

Guide and keys for the identification of Syllidae (Annelida, Phyllodocida) from the British Isles (reported and expected species)

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Abstract

In November 2012, a workshop was carried out on the taxonomy and systematics of the family Syllidae (Annelida: Phyllodocida) at the Dove Marine Laboratory, Cullercoats, Tynemouth, UK for the National Marine Biological Analytical Quality Control (NMBAQC) Scheme. Illustrated keys for subfamilies, genera and species found in British and Irish waters were provided for participants from the major national agencies and consultancies involved in benthic sample processing. After the workshop, we prepared updates to these keys, to include some additional species provided by participants, and some species reported from nearby areas. In this paper, we provide the revised keys to enable rapid identification of Syllidae from the seas around Britain and Ireland. One new combination, *Palposyllis propeweismanni*, is proposed.

Keywords

Identification, keys, NE Atlantic Ocean, Polychaeta

Introduction

Syllids are small to medium-sized polychaetes (from 2–3 mm long and 15–30 chaetigers, up to about 140 mm and 200 chaetigers). They are extremely abundant and diverse in benthic marine shallow habitats and also inhabit deep areas; however, they

are absent from fresh water and are not an important group in estuaries. They are very common on hard substrata, having an errant life among algae, biogenic structures, crevices, within porous rocks, etc. and they also inhabit marine sediments, especially coarse sand, where most species have an interstitial lifestyle. Also, numerous species are associated with other marine organisms, especially sponges and octocorals, mostly in tropical waters.

As syllids may constitute more than 50% (sometimes more than 70%) of the polychaete species that live in some substrata, they are very important in benthic studies. However, because of their small size, they are often overlooked, since most benthic ecology studies are devoted to macrofauna. Furthermore, they are difficult to identify because of their small size and the lack of taxonomic studies and monographs with keys and detailed descriptions for many areas. Syllids are very easy to recognize to family level, because they have a conspicuous modification of the gut, the proventriculus (=proventricle), which constitutes the autapomorphy of the family. The taxonomy and systematics are also complex and difficult, again because of their small size, numerous taxa (approximately 74 genera and 700 species), and the difficulty to correctly observe the characters. This paper is directed to participants of the NMBAQC Scheme and to all laboratory staff and students who need to familiarize themselves with the syllid fauna that may be found in benthic studies from British or Irish waters. Since the workshop, the keys have been modified and completed with the species identified during the workshop, many of which are not yet formally reported in the area. We have included reference numbers (in brackets after each species) to recommended descriptions cited in the references. Comparison of specimens with descriptions and figures is highly recommended. Also, it is necessary to note that fixed specimens lose their pigmentation after some time, and also that young, small specimens have appendages proportionally shorter than large, mature specimens. Also, note that the taxonomy and systematics are not yet completed and some changes and additions are probable in future years. Some genera need careful revision, and some species are only tentatively included in a particular genus, since they do not fit perfectly with the diagnosis of that genus.

Howson and Picton (1997) listed the following species as likely to be found in British water, which are herein arranged according to recent classifications (Aguado and San Martín 2009; Aguado et al. 2007, 2012; Nygren 2004; San Martín and Aguado 2014):

Subfamily **Anoplosyllinae** Aguado & San Martín, 2009: *Streptosyllis bidentata* Southern, 1914; *S. websteri* Southern, 1914; *Syllides benedicti* Banse, 1971; *S. longocirrata* Ørsted, 1845.

Subfamily **Eusyllinae** Malaquin, 1893: *Eusyllis assimilis* Marenzeller, 1875; *E. blomstrandii* Malmgren, 1867; *E. lamelligera* Marion & Bobretzky, 1875; *Nudisyllis divaricata* (Keferstein, 1862); *N. pulligera* (Krohn, 1852); *Odontosyllis ctenostoma* Claparède, 1868; *O. fulgurans* (Audouin & Milne-Edwards, 1833); *O. gibba* Claparède, 1863; *Opisthodonta longocirrata* (Saint-Joseph, 1886); *Pionosyllis compacta* Malmgren, 1867; *Synmerosyllis lamelligera* (Saint-Joseph, 1886).

Subfamily **Exogoninae** Langerhans, 1879: *Brania pusilla* (Dujardin, 1851); *Erinaceusyllis erinaceus* (Claparède, 1863); *Salvatoria clavata* (Claparède, 1863); *S. limbata* (Claparède, 1868); *S. swedmarki* (Gidholm, 1962); *Exogone dispar* (Webster, 1879); *E. naidina* Ørsted, 1845; *E. verugera* (Claparède, 1868); *Parexogone longicirris* (Webster & Benedict, 1887); *P. hebes* (Webster & Benedict, 1884); *Prosphaerosyllis tetralix* (Eliason, 1920); *Sphaerosyllis bulbosa* Southern, 1914; *S. hystrix* Claparède, 1863; *S. pirifera* Claparède, 1868; *S. taylora* Perkins, 1980.

Subfamily **Syllinae** Grube, 1850: *Eurysyllis tuberculata* Ehlers, 1864; *Haplosyllis spongicola* (Grube, 1855); *Syllis amica* Quatrefages, 1866; *S. armillaris* (O.F. Müller, 1771); *S. cornuta* Rathke, 1843; *S. gracilis* Grube, 1840; *S. garciai* (Campoy, 1981); *S. hyalina* Grube, 1863; *S. krohnii* Ehlers, 1864; *S. prolifera* Krohn, 1852; *S. variegata* Grube, 1860; *S. vittata* Grube, 1840; *Trypanosyllis coeliaca* Claparède, 1868; *T. zebra* (Grube, 1860).

Subfamily **Autolytinae** Langerhans, 1879: *Epigamia alexandri* (Malmgren, 1867); *Myrianida brachycephala* (Marenzeller, 1874); *M. edwardsi* (Saint-Joseph, 1886); *M. inermis* (Saint-Joseph, 1886); *M. langerhansi* (Gidholm, 1967); *M. pinnigera* (Montagu, 1808); *M. prolifera* (O.F. Müller, 1788); *M. quinquedecimdentata* (Langerhans, 1884); *M. rubropunctata* (Grube, 1860); *Proceraea aurantiaca* Claparède, 1868; *P. cornuta* (Agassiz, 1862); *P. picta* Ehlers, 1864; *P. prismatica* (O.F. Müller, 1776); *Procerastea halleziana* Malaquin, 1893; *P. nematodes* Langerhans, 1884.

Uncertain status: *Amblyosyllis formosa* (Claparède, 1863); *Dioplosyllis cirrosa* (Gidholm, 1962); *Palposyllis prosostoma* (Hartmann-Schröder, 1977); *Paraehlersia ferruginea* (Langerhans, 1881); *Streptodonta pterochaeta* (Southern, 1914).

Another 18 syllid taxa were also reported, but they are synonyms of other species, invalid, or doubtful species, or even not recognized as Syllidae.

This number of species is quite low for such an area and it is certain that many other species live in British waters. In the keys below, we have included all previously reported species (excluding invalid or doubtful ones) plus those that have been reported from nearby areas of the NE Atlantic and that could be also present in the study area. Some of these were noted at the NMBAQC workshop or since that time but are not yet formally recorded. It is important to remember the possibility that other species, not in the keys presented here, may yet be found in the area and reference should be made to additional literature for any specimens that do not fit descriptions. Books with keys for syllids of nearby areas include those by Fauvel (1923) (France), Hartmann-Schröder (1996) (Germany), and San Martín (2003) (Iberian Peninsula). A previous NMBAQC workshop (2006) included work on syllids led by Peter Garwood but the resulting key was not published or circulated via the website. Recently, Dietrich et al. (in press) revised the Autolytinae from the area (North Sea and NE Atlantic). Their results are followed here; we strongly recommend use of these keys as a complement to ours for that subfamily.

Main morphological characters

Body

Cylindrical in section (Fig. 1A, B, E, F), but may be flattened, ribbon-like (Fig. 1C). The surface is smooth (Fig. 1A–C, F), but may also bear papillae on the dorsal (Fig. 1E) and ventral surface, and on the parapodia. Some bear rugosities, tubercles, rows of cilia, etc.

Prostomium

Semicircular to pentagonal or oval and has four eyes and, sometimes, also a pair of ocular spots, three antennae, which may be smooth (Fig. 1B, E, F) or articulated (also known as moniliform) (Fig. 1A, C), short or long, and one pair of palps, triangular in shape, rounded or oval, that may be fully separated from each other (Fig. 1D), basally fused or fused along their entire length (Fig. 1E).

Tentacular (= peristomial) cirri

Usually two pairs (Fig. 1A–D, F), but in some genera only one pair (Fig. 1E), or absent, which may be smooth (Fig. 1B, E, F) or articulated (moniliform) (Fig. 1A, C, D), short or long.

Nuchal organs

Most commonly as ciliated pits (the most common) but also as nuchal lappets (nuchal epaulettes) (Fig. 1F).

Parapodia

Uniramous (except on some segments, during reproduction), with dorsal cirri, parapodial lobes, ventral cirri, chaetae, and aciculae (Fig. 2A–D).

Dorsal cirri

May be long or short, alternating between long and short, smooth (Figs 1B, E, F, 2B–D) or moniliform (Figs 1A, C, 2A). Typically filiform, but may be of different shapes.

Ventral cirri

Present, except in the subfamily Autolytinae, in which they appear to be absent (Fig. 2D) but are in fact fused to parapodial lobes.

Pharynx

Usually straight, but coiled in some genera, sometimes very slender and complex (Fig. 1F).

Pharyngeal armature

Absent in the subfamily Anoplosyllinae (Fig. 2E), but most often as a single pharyngeal tooth, or as a crown of denticles on the pharyngeal opening, i.e. the trepan, with (Fig. 2G) or without a pharyngeal tooth (Fig. 2F). The trepan may be complete or incomplete, and the denticles may be directed to the anterior or posterior parts of the body (Fig. 2H).

