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Research article

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Revision and morphological analysis of the Ragadidae (Insecta, Diptera)

Emma WAHLBERG

Department of Zoology, Swedish Museum of Natural History, P. O. Box 50007, SE-104 05 Stockholm, Sweden and Department of Zoology, Stockholm University, S-106 91 Stockholm, Sweden.

Email: emma.wahlberg@nrm.se

[urn:lsid:zoobank.org:author:CB7636CE-FC44-403A-BAFD-C9F7C22A57CE](https://zoobank.org/author/CB7636CE-FC44-403A-BAFD-C9F7C22A57CE)

Abstract. Several taxonomic groups within Empidoidea Latreille, 1809 have been subject to unclear phylogenetic assignments along with multiple parallel hypotheses causing difficulties in classification and morphological identification. This study reviews the internal classification of the Ragadidae and includes a diagnosis and description of all included subfamilies and genera based on the results of an analysis of morphological characters using maximum parsimony. Illustration of important characters and a key to all genera in the family is given. The genus *Hormopeza* Zetterstedt, 1838 is found to be most closely related to *Anthepiscopus* Becker, 1891 and *Iteaphila* Zetterstedt, 1838, and the subfamily Iteaphilinae Wahlberg & Johanson, 2018 is therefore expanded to also include that genus. *Hormopeza* is consequently excluded from Ragadinae Sinclair, 2016. This study provides diagnoses, descriptions and keys in a contribution to a thorough classification of the empidoid groups and increased ease in morphological recognition.

Keywords. Diptera, Empidoidea, Ragadidae, revision, taxonomy.

Wahlberg E. 2019. Revision and morphological analysis of the Ragadidae (Insecta, Diptera). *European Journal of Taxonomy* 521: 1–19. <https://doi.org/10.5852/ejt.2019.521>

Introduction

Chvála (1976) erected the subfamily Oreogetoninae Chvála, 1976 and included the genera *Anthepiscopus* Becker, 1891, *Hormopeza* Zetterstedt, 1838, *Gloma* Meigen, 1822, *Iteaphila* Zetterstedt, 1838, *Oreogeton* Schiner, 1860 and *Ragas* Walker, 1837. This subfamily was hypothesized to be the sister group to the remaining subfamilies (Chvála 1976, 1983) in Empididae Latreille, 1809. More than twenty years later, Sinclair (1999) proposed the erection of the ‘Ragas-group’ within the Empididae, and included the genera *Dipsomyia* Bezzi, 1909, *Hormopeza*, *Hydropeza* Sinclair, 1999, *Ragas* and *Zanclotus* Wilder, 1982. The monophyly of this group was supported by Sinclair & Cumming (2006) based on morphological analyses, and Sinclair (2016) later raised it to the rank of subfamily as Ragadinae Sinclair, 2016. The genus *Iteaphila*, earlier proposed by Chvála to be related to *Ragas*, was proposed by Sinclair & Cumming (2006) to be distantly related and they stated that *Iteaphila* together with *Anthepiscopus* are *incertae sedis* within the Empidoidea. The authors also left *Oreogeton* unplaced within the Empidoidea. The

genus *Gloma* was transferred to the Trichopezinae Sinclair, 1995 (Brachystomatidae Melander, 1908 *sensu* Sinclair & Cumming, 2006) by Sinclair (1995).

In a recent analysis (Wahlberg & Johanson 2018), the Ragadinae and the ‘*Iteaphila*-group’ were brought together within the family Ragadidae, and the ‘*Iteaphila*-group’ was included in the newly erected subfamily Iteaphilinae Wahlberg & Johanson, 2018. Supported by DNA sequence data, the Ragadidae were hypothesized to form the sister group to the Empididae. This recent change in taxonomic status and generic composition, however, left internal relationships unresolved. The objectives of this paper are to provide the results from an analysis of the internal relationships within the family, updated diagnostic characters to reflect the new classification, and determination keys to the included genera applicable to both males and females.

Material and methods

This study comprises all genera included in the Ragadidae and is based on material borrowed from the institutions listed under each taxon in the results. Each genus is represented by the type species, in most cases also the type material. For photographic purposes and detailed studies, non-types were applied to reduce the damage risk. Photographic equipment for dry material was a Nikon DS-Ri2 mounted on a motorized Nikon SMZ microscope. Automatic focus stacking was performed in Nikon NIS-Elements 5.10 connected to the camera. Dissected material was mounted in Euparal or glycerol and photographed using a Nikon D7100 mounted on a Leitz Orthoplan large field microscope, with manual focusing and subsequent stacking in Helicon Focus 6.8.0. Photos were edited and finalized in Adobe Photoshop CC 20.0.1. Pencil drawings were edited in Adobe Illustrator CC 23.0.1. A phylogenetic analysis based on 28 morphological characters, applied by Sinclair (1999, 2016), Sinclair & Cumming (2006) and Wahlberg & Johanson (2018) with the addition of new characters (Table 1), was executed in PAUP* ver. 4.0a164 (Swofford 2003). The most parsimonious trees were found using the heuristic search option with random stepwise addition with 1000 replicates and TBR branch swapping, MulTrees enabled, and 1000 bootstrap replications. All characters were unordered and unweighted, and the character matrix is presented in Table 2. The species of the Dolichopodidae Latreille, 1809 *Dolichopus unguulatus* Linnaeus, 1758, and two species of the Empididae, *Trichopeza longicornis* Meigen, 1822 and *Clinocera nigra* Meigen, 1804, were selected as outgroups to root the character transformations. Characters were mapped and visualized on the resulting tree in MacClade 4 (Maddison & Maddison 2001), and the tree was annotated in Adobe Illustrator CC 23.0.1. The terminology applied for morphological details follows Cumming *et al.* (1995) for the male terminalia, McAlpine (1981) for the morphology of adult and wing, and Stuckenberg (1999) for the antennae. In the case of the second anterior branch of the cubitus in the wing (traditionally referred to as CuA2), the more recent interpretation is followed (Cumming & Wood 2017). In this case the CuA2 is now referred to as CuA. The dorsal and ventral projections of the epandrium is interpreted as dorsal and ventral surstyli, respectively.

Abbreviations of morphological characters

CuA	=	anterior branch of cubital vein cubitus plus anal veins
R _s	=	radial sector
R ₁	=	anterior (first) branch of the radial vein
R ₄₊₅	=	branch 4 plus 5 of the radial vein
h	=	humeral crossvein

Table 1. Characters used in the analysis.

