheray, 1998; Speight, 2014; Mengual *et al.*, 2015a). Ståhls *et al.* (2004) stated a need to re-address the phylogenetic placement of the species *Pelecocera latifrons* Loew, 1856 as their phylogenetic analyses did not recover the taxon as a member of the genus *Pelecocera* (sensu Thompson, 1972). Mengual *et al.* (2015a) revised the Holarctic genus *Pelecocera* and described the male of *P. persiana* (Kuznetzov,

*Corresponding author. E-mail: snezana.radenkovic@dbe.uns.ac.rs
[Version of Record, published online 10 December 2018; http://zoobank.org/urn:lsid:zoobank.org:pub:A8CC9F24-937A-4079-A567-A4069DC67D1A]

1989). This study treated the *Chamaesyrphus* taxon as genus, and thus their revision included the taxa *Pelecocera tricincta* Meigen, 1822, *P. latifrons*, *P. pergandei* (Williston, 1884) and *P. persiana*.

Discovery of specimens of an unknown species from a high altitude locality in central Greece, exhibiting characteristics that clearly identified it as a member of the tribe Rhingiini, initiated the present study on the identity and systematic placement of this taxon. The taxon possesses a very distinctive, apomorphic combination of characters which are not concordant with members of any of the known Rhingiini genera.

Molecular phylogenetic studies of Syrphidae taxa have frequently employed the mitochondrial cytochrome c oxidase subunit I (hereafter *COI*), nuclear 28S and 18S ribosomal RNA genes, that proved to be informative for both generic and species levels (e.g. Mengual, Ståhls & Rojo, 2008, 2015b; Reemer & Ståhls, 2013; Vujić *et al.*, 2013).

We generated DNA sequences of these standard genes (*COI*, 28S and 18S) for multiple taxa representing 10 out of the total 11 Rhingiini genera and coded 35 morphological characters for all ingroup Rhingiini taxa and outgroups. The aims of the study are: 1) to evaluate the taxonomy and systematics of the unknown taxon found in Greece and of *Pelecocera latifrons* using morphological and molecular data, and 2) to resolve their phylogenetic affinities and placements within Rhingiini. We also provide an identification key to all genera of Rhingiini, and an extensive table describing and comparing informative morphological characters for diagnosing all genera.

MATERIAL AND METHODS

Morphological studies

The characters used in the description and drawings employ the terminology established by Speight (1987) and Thompson (1999), in addition to those relating to male genitalia that follow Claussen (2000) and Doczkal (2002). The male genitalia were extracted from dry specimens, cleared by boiling them in water-diluted KOH pellets, before using acetic acid to neutralize the KOH. Genitalia were stored in microvials containing glycerol. Drawings were made with an FSA 25 PE drawing tube attached to a binocular microscope (Leica MZ16). Photographs were taken using a camera (Leica DFC320) connected to a binocular microscope (Leica MZ16). Morphological characters used in combined molecular and morphological analysis are listed in Supporting information Appendix S2.

Molecular studies

Specimens used for both morphological and molecular studies (including GenBank accession numbers) are listed in Supporting information Table S1. For the molecular phylogenetic analyses, multiple representatives of all Rhingiini genera were included, except for the rare taxon *Ischyroptera bipilosa* Pokorny, 1887 because a specimen suitable for DNA analyses was not available. Included species were mainly from the Palaearctic region, with a few representatives from the Afrotropical, Nearctic and Neotropical regions. Some sequences generated by Ståhls *et al.* (2004) (the 3' part of mtDNA *COI* and 28S rDNA) were used in the present study (in boldface in Supporting information Table S1) in addition to new sequences of additional representative species (Supporting information Table S1).

Voucher specimens

Specimens with a labcode including the acronym MZH are deposited as DNA voucher specimens in the Zoological Museum of the Finnish Museum of Natural History, Helsinki, Finland and specimens are labelled accordingly. The remaining specimens are deposited in collections of the University of Novi Sad, Serbia (FSUNS), California State Collection of Arthropods, Sacramento, California, USA (CSCA; Martin Hauser), Zoologisches Forschungsmuseum A. Koenig Bonn, Germany (ZFMK) and the specimen of *Ischyroptera bipilosa* that is from the National Museum of Natural History, Smithsonian Institution, Washington DC, USA (USNM) (Supporting information Table S1).

Laboratory procedures

DNA was extracted from 1–3 legs of dry-pinned or ethanol-preserved specimens using the Nucleospin Tissue DNA extraction kit (Machery-Nagel, Düren, Germany) following the manufacturer's protocols and then resuspended in 50 µl of ultra-pure water.

PCR reactions were carried out using GE Ready-to-Go PCR beads in 25 µl reaction aliquots containing 2 µl DNA extract, 1 µl of each primer (at 10 pmol/µl) and ultrapure water. Thermocycler conditions were initial denaturing at 95°C for 2 min, 29 cycles of 30 s denaturing at 94°C, 30 s annealing at 49°C, 2 min extension at 72°C, followed by a final extension of 8 min at 72°C. The universally conserved primers used for amplifying and sequencing the *COI* fragments were LCO-1490 (5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO-2198 (5'-TAAACTTCAGGGTGACC AAAAAATCA-3') (Folmer *et al.*, 1994) for the 5'region of *COI* (hereafter COIa), and the forward primer C1-J-2183 (5'-CAA CAT TTA TTT TGA TTT TTT GG-3') (alias JERRY) and reverse primer TL2-N-3014 (5'-TCC AAT GCA CTA ATC TGC CAT ATT A-3') (alias PAT) (Simon *et al.*, 1994) for the 3'region (hereafter COIb). The D2-3 region of the nuclear ribosomal 28S rRNA gene was amplified with the forward

primer F2 (5'-AGA GAG AGT TCA AGA GTA CGT G-3') and reverse primer 3DR (5'-TAG TTC ACC ATC TTT CGG GTC-3'). The nuclear ribosomal 18S rRNA gene was amplified with the forward primer 2F (5'-AGGGTTCGATTCCGGAGAGGGAGC-3') and the reverse primer b2.9 (5'-TATCTGATCG CCTTCGAACCTCT-3').

Sequence alignment

The gap-free sequences of the protein-coding *COI* gene were assembled manually and trimmed to equal lengths to avoid missing data. The alignment of the 28S and 18S rDNA fragments was carried out using the E-INS-I strategy as implemented in MAFFT (Katoh *et al.*, 2005; Katoh, Asimenos & Toh, 2009) using the CIPRES Science Gateway (Miller, Pfeiffer & Schwartz, 2010) (http://www.phylo.org/sub_sections/portal/). The E-INS-I strategy was chosen because it is optimized for a small-scale alignment and recommended for sequences with multiple conserved domains and gaps, such as rRNA genes (Katoh *et al.*, 2009). The length of the obtained (unaligned) fragments of 18S among ingroup taxa varied between 672–676 bp, and the length of the D2–D3 region of 28S between 566–587 bp.

Phylogenetic analysis

We analysed the data as follows: 1) data set of 50 taxa including all the taxa for which *COI* sequences were available, (all *COI* analysis), 2) data set of 43 taxa for combined sequences of three genes (*COI*, 28S, 18S) (three-genes analysis) and 3) data set of 43 taxa for combined sequences of three genes and morphological data (combined analysis).

Eumerus flavitarsis Zetterstedt, 1843 (Syrphidae: Eristalinae: Merodontini) was used to root the trees, and six other Eristalinae taxa were included as additional outgroups (Supporting information Table S1). The *COI* only, three-genes and combined datasets were analyzed using maximum likelihood methods carried out with RAxML vs 8.2.10 HPC2 on XSEDE (Stamatakis, 2014) using CIPRES Portal Web Server http://www.phylo.org/sub_sections/portal/ on Cipres Science Gateway (Miller *et al.*, 2010).

RAxML analyses of DNA data and combined datasets used the GTR + G model for the DNA data and the MK model (Lewis, 2001) for morphological data. The option to conduct rapid bootstrapping and thorough search for the best-scoring ML-tree in a single program run was selected. Branch support was calculated with 1000 non-parametric bootstrap replicates. Trees were visualized and rooted using MEGA vs. 6 (Tamura *et al.*, 2013).

RESULTS

Molecular data

The mtDNA *COI* dataset (concatenated COIa and COIb) comprised 1344 nucleotides for 43 Rhingiini taxa and seven outgroups. Taxa for which we had only *COI* data are *Macropelecocera sanguinea* Doczkal, 2002 (only COIb), *Pelecocera willistoni* Snow, 1895 (only COIb), *Pelecocera* (*Chamaesyrphus*) sp. A and sp. B, *Portevinia dispar* (Hervé-Bazin, 1929) and *Rhingia trivittata* Curran, 1929 (see Supporting information Table S1). The length of the aligned 18S dataset was 680bp, and that of the 28S dataset was 614 nt. The three-genes dataset (*COI* and the aligned 28S and 18S sequences) comprised 2638 nucleotide positions,

Table 1. Review of taxa belonging to the tribe Rhingiini

Genus	Number of species (~)[b]	Distribution
Cheilosia Meigen, 1822	446	Holarctic, Oriental, Neotropic
Ferdinandea Rondani, 1844	17	Holarctic, Oriental
Ischyroptera Pokorny, 1887[a]	1	Palaearctic
Katara Vujić & Radenković **gen. nov.**	1	Palaearctic
Macropelecocera Stackelberg, 1952	4	Palaearctic
Pelecocera Meigen, 1822	11	Holarctic, Oriental
syn. nov. *Chamaesyrphus* Mik, 1895		
Pseudopelecocera Vujić & Radenković **gen. nov.**	2	Palaearctic
Portevinia Goffe, 1944	4	Palaearctic, Oriental
Psarochilosia Stackelberg, 1952	1	Palaearctic
Psarus Latreille, 1804	1	Palaearctic
Rhingia Scopoli, 1763	47	Holarctic, Oriental, Afrotropic, Neotropic

[a] generic status still unclear (unresolved)
[b] numbers are from Thompson, Rotheray, Zumbado (2010) and Ståhls & Barkalov (2017)

Table 2. Adult morphological characters of the genera of tribe Rhingiini (bold - character states shared with *Katara* **gen. nov.**; underlined - unique character state or apomorphy within the tribe)

	***Katara* gen. nov.**	*Pelecocera (Pelecocera)*	*Pelecocera (Chamaesyrphus)*	*Ferdinandea*	***Pseudopelecocera* gen. nov.**	*Macropelecocera*	*Portevinia*	*Psarochilosia*	*Psarus*	*Rhingia (Rhingia)*	*Rhingia (Eorhingia)*	*Cheilosia*	*Ischyroptera*
face (oral margin in comparison to facial tubercle in lateral view)	**less projected** (Fig. 4A)	more projected (as on Fig. 10B)	more projected (Fig. 10B)	**less projected**	more projected (Fig. 10D)	more projected (Fig. 10E)	**less projected** (Fig. 10A)	**less projected** (Fig. 10F)	**less projected** (Fig. 10C)	snout- like	snout-like	generally **less projected**	more projected (Fig. 10G)
hairs on eyes	**absent**	**absent**	**absent**	present	**absent**	**absent**	**absent**	**absent**	**absent**	**absent**	**absent**	variable	**absent**
eyes in male	**dichoptic** (Fig. 4D)	**dichoptic** (Fig. 11B)	**dichoptic** (Fig. 11C)	holoptic	**dichoptic** (Fig. 11A)	**dichoptic**	holoptic (approaching) (Fig. 11E)	**dichoptic**	**dichoptic** (Fig. 11D)	holoptic	**dichoptic**	holoptic	holoptic
antenna	**not modified** (Fig. 4C)	modified (as on Fig. 10B)	modified (Fig. 10B)	**not modified**	modified (Fig. 10D)	modified (Fig. 10E)	**not modified** (Fig. 10A)	**not modified** (Fig. 10F)	modified (Fig. 10C)	**not modified**	**not modified**	**not modified**	modified (Fig. 10G)
length of arista	**shorter or as long as baso-flagel-lomere** (Fig. 4C)	**shorter or as long as baso-flagel-lomere (as on** Fig. 10B)	**shorter or as long as baso-flagel-lomere** (Fig. 10B)	longer than baso-flagellomere	**shorter or as long as baso-flagellomere** (Fig. 10D)	**shorter or as long as baso-flagel-lomere** (Fig. 10E)	longer than baso-flagel-lomere (Fig. 10A)	**shorter or as long as baso-flag-ellomere** (Fig. 10F)	**shorter or as long as baso-flag-ellomere** (Fig. 10C)	longer than baso-flagel-lomere	longer than baso-flagel-lomere	mostly longer than baso-flagel-lomere	longer than baso-flagel-lomere (Fig. 10G)
antennal pits	**narrowly connected** (Fig. 7A)	**narrowly connected**	**narrowly connected**	confluent (Fig. 7C)	**narrowly connected**	**narrowly connected**	**narrowly connected**	confluent	confluent	confluent	confluent	variable (Fig. 7B, D)	**narrowly connected**
aristal insertion	**before basal 1/3** (Fig. 4C)	beyond basal 1/3 (as on Fig. 10B)	beyond basal 1/3 (Fig. 10B)	**before basal 1/3**	beyond basal 1/3 (Fig. 10D)	beyond basal 1/3 (Fig. 10E)	**before basal 1/3** (Fig. 10A)	**before basal 1/3** (Fig. 10F)	beyond basal 1/3 (Fig. 10C)	**before basal 1/3**	**before basal 1/3**	**before basal 1/3**	beyond basal 1/3 (Fig. 10G)
lunula	**almost straight** (Fig. 7A)	normal	normal	normal (Fig. 7C)	**almost straight**	normal	*very large* (Fig. 11E)	**almost straight**	normal	normal	normal	normal (Fig. 7B, D)	normal
frons	**protruded** (Fig. 4A)	not protruded (as on Fig. 10B)	not protruded (Fig. 10B)	**protruded**	**protruded** (Fig. 10D)	**protruded** (Fig. 10E)	**protruded** (Fig. 10A)	**protruded** (Fig. 10F)	*extremely protruded* (Fig. 10C)	not protruded	not protruded	**protruded**	protruded (Fig. 10G)
striae on frons	**present** (Fig. 4D)	absent (Fig. 11B)	absent (Fig. 11C)	absent	**present** (Fig. 11A)	inconspicious	inconspicious (Fig. 11E)	absent	absent (Fig. 11D)	absent	absent	generally absent	absent
width oforbital stripes	**normal** (Fig. 4A)	variable	variable	**normal**	**normal** (Fig. 10D)	wide (Fig. 10E)	wide (Fig. 10A)	**normal** (Fig. 10F)	narrow (Fig. 10C)	variable	narrow	variable	wide (Fig. 10G)