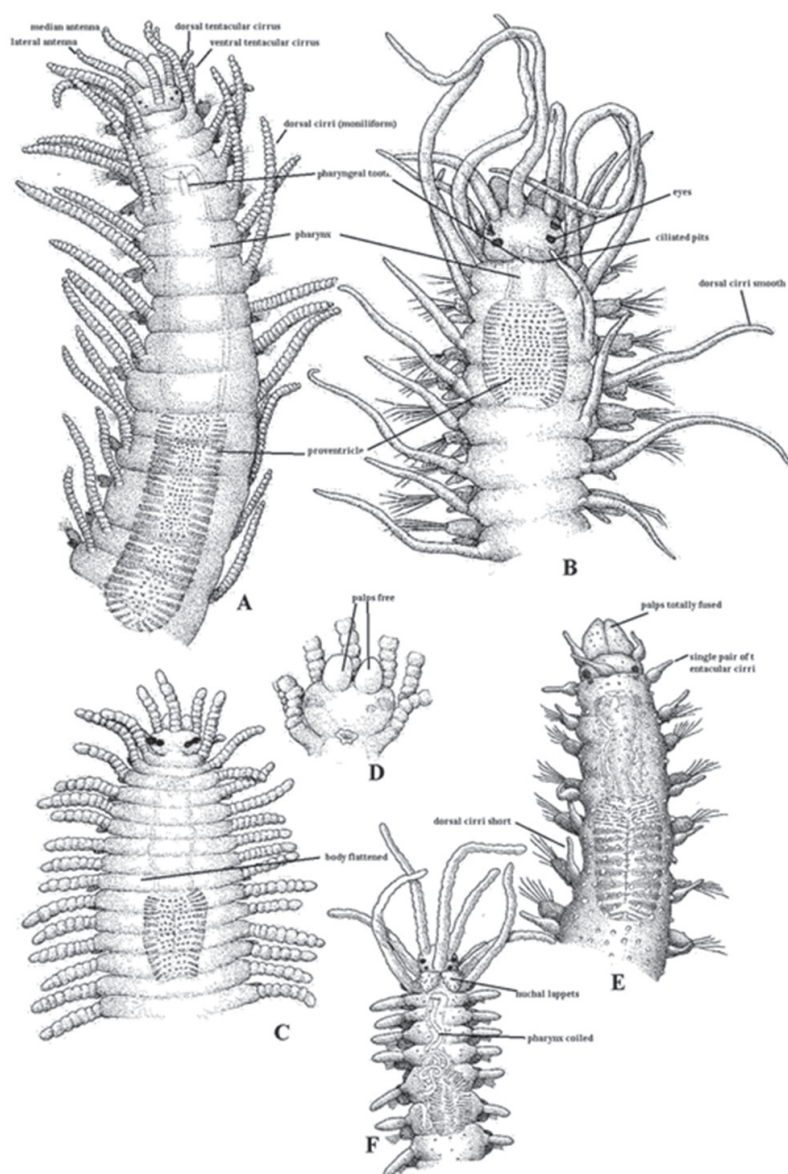


Figure 1. Anterior end of: **A** *Syllis amica* (SF. Syllinae), body cylindrical, smooth surface, two pairs of tentacular cirri, antennae, tentacular and dorsal cirri moniliform, nuchal organs as ciliated pits, palps basally fused **B** *Nudisyllis pulligera* (SF. Eusyllinae), body cylindrical, smooth surface, two pairs of tentacular cirri, antennae, tentacular and dorsal cirri smooth, nuchal organs as ciliated pits, palps free **C** *Trypanosyllis coeliaca* (SF. Syllinae), body flattened, smooth surface, two pairs of tentacular cirri, antennae, tentacular and dorsal cirri moniliform, nuchal organs as ciliated pits, palps free (see figure **D**) **D** Same species, prostomium in ventral view **E** *Sphaerosyllis pirifera* (SF. Exogoninae), body cylindrical, papillated surface, single pair of tentacular cirri, antennae, tentacular and dorsal cirri smooth and short, nuchal organs as ciliated pits, palps totally fused **F** *Myrianida convoluta* (SF. Autolytinae), body cylindrical, smooth surface, two pairs of tentacular cirri, antennae, tentacular and dorsal cirri smooth, nuchal lappets, palps totally fused, pharynx coiled.

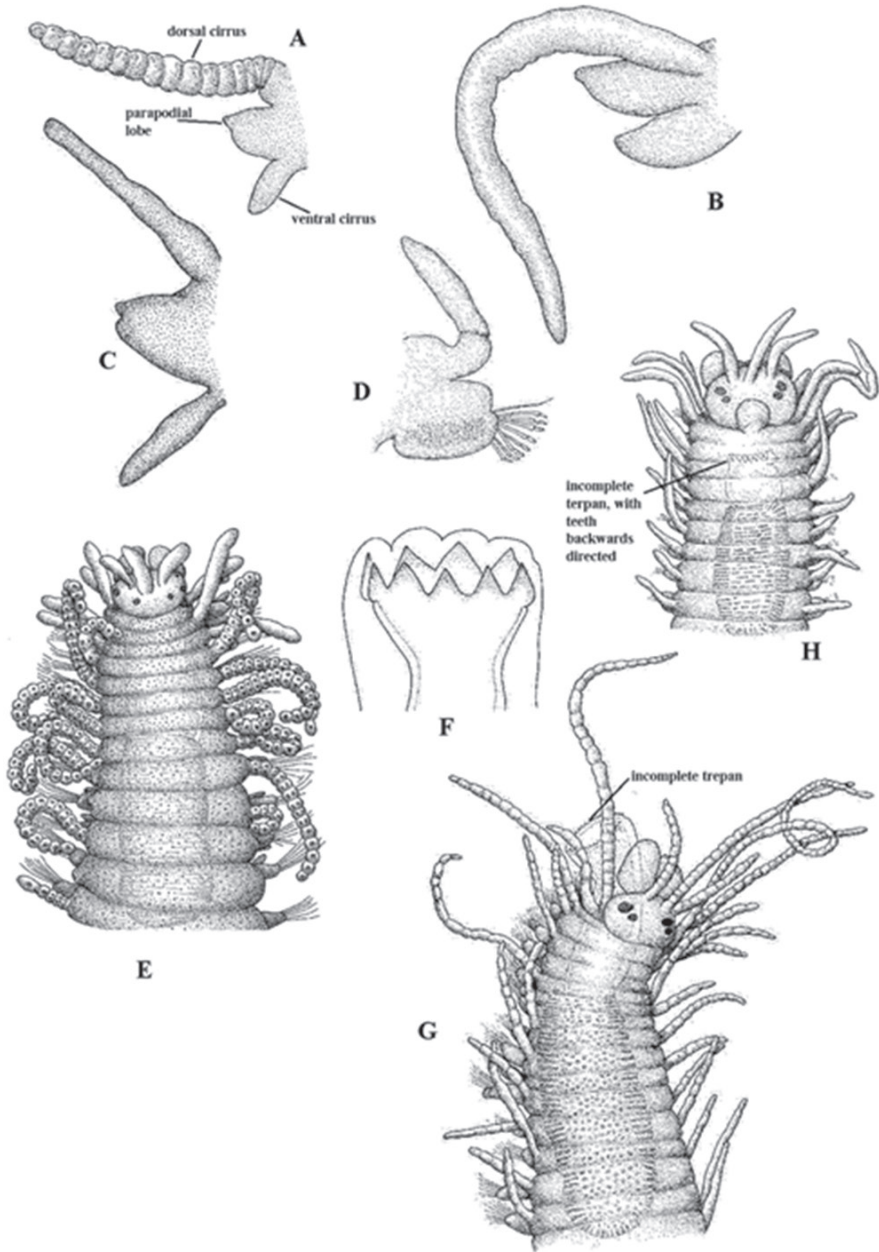


Figure 2. Lateral view of parapodia of: **A** *Syllis amica*, dorsal cirrus moniliform and long **B** *Nudisyllis puligera*, dorsal cirrus smooth and long **C** *Parapionosyllis brevicirra* (SF. Exogoninae), dorsal cirrus smooth and short **D** *Epigamia labordai* (SF. Autolytinae), dorsal cirrus smooth, short, without ventral cirrus **E** anterior end, dorsal view of *Syllides fulvus* (SF. Anoplosyllinae), without any pharyngeal armature **F** trepan, without middorsal tooth of *Myrianida convoluta* (SF. Autolytinae) **G** everted pharynx of *Eusyllis assimilis* (SF. Eusyllinae), showing an incomplete trepan and middorsal tooth **H** anterior end of *Odontosyllis fulgurans* (SF. Eusyllinae), with an incomplete trepan, teeth directed to posterior part of body.

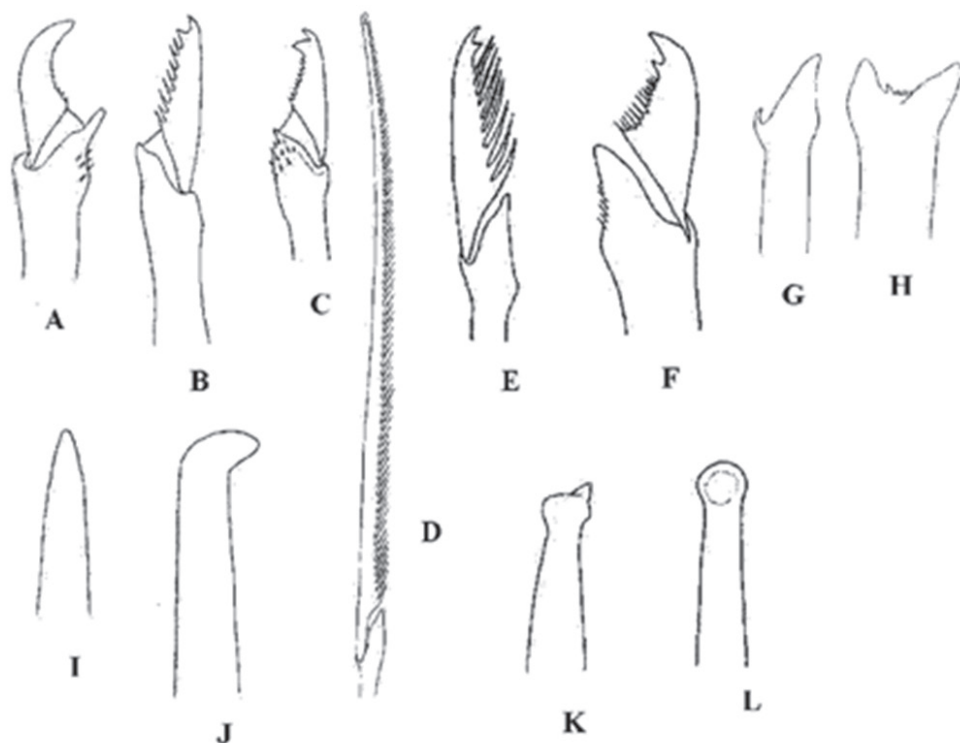


Figure 3. Compound chaetae of **A** *Sphaerosyllis pirifera* (falciger, unidentate, almost smooth on margin) **B** *Trypanosyllis coeliaca* (falciger, bidentate with both teeth similar, moderate spines on margin) **C** *Eusyllis assimilis* (falciger, bidentate, proximal tooth longer than distal one, short spines) **D** *Syllis garciai* (spiniger-like, long spines on margin); **E** *Syllis garciai* (falciger, bidentate, both teeth similar, long spines) **F** *Syllis krohnii* (falciger, bidentate, proximal tooth shorter than distal one, short spines on margin) **G** *Syllis amica* (thick simple chaeta by blade loss and shaft enlargement) **H** *Syllis gracilis* (thick simple chaeta by blade and shaft fusion). Aciculae of: **I** *T. coeliaca* (straight, pointed) **J** *E. assimilis* (distally bent at an angle) **K** *S. gracilis* (acuminate) **L** *Syllis prolifera* (distally rounded).