#	Character	State alternatives
1.	Male eyes type	1. holoptic; 2. dichoptic.
2.	Eye setation	1. bare; 2. pubescent.
3.	Scape setation	1. with setae; 2. bare.
4.	Shape of postpedicel	1. tapering; 2. ovate and broad.
5.	Length of postpedicel	1. at most 2.5 times as broad; 2. at least 3 times as wide.
6.	Shape of stylus	1. tapering; 2. cylindrical.
7.	Shape of labrum	1. straight; 2. recurved.
8.	Labrum apex shape	1. pointed; 2. truncate.
9.	Epipharyngeal blades	1. present; 2. absent.
10.	Ventroapical comb on labrum	1. present; 2. absent.
11.	Postgenal setae	1. with stout spine like setae; 2. bare or with setae, not spine like.
12.	Prosternum and proepisternum	1. prosternum fused with proepisternum; 2. prosternum separated from proepisternum.
13.	Laterotergite setation	1. with setae; 2. bare.
14.	Setation on anterior face of fore coxa	1. with at most slender and fine setae; 2. with stout, spine like setae.
15.	Inner ventral margin of fore trochanter	1. with spine like setae; 2. with trichoid setae.
16.	Tubercle on fore coxa	1. present; 2. absent.
17.	Male fore tarsal claws	1. present; 2. absent.
18.	Costal bristle	1. present; 2. absent.
19.	Subcosta shape	1. reaching, of fading just before, costa; 2. abruptly ending before costa; 3. curved towards R ₁ .
20.	Shape of Vein R ₄₊₅	1. branched; 2. unbranched.
21.	Shape of CuA	1. recurved; 2. truncate.
22.	Female: tergite 10	1. divided medially; 2. undivided; 3. divided and fused to cercus; 4. absent.
23.	Male: tergite 8 shape	1. slender; 2. broad; 3. absent.
24.	Male: postgonites	1. fused processes from hypandrium; 2. articulated to hypandrium.
25.	Male: presence of ventral surstylus	1. absent; 2. present.
26.	Male: ventral surstylus position	1. absent; 2. apical; 3. subapical, on inner margin of epandrium.
27.	Male: cercus sclerotization	1. thinly sclerotized; 2. heavily sclerotized.
28.	Male: apex of phallus	1. simple; 2. with membranous tube.

Institutional abbreviations

The following depository institutions are mentioned in the text below, following Evenhuis (2019).

MTD	=	Museum für Tierkunde, Dresden, Germany
NHRS	=	Naturhistoriska riksmuseet, Stockholm, Sweden
NHMW	=	Naturhistorisches Museum Wien, Vienna, Austria
MZLU	=	Lund University, Lund, Sweden
NZAC	=	New Zealand Arthropod Collection, Landcare Research, Auckland, New Zealand
USNM	=	National Museum of Natural History, Smithsonian Institution, Washington DC., USA

Table 2. Matrix of scored morphological characters used in analysis.

Character	111111111	22222222
Taxa	123456789	012345678
<i>Dolichopus unguata</i> (Linnaeus, 1758)	121211111	2211122113
<i>Trichopeza longicornis</i> Meigen, 1822	121121111	2212122112
<i>Clinocera nigra</i> Meigen, 1804	221111111	2211122111
<i>Anthepiscopus oedalinus</i> (Zetterstedt, 1838)	111122122	2222122121
<i>Iteaphila macquarti</i> Zetterstedt, 1838	111122122	2222122121
<i>Dipsomyia spinifera</i> Bezzi, 1909	211111221	1221222111
<i>Hormopeza obliterata</i> Zetterstedt, 1838	112212221	1222122211
<i>Hydropeza longipennae</i> (Miller, 1923)	221111221	2212222112
<i>Ragas unica</i> Walker, 1837	112112221	1122212121
<i>Zanclotus dioktes</i> Wilder, 1982	221111221	1122211121

Results

Phylogeny

The strict consensus tree based on a total of 14 trees (Fig. 1) from the maximum parsimony analysis (tree length = 54, consistency index = 0.611, retention index = 0.632, and rescaled consistency index = 0.386) showed that the Ragadidae form a monophyletic unit in relation to the outgroup taxa. *Anthepiscopus* and *Iteaphila* together form a monophyletic sister group to *Hormopeza*. The close relationship between *Hormopeza* and the Iteaphilinae is supported by unique characters in the male terminalia; tergite 8 is broad and rectangular (character 23:2) and has lost the differentiated ventral surstylus (character 25:1). The phylogenetic relationships between the remaining genera are presently unresolved.

Taxonomy

Order Diptera Linnaeus, 1758
Superfamily Empidoidea Latreille, 1809

Family **Ragadidae** Sinclair, 2016
Figs 2A–C, 3, 4A–C, 5

Diagnosis

The Ragadidae are separated from the Dolichopodidae and the Hybotidae Meigen, 1820 by the presence of unrotated and symmetrical male genitalia, and with a point of origin of R_5 at a distance from crossvein h being equal to, or longer than, crossvein h. The family is distinguished from the Atelestidae Hennig, 1970 in having a circumambient costa. It is separated from the Empididae by a prosternum that is separated from the proepisternum (except in species of *Hydropeza*). The representatives of *Hydropeza* are distinguished by the presence of a recurved labrum, which is straight in the Empididae.

Description

Labrum truncate apically. R_5 origins at a distance from crossvein h as long as or longer than crossvein h itself; subcosta reaches costa (except in *Hydropeza* spp.); R_{4+5} branched (except in *Anthepiscopus* spp.); costa circumambient. Prosternum separated from proepisternum (except in *Hydropeza* spp.);

laterotergite bare (except in *Dipsomyia* spp.). Males: terminalia symmetrical and unrotated; postgonites present; cercus weakly sclerotized.

Comments

The diagnostic characters showed below are based on the results of Wahlberg & Johanson (2018), reflecting the expanded concept of including the Iteaphilinae in the family. The Ragadidae are recorded from all the biogeographic regions except Antarctica, and fossil records in Baltic amber suggest this group to be at least 40 million years old (Sinclair 1999).