Table 2. (Continued)

	***Katara* gen. nov.**	*Pelecocera (Pelecocera)*	*Pelecocera (Chamaesyrphus)*	*Ferdinandea*	***Pseudopelecocera* gen. nov.**	*Macropelecocera*	*Portevinia*	*Psarochilosia*	*Psarus*	*Rhingia (Rhingia)*	*Rhingia (Eorhingia)*	*Cheilosia*	*Ischyroptera*
bristles on thorax	**absent**	present	present	present	**absent**	**absent**	present	**absent**	present	present	**absent**	present	present
triangular excavation on proepisternum of propleuron	**absent**	**absent**	**absent**	**absent**	**absent**	**absent**	**absent** (Fig. 16B)	**absent**	**absent**	**absent**	**absent**	*present* (Fig. 16A:*p*)	?
proepisternum	**bare**	hairy	hairy	hairy	**bare**	**bare**	hairy	hairy	hairy	hairy	hairy	hairy	?
metasternum	**bare**	**bare**	**bare**	hairy	**bare**	hairy	hairy	**bare**	**bare**	hairy	hairy	variable	**bare**
allula on wing	**reduced** (Fig. 8A:**x**)	**reduced** (Fig. 8B:**x**)	**reduced** (Fig. 8B:**x**)	not reduced	**reduced**	**reduced**	**reduced** (Fig. 8C:**x**)	**reduced**	**reduced**	not reduced	not reduced	generally not reduced (Fig. 8D:x)	not reduced
end of vein costa on wing	**before wing apex** (Fig. 8A:**y**)	beyond apex	beyond apex	around apex	beyond apex	**before apex**	**before apex**	around apex	around apex	beyond apex	beyond apex	beyond apex	**before apex**
position of vein r-m	**before middle of discal cell** (Fig. 8A)	**before middle of discal cell**	**before middle of discall cell**	at middle of discal cell	**before middle of discal cell**	**before middle of discal cell**	**before middle of discal cell**	**before middle of discal cell**	**before middle of discal cell**	**before middle of discal cell**	**before middle of discal cell**	**before middle of discal cell**	at middle of discal cell
vein dm-cu meeting CuA	**almost parallel to hind wing margin** (Fig. 8A)	at right angle	at right angle	**almost parallel to hind wing margin**	**almost parallel to hind wing margin**	at right angle	**almost parallel to hind wing margin**	**almost parallel to hind wing margin**	**almost parallel to hind wing margin**	**almost parallel to hind wing margin**	**almost parallel to hind wing margin**	**almost parallel to hind wing margin**	**almost parallel to hind wing margin**
subscutellar fringe	**absent**	**absent**	**absent**	reduced	**absent**	**absent**	reduced	reduced	reduced	present	present	present	present
tarsi p2 ventrally	**without black bristles**	with black bristles	with black bristles	with black bristles	**without black bristles**	**without black bristles**	with black bristles	with black bristles	with black bristles	with black bristles	with black bristles	with black bristles	with black bristles
tergites 3 and 4	**without lateral margin**	**without lateral margin**	**without lateral margin**	**without lateral margin**	**without lateral margin**	**without lateral margin**	**without lateral margin**	**without lateral margin**	**without lateral margin**	*with lateral margins*	**without lateral margin**	**without lateral margin**	**without lateral margin**
hypandrium	**elongate** (Fig. 6A)	normal	**elongate**	**elongate**	**elongate (Fig. 13)**	normal	**elongate**	normal	normal	**elongate**	normal	normal	**elongate**
hypandrium	**apically protruded** (Fig. 6)	normal	**apically protruded**	normal	**apically protruded** (Fig. 13C)	normal	**apically protruded**	normal	normal	normal	normal	normal	normal

Table 2. (Continued)

	***Katara* gen. nov.**	*Pelecocera (Pelecocera)*	*Pelecocera (Chamaesyrphus)*	*Ferdinandea*	***Pseudopelecocera* gen. nov.**	*Macropelecocera*	*Portevinia*	*Psarochilosia*	*Psarus*	*Rhingia (Rhingia)*	*Rhingia (Eorhingia)*	*Cheilosia*	*Ischyroptera*
ejaculatory apodeme	**spatula-like (Fig. 6C:f)**	fan-like (Fig. 12H)	fan-like (Fig. 12B)	**spatula-like**	**spatula-like (Fig. 13D): f, 12F)**	fan-like (Fig. 12G)	**spatula-like (Fig. 12A)**	**spatula-like (Fig. 12I)**	**spatula-like (Fig. 12C)**	fan-like	fan-like	mostly slender (stick-like) (Fig. 12D,E)	stick-like
ctenidium on gonostylus	**well developed (Fig. 6D)**	**well developed (Fig. 15E)**	**well developed (Fig. 15B)**	**well developed**	**well developed (Fig. 15D)**	**well developed**	**well developed (Fig. 15A)**	**well developed (Fig. 15F)**	**well developed (Fig. 15C)**	**well developed**	**well developed**	*variable*	**well developed**
gonostylus	**plate-like (Fig. 6D)**	**plate-like (Fig. 15E)**	sinuous (Fig. 15B)	**plate-like**	**plate-like (Fig. 15D)**	**plate-like**	**plate-like (Fig. 15A)**	elongate (Fig. 15F)	sinuous (Fig. 15C)	elongate	elongate	elongate	sinuous
spermal pump	**bifurcated (Fig. 6C:e)**	with lateral apodeme (Fig. 12H)	with lateral apodeme (Fig. 12B)	cap-like	**bifurcated (Fig. 13D): e, 12F)**	**bifurcated (Fig. 12G)**	**bifurcated (Fig. 12A)**	cap-like (Fig. 12I)	**bifurcated (Fig. 12C)**	cap-like	*multifurcated* (Fig. 12J)	with lateral apodeme (Fig. 12D,E)	with lateral apodeme
shape of distiphallus	**angulated (Fig. 6C:a)**	*fused with basiphallus* (Fig. 14F)	straight (Fig. 14B)	**angulated (Fig. 14D)**	**angulated (Fig. 14G)**	**angulated (Fig. 14E)**	**angulated (Fig. 14A)**	**angulated (Fig. 14H)**	**angulated (Fig. 14C)**	straight	**angulated**	straight (Fig. 14I)	straight
distiphallus	**dentate (Fig. 6C:a)**	**dentate (Fig. 14F)**	not dentate (Fig. 14B)	not dentate (Fig. 14D)	**dentate (Fig. 14G)**	**dentate (Fig. 14E)**	**dentate (Fig. 14A)**	not dentate (Fig. 14H)	not dentate (Fig. 14C)	not dentate	not dentate	not dentate (Fig. 14I)	**dentate**
basiphallus	**not dentate (Fig. 6C:b)**	**not dentate (Fig. 14F)**	**not dentate (Fig. 14B)**	*dentate* (Fig. 14D)	**not dentate (Fig. 14G)**	**not dentate (Fig. 14E)**	**not dentate (Fig. 14A)**	**not dentate (Fig. 14H)**	**not dentate (Fig. 14C)**	**not dentate**	**not dentate**	**not dentate (Fig. 14I)**	**not dentate**
basiphallus	**not forked (Fig. 6C)**	**not forked (Fig. 14F)**	**not forked (Fig. 14B)**	forked (Fig. 14D)	**not forked (Fig. 14G)**	**not forked (Fig. 14E)**	forked (Fig. 14A)	forked (Fig. 14H)	**not forked**	**not forked**	**not forked**	**not forked (Fig. 14I)**	**not forked**
lateral sclerites of distiphallus	**fused (Fig. 6C)**	free (Fig. 14F)	free (Fig. 14B:b)	**fused (Fig. 14D)**	**fused (Fig. 14G)**	**fused (Fig. 14E)**	**fused (Fig. 14A)**	**fused (Fig. 14H)**	**fused (Fig. 14C)**	**fused**	**fused**	*partly fused*	**fused**
surstylus	**without lateral carina (Fig. 6A)**	with lateral carina	with lateral carina	**without lateral carina**	**without lateral carina (Fig. 17B)**	**without lateral carina**	**without lateral carina**	with lateral carina	with lateral carina	**without lateral carina**	**without lateral carina**	variable (Fig. 17A:l)	**without lateral carina**
minis	*lateral arms not well developed (Fig. 6B:g)*	more divided apically (Fig. 17C)	more dived apically	more divided basally	more divided apically (Fig. 13F)	more divided apically	more divided apically	more divided basally	more divided basally (Fig. 17D)	more divided apically (Fig. 17E)	more divided apically	more dived apically	more divided apically

and combined dataset comprised 2638 nucleotide and 35 morphological characters (Supporting information Appendix S2) for 36 Rhingiini taxa and the seven outgroups.

Morphological studies

A differential diagnosis for all Rhingiini genera is presented Table 2, where apomorphic character states for each genus are highlighted. Based on our study of the morphology of the unknown taxon, it clearly belongs to the tribe Rhingiini. Due to its overall morphological and molecular uniqueness the new taxon merits generic rank and here we describe the new genus *Katara* gen. nov.

Phylogenetic analyses

The best fitting log likelihood obtained in the separate ML analysis of the *COI*-only data was -13 740.9050 (Fig. 1). The separate ML analysis of the *COI* only data resolved the Rhingiini taxa in two large groups, one comprising (*Macropelecocera*+(*Rhingia*+*Cheilosia*)) and another group with *Katara* gen. nov. and *Pseudopelecocera* gen. nov. resolved as sister group to the remaining Rhingiini taxa. The bootstrap support for (*Macropelecocera*+ (*Rhingia*+*Cheilosia*)) was <50%, and the support value for the second group was also low (66%) (Fig. 1). The focal taxa of this study, *Katara* gen. nov. and *Pseudopelecocera* gen. nov., were resolved together with moderate support (86%). The (*Ferdinandea* + (*Psarochilosia* + *Psarus*)) group was recovered with high bootstrap support (95%). The Nearctic taxon *Pelecocera willistoni* was resolved as sister to the (*Pelecocera* s.l. + *Portevinia*) with moderate support. The genus *Portevinia* was resolved as sister group to the Palaearctic peleocerines. The genus *Rhingia* was resolved in two groups, one comprising only taxa with Afrotropical distributions including *Rhingia* (*Eorhingia*) *cuthbertsoni* Curran, 1939, and the other clade comprising the remaining taxa with Neotropical and Palaearctic distribution. For several taxa we had obtained only partial mtDNA *COI* sequences and no 28S nor 18S rRNA data, e.g. *Macropelecocera sanguinea* and *Pelecocera* (*Chamaesyrphus*) sp. A + sp. B, thus we do not discuss nor evaluate the placements of these taxa based on the *COI* gene trees. In the following we mainly discuss the ML trees of the three-genes and combined data analyses.

The best fitting log likelihood for the RAxML analysis of the three-genes dataset was -18 653.626726, and for combined data analysis -19 200.415494 (Figs 2, 3).

The topologies of the ML analysis of the three-genes data and the combined data were almost identical, only resolving *Portevinia* with different placements. The first ingroup node (first dichotomy) of the ML trees resolves the Rhingiini taxa in two large clades, one clade with *Rhingia* + *Cheilosia* and the other clade including the remaining Rhingiini taxa. The bootstrap support for the *Rhingia* + *Cheilosia* clade in three genes analysis was <50% and in combined analysis 68%, and the support value for the other clade was 89% and 99%, respectively (Figs 2, 3). For the genus *Cheilosia* the analysis included only 1–3 representatives for most of the described subgenera and the present analyses do not constitute a test of the monophyly of the subgenera, but we found that taxa either placed in the subgenera *Eucartosyrphus* or *Taeniocheilosia* were not resolved as monophyletic.

The focal taxa of the present study, *Katara* gen. nov. and *Pseudopelecocera* gen. nov., were placed together in the *COI* gene tree, and also resolved as sister taxa in both the three genes and the combined analyses with high bootstrap support, 92% (Fig. 2) and 100% (Fig. 3), respectively.

Description

Family Syrphidae Latreille, 1802

Tribe Rhingiini Meigen, 1822

Genus ***Katara*** Vujić & Radenković **gen. nov.**

(Figs 4–8)

The taxon shares the following adult morphological characters with all Rhingiini taxa: pilose postpronotum; two-segmented aedeagus of male genitalia; face with well-defined parafacia; antenna shorter than head; wing: cell R4 + 5 acute, with long petiole; anterior crossvein (r-m) before middle of cell DM (but r-m at middle position in *Ferdinandea*); upper outer cross vein (M_1) more or less straight; vein R_{4+5} almost straight.