Proventriculus (= Proventricle)

Rectangular, squared or barrel-shaped. Size (number of segments) and number of muscle cell rows vary between species.

Chaetae

Typically, compound heterogomph, with capillary dorsal and ventral simple chaetae on posterior parapodia but many modifications may occur. Some may be elongated and similar to the spinigers of nereidids, known as spiniger-like (Fig. 3D), or pseudospingers. Falcigers usually bidentate, with both teeth similar (Fig. 3B), the proximal teeth either smaller than the distal (Fig. 3F) or larger (Fig. 3C). Blades may also be unidentate (Fig. 3A). The blades may be smooth, or have a row of marginal spines, which may be long (Fig. 3E) or short (Fig. 3C, F).

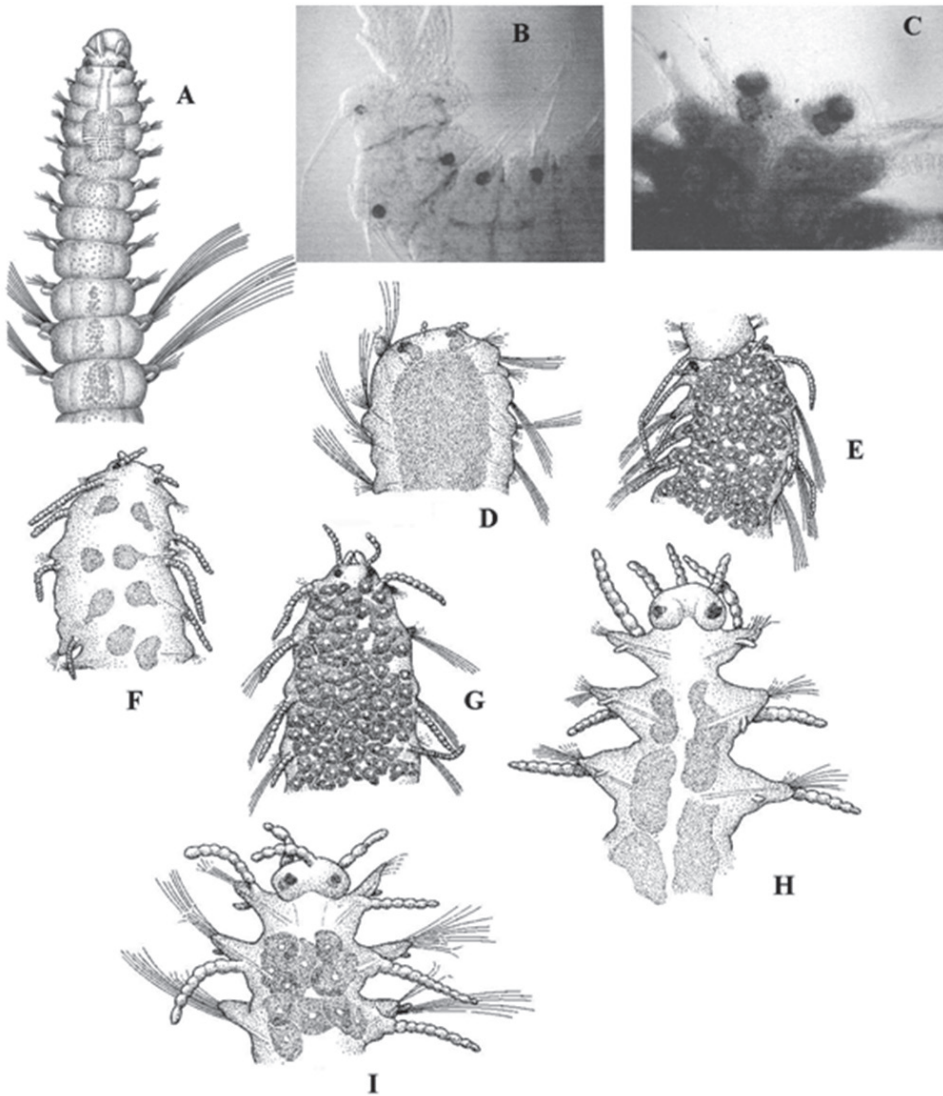


Figure 4. **A** epigamic male of *Exogone naidina*. Anterior end of stolons **B** acephalous (male, still attached to parental), *Haplosyllis spongicola* **C** acerous (male), *Trypanosyllis zebra* **D** dicerous (male), *Syllis prolifera* **E** dicerous (female, still attached to parental), *S. prolifera* **F** tetracerous (male), *Syllis pulvinata* **G** tetracerous (female), *S. pulvinata* **H** pentacerous (male), *Syllis hyalina* **I** pentacerous (female), *S. hyalina*. All, dorsal view, except **H** ventral view.

Sometimes, there may be thick simple chaetae due to the loss of blades and enlargement of shafts (Fig. 3G) or by fusion of blade and shaft (Fig. 3H). The capillary dorsal and ventral simple chaetae are usually very slender, bifid or entire, with or without subdistal spines. Typically, these capillary simple chaetae are present only on posterior parapodia.

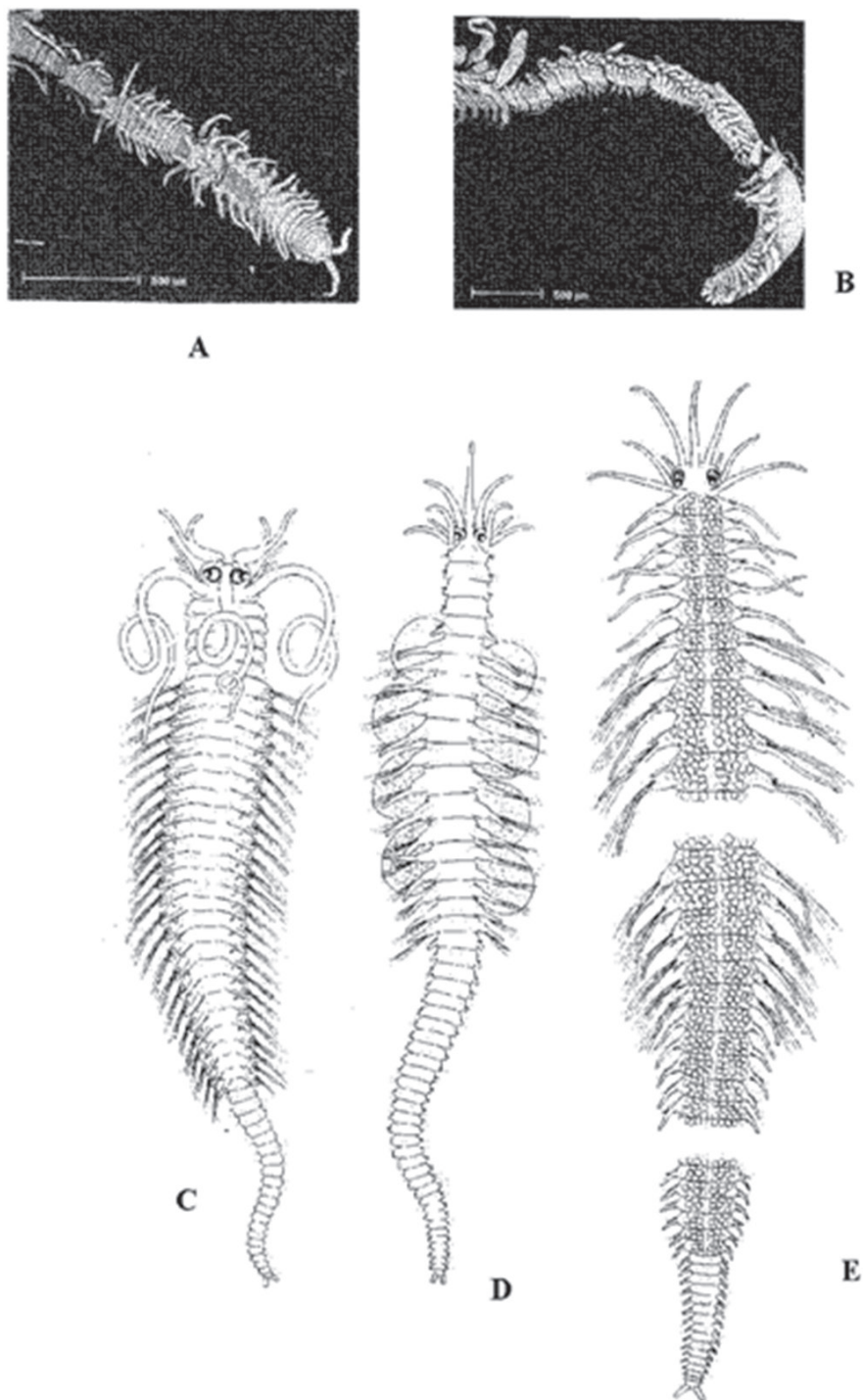


Figure 5. **A, B** Chain of stolons (*Myrianida* spp.) **C** *Polybostrichus* **D** *Sacconereis*, with brooding ventral sac **E** *Sacconereis*.