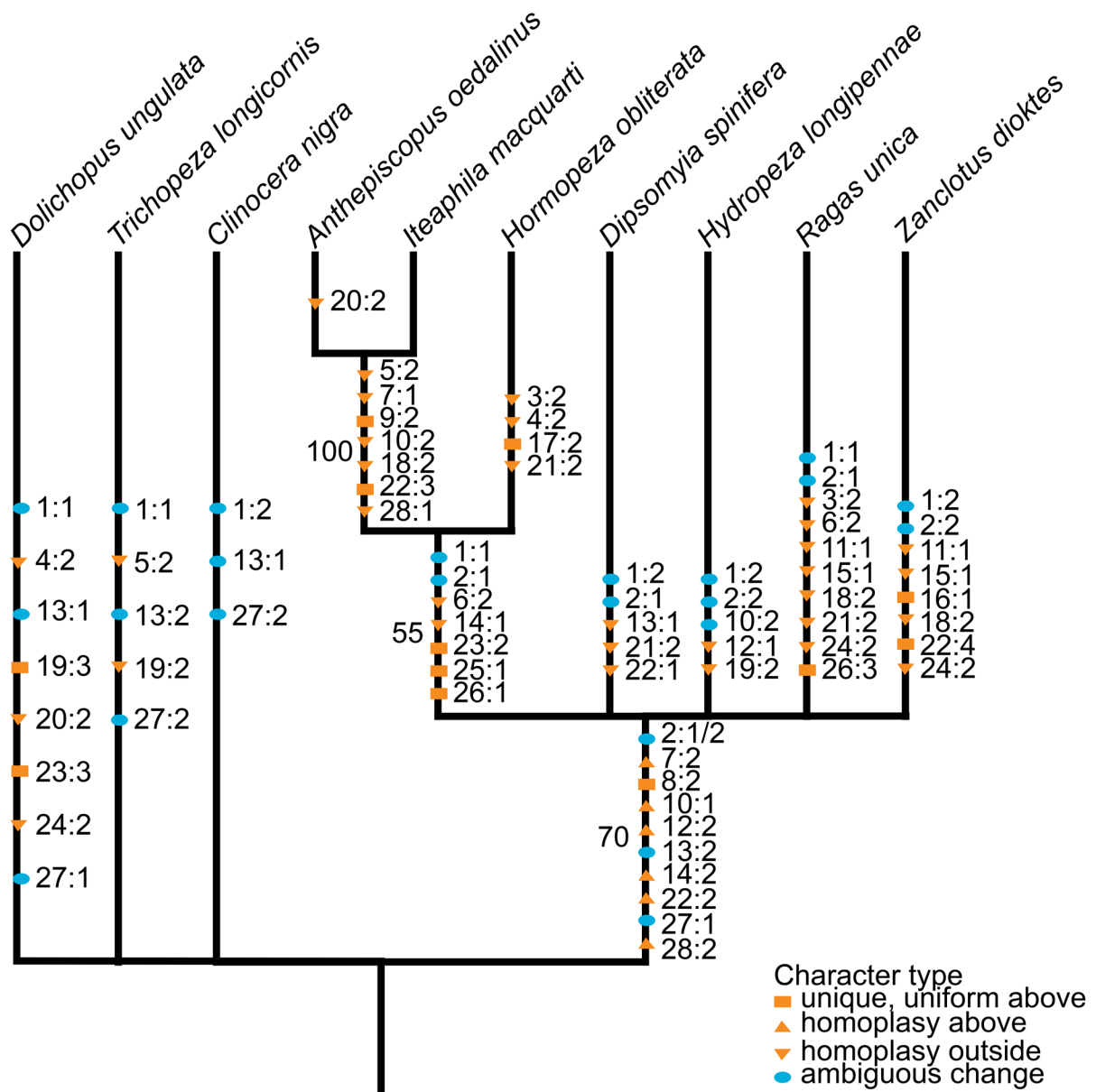


Fig. 1. The strict consensus tree from maximum parsimony analysis with characters mapped. Numbers to the right of character symbols and character numbers show bootstrap support values.

Included subfamilies

Subfamily Ragadinae Sinclair, 2016.

Subfamily Iteaphilinae Wahlberg & Johanson, 2018.

Key to the subfamilies and genera

- 1. Fore coxa with stout spine like setae on anterior face (Fig. 6A)(Ragadinae) 2
- Stout spine like setae on anterior face of fore coxa absent (Fig. 6C)(Iteaphilinae) 5



Fig. 2. Habitus, lateral view. **A.** *Ragas unica* Walker, 1837, ♀, lectotype (UZIL 2629:1; photo courtesy of Rune Bygebjerg, UZIL). **B.** *Ragas unica*, 1 ♀ (NHRS). **C.** *Dipsomyia spinifera* Bezzi, 1909, ♀, holotype (MTD).

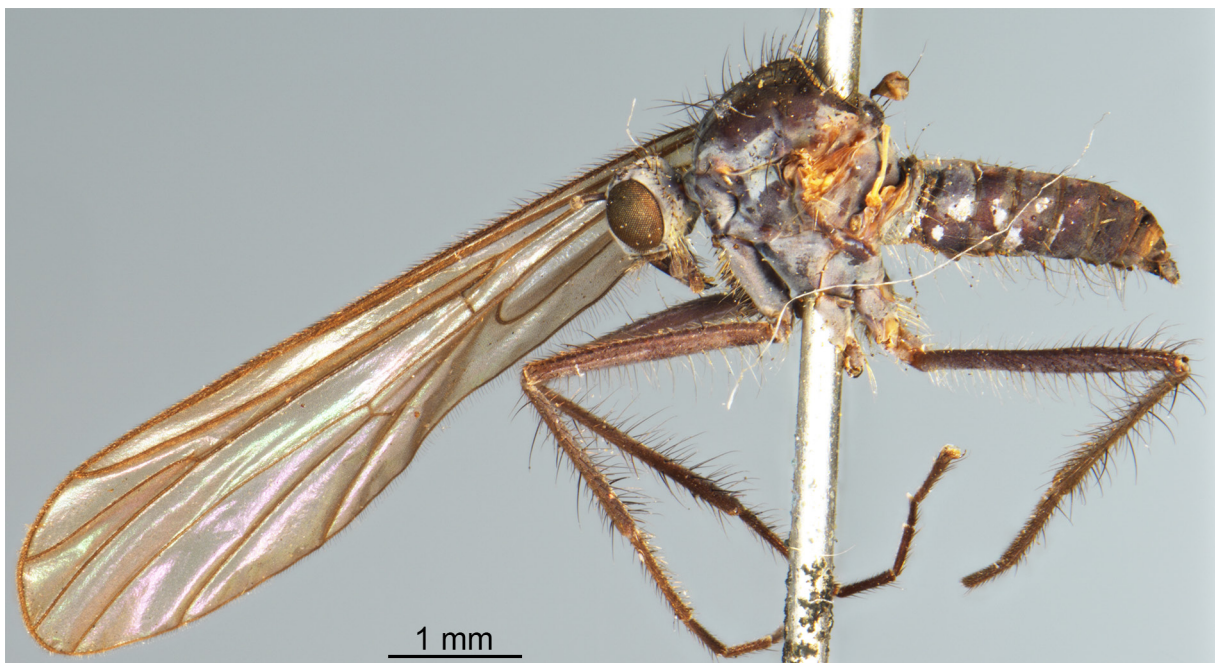


Fig. 3. *Hydropeza longipennae* (Miller, 1923), ♀, holotype, habitus, lateral view (NZAC 04021412).

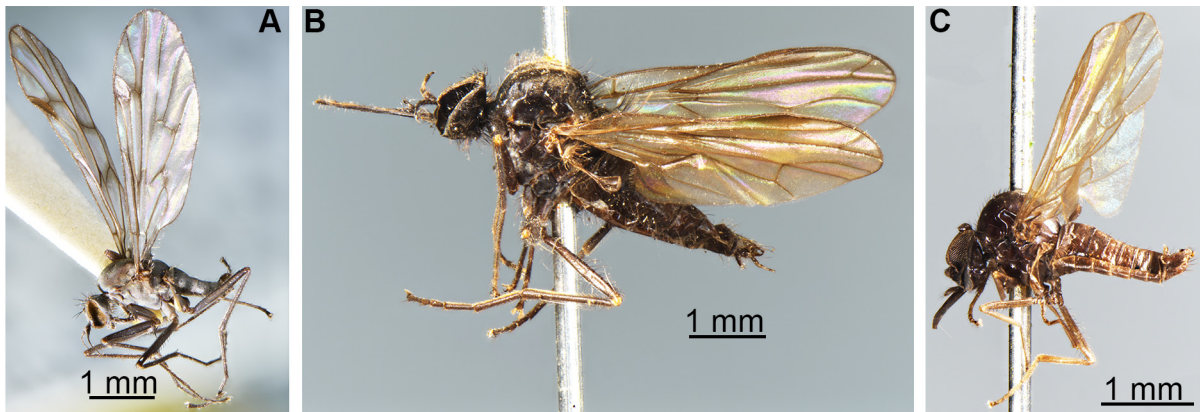


Fig. 4. Habitus, lateral view. **A.** *Zanclostus dioktes* Wilder, 1982, ♂, holotype (USNM). **B.** *Iteaphila macquarti* Zetterstedt, 1838, ♀, holotype (MZLU 3028:1). **C.** *Anthe piscopus oedalinus* (Zetterstedt, 1838), ♂ (NHRS-GULI000058764).



Fig. 5. *Hormopeza obliterata* Zetterstedt, 1838, ♂, holotype, habitus, lateral view (MZLU 5863:1).