Diagnosis: Katara Vujić & Radenković **gen. nov.** possesses a unique combination of character states that clearly discriminates it from all other Rhingiini genera: eye dichoptic in both sexes (Fig. 4D, E) and abdomen distinctly broader than thorax in both sexes (1.3–1.4 times wider than thorax) (Fig. 5C–F); basoflagellomere small, rounded, with a short, slightly thickened arista almost as long as the length of antenna (Fig. 4C), proepisternum and proepimeron bare of pilosity in both sexes; and male genitalia with elongated surstylus and epandrium (Fig. 6A, B). Other generic diagnostic characters that discriminate *Katara* **gen. nov.** from other Rhingiini genera are: face not protruded (Fig. 4A); frons protruded (Fig. 4A) with transverse striae (Fig. 4D); eye bare; antennal pits narrowly connected (Fig. 7A); the ventral margin of lunula is almost straight without a medial process

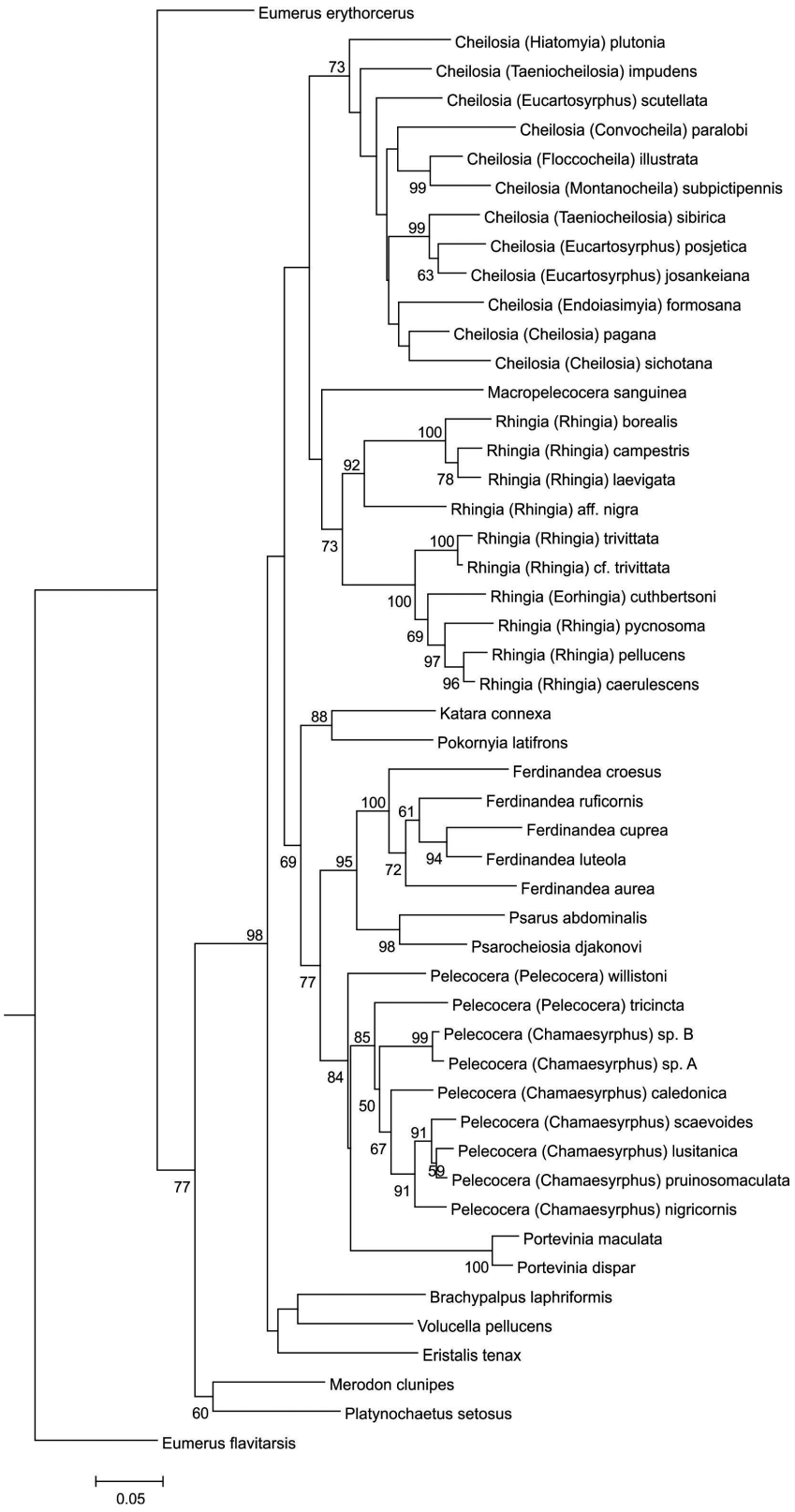

Figure 1. RAxML likelihood tree of mtDNA *COI* sequences, with bootstrap values >50% indicated above branches.

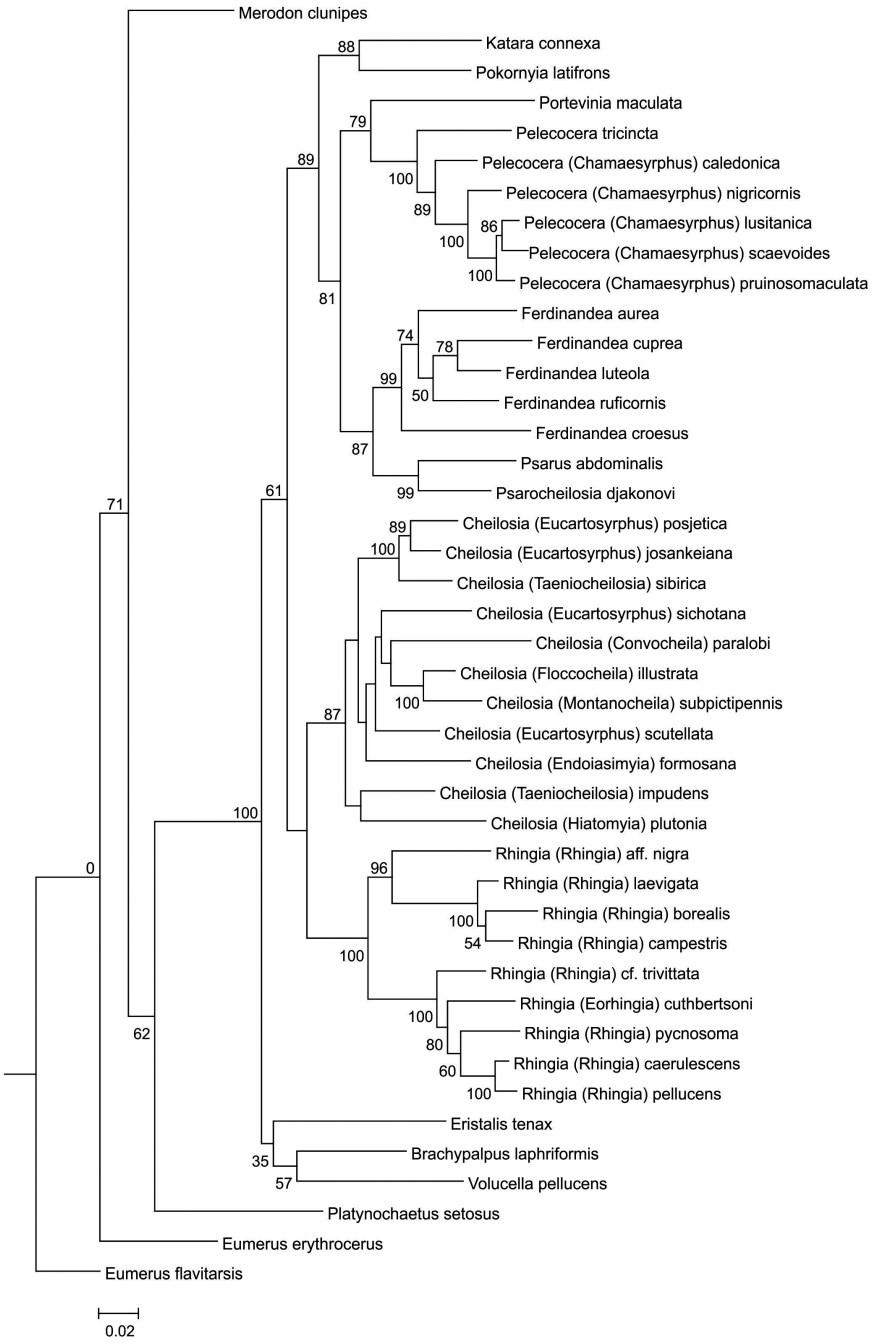

Figure 2. RAxML likelihood tree of combined mtDNA *COI*, nuclear 28S and 18S sequences, with bootstrap values >50% indicated above branches.

(Fig. 7A); thorax without bristles; metasternum bare; alula reduced (Fig. 8A:x); costal vein ending before wing apex (Fig. 8A:y); anterior crossvein (r-m) placed before mid of cell DM (Fig. 8A); subscutellar fringe absent; tarsomeres of mesolegs ventrally without black bristles; male genitalia with hypandrium apically protruded (Fig. 6), ejaculatory apodeme spatulate (Fig. 6C:f), gonostylus plate-like (Fig. 6D), ctenidium on gonostylus well developed (Fig. 6D), spermal pump bifurcated (Fig. 6C:e), distiphallus angulated (Fig. 6C:a) and dentate (Fig. 6C:a), lateral sclerites of distiphallus fused (Fig. 6C), surstylus without

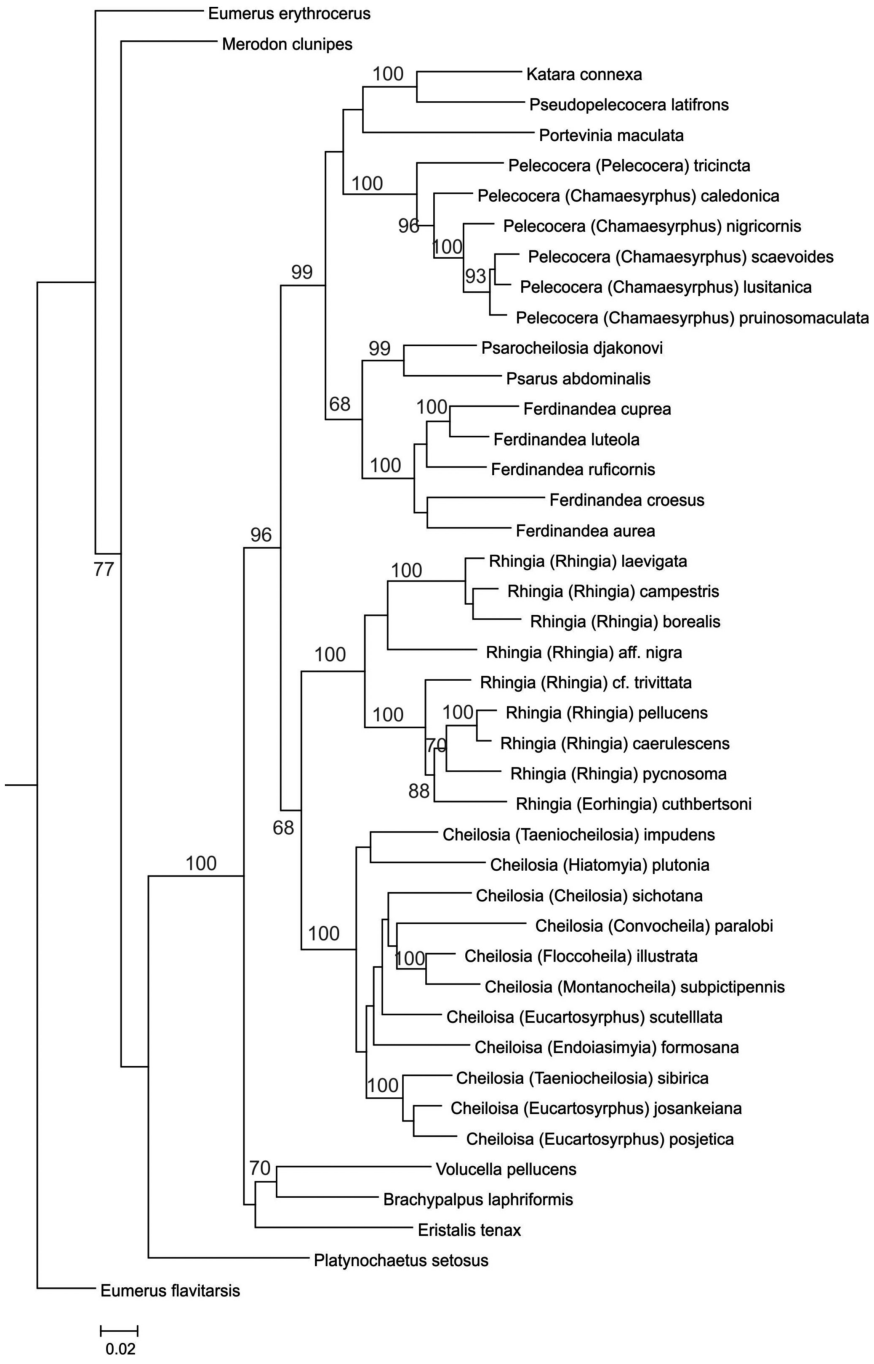

Figure 3. RAxML likelihood tree of combined mtDNA *COI*, nuclear 28S, 18S sequences, and morphological data with bootstrap values >50% indicated above branches.

lateral carina (Fig. 6A), lateral arms of minis not well developed (Fig. 6B:g).

Etymology: The new genus is named based on type locality, an area between Katara pass and Kampos Despoti, in PindosMountains, central Greece. Word '*Katara*' is latinized from the Greek word '*Kataras*'. The name is to be considered as feminine. It means 'curse' in Greek language, indicating the dangerous high mountain pass.

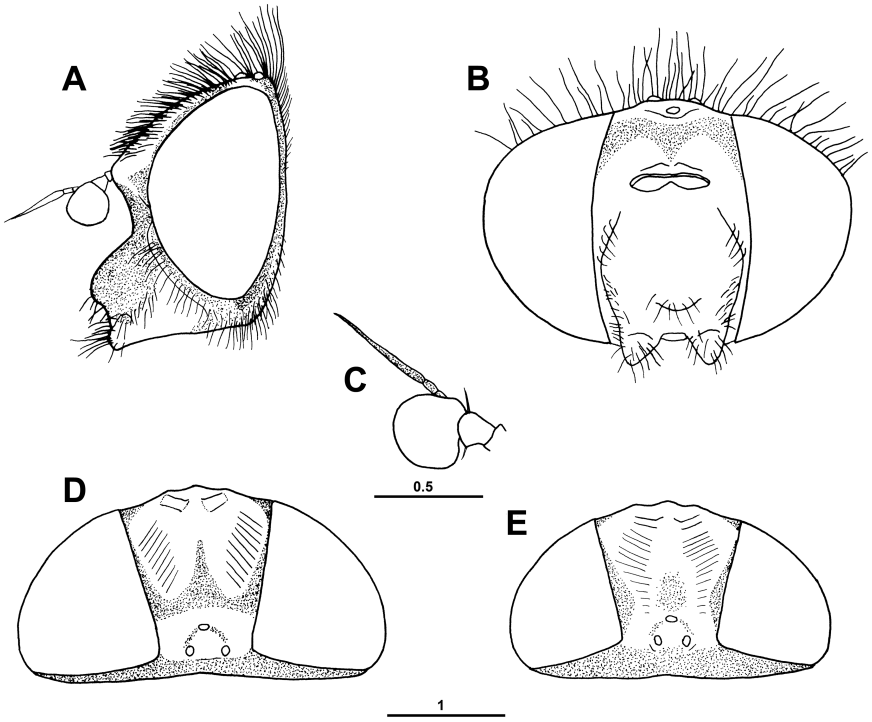

Figure 4. ***Katara connexa*** Vujić & Radenković **sp. nov.** A, male head, lateral view; B, male head, anterior view; C, male antenna, inner view; D, male head, dorsal view; E, female head, dorsal view. Scale in mm.