Aciculae

Numerous different kinds of tips may be present: straight and pointed (Fig. 3I), acuminate (Fig. 3K), bent at an angle (Fig. 3J), distally rounded (Fig. 3L), and other variations.

Reproduction

There are two main reproductive strategies in syllids: Epigamy and Schizogamy.

Epigamy in syllids is quite similar to that of other polychaetes but long, slender notochaetae appear for swimming (natatory chaetae) (Fig. 4A) in some parapodia (from the mid-body backwards). There are two kinds of epigamy: without brooding or with brooding eggs. Brooding eggs may be dorsal (attached by capillary notochaetae) or ventral (attached to nephridial openings). In the latter, juveniles grow attached to mother's body.

Schizogamy by means of sexual stolons. Stolons are detached individuals budded off from the adult, without gut, composed of few segments, filled with gametes: a short life, purely for reproduction. There are two kinds of schizogamy: scissiparity (formation of a single stolon) and gemmiparity (formation of a chain of stolons) (Fig. 5A, B).

Stolons of the Syllinae have no sexual dimorphism, but are easily distinguished because males store spermatozoa and females store oocytes; there are different kinds of stolons: acephalous (without 'head') (Fig. 4B), acerous (= '*Tetraglene*') (a 'head' without appendages, and with two pairs of eyes) (Fig. 4C), dicerous (= '*Chaetosyllis*') (a bilobed 'head' with two pairs of eyes and two antennae) (Fig. 4D, E), tetracerous (a 'head' with two palps and two antennae) (Fig. 4F, G), pentacerous (= '*Ioida*') (a 'head' with two pairs of eyes, three antennae, and two palps) (Fig. 4H, I).

Stolons of the Autolytinae have marked sexual dimorphism. Male stolons ('*Polypostrichus*') have a 'head' with two pairs of eyes, two bifid, elongated palps and three antennae, the median one long and spiral (Fig. 5C). Female stolons ('*Sacconereis*') have a 'head' with two pairs of eyes, two short, simple palps, and three antennae (Fig. 5D, E). Both also have two pairs of 'tentacular cirri'.

Viviparity has also been reported in some species.

Key to subfamilies and 'incertae sedis' genera

- 1 Nuchal organs as two occipital lappets. Pharynx more or less sinuous and coiled.....**2**
- Nuchal organs as two ciliated pits (difficult to observe; occipital lappets absent or, if present, with transversal ridges) between prostomium and peristomium. Pharynx straight**4**
- 2 Body composed of few, rhomboidal segments. Ventral cirri well developed. Last segment without chaetae, with two pairs of long cirri***Amblyosyllis***
- Body composed of numerous, cylindrical segments. Ventral cirri absent or fused to parapodial lobes. All segments (except peristomium) chaetigerous.... **3**

- 3 Two antennae. Ventral cirri distinct, fused along ventral side of parapodial lobes. Compound chaetae with long, filiform, unidentate blades. Reproduction unknown.....***Acritagasyllis***
- Three antennae. Ventral cirri apparently absent (totally fused with parapodial lobes?). Compound chaetae with short blades, usually with proximal tooth longer than distal. Reproduction by epigamy or schizogamy.....
.....**Subfamily Autolytinae**
- 4 Pharynx unarmed **5**
- Pharynx with mid-dorsal tooth, trepan or both..... **6**
- 5 Palps fused along their entire length. Antennae and tentacular cirri minute, papilliform. Single pair of tentacular cirri. Reproduction by epigamy.....***Anguillosyllis***
- Palps fused basally. Antennae and tentacular cirri more or less club-shaped. Two pairs of tentacular cirri. Reproduction by epigamy or brooding eggs ventrally.....**Subfamily Anoplosyllinae**
- 6 Antennae, tentacular cirri and dorsal cirri distinctly articulated, usually long (two genera with only one spherical article). Reproduction by schizogamy (some viviparous)..... **Subfamily Syllinae**
- Appendages smooth or weakly articulated on anterior part of body. Reproduction by epigamy (but unknown in several genera) **7**
- 7 Palps fused entirely or at least to mid way along their length. Antennae, tentacular cirri and dorsal cirri short (sometimes papilliform). Eggs brooded dorsally on capillary notochaetae, or ventrally, attached to nephridial pores.....
.....**Subfamily Exogoninae**
- Palps not completely fused. Appendages long, filiform. No brooding of eggs; reproduction by epigamy (or unknown)
.....**Subfamily Eusyllinae** (plus some *incertae sedis* genera)

Genus *Amblyosyllis* Grube, 1857

- 1 Nuchal lappets short, more or less spherical. Trepan with 6 pentacuspide teeth ***A. madeirensis* Langerhans, 1879 (1)**
- Nuchal lappets long, reaching the level of chaetiger 2. Teeth of trepan otherwise **2**
- 2 Trepan with 6 monocuspid teeth, each with a basal spine on each side, more or less developed on larger specimens..... ***A. formosa* (Claparède, 1863) (1)**
- Trepan with 6 teeth, each with 11 cusps
..... ***A. finmarchica* (Malmgren, 1867) (2)**

Genus *Acritagasyllis* Lucas, San Martín & Sikorski, 2010

A. longichaetosa Lucas, San Martín & Sikorski, 2010 (3)

Genus *Anguillosyllis* Day, 1963*A. pupa* (Hartman, 1965) (4)**Key to genera of Anoplosyllinae Aguado & San Martín, 2009**

- 1 Aciculae of some anterior parapodia enlarged, with inflated tips (one exception) ***Streptosyllis***
- Aciculae unmodified, without inflated tips..... **2**
- 2 Dorsal cirri all smooth, more or less club-shaped ***Anoplosyllis***
- Dorsal cirri from chaetiger 3 distinctly annulated ***Syllides***

Genus *Streptosyllis* Webster & Benedict, 1884

- 1 Aciculae not enlarged. Blades of compound chaetae with distinct hoods
 ... ***S. nunezi* Faulwetter, Vasileiadou, Papageorgiou & Arvanatidis, 2008** (18)
- Aciculae of some anterior segments enlarged. Blades of compound chaetae without hoods..... **2**
- 2 Compound chaetae with indistinctly bidentate blades. Enlarged aciculae in chaetigers 2–5..... ***S. websteri* Southern, 1914** (1)
- Compound chaetae with distinctly bidentate blades. Enlarged aciculae in chaetigers 2–6..... **3**
- 3 Blades of compound chaetae with both teeth similar and close to each other. Aciculae of chaetiger 7 only slightly more slender than those of chaetiger 6..
 ***S. bidentata* Southern, 1914** (1)
- Blades of compound chaetae with proximal teeth longer and well separated. Aciculae of chaetiger 7 distinctly more slender than those of chaetiger 6.....
 ***S. campoyi* Brito, Núñez & San Martín, 2000** (1)

Genus *Anoplosyllis* Claparède, 1868*A. edentula* Claparède, 1868 (1)**Genus *Syllides* Ørsted, 1845**

- 1 Blades of some compound chaetae with one or more long basal spines **2**
- Blades of all compound chaetae with short, uniform spines on margin **4**
- 2 Longer blades of each parapodium with 2–3 long basal spines
 ***S. japonica* Imajima, 1966** (1)
- Blades of some compound chaetae with single, long basal spine..... **3**

- 3 Blades of medium length compound chaetae with a long basal spine. Tips of dorsal simple chaetae blunt ***S. bansei* Perkins, 1981** (1)
- Blades of longest and second pairs of compound chaetae with a long basal spine. Tips of dorsal simple chaetae enlarged and rounded, with some minute spines dorsally..... ***S. benedicti* Banse, 1971** (1)
- 4 Shafts of compound chaetae distally with 1–2 spines distinctly long and thick. Tips of dorsal simple chaetae enlarged and rounded..... ***S. convoluta* Webster Benedict, 1884** (1)
- Distal part of shafts with few, thin spines or smooth. Dorsal simple chaetae ending in a blunt tip ***S. fulva* (Marion & Bobretzky, 1875)** (1)

Syllides longocirrata Ørsted, 1845 is the type-species of the genus but it is poorly known. Later descriptions and reports of this species actually belong to a recently described species of another genus (*Streptospinigera* Kudenov, 1983) (Olivier et al. 2013).

Key to genera Autolytinae Langerhans, 1879

- 1 Dorsal cirri absent on some chaetigers **2**
- Dorsal cirri on all chaetigers..... **3**
- 2 Antennae, tentacular cirri and dorsal cirri present on chaetiger 1; appendages absent on other chaetigers. Both simple and compound chaetae present ***Procerastea***
- Dorsal cirri absent on chaetigers 2–5. Cirrostyles foliaceous. All chaetae simple ***Imajimaea***
- 3 Large, clavate, dorsal cirri alternate with much smaller, cylindrical or clavate cirri. Nuchal epaulettes on special outgrowths ***Virchowia***
- Not as above..... **4**
- 4 Reproduction by epigamy ***Epigamia***
- Reproduction by schizogamy **5**
- 5 Trepan in two rows. Bayonet chaetae distally thick. Reproduction by anterior scissiparity..... ***Proceraea***
- Trepan in single row. Bayonet chaetae distally slender. Reproduction by gemmiparity or anterior scissiparity ***Myrianida***

Genus *Procerastea* Langerhans, 1884

- 1 Antennae, tentacular and dorsal cirri club-shaped. Trepan with 16–28 teeth. Chaetigers 1–4 with both unidentate and bidentate chaetae ***P. balleziana* Malaquin, 1893** (1, 5)
- Antennae, tentacular and dorsal cirri cylindrical. Trepan with 6–10 teeth. Chaetigers 1–4 with bidentate chaetae only ***P. nematodes* Langerhans, 1884** (1, 5)

Genus *Virchowia* Langerhans, 1879*V. clavata* Langerhans, 1879 (1, 5)**Genus *Imajimaea* Nygren, 2004***I. draculai* (San Martín & López, 2002) (1, 5, 16)**Genus *Epigamia* Nygren, 2004**