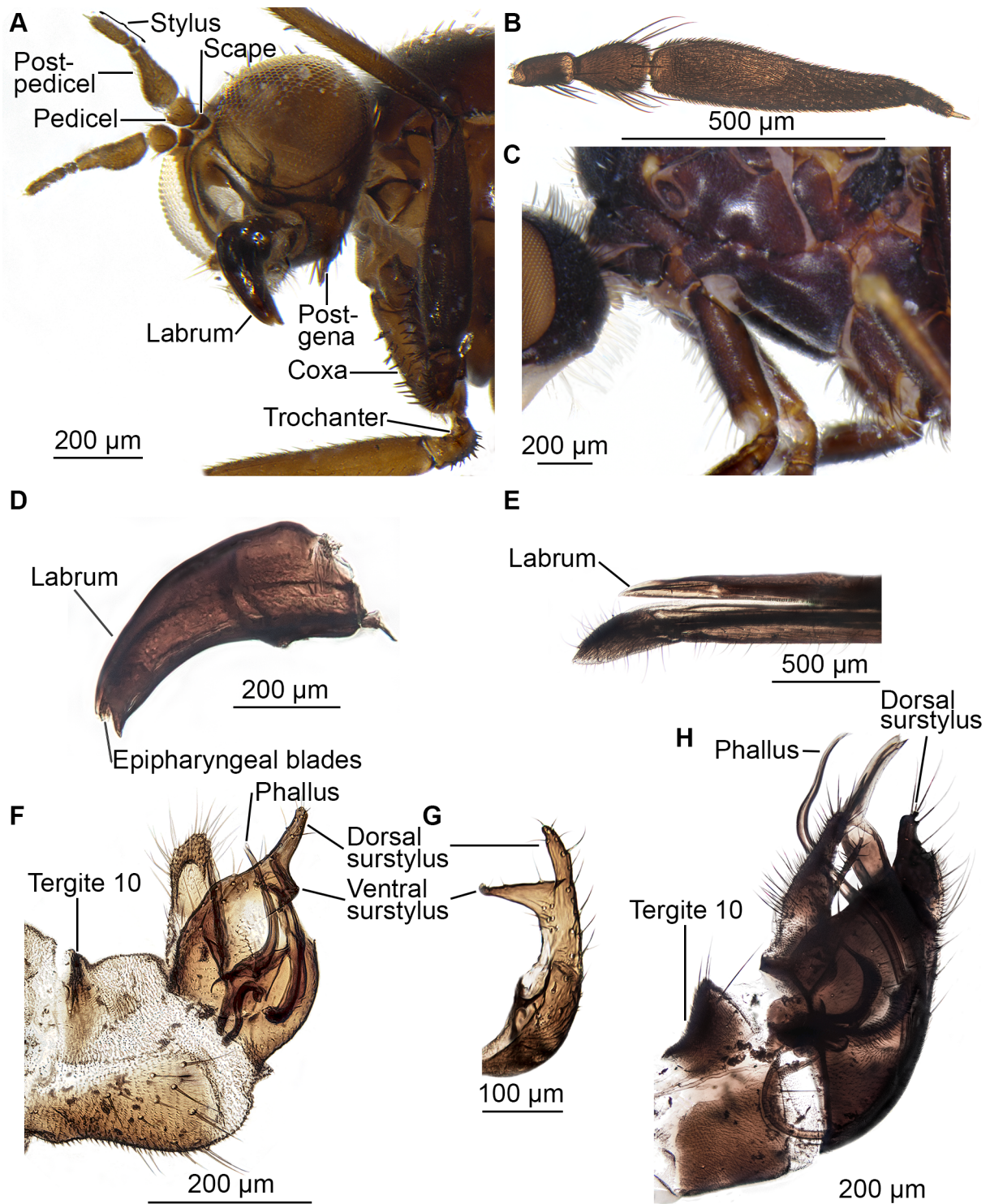


Fig. 6. Habitus, lateral view. **A.** *Ragas unica* Walker, 1837, head and fore leg (NHRS). **B.** *Iteaphila macquarti* Zetterstedt, 1838, antenna (NHRS). **C.** *Iteaphila macquarti*, head and fore leg (NHRS). **D.** *Ragas unica*, mouthparts (NHRS). **E.** *Iteaphila macquarti*, mouthparts (NHRS). **F.** *Ragas unica*, 1 ♂, genitalia, lateral (NHRS). **G.** *Ragas unica*, 1 ♂, right epandrial lobe, dorsal (NHRS). **H.** *Iteaphila macquarti*, 1 ♂, genitalia, lateral (NHRS).

2. Postgena with stout spine like setae (Fig. 6A, 7C); wings without costal bristle; spine like setae present on inner ventral margin of fore trochanter (Figs 6A, 7G)3
 - Postgena bare or with setae, not spine like (Figs 6C, 7A–B); costal bristle present; fore trochanter without spine like setae on inner margin (Figs 6C, 7F)4
3. Eyes pubescent (Fig. 7C); in wings, CuA recurved (Fig. 9D); fore coxa with tubercle (Fig. 7G)*Zanclotus* Wilder, 1982
 - Eyes bare (Fig. 6A); in wings, CuA straight (Fig. 9A); fore coxa without tubercle (Fig. 6A, cf. 7D–F)*Ragas* Walker, 1837
4. Eyes pubescent (Fig. 7B); prosternum fused with proepisternum forming a precoxal bridge (Fig. 7E); laterotergite without setae*Hydropeza* Sinclair, 1999
 - Eyes bare (Fig. 7A); prosternum separated from proepisternum forming an isolated sclerite (Fig. 7D); laterotergite with setae *Dipsomyia* Bezzi, 1909
5. In wings, costal bristle present; CuA straight (Fig. 9G); scape always bare (Fig. 8A) *Hormopeza* Zetterstedt, 1838
 - In wings, costal bristle absent; CuA recurved (Figs 9E–F); scape always with setae (Fig. 6B) ...6
6. In wings, R₄₊₅ branched into R₄ and R₅ (Fig. 9E) *Iteaphila* Zetterstedt, 1838
 - In wings, R₄₊₅ unbranched (Fig. 9F)*Anthepiscopus* Becker, 1891