KATARA CONNEXA VUJIĆ & RADENKOVIĆ **SP. NOV.**

Type-material: Holotype, ♂, GREECE; Pindos Mountains, Kampos Despoti, 39.8028N 21.2721E, 1470.5 m.a.s.l., 15.v.2011, *A. Vujić* (MZH; http://id.luomus.fi/GJ.2035).
Paratypes, GREECE: 1 ♂, Pindos Mountains, Kampos Despoti, 39.8028N 21.2721E, 1470.5 m., 20.v.1997, (*S. Radenković*) (FSUNS); 2 ♀, (*S. Šimić*), 15.v.2011, 11 ♂, 7 ♀ (*A. Vujić*) (FSUNS); 3 ♂, Katara Pass, 39.7968N, 21.2292E, 1717 m, 26.v.2012, (*A. Vujić*) (FSUNS).
Size (n = 16 ♂, 9 ♀): body length 8.8–9.1 mm, wing length: 7.3–7.5 mm.

Diagnosis: Shiny, black species with broad, oval abdomen (Fig. 9).

Description of male: Head (Fig. 4A–D). Antenna (Fig. 4C) dark brown with gray pollinosity. Basoflagellomere small, rounded, 0.85 times longer than wide. Arista inserted dorsally at the basal 1/3 of basoflagellomere, thickened in basal 1/2, about as long as antenna (1.2 times longer). Antennal pits almost separated by a cuticular extension of the face (Fig. 4B). Lunula wide (0.54 times width of frons), with an almost straight posterior margin except for a notch medially. Eyes bare, separated (Fig. 4D). Frons broad (0.4 times width of head), with transverse rugosity on lateral parts and with very rough punctuation; partly pollinose (in front of ocellar triangle and along eye margins, but lacking on rugose areas) (Fig. 4D). Most of the vertex non-pollinose, except on posterior part. Occiput entirely gray pollinose. Ocellar triangle equilateral (Fig. 4D). In contrast to the black colour of the whole head, there is a light brown narrow line dorsally along eye margin. Face below antennae concave, with well-developed facial tubercle and parafacia (Fig. 4A); gray pollinose, except for shiny lateral stripes in lower parts (Fig. 9). Long hairs on parafacia; lower part of face and mouth edge are mainly pale, as for postcranium, whereas pilosity of the frons, vertex and occiput is mainly black.

Thorax (Fig. 5A, C). Mesonotum shiny, with fine punctuation, except for three gray pollinose longitudinal stripes (two wider lateral stripes and one narrow central) reaching the level of the transverse suture (Fig. 5C). Hairs on mesonotum long (Fig. 5A) and predominantly black, with some intermingled light yellow ones; without strong bristles. Pleurae gray pollinose, with posterior anepisternum and anterior anepimeron covered with black hairs, katepisternum with pale hairs; dorsal and ventral hair patches on katepisternum widely separated; the following areas lack hairs: anterior anepisternum, proepimeron, katepimeron, posterior anepimeron, meron and katatergum. Metasternum bare. Median postnotal sclerite of mesonotum gray pollinose except for shiny triangular area extending from central part to

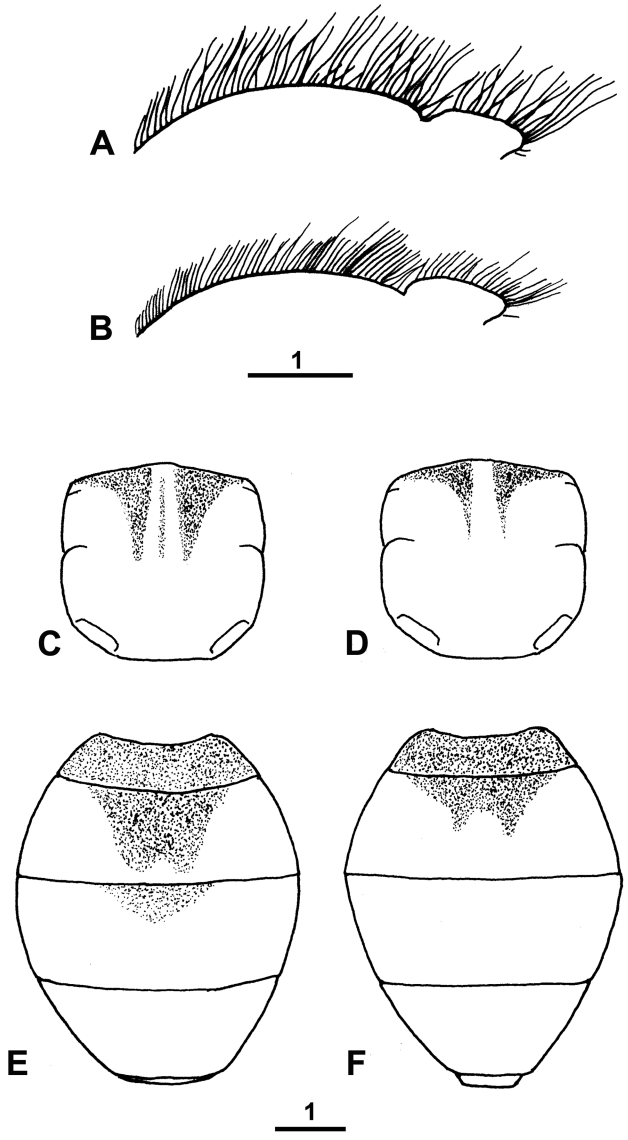

Figure 5. ***Katara connexa*** Vujić & Radenković **sp. nov.** A, male mesonotum, lateral view; B, female mesonotum, lateral view; C, male mesoscutum, dorsal view; D, female mesoscutum, dorsal view; E, male abdomen, dorsal view; F, female abdomen, dorsal view. Scale in mm.

posterior margin. Wing brown hyaline, with black veins; completely covered with dense and strong microtrichia. Alula very narrow (Fig. 8A:x); vein R_{4+5} meets costal vein before apex of wing (Fig. 8A:y); upper outer cross-vein (M1) joins vein R_{4+5} at an angle of 80° (Fig. 8A:M1). Calypter yellow, with some black marginal hairs. Halter pale-brownish. Legs black, except for pale apex of femora and basal 1/2-1/3 of pro- and mesotibiae, and basal 1/3-1/4 of metatibia. Hairs on legs a mix of black and light yellow (pale hairs predominantly on anterior part of pro- femur and tibia, basal 1/4 of mesofemur, posteriorly on metafemur, ventral part of meso- and meta- tibiae, and on all tarsi).

Abdomen (Fig. 5E) broad and oval; clearly broader than thorax at the level of posterior margin of tergite 2. Tergites and sternites shiny black, except for dull gray pollinose zones on tergites 1–3 (almost whole of tergite 1, central area on tergite 2 in the form of an inverted trapezoid ending slightly before posterior margin, and a small triangular area antero-medially on tergite 3) (Fig. 5E); punctuation on tergites fine as on mesonotum. Abdominal hairs erect (except adpressed hairs on dull areas of tergites 1 and 2), predominantly pale, except for some black hairs on posterior 1/2 of tergites 3 and 4 and on pregenital segments; pale-haired parts can have a few intermingled black hairs.

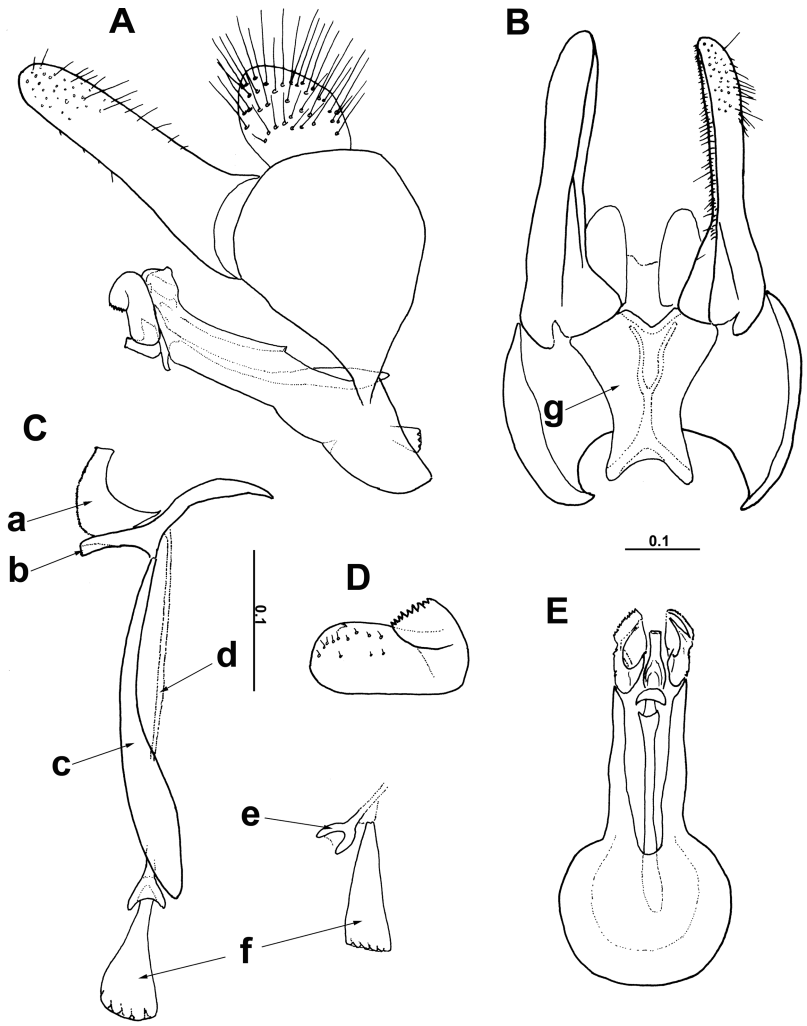

Figure 6. ***Katara connexa*** Vujić & Radenković **sp. nov.** A, male genitalia, lateral view; B, epandrium, ventral view; C, aedeagus with phallapodeme, lateral view; D, gonostylus, lateral view; E, hypandrium, ventral view. Abbreviations: a, distiphallus; b, basiphallus; c, phallapodeme; d, ejaculatory duct; e, spermal pump; f, ejaculatory apodeme; g, minis. Scale in mm.

Male genitalia (Fig. 6): hypandrium elongated, especially distally extended (Fig. 6A); gonostylus plate-like, with developed ctenidium (Fig. 6D); distiphallus dentate, in the form of an angulated tubus (Fig. 6C:a); spermal pump bifurcated (Fig. 6C:e); ejaculatory apodeme small, in the shape of a narrow spatula (Fig. 6C:f); surstyli elongated (Fig. 6A, B); minis fused, only slightly divided apically and concave ventrally (Fig. 6B:g).

Description of female: Very similar to male, except for the following characters: basoflagellomere and arista reddish-brown, except for dark apical part of arista; frons slightly broader (0.42 times width of head), less pollinose in central part (Fig. 4E), covered with shorter pale hairs; hairs on thorax predominantly pale; mesoscutum with shorter hairs (Fig. 5B), less pollinose (only two short, narrow longitudinal stripes present) (Fig. 5D); legs predominantly pale-haired; apex of femora and basal and distal parts of tibiae paler; tergites with smaller pollinose areas (tergite 3 without pollinosity) (Fig. 5F); abdominal hairs predominantly pale, except for a few black hairs on the last segments.

Etymology: The new species is named according to the Latin word '*connexa*' indicating the connection of the taxon to the other taxa of the tribe based on its characters. It is the participle of the verb '*connecto*' in the nominative singular and agrees in feminine gender with the corresponding genus name.

Distribution: The specimens of *Kataria connexa* **sp. nov.** were collected at 1300–1700 m altitude in the Pindos Mountains of Central Greece. This area belongs

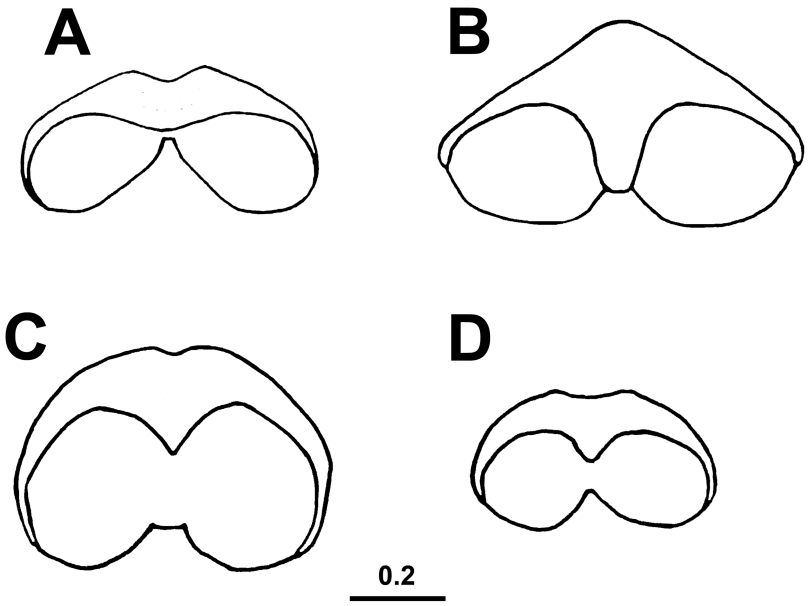

Figure 7. Antennal pits and lunulae. A, ***Katara connexa*** Vujić & Radenković **sp. nov.**; B, *Cheilosia illustrata* (Harris, 1780); C, *Ferdinandea cuprea* (Scopoli, 1763); D, *Cheilosia (Taeniocheilosia) nigripes* (Meigen, 1822). Scale in mm.