- 1 Trepan with two sizes of teeth, alternating between 1 large and 3–4 much smaller. Blades of compound chaetae with both teeth similar *E. alexandri* (Malmgren, 1867) (5)
- Trepan with three sizes of teeth, alternating between 1 large with 2 of medium size, or between 1 large, 1 small and 1 medium. Blades of compound chaetae with proximal tooth distinctly longer than distal *E. labordai* (San Martín & López, 2002) (1, 5)

Genus *Proceraea* Ehlers, 1864

- 1 Body without colour pattern.....2
- Body with colour pattern3
- 2 Blades of compound chaetae with both teeth similar *P. aurantiaca* Claparède, 1868 (5)
- Blades of compound chaetae with both teeth distinctly different; distal tooth smaller than proximal tooth..... *P. cornuta* (Agassiz, 1862) (5)
- 3 Colour pattern of 3 lines.....*P. prismatica* (O. F. Müller, 1776) (5)
- Colour pattern otherwise4
- 4 Colour pattern of 2 lines and brown squares..... *P. picta* Ehlers, 1864 (5)
- Dorsum yellow with 2 black longitudinal lines on each side *P. scapularis* (Claparède, 1864) (5)

Genus *Myrianida* Milne Edwards 1845

- 1 Dorsal cirri distinctly flattened.....*M. pinnigera* (Montagu, 1808) (1, 5)
- Dorsal cirri cylindrical2
- 2 Pharynx with several sinuations3
- Pharynx with 1–2 sinuations.....4

- 3 Cirrophores swollen; cirrostyles attached subterminally on cirrophores. Trepan with indistinct teeth *M. inermis* (Saint-Joseph, 1886) (5)
- Cirrophores not swollen; cirrostyles attached terminally on cirrophores. Trepan with 9 distinct teeth *M. convoluta* (Cognetti, 1953) (1, 5)
- 4 Cirrophores on both short and long cirri longer than cirrostyles in median chaetigers *M. sanmartini* Dietrich, Hager, Bönsch, Winkelman, Schmidt & Nygren, in press (17)
- Cirrophores on at least short cirri shorter than cirrostyles in all chaetigers... 5
- 5 Teeth of trepan unequal..... 6
- Teeth of trepan all of equal size..... 8
- 6 Colour pattern of 4 red spots on each segment. Trepan with 30–35 unequal teeth, 4–5 large and 26–30 small *M. rubropunctata* (Grube, 1860) (5)
- Not as above..... 7
- 7 Trepan with 22–29 teeth, alternating 1 large and 1–3 short *M. brachycephala* (Marenzeller, 1874) (1, 5)
- Trepan with 4–5 large teeth and 25–39 short *M. langerhansi* (Gidholm, 1967) (5)
- 8– Trepan with 12–24 teeth *M. quinquedecimdentata* (Langerhans, 1884) (1, 5)
- Trepan with 24–34 teeth 9
- 9 Cirri with more or less distinct alternation in length along body. Cirrophores on long cirri slightly longer than parapodial lobes *M. prolifera* (O. F. Müller, 1788) (1, 5)
- Cirri similar along body. Cirrophores on long cirri equal to parapodial lobes ... *M. edwardsi* (Saint-Joseph, 1886) (1, 5)

Keys to genera of Exogoninae Langerhans, 1879

Key based on reproductive and morphological characters

- 1 Females brooding dorsally..... 2
- Females brooding ventrally, developing juveniles, or viviparous 4
- 2 Two pairs of tentacular cirri. Body smooth..... *Salvatoria*
- Single pair of tentacular cirri. Body with papillae..... 3
- 3 Some dorsal cirri with a retractile cirrostyle. Antennae short. Pharynx relatively long and wide; pharyngeal tooth usually located far from anterior margin. Compound chaetae always with short, unidentate blades..... *Prosphaerosyllis*
- Antennae and dorsal cirri more or less elongate, without distal cirrostyle. Pharynx relatively slender; pharyngeal tooth usually located near anterior margin. Compound chaetae with elongate blades, bidentate, unidentate, or both..... *Erinaceusyllis*

4	Body smooth	5
–	Body covered with papillae	<i>Sphaerosyllis</i>
5	Two pairs of tentacular cirri.....	<i>Brania</i>
–	Single pair of tentacular cirri.....	6
6	Palps basally fused to half or 2/3 of their length. Dorsal cirri bowling-pin shaped. Distinct parapodial glands.....	<i>Parapionosyllis</i>
–	Palps fused along their entire length or with terminal notch. Dorsal cirri small, papilliform. Parapodial glands indistinct or minute, apparently absent.....	7
7	Compound chaetae all bidentate falcigers, with both teeth similar; some species may have elongate, spiniger-like blades on some chaetae but their structure is similar to that of the shorter falcigers.....	<i>Parexogone</i>
–	Blades of compound chaetae of 2 different types; some elongated, spiniger-like, others short falcigers; some with blades missing or fused to shafts	<i>Exogone</i>

Key based exclusively on morphological features

1	Two pairs of tentacular cirri.....	2
–	Single pair of tentacular cirri.....	3
2	Palps basally fused to half or 2/3 of their length. Dorsal cirri bowling-pin shaped or truncate. Parapodial glands distinct, sometimes inside dorsal cirri. Aciculae distally rounded, apparently hollow at tip. Pharynx slender, with distal soft papillae. Pharyngeal tooth conical, located at opening.....	<i>Brania</i>
–	Palps joined along most or all of their length by a dorsal membrane. Dorsal cirri spindle-shaped, usually elongate. Parapodial glands absent. Aciculae acuminate. Pharynx long and wide; usually without papillae on pharyngeal opening. Pharyngeal tooth rhomboidal to ovate, usually located far from pharyngeal opening.....	<i>Salvatoria</i>
3	Body without papillae.....	4
–	Body papillated.....	6
4	Palps basally fused to half or 2/3 of their length. Dorsal cirri bowling-pin shaped. Parapodial glands distinct. Dorsal simple chaetae distally serrated....	<i>Parapionosyllis</i>
–	Palps fused along their entire length or with a distal, short notch. Dorsal cirri small, papilliform. Parapodial glands indistinct. Dorsal simple chaetae not as above.....	5
5	Compound chaetae all bidentate falcigers, with both teeth similar; some species may have elongate, spiniger-like blades on some chaetae but their structure is similar to that of the shorter falcigers.....	<i>Parexogone</i>
–	Blades of compound chaetae of 2 different types; some elongated, spiniger-like, others short falcigers; some with blades missing or fused to shafts	<i>Exogone</i>

- 6 Prostomium with 4 eyes, no additional eyespots. Proventriculus short, with few large muscular bands. Pharynx slender; pharyngeal tooth small, conical, located on anterior rim of pharynx. Aciculae with tip forming an angle (bulbous in one species) ***Sphaerosyllis***
- Four eyes and 2 anterior eyespots on prostomium (sometimes difficult to see). Proventriculus barrel-shaped, long and relatively wide, with numerous, slender muscular bands. Pharynx relatively wide. Aciculae acuminate 7
- 7 Pharynx distinctly wide, without papillae. Pharyngeal tooth rhomboidal to oval, long, usually located far from anterior rim. Antennae and dorsal cirri typically having a retractile cirrostyle. Compound chaetae always with short, unidentate falcigers ***Prospiraerosyllis***
- Pharynx proportionally more slender, sometimes with soft papillae surrounding opening. Pharyngeal tooth small, located near anterior rim. Antennae and dorsal cirri always without retractile cirrostyle. Compound chaetae usually with elongate blades bidentate, unidentate or both ***Erinaceusyllis***

Genus *Salvatoria* McIntosh, 1885

- 1 Dorsal cirri short, absent from chaetiger 2 ***S. swedmarki* (Gidholm, 1962) (1)**
- Dorsal cirri elongated, present on all chaetigers 2
- 2 Blades of compound chaetae smooth on margin, unidentate or with a minute subdistal spine; 1–2 compound chaetae on each parapodium with longer blades having some long basal spines ***S. limbata* (Claparède, 1868) (1)**
- Compound chaetae with bidentate blades ***S. clavata* (Claparède, 1863) (1)**

Genus *Prospiraerosyllis* San Martín, 1984

- 1 Antennae, tentacular and dorsal cirri minute, papilliform ***P. giandoi* (Somaschini & San Martín, 1994) (6)**
- Antennae, tentacular and dorsal cirri typical of the genus, with a papilliform cirrostyle and a bulbous cirrophore 2
- 2 Blades of compound chaetae all short; dorsal ones with long spines, ventral ones smooth or very slightly spinulose ***P. campoyi* (San Martín, Acero, Contonente & Gómez, 1982) (1)**
- Blades of compound chaetae without long spines 3
- 3 Dorsal papillae of two lengths, arranged in four longitudinal rows ***P. tetralix* (Eliason, 1920) (1)**
- Dorsal papillae all similar, not arranged in longitudinal rows 4

- 4 Palps densely papillated. Dorsal papillae small, rounded. Without long papillae on dorsal cirri..... ***P. laubieri* Olivier, Grant, San Martín, Archambault & McKindsey, 2011 (7)**
- Palps with few papillae. Dorsal papillae digitiform..... **5**
- 5 One long, distinct papilla on dorsal cirrus ***P. chauseyensis* Olivier, Grant, San Martín, Archambault & McKindsey, 2011 (7)**
- Without papillae on dorsal cirri.. ***P. xarifae* (Hartmann-Schröder, 1960) (1)**

Genus *Erinaceusyllis* San Martín, 2005

- Blades of compound chaetae unidentate
..... ***E. erinaceus* (Claparède, 1863) (8) (19)**
- Chaetal blades bidentate ***E. cryptica* (Ben-Eliahu, 1977) (1)**

Genus *Sphaerosyllis* Claparède, 1863

- 1 Aciculae straight, with a bulbous distal swelling. Mid body parapodia with simple chaetae by loss of blades and shaft enlargement.....
..... ***S. bulbosa* Southern, 1914 (1)**
- Aciculae distally bent at an angle. Without enlarged chaetae **2**
- 2 Antennae, tentacular and dorsal cirri minute, bulbous. Blades of mid body and posterior compound chaetae with smooth margins, with a long subdistal spine ***S. parabulbosa* San Martín & López, 2002 (1)**
- Antennae, tentacular and dorsal cirri not so small, with longer tips. Blades otherwise **3**
- 3 Without parapodial glands..... **4**
- With parapodial glands from chaetiger 4 **5**
- 4 Proventriculus rectangular. Compound chaetae of posterior parapodia with short, hooked, smooth blades ***S. pirifera* Claparède, 1868 (1)**
- Proventriculus almost square. Compound chaetae with blades elongated throughout body..... ***Sphaerosyllis* sp.**
- 5 Parapodial glands with granular material ***S. glandulata* Perkins, 1981 (1) (*)**
- Parapodial glands with fibrillar material (rods)..... **6**
- 6 Blades of compound chaetae with distinct dorsoventral gradation in length, especially on anterior parapodia ***S. hystrix* Claparède, 1863 (1)**
- Blades of compound chaetae with, at most, very slight dorsoventral gradation in length; all blades short, those of dorsal compound chaetae with long spines on margin ***S. taylori* Perkins, 1981 (1) (*)**

(*) Stained specimens of species with fibrillar material can appear as *S. glandulata*; parapodial glands with granular material are small, rounded and sometimes difficult to see; those with fibrillar material are ovate, large and easy to see.