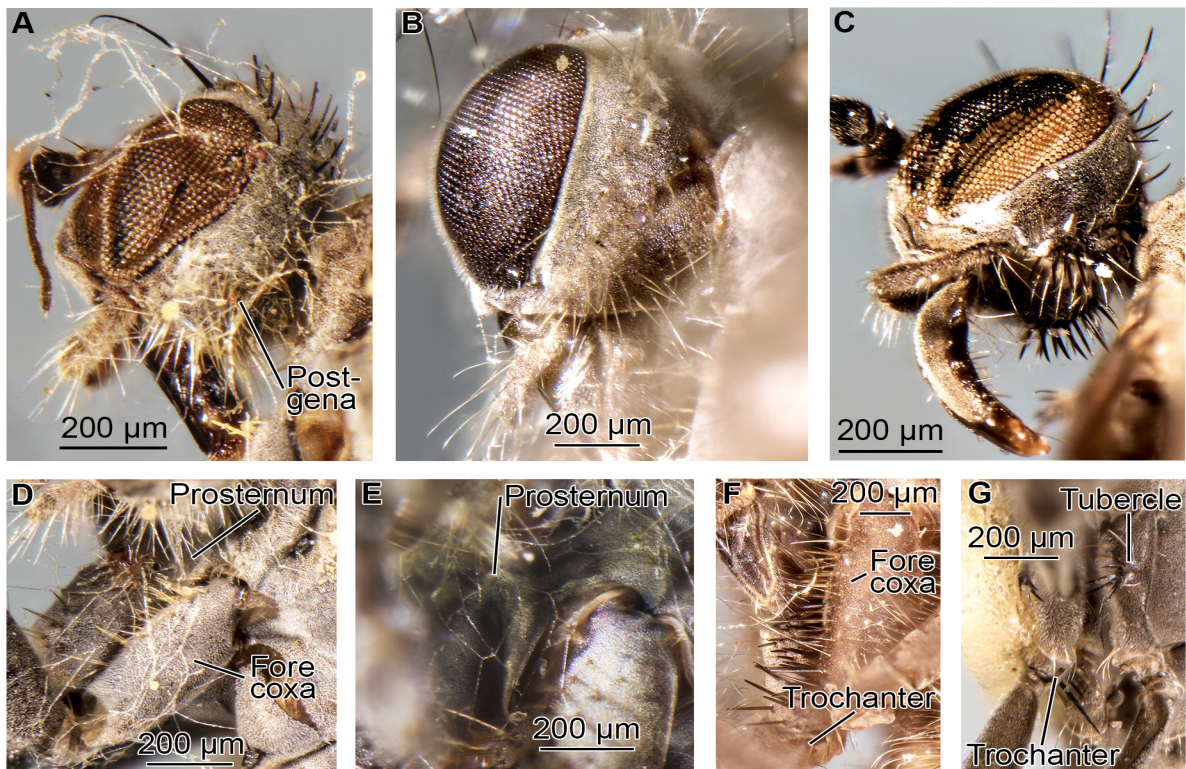


Fig. 7. A–C. Eye and postgena. A. *Dipsomyia spinifera* Bezzi, 1909 (MTD). B. *Hydropeza longipennae* (Miller, 1923) (NZAC 04021412). C. *Zanclotus dioktes* Wilder, 1982 (USNM). D. *Dipsomyia spinifera*, prosternum and fore coxa (MTD). E. *Hydropeza longipennae*, prosternum (NZAC 04021412). F–G. Fore coxa and trochanter. F. *Hydropeza longipennae* (NZAC 04021412). G. *Zanclotus dioktes* (USNM).

Subfamily **Ragadinae** Sinclair, 2016

Figs 2A–C, 3, 4A, 9A–D

Diagnosis

The species of the subfamily Ragadidae are distinguished from those of the Iteaphilinae by the length of the postpedicel and the shape of tergite 8 in males (see the description below and the key above for details). The stout and spine-like setae on fore coxa are synapomorphies for this group. Its included species can be further distinguished by the presence of a recurved labrum in both males and females (in the Iteaphilinae, the labrum is recurved only in the females of *Hormopeza*).

Type genus

Ragas Walker, 1837.

Description

Postpedicel always at most two and a half times as long as broad (Fig. 6A). Labrum recurved in both males and females (Fig. 6D). Anterior of fore coxa with stout, spine like setae (Fig. 6A). Males: tergite 8 slender in shape (Fig. 6F); ventral surstylus distinguishable (Fig. 6G).

Comments

The first formal description of this group included the genera *Dipsomyia*, *Hormopeza*, *Hydropeza*, *Ragas*, and *Zanclotus* (Sinclair 2016). In the analysis herein, it is found that this subfamily, excluding *Hormopeza*, can be distinguished only by a few diagnostic characters.

Included genera

Ragas Walker, 1837.

Dipsomyia Bezzi, 1909.

Hydropeza Sinclair, 1999.

Zanclotus Wilder, 1982.

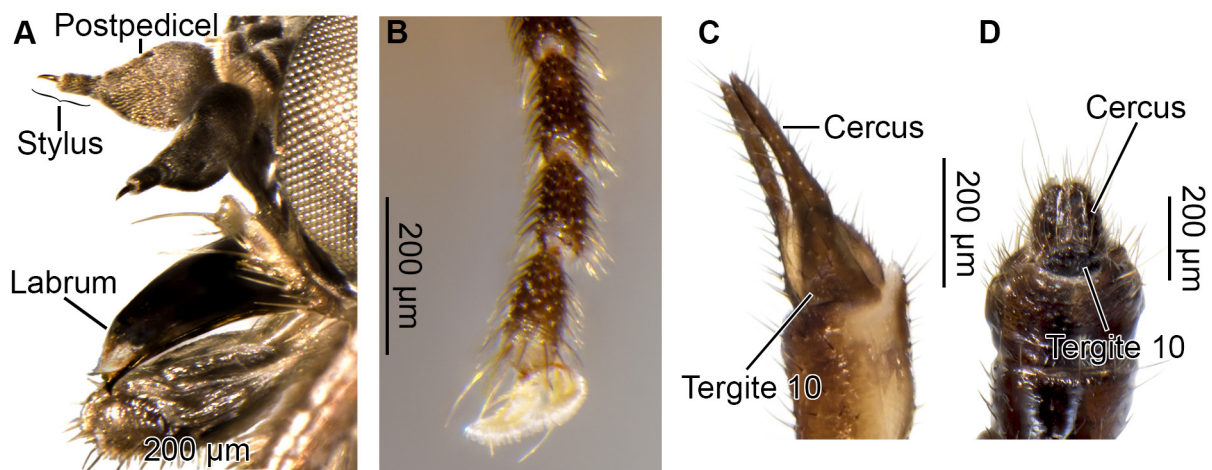


Fig. 8. A–B. *Hormopeza obliterated* Zetterstedt, 1838. A. Antennae and mouthparts, ♀ (NHRS-000061621). B. Apical part of tarsus, ♂ (NHRS-000061670). C–D. Terminalia, ♀. C. *Iteaphila macquarti* Zetterstedt, 1838, dorsolateral (NHRS). D. *Hormopeza obliterated*, dorsal (NHRS-000061621).

Genus *Ragas* Walker, 1837
Figs 2A–B, 6A, D, F–G, 9A

Diagnosis

The species in the genus *Ragas* are recognized by having spine like setae on the postgena and on the inner ventral margin of the fore trochanter, and lack costal bristles. These character stages are shared with species in the genus *Zanclotus*, from which they can be distinguished by having bare instead of pubescent eyes, and straight instead of recurved CuA.

Type species

Ragas unica Walker, 1837.