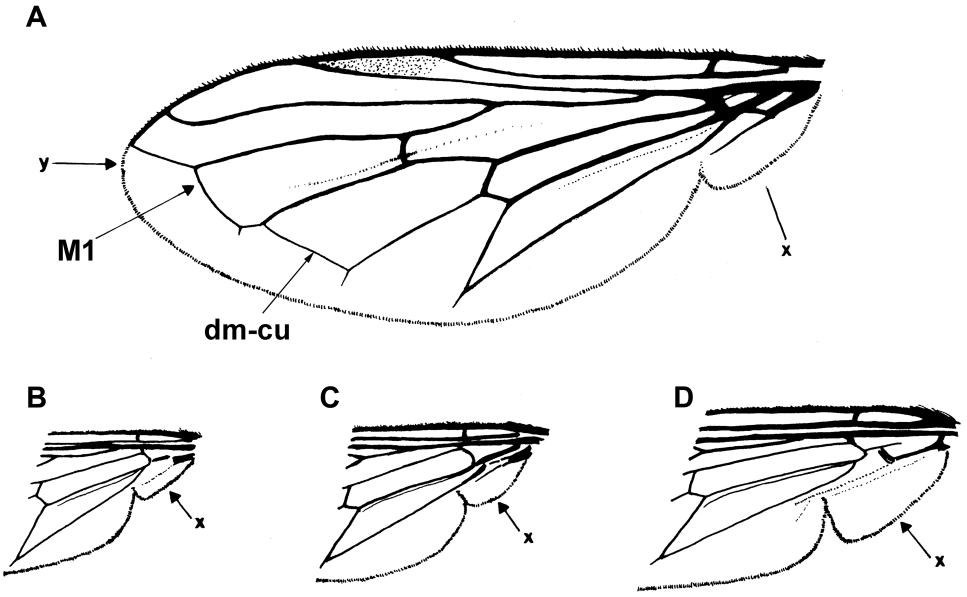

Figure 8. Wing. A, ***Katara connexa*** Vujić & Radenković **sp. nov.**; B, *Pelecocera* sp.; C, *Portevinia* sp.; D, *Cheilosia* sp. Abbreviations: x, alula; y, apex; M_1, upper outer cross vein; dm-cu, lower outer cross vein. Scale in mm.

to the Oro-Mediterranean mountain biome that is rich in pre-glacial habitats and many pre-glacial relict plant and animal taxa. The species *Cheilosia katara* Claussen et Vujić, 1993, an endemic (relict) species occurring only at Pindos, was described by Claussen &Vujić (1993) from the same locality (Katara Pass, 1300 m). These taxa are only known from relict coniferous forests with *Pinus heldreichii* H. Christ and *Pinus nigra* J. F. Arnold subsp. *pallasiana* (Lamb.) Holmboe.

PSEUDOPELECOCERA VUJIĆ & RADENKOVIĆ **GEN. NOV.**

Type: Pelecocera latifrons Loew, 1856: 46; Mengual *et al.* (2015a) (lectotype des.).

The phylogenetic analyses of both the three-genes and combined data (and also separate analysis of *COI* gene tree) agreed with the results of Ståhls *et al.* (2004) in not resolving the *Pelecocera latifrons* taxon in the *Pelecocera* sensu lato (sg. *Chamaesyrphus* + *Pelecocera* s. str.) clade.

Morphological characters (listed in Table 2) confirm its distinctness from *Pelecocera* and *Chamaesyrphus*. For *Pelecocera latifrons,* here we erect the new genus *Pseudopelecocera* Vujić & Radenković **gen. nov.** We also place the species *Pelecocera persiana* in the new genus *Pseudopelecocera* based on descriptive data and illustrations given in Kuznetzov (1989) and Mengual *et al.* (2015a), as morphological characters agree well with those of *P. latifrons*. Morphological closeness between these two taxa was previously noted by Doczkal (2002).

Diagnosis: Basoflagellomere large, triangular, with a thick dorso-apical arista (Fig. 10D); eye dichoptic in both sexes; frons wide (as wide as eye), with distinct transversal striae (Fig. 11A); dorsal margin of lunula almost straight; no thoracic bristles; bare proepisternum; mesotarsi without black bristles ventrally; vein dm-cu almost parallel to hind margin; spermal pump bifurcated (Fig. 12F); ejaculatory apodeme in the shape of a spatula (not fan- or stick-like) (Fig. 12F); distiphallus angulated and not fused with basiphallus (Fig. 13D:a); lateral sclerites of distiphallus fused; surstylus without ridge (Fig. 13E).

Etymology: The new genus is named after the former genus *Pelecocera* from which it is separated, with prefix *pseudo* from the ancient Greek word *pseudēs* meaning pretending or having a close resemblance. The name is to be considered as feminine.

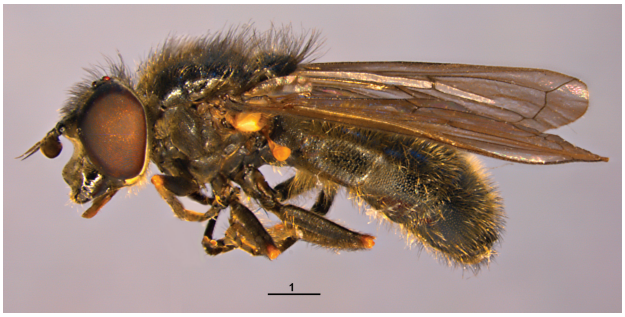

Figure 9. ***Katara connexa*** Vujić & Radenković **sp. nov.**, male, lateral view. Scale in mm.

Pelecocera Meigen, 1822

Chamaesyrphus Mik, 1895 **stat. nov.**

The ML analyses of the three-genes and combined data sets (Figs 2, 3) resolved the type species of genus *Pelecocera* (*P. tricincta*) as sister group to Palaearctic taxa of the subgenus *Chamaesyrphus*. This result is congruent with the results of the study of Ståhls *et al.* (2004) on a more limited taxon set (four species in total). There is no clear molecular and morphological evidence for treating these taxa as separate genera (Table 2). Our results support a division of the Palaearctic taxa of the clade into two subgenera, the nominal subgenus

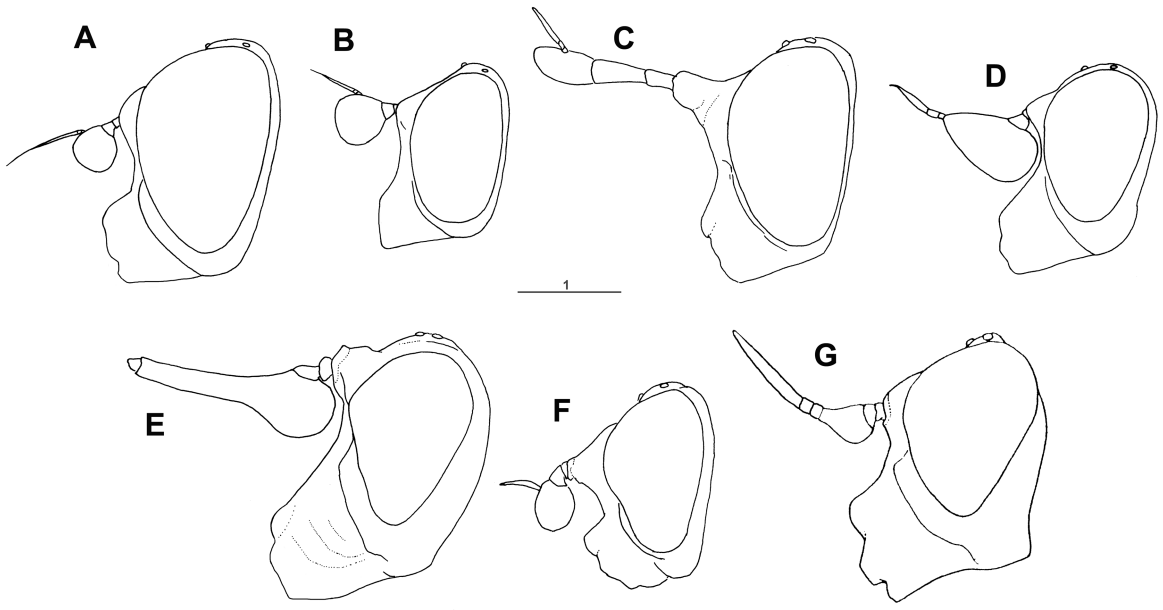

Figure 10. Male head, lateral view. A, *Portevinia* Goffe, 1944; B, *Pelecocera* (*Chamaesyrphus*) *scaevoides* (Fallen, 1817); C, *Psarus* Latreille, 1804; D, *Pseudopelecocera latifrons* (Loew, 1856); E, *Macropelecocera* Stackelberg, 1952; F, *Psarochilosia* Stackelberg, 1952; G, *Ischyroptera bipilosa* Pokorny, 1887. Scale in mm.

KEY TO RHINGIINI GENERA OCCURRING IN THE PALAEARCTIC REGION

1. Basoflagellomere unmodified, with dorsal arista, which is thin and usually basal, never apical (Fig. 10A, B) 4
– Basoflagellomere modified, usually with terminal style or a thick, apical arista (Fig. 10D, E, G) 2
2. Arista longer than basoflagellomere (Fig. 10G); frons less protruded (Fig. 10G); bristles on thorax present; alula of wing not narrow; subscutellar fringe present; eyes in male holoptic; gonostylus plate sinuous (as on Fig. 15C); spermal pump with lateral apodeme (as on 12D); distiphallus straight (as on Fig. 14I) ..... *Ischyropt*era
– Arista shorter or as long as basoflagellomere (Fig. 10D, E); frons protruded (Fig. 10D, E); bristles on thorax absent; alula on wing narrow; subscutellar fringe absent; eyes in male dichoptic (Fig. 11A); gonostylus plate-like (Fig. 15D); spermal pump bifurcated (Figs 12F, G, 3D:e); distiphallus angulated (Fig. 14G) 3
3. Lunula almost straight; striae on frons present (Fig. 11A); width of parafacia moderate (Fig. 10D); hypandrium elongate apically protruded (Fig. 13C); ejaculatory apodeme spatula-like (Figs 12F, 13D:f) ....*Pseudopelecocera* **gen. nov.**
– Lunula normal, wavy; striae on frons inconspicuous; parafacia wider, hypandrium with usual shape, ejaculatory apodeme plate-like ..... *Macropelecocera*
4. Head with a distinct frontal prominence (Fig. 10C, F) 5
– Head without a distinct frontal prominence (Fig. 10A, B) 6
5. Antenna modified, scapus and pedicel elongated (Fig. 10C); arista inserted beyond basal 1/3 (Fig. 10C); gonostylus sinuous (Fig. 15C); spermal pump bifurcated (Fig. 12C); basiphallus and distiphallus not forked (Fig. 14C) ..... *Psarus*
– Antenna not modified (Fig. 10F); arista inserted before basal 1/3 (Fig. 10F); gonostylus elongate (Fig. 15F); spermal pump cap-like (Fig. 12I); basiphallus and distiphallus forked (Fig. 14H) .....*Psarochilosia*
6. Lunula very large (Fig. 11E); parafacia wide (Fig. 10A); eyes bare, in male dichoptic (Fig. 11E)..... *Portevin*ia
– Lunula of usual size (Fig. 7A–D); parafacia usually less wide (as on Fig. 10B, C) 7
7. Triangular excavation on proepisternum of propleuron present (Fig. 16A:p); ejaculatory apodeme mostly slender (stick-like) (Fig. 12D, E); lateral sclerites of distiphallus partly fused .....*Cheilosia*
– Triangular excavation on proepisternum of propleuron absent (Fig. 16B); ejaculatory apodeme spatula-like (Fig. 6C:f) or fan-like (Fig. 12B, H); lateral sclerites of distiphallus fused (Figs 6C, 14D) or free (Fig. 14B, F) 8
8. Antennal pits confluent (Fig. 7C); metasternum hairy; alula of wing not reduced; eyes in male holoptic..... 10
– Antennal pits narrowly connected (Fig. 7A); metasternum bare; alula of wing reduced (Fig. 8A:x); eyes in male dichoptic (Figs 4D, 11B, C) 9
9. Aristal insertion before basal 1/3 (Fig. 4C); lunula almost straight (Fig. 7A); frons protruded (Fig. 4A); striae on frons present (Fig. 4D); bristles on thorax absent; proepisternum bare; ejaculatory apodeme spatula-like (Fig. 6C:f); lateral sclerites of distiphallus fused (Fig. 6C); lateral arms of minis not well developed (Fig. 6B:g) ..... *Katara* **gen. nov.**
– Aristal insertion beyond basal 1/3 (Fig. 10B); lunula as on Fig. 7C; frons not protruded (Fig. 10B); striae on frons absent (Fig. 11B, C); bristles on thorax present; proepisternum hairy; ejaculatory apodeme fan-like (Fig. 12B, H); lateral sclerites of distiphallus free (Fig. 14B, F); lateral arms of minis divided apically (Fig. 17C) ..... *Pelecocera*
10. Oral margin elongated into a long snout; eyes pilose; frons not protruded; tergites 3 and 4 with lateral margins;ejaculatory apodeme fan-like (Fig. 12J); basiphallus not dentate and not forked (as on Fig. 14I) .....*Rhingia*
– Oral margin not elongated into a long snout; eyes bare; frons protruded; tergites 3 and 4 without lateral margins; ejaculatory apodeme spatula-like; basiphallus dentate and forked (Fig. 14D).....*Ferdinandea*

Pelecocera and subgenus *Chamaesyrphus*. The main morphological character distinguishing these subgenera is the shape of phallus, divided in basi- and distiphallus in *Chamaesyrphus* (Fig. 14B) and fused in *Pelecocera* (Fig. 14F). In the *COI* gene tree the Nearctic species *Pelecocera willistoni* was resolved as sister to all *Peleococera* (including *Chamaesyrphus*) (Fig. 1). To establish the phylogenetic placement of the Nearctic *Pelecocera* taxa, additional character and taxon sampling is necessary.