Genus *Brania* Quatrefages, 1865

- Dorsal cirri truncate, with inclusions of fibrillar material
..... ***B. pusilla* (Dujardin, 1851) (1)**
- Dorsal cirri bowling pin-shaped, with glands on parapodial bases
..... ***B. arminii* Langerhans, 1881(1)**

Genus *Parapionosyllis* Fauvel, 1923

- 1 Compound chaetae with long blades; longer blades on each parapodium more than 3 times as long as shorter ones **2**
- Chaetae with shorter blades **3**
- 2 Peristomium with a swelling partially covering the prostomium. Spines on long blades of compound chaetae short and straight. Two kinds of parapodial glands ***P. brevicirra* Day, 1954 (1)**
- Without swelling. Spines on long blades moderately long, distally dressed. Parapodial glands one kind, all with granular material
..... ***Parapionosyllis macaronesiensis* Brito, Núñez & San Martín, 2000 (15)**
- 3 Blades of uppermost compound chaetae in each parapodium twice as long as those of shortest chaetae, with long spines on margin
..... ***P. elegans* (Pierantoni, 1903) (1)**
- Blades of uppermost compound chaetae on each parapodium more than twice as long as those of shortest chaetae, without long spines **4**
- 4 Blades of uppermost compound chaetae distinctly longer than others on each parapodium, about 3 times longer than of the most ventral.
..... ***P. minuta* (Pierantoni, 1903) (1)**
- Blades of uppermost compound chaetae longer than other blades on each parapodium but with a gradual and homogeneous gradation in size
..... ***P. cabezali* Parapar, San Martín & Moreira, 2000 (1)**

Genus *Parexogone* Mesnil & Caullery, 1918

- 1 Compound chaetae of all parapodia with short blades, all similar or with slight dorsal to ventral gradation..... ***P. hebes* (Webster & Benedict, 1884) (1, 8)**
- Some compound chaetae (1–3) with long blades, at least on anterior parapodia **2**
- 2 Dorsal simple chaetae with few (1–3) very long, thin spines (aristae), extending beyond the tips
..... ***Parexogone longicirris* (Webster & Benedict, 1887) (2)**
- Dorsal simple chaetae without aristae **3**
- 3 All blades of compound chaetae elongated, slender, unidentate, with long, thin spines on margin. Aciculae with thin tips
..... ***P. campoyi* San Martín, Ceberio & Aguirrezabalaga, 1996 (1)**

- Most compound chaetae with short blades, without long spines on margin. Aciculae rounded distally **4**
- 4 Lateral antennae minute; median antenna shorter than prostomium and palps combined..... ***P. caribensis* San Martín, 1991** (1)
- Lateral antennae similar in length to prostomium; median antenna longer than prostomium and palps combined.... ***P. convoluta* (Campoy, 1982)** (1)

Genus *Exogone* Ørsted, 1845

- 1 Spiniger-like compound chaetae modified, with enlarged, spinous shafts and short, triangular blades.....
..... ***E. mompasensis* Martínez, Adarraga & San Martín, 2002** (1)
- Chaetae not modified **2**
- 2 Simple chaetae and blades of compound chaetae with long, thin spines extending beyond tips ***E. sorbei* San Martín, Ceberio & Aguirrezabalaga, 1996** (1)
- Simple chaetae without these spines..... **3**
- 3 Blades of falcigers with some long spines, extending beyond distal tooth
..... ***E. lopezi* San Martín, Ceberio & Aguirrezabalaga, 1996** (1)
- Without long spines on falcigers **4**
- 4 Compound chaetae of 2–3 most anterior parapodia with blades very different from the others: very short, unidentate with a long basal spine
..... ***E. naidina* Ørsted, 1845** (1)
- Compound chaetae similar throughout..... **5**
- 5 Median antenna distinctly longer than lateral antennae
..... ***E. dispar* (Webster, 1879)** (1)
- Median antenna small, similar to lateral antennae.....
..... ***E. verugera* (Claparède, 1868)** (1)

Key to genera of Syllinae Grube, 1850

- 1 All chaetae simple, usually thick..... ***Haplosyllis***
- Compound and capillary chaetae present dorsally and ventrally (sometimes some chaetae in mid body appear simple by blade and shaft fusion but typical compound chaetae also present anteriorly)..... **2**
- 2 Body small, dorso-ventrally flattened. Antennae, tentacular and dorsal cirri reduced to a single, spherical article **3**
- Body of medium to large size, cylindrical or flattened. Antennae, tentacular and dorsal cirri with several articles (moniliform)..... **4**
- 3 Palps fused. Two dorsal rows of spherical tubercles, similar to dorsal cirri....
..... ***Eurysyllis***
- Palps separated. Without dorsal tubercles ***Plakosyllis***

- 4 Body cylindrical..... **Syllis**
- Body dorso-ventrally flattened **5**
- 5 Dorsum, as well as antennae and dorsal cirri, with papillae and longitudinal grooves. Pharynx unarmed..... **Xenosyllis**
- Without longitudinal grooves on dorsum (minute transverse rows of papillae, difficult to see) (one species densely papillated). Pharynx with a trepan and, occasionally, a tooth..... **Trypanosyllis**

Genus *Haplosyllis* Langerhans, 1879

H. spongicola (Grube, 1855) (9)

Genus *Eurysyllis* Ehlers, 1864

- 1 Compound chaetae with blades short and curved, smooth or with short spines on margin..... ***E. tuberculata* Ehlers, 1864** (1)
- Compound chaetae with blades elongated, with long spines on margin of anterior chaetae..... ***E. mercuryi* Lucas, San Martín & Parapar, 2012** (10)

Genus *Plakosyllis* Hartmann-Schröder, 1956

P. brevipes Hartmann-Schröder, 1956 (1)

Genus *Syllis* Lamarck, 1818

- 1 Thick simple, Y-shaped chaetae in mid body (enlargement and fusion of shafts and blades)..... ***S. gracilis* Grube, 1840** (1)
- Without these thick simple chaetae..... **2**
- 2 Aciculae of posterior parapodia distally rounded and hollow. Pharyngeal tooth distinctly back from the pharyngeal opening **3**
- Aciculae not as above. Pharyngeal tooth located on anterior margin **4**
- 3 Compound chaetae distinctly bidentate, with both teeth similar..... ***S. prolifera* Krohn, 1852** (1)
- Compound chaetae with unidentate blades or with minute, spine-like proximal tooth..... ***S. vivipara* Krohn, 1869** (1)
- 4 With spiniger-like compound chaetae..... **5**
- Without spiniger-like compound chaetae **12**
- 5 Aciculae of posterior parapodia thick, straight, acute, protruding from the parapodial lobes..... **6**

- Aciculae otherwise7
- 6 Mid body dorsal cirri elongated. Mid body spiniger-like chaetae distinctly bidentate.....***S. cornuta* Rathke, 1843** (11)
- Mid body dorsal cirri fusiform. Mid body spiniger-like chaetae indistinctly bidentate.....***S. mercedesae* Lucas, San Martín & Parapar, 2012** (10)
- 7 Proximal tooth of spiniger-like chaetae and falcigers distinct, forming a narrow angle with distal teeth (both teeth almost parallel); apparently without eyes.....***S. caeca* (Katzmann, 1973)** (11)
- Chaetae not as above; eyes present8
- 8 Mid body dorsal cirri thick, short and fusiform***S. parapari* San Martín & López, 2000** (1)
- Dorsal cirri slender, more or less elongated9
- 9 Posterior aciculae distally bent at an angle. Dorsal simple chaetae truncate. Short spiniger-like chaetae, distally rounded and unidentate from mid body ..
..... ***S. rosea* (Langerhans, 1879)** (1, 11)
- Aciculae acuminate. Dorsal simple chaetae acute. Arrangement and shape of spiniger-like chaetae not as above.....10
- 10 Spiniger-like chaetae very short, only present on anterior and mid body segments; spiniger-like chaetae and falcigers unidentate, sometimes with a long, slender subdistal spine..... ***S. oerstedii* (Malmgren, 1867)**
- Chaetae not as above11
- 11 Blades of falcigers with long spines on margin, especially distally, extending beyond level of proximal tooth ***S. garciai* (Campoy, 1982)** (1)
- Spines of blades not so long, decreasing distally, not reaching level of proximal tooth..... ***S. mauretana* (Licher, 1999)** (11)
- 12 On mid body, one thick simple chaeta on each parapodium, formed by blade loss and shaft enlargement ***Syllis amica* Quatrefages, 1866** (1)
- Without thickened, simple chaetae13
- 13 Posterior aciculae distally bent at an angle. Dorsal simple chaetae truncate....14
- Without the above characters.....15
- 14 Proventriculus long, through about 5 segments or more. Two dorsal glands after proventriculus..... ***S. pulvinata* (Langerhans, 1881)** (1)
- Short proventriculus, through 3 segments. Dorsal glands absent.....
..... ***S. gerlachi* (Hartmann-Schröder, 1960)** (1)
- 15 Dorsal cirri of mid body short, fusiform14
- All dorsal cirri elongated, not fusiform.....16
- 14 Dorsal cirri strongly fusiform. Mid body compound chaetae almost unidentate, with a short, small proximal tooth.....
..... ***S. armillaris* (O.F. Müller, 1771)** (1, 11)
- Dorsal cirri not so strongly fusiform. Mid body compound chaetae bidentate ***S. hyalina* Grube, 1863** (1, 11)
- 16 Aciculae of posterior parapodia thick, straight, acute, protruding from the parapodial lobes17