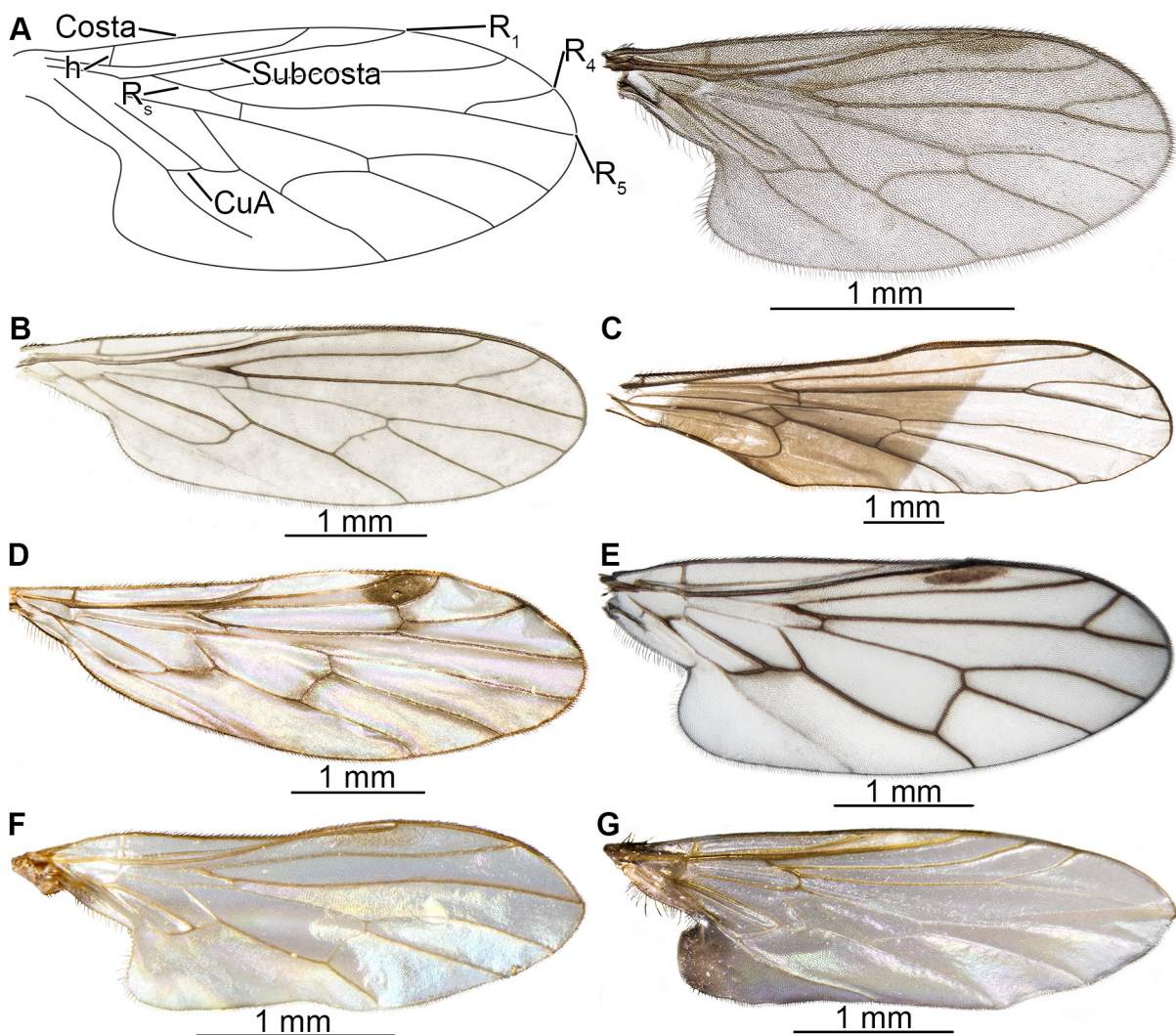


Fig. 9. Right wing. **A.** *Ragas unica* Walker, 1837, drawing with terminology on characters (left) and photo (right) (NHRS). **B.** *Dipsomyia spinifera* Bezzi, 1909 (MTD). **C.** *Hydropeza longipennae* (Miller, 1923) (dark colour is from underlying board to which the wing is glued) (NZAC 04021412). **D.** *Zanclotus dioktes* Wilder, 1982 (USNM). **E.** *Iteaphila macquarti* Zetterstedt, 1838 (NHRS). **F.** *Anthepiscopus oedalinus* (Zetterstedt, 1838) (NHRS-GULI000058764). **G.** *Hormopeza obliterated* Zetterstedt, 1838 (NHRS-000061621).

Material examined of *Ragas unica*

Lectotype

SWEDEN • 1 ♀; UZIL 2629:1.

Paralectotype

SWEDEN • 1 ♀; UZIL 2629:2.

Other material

SWEDEN • 1 ♂; Västerbotten, Vindelns kommun, Kulbäckslidens trail park; 2 Dec. 2003–16 Jun. 2004; Swedish Malaise Trap Project leg.; Malaise trap, dense, 25 years old mixed coniferous forest; DNA voucher AB7E, NHRS • 1 ♀; Småland, Högsby kommun, Hornsö kronopark, vicinity of Skärsgölorna, near end of Nya Kringlavägen; 30 Jun.–10 Jul. 2004; Swedish Malaise Trap Project leg.; Malaise trap, birch fen; DNA voucher AS9E, NHRS.

Description

Eyes bare; males holoptic (Fig. 6A). Scape bare; postpedicel tapering; stylus cylindrical (Fig. 6A). Epipharyngeal blades (Fig. 6D) and ventroapical comb present. Postgena with stout spine-like setae (Fig. 6A). Prosternum separated from proepisternum forming an isolated sclerite; laterotergite bare. Stout spine-like setae on anterior face of fore coxa and on inner ventral margin of fore trochanter present (Fig. 6A); tubercle on fore coxa absent; male fore tarsal claws present. In wings, costal bristle absent; subcosta reaching costa; R_{4+5} divided (or branching) into R_4 and R_5 ; CuA straight (Fig. 9A). Females: tergite 10 undivided. Males: postgonites articulated to hypandrium; ventral surstylus position subapical, on inner margin of epandrium (Fig. 6G); apex of phallus membranous (Fig. 6F).

Distribution

Holarctic, with records from North America through Europe and Russia to East Asia (Sinclair & Saigusa 2001).

Genus *Dipsomyia* Bezzi, 1909

Figs 2C, 7A, D, 9B

Diagnosis

Species in the genus *Dipsomyia* are distinguished from those in *Ragas* and *Zanclotus* by the lack of stout setae on postgena and the fore trochanter. The lack of pubescence on the eyes, the setose laterotergite and the isolated prosternum separates the species of *Dipsomyia* from *Hydropeza*.

Type species

Dipsomyia spinifera Bezzi, 1909.

Material examined of *Dipsomyia spinifera*

Holotype

CHILE • ♀; [Quillota]; [1000 m a.s.l.]; 22 Sep. 1902; W. Schnuse leg.; MTD.

Description

Eyes bare (Fig 7A); males dichoptic (Sinclair 1999). Scape with setae; postpedicel tapering; stylus tapering. Epipharyngeal blades and ventroapical comb present. Postgena bare or with setae, not spine like (Fig. 7A). Prosternum separated from proepisternum forming an isolated sclerite (Fig. 7D); laterotergite with setae. Stout spine like setae on anterior face of fore coxa present; spine like setae on inner ventral

margin of fore trochanter absent; tubercle on fore coxa absent (Fig. 7D); male fore tarsal claws present. In wings, costal bristle present; subcosta reaching costa; R_{4+5} branched; CuA straight (Fig. 9B). Females: tergite 10 divided medially. Males: postgonites as fused processes from hypandrium; ventral surstylus position apical; apex of phallus membranous (Sinclair 1999).

Distribution

The only known species in this genus is endemic to Chile.

Genus *Hydropeza* Sinclair, 1999

Figs 3, 7B, 7E–F, 9C

Diagnosis

The species in the genus *Hydropeza* resemble those of *Dipsomyia* by lacking the stout setae on the postgena, and the fore trochanter that is present in species in the genera *Ragas* and *Zanclotus*. Species in *Hydropeza* are distinguished from those in *Dipsomyia* by having pubescent eyes, a bare laterotergite, and a prosternum that is fused with the proepisternum and forming a precoxal bridge.