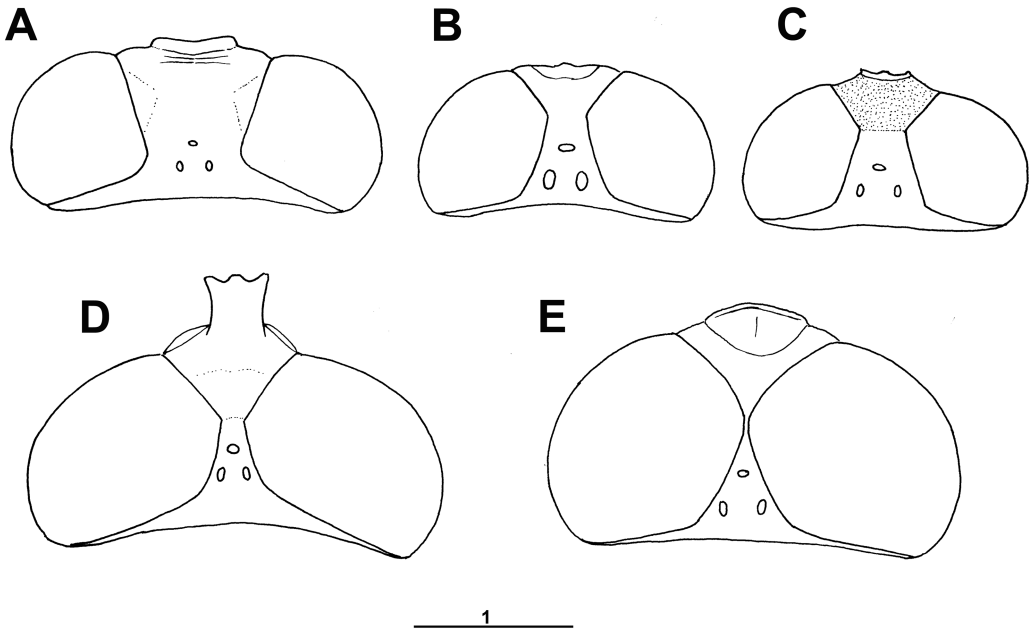

Figure 11. Male head, dorsal view. A, *Pseudopelecocera latifrons* (Loew, 1856); B, *Pelecocera tricincta* Meigen, 1822; C, *Pelecocera* (*Chamaesyrphus*) *scaevoides* (Fallen, 1817); D, *Psarus* Latreille, 1804; E, *Portevinia* Goffe, 1944. Scale in mm.

DISCUSSION

PHYLOGENETIC AFFINITIES AND PLACEMENTS OF RHINGIINI GENERA

Ståhls *et al.* (2004) included a large number of *Cheilosia* species in their molecular and combined genes+morphology phylogenetic analyses, but a lower number of other representatives of Rhingiini. Their results suggested that *Pelecocera latifrons* is not a member of the genus *Pelecocera*, and this result is supported by the present study (with a larger representation of Rhingiini taxa and a more limited set of *Cheilosia* species). In the different analyses (parsimony, optimisation alignment with different character weighting schemes) conducted by Ståhls *et al.* (2004), *Pelecocera latifrons* was resolved either in a basal polytomy or as sister taxon to *Macropelecocera*.

Our phylogenetic analyses consistently resolved *Katara* **gen. nov.** and *Pseudopelecocera* **gen. nov.** as sister taxa (Figs 2, 3). These taxa share the following characters: narrowly connected antennal pits and almost straight dorsal margin of lunula; presence of conspicuous striae on frons; hypandrium of male genitalia apically protruded. *Katara* **gen. nov.** exhibits a combination of diagnostic characters clearly different from *Pseudopelecocera* **gen. nov.** (Table 3) supporting the valid generic status of both taxa.

The three-genes analysis resolved genus *Portevinia* as sister to genus *Pelecocera* (Fig. 2, bootstrap support 79%), while the combined analysis placed the taxon as sister to *Pseudopelecocera* **gen. nov.** + *Katara* **gen. nov.,** but lacking support (Fig. 3). Genus *Portevinia* shares with *Pseudopelecocera* **gen. nov.**, *Macropelecocera* and *Katara* **gen. nov.**the following character states: narrowly connected antennal pits, reduction of alula, and similar shapes of the spermal pump and gonostylus (Figs 4C, 6C:e, 6D, 8A, 8C:x, 10A, 10E, 12A, 12G, 15A). Many characters of *Katara* **gen. nov.** are similar to those of the genus *Portevinia* such as the shape of antennae (Figs 4A, 10A), vein R_{4+5} meeting the costal vein before the tip of wing (Fig. 8A:y), similarly reduced alula of wing (Fig. 8A, C), and the same type of aedeagus (Figs 6C, 14A). Genus *Portevinia* was previously variously classified as a member of the subtribe Cheilosiina (Thompson, 1972) or Psarina (Shatalkin, 1975). The taxon has many key characters in common with the other genera of tribe Rhingiini, e.g. eyes bare, antennal pits confluent, partly reduced alula (Fig. 8C), and gonostylus with developed ctenidium (Fig. 15A).

Genera *Pseudopelecocera* **gen. nov.**, *Macropelecocera* and *Katara* **gen. nov.** also share with the genus *Psarus* the dichoptic eye in male, a reduced alula and a similarly shaped spermal pump (Figs 4D, 6C:e, 11A, 12C, 12F, 12G, 13D:e), but there are not resolved together in our analyses (Figs 2, 3).

Katara **gen. nov.** shares some important characters (dichoptic eyes in both sexes, bare metasternum, more or less reduced alula and structure of male genitalia) individually with several other genera (Table 2).

Genus *Cheilosia* exhibits the highest number of apomorphic characters (triangular excavation present on proepisternum of propleuron, lateral sclerites of

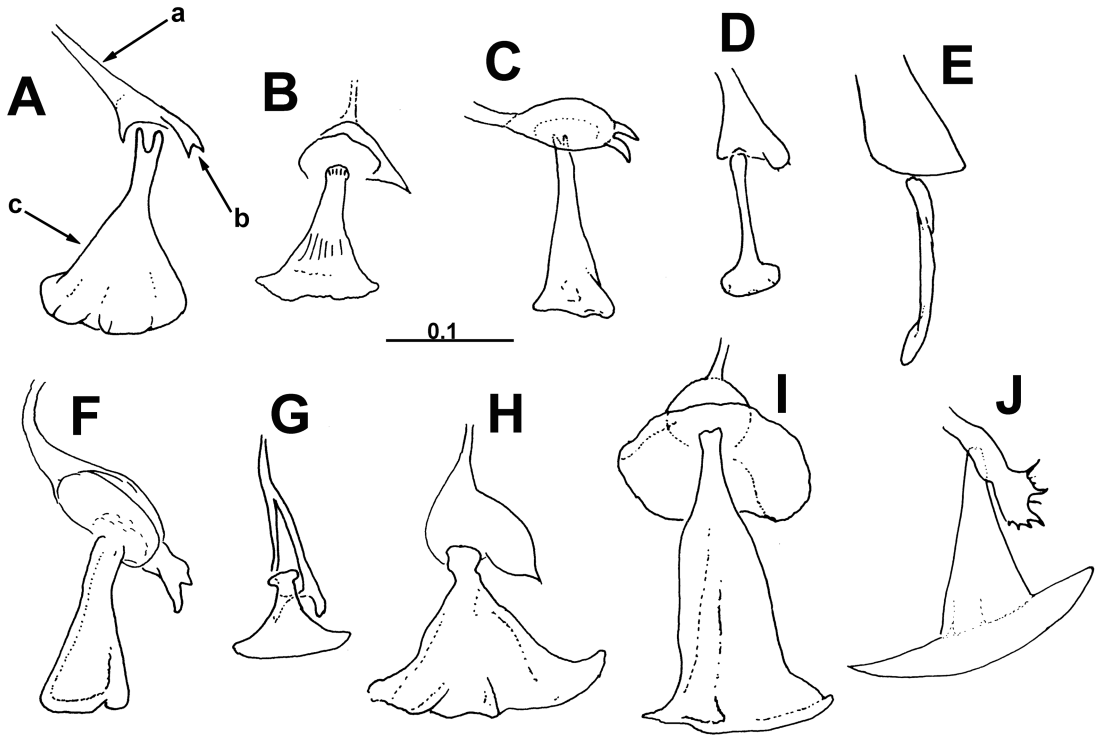

Figure 12. Parts of ejaculatory complex. A, *Portevinia* Goffe, 1944; B, *Pelecocera* (*Chamaesyrphus*) *scaevoides* (Fallen, 1817); C, *Psarus* Latreille, 1804; D, *Cheilosia laticornis* (Rondani, 1857); E, *Cheilosia* (*Hiatomyia*) (Shannon, 1922); F, *Pseudopelecocera latifrons* (Loew, 1856); G, *Macropelecocera* Stackelberg, 1952; H, *Pelecocera tricincta* Meigen, 1822; I, *Psarochilosia* Stackelberg, 1952; J, *Rhingia* (*Eorhingia*) (Hull, 1949). Abbreviations: a, ejaculatory duct; b, spermal pump; c, ejaculatory apodeme. Scale in mm.

distiphallus partly fused and ctenidium on gonostylus reduced) (Table 2). *Cheilosia* is characterized by high morphological character variability and an exceptional diversity of taxa, with 446 described species worldwide (Ståhls & Barkalov, 2017). The ML analyses resolved the genus *Cheilosia* as monophyletic with high bootstrap support (Figs 2, 3).

The only synapomorphy in common to all genera except *Cheilosia* is the angulated shape of the distiphallus. The morphologically most distinct genus within Rhingiini is *Ferdinandea*, which is different from all other taxa in the following combination of characters: metasternum bare, males dichoptic (or eyes meeting at one point, as in *Portevinia*); alula reduced; eyes bare (all these characters are the opposite in *Ferdinandea*). Here, the studied Palaearctic and Neotropical taxa of the genus *Rhingia* were resolved as one clade, and selected Afrotropical *Rhingia* taxa, including *Rhingia* (*Eorhingia*) *cuthbertsoni,* as its sister clade. The Afrotropical *R. (E.) cuthbertsoni* has dichoptic eyes in males, while the other Afrotropical taxa are holoptic. A possible subgeneric division of the genus deserves a separate study also including representatives also from the Oriental region which has the greatest species abundance (Thompson, 1972), and additional samples from the New World, which was beyond the scope of the present paper.

Rhingiini: subtribal classification

The previously proposed divisions of tribe Rhingiini into subtribes (Thompson, 1972; Shatalkin, 1975) was not supported by the molecular and morphological results of Ståhls *et al.* (2004). Thompson (1972) distinguished two subtribes – Cheilosiina (comprising the genera *Cartosyrphus* Bigot, 1883, *Cheilosia*, *Ferdinandea*, *Hiatomyia*, *Portevinia*, *Psarochilosia* and *Rhingia*) and Pelecocerina (comprising *Chamaesyrphus*, *Ischyroptera*, *Macropelecocera* and *Pelecocera*) within the tribe Rhingiini, but with unplaced genus *Psarus*. Shatalkin (1975) classified the tribe Rhingiini into three subtribes: Psarina (*Ferdinandea*, *Rhingia*, *Portevinia* and *Psarus*), Pelecocerina (*Chamaesyrphus*, *Pelecocera* and *Macropelecocera*) and Cheilosiina (*Cheilosia*, with three subgenera *Cheilosia*, *Hiatomyia* and *Nigrocheilosia* Shatalkin, 1975) based on the structure of the male genitalia. The main clades resolved in the ML trees presented here (Figs 2, 3), do not agree

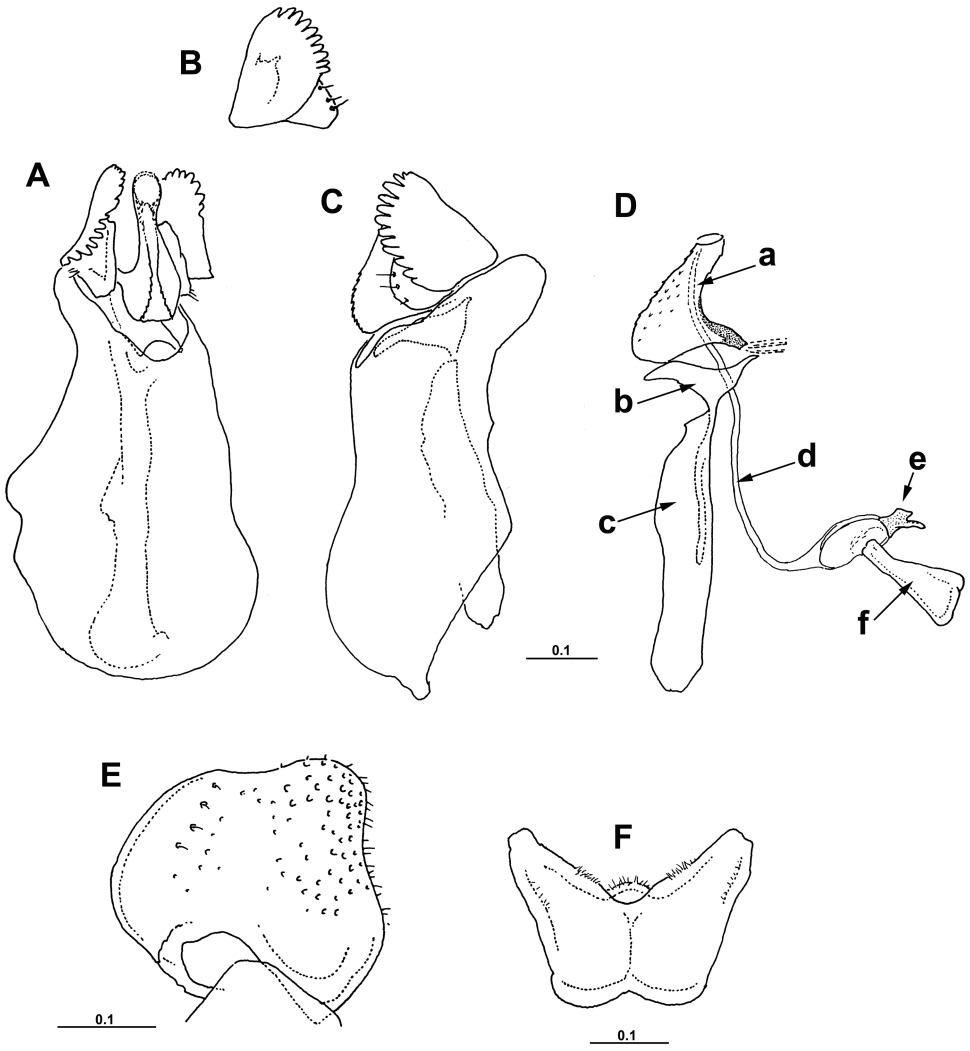

Figure 13. *Pseudopelecocera latifrons* (Loew, 1856), male genitalia. A, hypandrium, ventral view; B, gonostylus, lateral view; C, hypandrium, lateral view; D, phallus, lateral view; E, surstylus; F, minis. Abbreviations: a, distiphallus; b, basiphallus; c, phallapodeme; d, ejaculatory duct; e, spermal pump; f, ejaculatory apodeme. Scale in mm.

with the previously proposed subtribal divisions of Shatalkin (1975) or Thompson (1972). Ståhls *et al.* (2004) resolved *Rhingia*+*Cheilosia* as sister groups in several of their analyses (parsimony analysis of only *COI* sequences, parsimony analysis of adult morphological characters+two genes under both dynamic alignment and static alignments), agreeing with the present results of three-genes and combined data analysed under ML. Ståhls *et al.* (2004) resolved *Psarus* + *Psarocheilosia* as sister taxa, and *Pelecocera* as monophyletic in their different analyses, but *Portevinia* and *Macropelecocera* were resolved in different positions. More recent studies including a very limited number of Rhingiini taxa (four in Mengual *et al.*, 2015b; and three in Young *et al.*, 2016) recovered the tribe Rhingiini as monophyletic but presented variable placements of the included taxa. To conclude, the monophyly of the tribe has not been questioned, but neither of the proposed subtribal classifications were supported in subsequent studies.