- Aciculae otherwise20
- 17 Blades of compound chaetae unidentate (or slightly bidentate on anterior parapodia).....18
- Blades distinctly bidentate19
- 18 Dorsal cirri long. Blades distally more or less hooked.....
.....*S. fasciata* (Malmgren, 1867) (11)
- Dorsal cirri short, slender, delicate. Blades short, triangular
..... *S. licheri* Ravara, San Martín & Moreira, 2004 (1)
- 19 Dorsal cirri short, slender, delicate. Posterior aciculae distally bent, oblique, although pointed. Without colour pattern
.....*S. pontxioi* San Martín & López, 2000 (1)
- Dorsal cirri longer. Aciculae straight. Strong pigmentation on anterior segments, as ∞ *S. variegata* Grube, 1860 (1, 11)
- 20 Compound chaetae all unidentate, distally acute
.....*S. vittata* Grube, 1840 (1, 11)
- At least anterior compound chaetae bidentate.....21
- 21 Long dorsal cirri of anterior segments distinctly thicker than others. Compound chaetae of posterior segments distinctly enlarged, unidentate or with a small proximal tooth. Anterior segments pigmented with distinct transverse red bands*S. krohnii* Ehlers, 1864 (1, 11)
- Dorsal cirri of similar thickness throughout body. Pigment pattern otherwise22
- 22 Posterior compound chaetae unidentate by reduction and loss of distal tooth. Prostomium, peristomium and chaetiger 1 with dark red pigment, sometimes also a small red band on some anterior segments
..... *S. torquata* Marion & Bobretzky, 1875 (1)
- Without such colour pattern nor such chaetae23
- 23 Compound chaetae strongly bidentate. Colour pattern: one rhomboidal red mark on dorsum and a slight line on each border of each segment.....
..... *S. columbretensis* (Campoy, 1982) (1)
- Compound chaetae slightly bidentate Colour pattern forming ∞ on anterior segments*S. westheidei* (San Martín, 1982) (1, 11)

Genus *Xenosyllis* Marion & Bobretzky, 1875

X. scabra (Ehlers, 1864) (1)

Genus *Trypanosyllis* Claparède, 1864

- 1 Body densely papillated
..... *T. troll* Ramos, San Martín & Sikorski, 2010 (12)
- Body non-papillated2

- 2 Medium sized. Without colour pattern. Dorsal cirri short *T. coeliaca* Claparède, 1868 (1)
- Large. With colour pattern. Dorsal cirri long 3
- 3 Thin reddish transverse stripes on anteriormost segments. Some anterior dorsal cirri distinctly thicker and longer than others. Blades of compound chaetae slightly bidentate *T. aeolis* Langerhans, 1879 (1)
- Distinct colour pattern of transverse red stripes. Dorsal cirri long and red, all of similar thickness. Blades distinctly bidentate *T. zebra* (Grube, 1860) (1)

Key to genera of Eusyllinae Malaquin, 1893 (and some “incertae sedis” genera)

- 1 Pharyngeal tooth absent; pharynx with an incomplete trepan formed by few teeth, backwardly directed *Odontosyllis*
- Pharyngeal tooth present, with or without trepan 2
- 2 Pharynx with mid dorsal tooth and an incomplete arc of small denticles, frontally directed 3
- Pharynx without denticles, only the mid dorsal tooth 4
- 3 All dorsal cirri long to very long, coiled over dorsum. Pharyngeal armature composed of a mid dorsal tooth and an incomplete arc of few (5–6) denticles *Dioplosyllis*
- Dorsal cirri not so long. Mid dorsal tooth and incomplete (sometimes complete) arc of numerous (around 30–40) pharyngeal denticles *Eusyllis*
- 4 Antennae, tentacular cirri and dorsal cirri of chaetiger 1 long; subsequent dorsal cirri short 5
- All appendages long 6
- 5 Body minute; strictly interstitial. Without enlarged, aciculiform ventral simple chaetae *Neopetitia*
- Body not so small; found on hard substrata. With enlarged, aciculiform, ventral simple chaetae *Brevicirrosyllis*
- 6 Pharyngeal tooth on middle or posterior position or distinctly retarded 7
- Pharyngeal tooth located on anterior margin 8
- 7 A number of anterior parapodia with enlarged aciculae, distally knobbed *Streptodonta*
- Without these enlarged aciculae *Opisthodonta*
- 8 Segments posterior to proventriculus fused in units of 2–3 segments. Palps completely separated *Synmerosyllis*
- Segments not fused. Palps separated or basally fused 9
- 9 Without eyes (nuchal pigment patches may be present on prostomium). Palps long, fused to prostomium. Dorsal cirri of midbody short .. *Palposyllis*
- With eyes. Palps not so long nor fused to prostomium. Dorsal cirri long throughout body 10

- 10 Antennae and anterior dorsal cirri more or less articulated. A digitiform, sub-cirral papilla, below the bases of dorsal cirri ***Paraehlersia***
 – All appendages smooth. Without subcirral papillae..... 11
 11 Small to minute size (< 5 mm in length). Palps separated. Pharynx shorter than proventriculus, with a long tooth. Compound chaetae unidentate or with small, spine-like proximal teeth..... ***Nudisyllis***
 – Medium to large size (> 5 mm in length). Palps fused basally. Pharynx similar in length or longer than proventriculus. Compound chaetae bidentate
 ***Pionosyllis***

Genus *Odontosyllis* Claparède, 1863

- 1 Blades of compound chaetae elongated and unidentate.....
 ***O. gibba* Claparède, 1863 (1)**
 – Blades short and hooked, uni- or bidentate..... **2**
 2 Blades strongly bidentate
 ***O. fulgurans* (Audouin & Milne Edwards, 1833) (1)**
 – Blades unidentate..... ***O. ctenostoma* Claparède, 1868 (1)**

Genus *Dioplosyllis* Gidholm, 1962

D. cirrosa Gidholm, 1962 (1)

Genus *Eusyllis* Malmgren, 1867

- 1 Blades of compound chaetae all short and similar
 ***E. blomstrandii* Malmgren, 1867 (1, 8)**
 – Compound chaetae with elongated and short blades on each parapodium.... **2**
 2 Ventral cirri of chaetiger 1 similar to remaining ones. Blades of compound chaetae of two distinctly different sizes. Aciculae thick, distally curved.....
 ***E. assimilis* Marenzeller, 1875 (1)**
 – Ventral cirri of chaetiger 1 flattened, different from remaining ones. Blades of compound chaetae decreasing gradually in size on each parapodium. Aciculae slender, tricuspid ***E. lamelligera* Marion & Bobretzky, 1875 (1)**

Genus *Neopetitia* San Martín, 2003

N. amphophthalma (Siewing, 1956) (1)

Genus *Brevicirrosyllis* San Martín, López & Aguado, 2009*B. weismanni* (Langerhans, 1879) (1, 13)**Genus *Streptodonta* San Martín & Hutchings, 2006**

- 1 All chaetal blades short. Blades of compound chaetae and dorsal simple chaetae with a translucent hood. Pharyngeal tooth located very far from anterior margin ***S. pterochaeta* (Southern, 1914) (1)**
- Some chaetal blades distinctly longer than others. Chaetae without hood. Pharyngeal tooth located more anteriorly ***S. exsulis* Ramos, San Martín & Sikorski, 2010 (12)**

Genus *Opisthodonta* Langerhans, 1879

- 1 Some blades of compound chaetae with proximal tooth curved, almost connecting with blade edge. Pharyngeal tooth on anterior 1/3 of pharynx **2**
- Proximal tooth not so curved. Pharyngeal tooth about half way along pharynx ***O. morena* Langerhans, 1879 (1)**
- 2 Blades of compound chaetae on mid body and posterior segments with distal tooth somewhat smaller than subdistal one ***O. serratisetosa* López, San Martín & Jiménez, 1997 (1)**
- Distal tooth on blades minute or absent ***O. longocirrata* (Saint-Joseph, 1886) (1, 13)**

Genus *Synmerosyllis* San Martín, López & Aguado, 2009*S. lamelligera* (Saint-Joseph, 1886) (1, 13)**Genus *Palposyllis* Hartmann-Schröder, 1977**

- 1 Dorsal cirri absent from chaetiger 2. Palps distinctly long. Body with retractile papillae ***P. prosostoma* Hartmann-Schröder, 1977 (1)**
- Dorsal cirri present on chaetiger 2. Palps not so long. Without retractile papillae ***P. propeweismanni* (Dauvin & Lee, 1983), comb. n. (14) (*)**

(*) San Martín et al. (2009) considered this species as synonymous with *P. prosostoma*; however, after examination of new material during the NMBAQC Workshop, it seems to be a different species.

Genus *Paraehlersia* San Martín, 2003

- 1 Blades of posterior compound chaetae short, with proximal tooth distinctly longer than distal tooth.....*P. ferrugina* (Langerhans, 1881) (1)
- Blades similar throughout, with proximal tooth shorter than distal.....
.....*P. dionisi* Núñez & San Martín, 1991 (1, 13)

Genus *Nudisyllis* Knox & Cameron 1970

- 1 Long blades of compound chaetae bidentate, with both teeth similar. Short blades unidentate.....*N. pulligera* (Krohn, 1852) (1, 13)
- All blades unidentate or with minute, spine-like subdistal tooth
.....*N. divaricata* (Keferstein, 1862) (1, 13)

Genus *Pionosyllis* Malmgren, 1867

- 1 Small size (up to 10 mm long). Teeth of blades of compound chaetae close to each other*P. compacta* Malmgren, 1867 (13)
- Large size (up to 31 mm long. Teeth of blades well separated
.....*P. enigmatica* (Wesenberg-Lund, 1950) (1, 13)

Acknowledgments

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Three new species of *Tasmaniosoma* Verhoeff, 1936 (Diplopoda, Polydesmida, Dalodesmidae) from northeast Tasmania, Australia

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Abstract

The small-range millipedes *Tasmaniosoma anubis* sp. n., *T. interfluminum* sp. n. and *T. nicolaus* sp. n. are described, and the colour of live *T. barbatulum* Mesibov, 2010 is documented.