Type species

Trichopeza longipennae (Miller, 1923).

Material examined of *Trichopeza longipennae*

Lectotype

NEW ZEALAND • 1 ♀; Otira; 10 Jan. 1920; NZAC 04021412.

Paralectotype

NEW ZEALAND • 2 ♀♀; same data as for lectotype; NZAC 04021441, NZAC 04021437.

Other material

NEW ZEALAND • 1 ♂; Mount Arthur, Flora Street; 3000 ft; 20 Nov. 1969; B.M. May leg.; on surface; NZAC • 2 ♀♀; same data as for preceding; NZAC.

Description

Eyes pubescent (Fig. 7B); males dichoptic. Scape with setae; postpedicel tapering; stylus tapering. Epipharyngeal blades present; ventroapical comb on labrum absent. Postgena bare or with setae (Fig. 7B), not spine like. Prosternum fused with proepisternum forming a precoxal bridge (Fig. 7E); laterotergite bare. Stout spine like setae on anterior face of fore coxa present; spine like setae on inner ventral margin of fore trochanter absent; tubercle on fore coxa absent (Fig. 7F); male fore tarsal claws present. In wings, costal bristle present; subcosta abruptly incomplete; R_{4+5} branched; CuA recurved (Fig. 9C). Females: tergite 10 undivided. Males: postgonites as fused processes from hypandrium; ventral surstylus position apical; apex of phallus membranous.

Distribution

This genus is known from Chile, west Australia and New Zealand (Sinclair 2016).

Genus *Zanclotus* Wilder, 1982
Figs 4A, 7C, 7G, 9D

Diagnosis

The species in the genus *Zanclotus* are most similar to those in the genus *Ragas*, particularly by the presence of spine-like setae on postgena, and the inner margin of the fore trochanter. The species are distinguished from the species of *Ragas* by the pubescent eyes and recurved CuA in the wings. A unique character of species of *Zanclotus* is the presence of a tubercle on the coxa of each fore leg.

Type species

Zanclotus dioktes Wilder, 1982.

Material examined of *Zanclotus dioktes*

Holotype

USA • ♂; Washington, Mt. Rainer Nat. Park, Edith Cr. at Paradise Park; 1650 m a.s.l.; 11 Oct. 1979; D. Wilder leg.; USNM.

Allotype

USA • 1 ♀; same data as for holotype; USNM.

Description

Eyes pubescent (Fig. 7C); males dichoptic. Scape with setae, postpedicel tapering; stylus tapering. Epipharyngeal blades and ventroapical comb present. Postgena with stout spine like setae (Fig. 7C). Prosternum separated from proepisternum forming an isolated sclerite; laterotergite bare. Stout spine like setae on anterior face of fore coxa and on inner ventral margin of fore trochanter present; tubercle on fore coxa present (Fig. 7G); male fore tarsal claws present. In wings, costal bristle absent; subcosta reaching costa; R₄₊₅ branched; CuA recurved (Fig. 9D). Female: tergite 10 absent. Male: postgonites articulated to hypandrium; ventral surstylus position apical; apex of phallus membranous.

Distribution

Only two species are known, both from Washington State, USA.

Subfamily **Iteaphilinae** Wahlberg & Johanson, 2018
Figs 4B–C, 5, 9E–G

Diagnosis

The species in this subfamily are recognized by the broad and rectangular tergite 8 in the males. All species lack spine like setae on fore coxa, in contrast to species in the subfamily Ragadinae, and the labrum is straight, except for females in the genus *Hormopeza*.

Type genus

Iteaphila Zetterstedt, 1838.

Description

Postpedicel (Fig. 6B) at least three times as long as wide (except for *Hormopeza*). Labrum straight in males (Fig. 6E). Lacking anterior stout, spine like setae on the fore coxa, at most slender setae are present (Fig. 6C). Male: tergite 8 broad and rectangular in shape; ventral surstylus absent (Fig. 6H), except for the '*Iteaphila setosa*-group'.

Included genera

Iteaphila Zetterstedt, 1838.
Anthepiscopus Becker, 1891.
Hormopeza Zetterstedt, 1838.

Genus *Iteaphila* Zetterstedt, 1838
 Figs 4B, 6B, 6E, 6H, 8C

Diagnosis

The synapomorphies of this genus and *Anthepiscopus* are the loss of epipharyngeal blades and the tergite 10 fused with the cercus in females. Both males and females possess a straight labrum, in contrast to *Hormopeza* spp., where only males possess a straight labrum. Further similarities with species in *Anthepiscopus* are the setose scape, the loss of costal bristle and the recurved CuA in the wings (except for '*Iteaphila setosa*-group' for the latter two characters). The species in the genus are distinguished from those of *Anthepiscopus* by having a branched R₄₊₅.

Type species

Iteaphila macquarti Zetterstedt, 1838.

Material examined of *Iteaphila macquarti***Lectotype**

NORWAY • 1 ♂; "Werdalen, Naes"; [4 Jun.]; D. Boheman leg.; MZLU 3028:1.

Other material

SWEDEN • 1 ♂; Lappland, Kiruna kommun, Abisko nationalpark, Nuolja; 26 Jun.–15 Jul. 2006; Swedish Malaise Trap Project leg.; Malaise trap, bare mountain; DNA voucher AD7E; NHRS • 23 ♀♀; same data as for preceding; NHRS.

Description

Eyes bare; males holoptic. Scape with setae; postpedicel tapering, at least 3 times as long as wide; stylus cylindrical (Fig. 6B). Labrum straight in both sexes (6E); epipharyngeal blades and ventroapical comb absent. Postgena bare or with setae, not spine like (Fig. 6C). Prosternum separated from proepisternum and forming an isolated sclerite; laterotergite bare. Stout spine-like setae present on anterior face of fore coxa and inner ventral margin of fore trochanter absent (Fig. 6C); tubercle lacking on fore coxa; male fore tarsal claws present. Costal bristle absent; subcosta reaching costa; R₄₊₅ branched; CuA recurved (Fig. 9E). Females: tergite 10 fused to cercus (Fig. 8C). Males: postgonites form fused processes from hypandrium; the apex of the phallus is simple (Fig. 6H).

Distribution

The genus *Iteaphila* is the most widely spread group within the Ragadidae, with representatives in the Nearctic, Palearctic and Oriental regions (Shamshev & Sinclair 2009; Sinclair & Shamshev 2012).

Comments

Sinclair & Saigusa (2001) transferred *Ragas setosa* (Bezzi 1924) to the genus *Iteaphila* based on the presence of a straight labrum, the absence of spine like setae on fore coxa and postgena, the palpus projection and the shape of the male terminalia. Shamshev & Sinclair (2009) assigned this species together with several other from the southern Europe, the northern Africa and the Middle East to the '*Iteaphila setosa*-group'. This group, however, possesses species with numerous peculiar characters

such as both ventral and dorsal surstyli, costal bristle, antennal shape and modification in male hind femur, and its affinity to other species in *Iteaphila* is unclear. For the analysis herein, the characters present in the type species were used and the above listed characters treated as uniquely or possibly secondarily derived in the group. Further examination of morphological characters such as mouthparts, as well as DNA data is needed to clarify the phylogenetic position of this group.