We found that the morphological characters studied herein among all Rhingiini taxa offer only limited information for a subtribal division (see Table 2). Our three-genes analysis and combined data set recovered all speciose Rhingiini genera as monophyletic with high bootstrap support, namely the genus *Rhingia* with two groups, comprising Palaearctic+Neotropical and Afrotropical taxa, respectively, the genus *Cheilosia* with its subgenera, *Ferdinandea* and *Pelecocera* with its subgenera (Figs 2, 3). Phylogenetic analyses support the presence of three main lineages within the tribe: (1) genus *Rhingia*, (2) genus

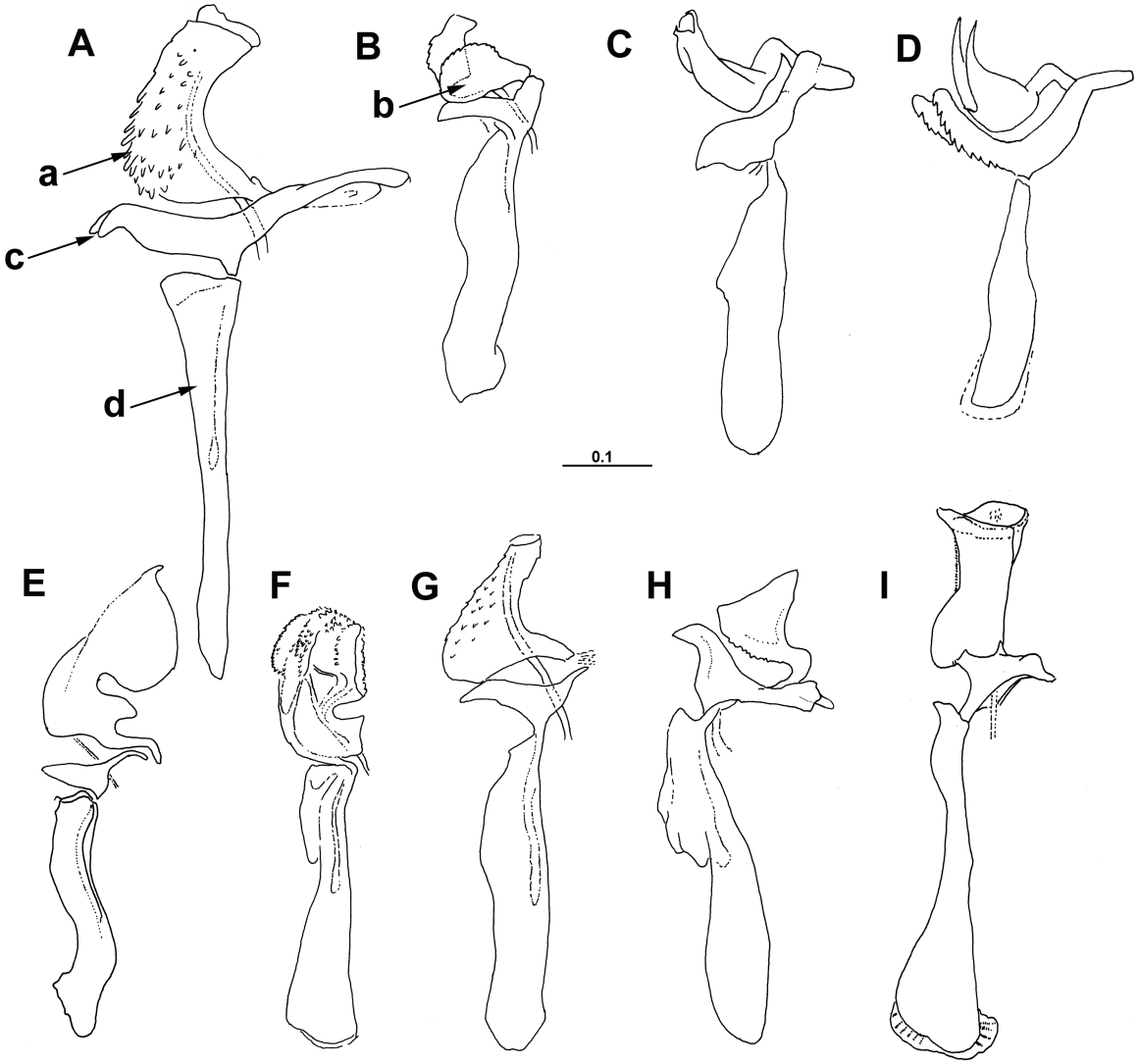

Figure 14. Aedeagus with phallapodeme, lateral view. A, *Portevinia maculata* (Fallen, 1817); B, *Pelecocera* (*Chamaesyrphus*) *scaevoides* (Fallen, 1817); C, *Psarus abdominalis* (Fabricius, 1794); D, *Ferdinandea cuprea* (Scopoli, 1763); E, *Macropelecocera* Stackelberg, 1952; F, *Pelecocera tricincta* Meigen, 1822; G, *Pseudopelecocera latifrons* (Loew, 1856); H, *Psarochilosia* Stackelberg, 1952; I, *Cheilosia derasa* Loew, 1857. Abbreviations: a, distiphallus; b, lateral sclerite of distiphallus; c, basiphallus; d, phallapodeme). Scale in mm.

Cheilosia, and (3) lineage with remaining genera (*Pseudopelecocera* **gen. nov.**, *Katara* **gen. nov.**, *Ferdinandea*, *Psarochilosia*, *Psarus*, *Portevinia* and *Pelecocera*). *Macropelecocera* and *Ischyroptera* are currently *incertae sedis*. We refrain from proposing a subtribal division of Rhingiini in the present study. In forthcoming studies at least Oriental taxa of the speciose genera of the tribe are necessary to include, as this region is the likely origin for most lineages, but material for molecular analyses has not been available.

RHINGIINI: HIGH TAXONOMIC DIVERSITY

Based on molecular and morphological evidence (e.g. Thompson, 1972, this study), the tribe Rhingiini is undoubtedly monophyletic. The tribe includes genera with remarkably high morphological variability and species richness (Table 1). *Cheilosia* is the most speciose hoverfly genus of the Syrphidae family (or next to it), comprising at least 446 species (Ståhls & Barkalov, 2017) classified into thirteen subgenera (Barkalov, 2002, 2007). Numerous recent studies concerning the *Cheilosia* fauna of the Palaearctic region

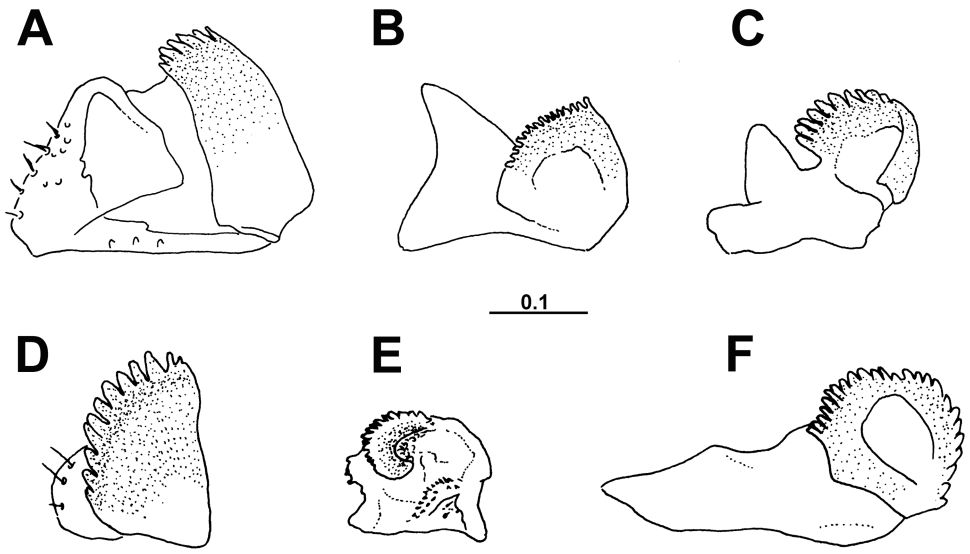

Figure 15. Gonostylus, lateral view. A, *Portevinia* Goffe, 1944; B, *Pelecocera* (*Chamaesyrphus*) *scaevoides* (Fallen, 1817); C, *Psarus* Latreille, 1804; D, *Pseudopelecocera latifrons* (Loew, 1856); E, *Pelecocera tricincta* Meigen, 1822; F, *Psarochilosia* Stackelberg, 1952. Scale in mm.

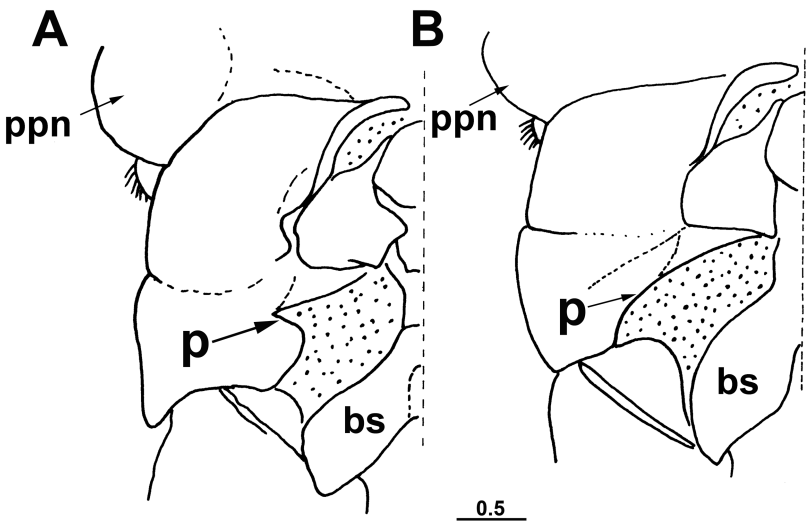

Figure 16. Thorax, anterior view. A, *Cheilosia* Meigen, 1822; B, *Portevinia* Goffe, 1944. Abbreviations: p, inner margin of proepisternum of propleuron; ppn, postpronotum; bs, protoracic basisternum. Scale in mm.

have continued to add new taxa to the genus (e.g. Claussen, 2000; Barkalov & Cheng, 2004; Claussen & Ståhls, 2007; Vujić *et al.*, 2013; Barkalov & Ståhls, 2015). *Rhingia*, *Pelecocera*, and *Ferdinandea* are genera with wide distributions and moderately high numbers of species (Table 1), but with few recent descriptions of taxa new to science (e.g. Kassebeer, 1999; Mutin & Barkalov, 1999, Claussen & Weipert, 2003). *Portevinia* is a genus with only four described species distributed in Palaearctic and Oriental regions. However, the Rhingiini tribe also comprises surprisingly many monotypic genera, namely *Ischyroptera*, *Katara* **gen. nov.**, *Psarochilosia* and *Psarus*, three of which are long-recognized taxa. Of these monotypic genera three are distributed in isolated mountain ranges in the Palaearctic area, probably as relict taxa, being *Ischyroptera* in the Alps, *Katara* **gen. nov.** in Central Greek Mountains, and

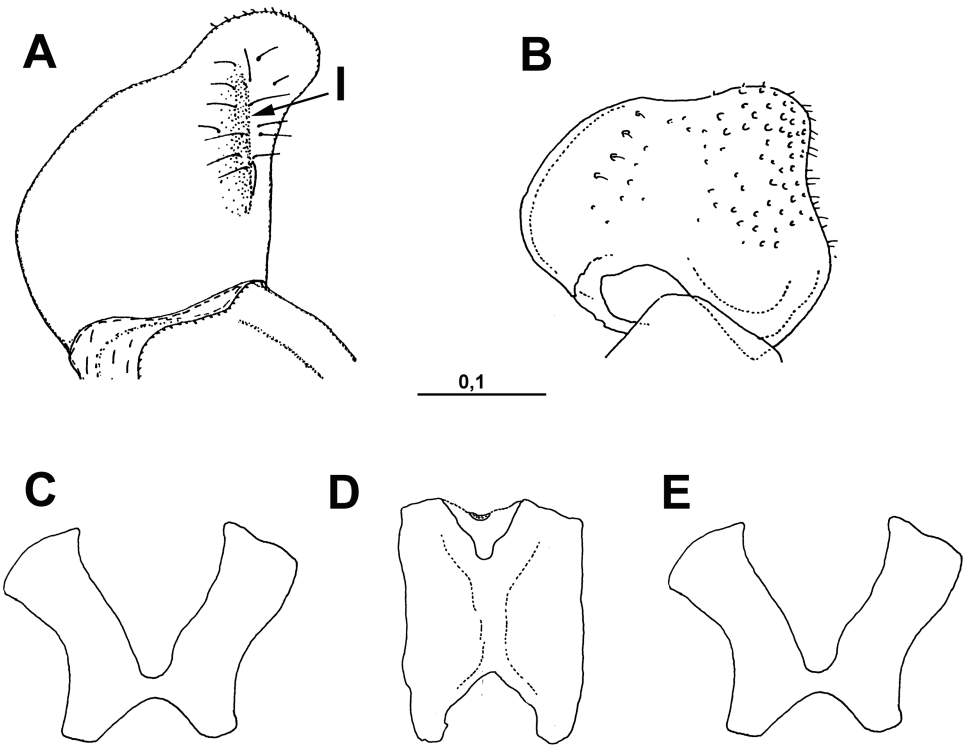

Figure 17. Parts of epandrium: surstylus (A-B), minis (C-E). A, *Cheilosia morio* (Zetterstedt, 1838); B, *Pseudopelecocera latifrons* (Loew, 1856); C, *Pelecocera tricincta* Meigen, 1822; D, *Psarus abdominalis* (Fabricius, 1794); E, *Rhingia campestris* Meigen, 1822. Abbreviation: l, lateral carina. Scale in mm.

Table 3. Diagnostic morphological differences between ***Katara* gen. nov.** and ***Pseudopelecocera* gen. nov.**

	***Katara* gen. nov.**	***Pseudopelecocera* gen. nov.**
1	Integument black without any trace of red or yellow marks	Face in both sexes and male abdomen with yellow reddish marks
2	Body stocky, abdomen broad (Fig. 5E, F)	Narrow abdomen
3	Both sexes very similar in morphology	Clear sexual dimorphism
4	Antennae unmodified (Fig. 4C)	Antennae strongly modified (Fig. 10D)
5	Face not protruded (Fig. 4A)	Face protruded (Fig. 10D)
6	Arista inserted before basal third (Fig. 4C)	Arista inserted beyond basal third (Fig. 10D)
7	Costal vein ending before wing apex	Costal vein ending beyond wing apex
8	Male genitalia: surstylus and hypandrium elongated, aedagus and minis with distinct shape; minis with reduced lateral arms (Fig. 6)	Male genitalia: surstylus and hypandrium short, aedagus and minis with different shape (Fig. 13)

Psarochilosia in the Russian Far East. Species of the genus *Macropelecocera*, *M. paradoxa* Stackelberg, 1952, *M. pulchella* Kuznetzov, 1990, *M. sanguinea*, and *M. stackelbergi* Kuznetzov, 1990 have similar types of restricted distributional ranges; *M. paradoxa* in Russian high mountains, *M. pulchella* in Kazakstan, *M. sanguinea* in mountains in Kyrgyz Republic, and *M. stackelbergi* in Tajikistan. *Psarus* is widely distributed in lowland areas in Central and South Europe (reviewed in Mengual & Ssymank, 2015). *Pseudopelecocera* **gen. nov.** comprises two known species from remotely situated areas; *P. latifrons* in the Eastern Palaearctic, Central Europe and Lebanon, and *P. persiana* with a distribution in Iran.

CONSERVATION

Katara connexa **gen. et sp. nov.** and *Psarus abdominalis* (Fabricius, 1794) are rare and unique species and hence may become extinct in the wild. Both taxa are endemic to Europe. *Psarus abdominalis* has long been known from many localities in Europe, but is rare across its entire distributional range (Mengual & Ssymank, 2015).The discovery of *Katara connexa* **sp. nov.** from Pindos Mountains in Greece is a remarkable finding from a European perspective, given that it has been more than 30 years since the last two new European hoverfly genera were described (*Cryptopipiza* Mutin, 1998, a new name for *Pseudopipiza* Violovitsh, 1985; and *Primoceroides* Violovitsh, 1985) and, prior to those, it was in the first half of the 20th century that the next most recent genus was discovered (*Rohdendorfia* Smirnov, 1924). Appropriate conservation measures to protect *Katara connexa* **sp. nov.** highlight the importance of nature conservation in Greece and in particular the protection of the mountainous habitats of the PindosMountains. These habitats harbor numerous glacial relict species, with *Katara connexa* **sp. nov.** and *Cheilosia katara* as significant representatives of the Syrphidae (Diptera).

ACKNOWLEDGEMENTS

We are sincerely grateful to National Museum of Natural History; Smithsonian Institution, Washington DC, USA (USNM) for loan of specimen of *Ischyroptera bipilosa* necessary to complete the present study. We thank Claus Claussen (Flensburg, Germany) for his valuable comments and support. This work was funded by projects of the Ministry of Education, Science and Technological Development of the Republic of Serbia (OI173002 and III43002) and The Provincial Secretariat for Higher Education and Scientific Research of the Republic of Serbia ("Evaluation of Ecological Networks in AP Vojvodina as support for nature conservation"). We thank Menno Reemer (Leiden, Netherlands), Ximo Mengual and Axel Ssymank (Bonn, Germany) for providing some species of Rhingiini for molecular work, and Jeff Skevington (Ottawa, Canada) for permission to use CNC barcode sequences. We are grateful to John O'Brien for English proofreading.

REFERENCES

Barkalov AV. 2002. Subgeneric classification of the genus *Cheilosia* Meigen, 1822 (Diptera, Syrphidae). *Entomological Review* **82:** 518–531.

Brakalov AV. 2007. A new species, a new synonym, and new records of the hover-fly genus *Cheilosia* Meigen (Diptera, Syrphidae). *Entomological Review* **87:** 368–375.

Barkalov AV, Cheng X-Y. 2004. Revision of the genus *Cheilosia* Meigen, 1822 (Diptera: Syrphidae) of China. *Contributions on Entomology, International* **5:** 266–421.

Barkalov AV, Ståhls G. 2015. Descriptions of three new species of the genus *Cheilosia Meigen* from China (Diptera, Syrphidae). *Zootaxa* **3972:** 280–290.

Claussen C. 2000. Eine neue Art der Gattung *Cheilosia* Meigen, 1822 (Diptera, Syrphidae) aus Bulgarien und ihre Verwandtschaftsbeziehungen. *Volucella* **5:** 1–14.

Claussen C, Vujić A. 1993. *Cheilosia katara* n. sp. aus Zentralgriechenland (Diptera: Syrphidae). *Entomologische Zeitschrift* **103:** 341–346.

Claussen C, Weipert J. 2003. Zur Schwebfliegenfauna Nepals (Insecta: Diptera: Syrphidae) unter besonderer Berücksichtigung Westnepals. In: Hartmann M, Baumbach H, eds. *Biodiversität und Naturausstattung im Himalaya*. Erfurt: Verein der Freunde und Förderer des Naturkundemuseums Erfurt e. V., 343–380.

Claussen C, Ståhls G. 2007. A new species of *Cheilosia* Meigen from Thessaly/Greece, and its phylogenetic position (Diptera, Syrphidae*). Studia Dipterologica* **3:** 275–281.

Doczkal D. 2002. Description of *Macropelecocera sanguinea* spec. nov. from Kirghizia (Diptera, Syrphidae). *Volucella* **6:** 45–51.

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* **3:** 294–299.

Kassebeer CF. 1999. Eine neue Art der Gattung *Ferdinandea* Rondani, 1844 (Diptera, Syrphidae) aus Nordafrika. *Beitrage zur Schwebfliegen Marokkos 9, Dipteron* **2:** 153–162.

Katoh K, Kuma K, Toh H, Miyata T. 2005. MAFFT version **5**: improvement in accuracy of multiple sequence alignment. *Nucleic Acids Research* **33:** 511–518.

Katoh K, Asimenos G, Toh H. 2009. Multiple alignment of DNA sequences with MAFFT. In: Posada D. ed. *Methods in Molecular Biology. Bioinformatics for DNA Sequence Analysis*. New York: Springer, Humana Press, 39–64.

Kuznetzov SY. 1989. Hover-flies of the genus *Pelecocera* Mg. (Diptera, Syrphidae). *Latvijas Entomologs* **32:** 80–85.

Lewis PO. 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biology* **50:** 913–925.

Mengual X, Ssymank A. 2015. New records of *Psarus abdominalis* (Fabricius) (Diptera: Syrphidae), a threatened species in Europe. *Annales de la Société entomologique de France (N.S.)* **51:** 197–207.

Mengual X, Ståhls G, Rojo S. 2008. First phylogeny of predatory flower flies (Diptera, Syrphidae, Syrphinae) using mitochondrial COI and nuclear 28S rRNA genes: conflict and congruence with the concurrent tribal classification. *Cladistics* **24:** 543–562.

Mengual X, Kazerani F, Talebi AA, Gilasian E. 2015a. A revision of the genus *Pelecocera* Meigen with the description

of the male of *Pelecocera persiana* Kuznetzov from Iran (Diptera: Syrphidae). *Zootaxa* **3947:** 99–108.

Mengual X, Ståhls G, Rojo S. 2015b. Phylogenetic relationships and taxonomic ranking of pipizine flower flies (Diptera: Syrphidae) with implications for the evolution of aphidophagy. *Cladistics* **31:** 491–508.

Miller MA, Pfeiffer W, Schwartz T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Proceedings of the Gateway Computing Environments Workshop(GCE), 14 Nov. 2010, New Orleans, LA, 1–8.

Mutin VA, Barkalov AV. 1999. Family Syrphidae. In: Ler PA, ed. *Key to the insects of Russian Far East, 6, Diptera and Siphonaptera*. Valdivostok: Dal'nauka, 1–665.

Peck LV. 1988. Syrphidae. In: Soos A, Papp L, eds. *Catalogue of Palaearctic Diptera.* Budapest: Akad. Kiado, 11–230.

Reemer M, Ståhls G. 2013. Phylogenetic relationships of Microdontinae (Diptera: Syrphidae) based on molecular and morphological characters. *Systematic Entomology* **38:** 661–688.

Rotheray GE, Gilbert FS. 1999. Phylogeny of Palaearctic Syrphidae (Diptera): evidence from larval stages. *Zoological Journal of the Linnean Society* **127:** 1–112.

Shatalkin AI. 1975. A taxonomic analysis of the hover flies (Diptera, Syrphidae). II. *Entomological Review* **54:** 127–134.

Simon C, Frati F, Beckenbach A, Crespi B, Liu H, Flook P. 1994. Evolution, weighting and phylogenetic utility of mitochondrial gene-sequences and a compilation of conserved polymerase chain-reaction primers. *Annals of the Entomological Society of America* **87:** 651–701.

Stamatakis A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* doi: 10.1093/bioinformatics/btu033. Available at: http://bioinformatics.oxfordjournals.org/content/early/2014/01/21/bioinformatics.btu033.abstract. Accessed 16 November 2017.

Stuke J-H. 2000. Phylogenetische Rekonstruktion der Verwandtschaftsbeziehungen innerhalb der Gattung *Cheilosia* Meigen, 1822 anhand der Larvenstadien (Diptera: Syrphidae). *Studia Dipterologica Suppl*. **8:** 1–118.

Ståhls G, Stuke J-H, Vujić A, Doczkal D, Muona J. 2004. Phylogenetic relationships of the genus *Cheilosia* and the tribe Rhingiini (Diptera, Syrphidae) based on morphological and molecular characters. *Cladistics* **20:** 105–122.

Ståhls G, Barkalov AV. 2017. Taxonomic review of the Palaearctic species of the *Cheilosia caerulescens*-group (Diptera, Syrphidae). *ZooKeys* **662:** 137–171.

Speight MCD. 1987. External morphology of adult Syrphidae (Diptera). *Tijdschrift Voor Entomologie* **130:** 141–175.

Speight MCD. 2014. Species accounts of European Syrphidae (Diptera), 2014. *Syrph the Net, the database of European Syrphidae*. Dublin: Syrph the Net Publications **78**, 321.

Tamura K, Stecher G, Peterson D, Filipski A, Kumar S. 2013. MEGA6: molecular evolutionary genetics analysis version 6.0. *Molecular Biology and Evolution* **30:** 2725–2729.

Thompson FC. 1972. A contribution to a generic revision of the Neotropical Milesinae (Diptera, Syrphidae). *Arquivos de Zoologia* **23:** 73–215.

Thompson FC. 1999. A key to the genera of the flower flies (Diptera: Syrphidae) of the Neotropical Region including descriptions of new genera and species and a glossary of taxonomic terms. *Contributions on Entomology, International* **3:** 319–378.

Thompson FC, Rotheray GE, Zumbado MA. 2010. Syrphidae. In: Brown BV, Borkent A, Cumming JM, Wood DM, Woodley NE, Zumbado MA. eds. *Manual of Central American Diptera*. Ottawa, Canada: NRC Research Press, 763–792.

Thompson FC, Rotheray G. 1998. Family Syrphidae. In: Papp L, Darvas B, eds. *Contributions to a manual of Palaearctic Diptera (with species reference to flies of economic importance)*. Budapest: Science Herald, 81–139.

Vujić A, Radenković S, Trifunov S, Nikolić T. 2013. Key for European species of the *Cheilosia proxima* group (Diptera, Syrphidae) with a description of a new species. *ZooKeys* **269:** 33–50.

Young AD, Lemmon AR, Skevington JH, Mengual X, Ståhls G, Reemer M, Jordaens K, Kelso S, Lemmon EM, Hauser M, Meyer MD, Misof B, Wiegmann BM. 2016. Anchored enrichment dataset for true flies (order Diptera) reveals insights into the phylogeny of flower flies (family Syrphidae). *BMC Evolutionary Biology* **16:** 143. doi: 10.1186/s12862-016-0714-0.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Specimens used for morphological and molecular studies (including GenBank accession numbers).
Appendix S2. Character state descriptions (character descriptions and states as in Ståhls *et al.* (2004) study with character number in boldface).