Genus *Anthepiscopus* Becker, 1891

Figs 4C, 9F

Diagnosis

The species of this genus share synapomorphies and similarities with the species of the genus *Iteaphila*, which also separate these two genera from *Hormopeza*. These characteristics include the lack of epipharyngeal blades, the straight labrum in both sexes, the setose scape, the loss of costal bristle in the wings, the recurved CuA, and the tergite 10 fused to the cercus in females. The species of this genus are distinguished from those of *Iteaphila* by the presence of an unbranched R_{4+5} .

Type species

Anthepiscopus ribesii Becker, 1891.

Material examined of *Anthepiscopus ribesii*

AUSTRIA • 2 ♂♂; Admont, Styria; 1896; Strobl leg.; NHMW.

Material examined of *Anthepiscopus oedalinus* (Zetterstedt, 1838)

SWEDEN • 1 ♀; [Lapponia inferior, Lappland]; [D. Boheman leg.]; NHRS-GULI000058763 • 1 ♂; same data as for preceding; NHRS-GULI000058764.

Description

Eyes bare; males holoptic. Scape with setae; postpedicel tapering, at least three times as long as wide; stylus cylindrical. Labrum straight in both sexes; epipharyngeal blades and ventroapical comb absent. Postgena bare or with setae, not spine like. Prosternum separated from proepisternum forming an isolated sclerite; laterotergite bare. Stout spine like setae on anterior face of fore coxa and on inner ventral margin of fore trochanter absent; tubercle on fore coxa absent; male fore tarsal claws present. In wings, costal bristle absent; subcosta reaching costa; R_{4+5} unbranched; CuA recurved (Fig. 9F). Female: tergite 10 fused to cercus. Male: postgonites as fused processes from hypandrium; apex of phallus simple.

Distribution

This genus is represented in the Nearctic and west Palearctic. In addition, one species is recorded from Australia.

Genus *Hormopeza* Zetterstedt, 1838

Figs 5, 8A–B, 8D

Diagnosis

The species of the genus *Hormopeza* are separated from the species of *Iteaphila* and *Anthepiscopus* by the presence of epipharyngeal blades and costal bristle, the scape is bare and CuA straight. Males lack claws on the fore legs, and females have a recurved labrum a tergite 10 separate from to cercus.

Type species

Hormopeza obliterated Zetterstedt, 1838.

Material examined of *Hormopeza obliterated***Holotype**

FINLAND • ♂; Turtola; [25 Aug. 1821]; MZLU 5863:1.

Other material

SWEDEN • 1 ♂; Dalarna, Falun, Svartnäs, Lill-Sixen, burnt 1999; 15–17 Jun. 1999; Malaise trap; NHRS-000061670 • 1 ♀; same data as for preceding; NHRS-000061621.

Description

Eyes bare; male eyes holoptic. Scape bare; postpedicel ovate and broad, at most two and a half times as long as broad; stylus cylindrical (Fig. 8A). Labrum recurved in females only; epipharyngeal blades and ventroapical comb present (Fig. 8A). Postgena bare or with setae, not spine like. Prosternum separated from proepisternum forming an isolated sclerite; laterotergite bare. Stout spine like setae on anterior face of fore coxa and inner ventral margin of fore trochanter absent; tubercle on fore coxa absent; male fore tarsal claws absent (Fig. 8B). Costal bristle present; subcosta reaching costa; R₄₊₅ branched; CuA straight. Female: tergite 10 undivided (Fig. 8D). Male: postgonites form fused processes from hypandrium; apex of phallus membranous.

Distribution

Hormopeza spp. are known from the Nearctic, Palaearctic, Oriental and Neotropical regions (Daugeron 1999).

Discussion

When Chvála described the subfamily Oreogetoninae (Chvála 1976), he expressed a probable close relationship between the genera *Anthepiscopus* and *Iteaphila* and the genera *Hormopeza* and *Ragas*. However, more recent authors considered the groups of *Iteaphila* and *Ragas* only as distant relatives with the ‘*Iteaphila*-group’ as *incertae sedis* within the Empidoidea, and the ‘*Ragas*-group’ as *incertae sedis* within the Empididae (Sinclair & Cumming 2006), or later as a subfamily within the Empididae (Sinclair 2016). In Wahlberg & Johanson (2018), the close relationship between *Anthepiscopus*, *Iteaphila* and *Ragas* was re-established, and the family Ragadidae was established based on the molecular distances separating this group and the Empididae. The present study further explores this concept, and the analysis of morphological data indicates a distinct clade including *Iteaphila*, *Anthepiscopus* and *Hormopeza* separate from the remaining Ragadidae. The synapomorphy of this group including *Hormopeza* in the ‘*Ragas*-group’, according to Sinclair (1999) and Sinclair & Cumming (2006), is a membranous distiphallus. However, this character may vary in different degree of sclerotization and form, even within empidoid genera (e.g., in *Hesperemis* Melander, 1906, see Cumming *et al.* 2013). The recurved labrum is found to be a homoplastic character in the phylogenetic analysis in the present study. The genus *Hormopeza* is therefore transferred from this subfamily. The diagnosis and description of the Iteaphilinae and the Ragadinae are updated to reflect the results herein, based on labrum shape, chaetotaxy of fore coxa, and characters in male genitalia. The monophyly of the genus *Iteaphila* in relation to *Anthepiscopus* is dubious (Sinclair & Shamshev 2012), which was also indicated in Walberg & Johanson (2018). Further molecular studies including a broader taxon sampling are required to resolve this relationship, as well as the monophyly in regard to the ‘*Iteaphila setosa*-group’. The morphological similarities reviewed herein between *Ragas* and *Zanclotus* is coherent with the results in Sinclair (1999). The spine like setae on fore coxa and postgena, and the fore coxal tubercle in *Zanclotus*, are hypothesized to be morphological adaptations to catch and handle prey. The presence

of epipharyngeal blades strengthens the notion of a predatory lifestyle as these may be used in cutting prey tissue (Bletchly 1954; McAlpine 1981). Species in the genus *Hormopeza* lack the spine-like setae on for coxa present in species of the Ragadinae, and species in *Anthepiscopus* and *Iteaphila* also lack epipharyngeal blades. *Iteaphila* has been observed feeding on flowers (Shamshev & Sinclair 2009), especially in early spring and may be an early pollinator. Many of the species of the Ragadidae are rarely collected, and there have been few observations of feeding and mating behaviour. A few genera remain unplaced, e.g., *Oreogeton* within the Empidoidea. Further studies, preferably combinations of molecular and morphological methods, are warranted to properly assign *Oreogeton* and the other unplaced genera to formal taxonomic groups. Steps towards accessible and thorough classification, not only in this group, but also within other groups within the Empidoidea, together with up-to-date determination keys may, hopefully, lead to more attention to these flies and their roles in ecological systems.

Acknowledgements

The following people are thanked for assistance in loans of material used in this study: Rune Bygebjerg (MZLU), Dr. Torsten Dikow (USNM), Dr. Allen L. Norrbom (USNM), Dr. Michael Ohl (MTD), and Dr. Darren Ward (NZAC). Dr. Bradley Sinclair (Canadian National Collection of Insects and Canadian Food Inspection Agency) have provided interesting feedback and insights in empidoid systematics and taxonomy.

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Manuscript received: 18 March 2019

Manuscript accepted: 4 April 2019

Published on: 29 April 2019

Topic editor: Gavin Broad

Desk editor: Alejandro Quintanar

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