Keywords

Diplopoda, Polydesmida, Dalodesmidae, millipede, Australia, Tasmania

Introduction

When reviewing *Tasmaniosoma* Verhoeff, 1936 several years ago I wrote that “more small-range species may remain to be discovered” (Mesibov 2010: 32). Here I describe three new *Tasmaniosoma* from northeast Tasmania with known range envelopes of <12, <40 and ca 100 km². *Tasmaniosoma* now contains 22 species, or about one quarter of the 86 species in the suborder Dalodesmidea so far described from Tasmania (Mesibov 2006–2015).

Methods

“Male” and “female” in the text refer to adult (stadium 7) individuals. All specimens are stored in 75–80% ethanol in their respective repositories. Gonopods were cleared in 80% lactic acid and temporarily mounted in a 1:1 glycerol:water mixture for examination by optical microscopy. Body measurements were estimated with a Nikon SMZ800 binocular dissecting microscope using an eyepiece scale. Colour photographs were taken with a Canon EOS 1000D digital SLR camera mounted on the same microscope fitted with a beam splitter. The colour images in Figs 1 and 9 are manually stacked composites processed with Zerene Stacker 1.04. Scanning electron microscope images were acquired digitally using a FEI Quanta 600 (Fig. 2) or a Hitachi SU-70 (Figs 3, 6, 8); specimens were examined after air-drying and sputter-coating with platinum. Images and drawings were prepared for publication using GIMP 2.8.

The Suppl. material 1 tabulates data for known specimen lots of all *Tasmaniosoma* species as of 15 February 2015 (data also available online in Mesibov 2006–2015). Locality details are given with latitude and longitude based on the WGS84 datum. My estimate of the uncertainty for each locality is the radius of a circle around the given position, in metres or kilometres.

Abbreviations in text: QVMAG = Queen Victoria Museum and Art Gallery, Launceston, Tasmania, Australia; Tas = Tasmania; WAM = Western Australian Museum, Perth, Western Australia, Australia.

Results

Taxonomy

Order Polydesmida Pocock, 1887

Suborder Dalodesmidea Hoffman, 1980

Family Dalodesmidae Cook, 1896

Tasmaniosoma Verhoeff, 1936

Tasmaniosoma Verhoeff 1936: 11. Attems 1940: 442. Jeekel 1971: 355; 1982: 12; 1983: 146; 1984: 85; 1985: 52. Hoffman 1980: 150, 185. Mesibov 2010: 33.

Type species. *Tasmaniosoma armatum* Verhoeff, 1936, by monotypy.

Other assigned species. *T. alces* Mesibov, 2010, *T. anubis* sp. n., *T. aureorivum* Mesibov, 2010, *T. australe* Mesibov, 2010, *T. barbatulum* Mesibov, 2010, *T. brunniense* Mesibov, 2010, *T. cacophonix* Mesibov, 2010, *T. clarksonorum* Mesibov, 2010, *T. compitale* Mesibov, 2010, *T. decussatum* Mesibov, 2010, *T. fasciculum* Mesibov, 2010, *T. fragile* Mesibov, 2010, *T. gerdiorivum* Mesibov, 2010, *T. hesperium* Mesibov, 2010, *T. hickmanorum* Mesibov, 2010, *T. interfluminum* sp. n., *T. laccobium* Mesibov,

2010, *T. maria* Mesibov, 2010, *T. nicolaus* sp. n., *T. orientale* Mesibov, 2010, *T. warra* Mesibov, 2010.

***Tasmaniosoma anubis* sp. n.**

<http://zoobank.org/FCFF46F0-6D36-4DC4-A0D9-5E89868D26CC>

Figs 1A, D, 2A, D, E, 3

Holotype. Male, Trevallyn Nature Recreation Area, Tas, -41.4417 147.0800 ±25 m (Google Earth), 150 m a.s.l., 21 June 2014, R. Mesibov, QVM 23:53863 (ex QVM 23:53817)

Paratypes. 15 males, 28 females, details as for holotype, QVM 23:53817.

Other material. 41 males and 51 females (see Suppl. material 1 for details).

Diagnosis. Nominate member of the “*anubis* group” within *Tasmaniosoma* (see Discussion), distinguished from *T. clarksonorum*, *T. compitale*, *T. fasciculum*, *T. hickmanorum* and *T. nicolaus* sp. n. by the absence of a distally directed cluster of stout, rod-like setae on the posterior surface of the gonopod telopodite; from *T. barbatulum* by the presence of a lateral apical process and by the absence of a setal cluster on the anterior telopodite surface; from *T. fragile* by the absence of a setal cluster on the anterior telopodite surface; and from all other “*anubis* group” members by the presence of an anteromedially directed tab on the anterior telopodite surface.

Description. Male/female approximate measurements: length 10/10 mm, mid-body paranota width 1.2/1.1 mm, maximum vertical diameter 1.1/1.1 mm. Live and freshly preserved adults with reddish brown head and antennae; body (Fig. 1A, D) with pale, yellowish brown ground colour, reddish brown anterolateral margins on paranota, reddish brown paramedian spots or short oblique streaks dorsally; legs darkening to light reddish brown distally. Reddish brown colouring fades in alcohol; long-preserved animals more or less uniformly pale yellowish brown, sometimes with a pair of yellowish paramedian spots on each metatergite.

Male with head sparsely setose; antennal sockets slightly impressed, separated by ca 2× socket diameter; antennal groove short and shallow. Antenna slender, slightly clavate, when manipulated reaching back to ring 3; antennomere 6 widest, relative antennomere lengths (2,3,6)>(4,5). Collum from above reniform, convex anteriorly, posterior corner rounded. Tergites 2–4 distinctly narrower than more posterior metatergites; overall ring widths 6>(5,head)>(2,4)>(3,collum); rings 6–15 about same width, 16–18 narrowing. In lateral view, margin of ring 2 tergite slightly lower than margins of collum and ring 3 tergite. Ring 2 ventrally on either side without obvious pit. Ring suture and waist distinct on diplosegments (Fig. 1D), no longitudinal striations on waist; prozonites smooth; metatergites with three transverse rows of ca 12 low, rounded tubercles; posterior metatergal margin slightly emarginate medially. Limbus (Fig. 2E) composed of minute, sharply pointed triangular tabs with jagged, pointed margins. Midbody paranota extend metatergite to ca 1.3× width of prozonite; paranota slightly inflated, marginal groove distinct, anterior corner smoothly convex, posterior corner smoothly convex without

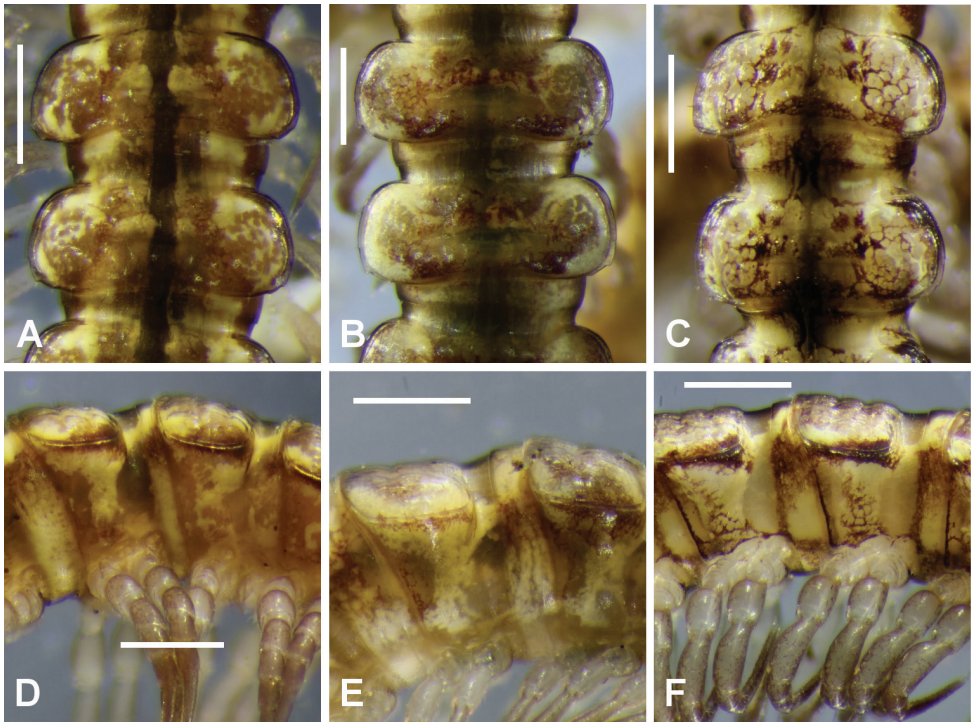


Figure 1. Dorsal **A–C** and right lateral **D–F** views of midbody rings of freshly killed males **A, D** *Tasmaniosoma anubis* sp. n., ex QVM 23:53865 **B, E** *T. interfluminum* sp. n., ex QVM 23:53866 **C, F** *T. nicolaus* sp. n., paratype ex QVM 23:53860. Scale bars = 0.5 mm.

projecting posteriorly on any rings, with 1–2 very small tooth-like projections, each bearing small seta; lateral margin very slightly convex, in lateral view slightly oblique (anterior lower) at ca 3/4 ring height. Pore formula 5, 7, 9, 10, 12, 13, 15–18; ozopore small, round, opening dorsolaterally close to margin near posterior corner of paranotum. Spiracles (Fig. 2D) small, round, opening on low, dome-like projections; on diplosegments, projections arise just above and anterior to first leg and about midway between leg bases. Sternites moderately setose with setae longer on anterior rings; sternite wider than long, transverse impression distinct, longitudinal impression indistinct. Anterior legs with prefemur greatly swollen dorsally, femur less so; swellings begin leg 3, decrease gradually to ca leg 15. Midbody legs with tarsus long, slightly curved, ca 1.6× as long as femur; relative podomere lengths tarsus>femur>prefemur>(postfemur, tibia). Sphaerotrichomes on tarsus and tibia of anterior legs, shafts tapering to point and inclined strongly towards podomere surface. Sparse brush setae on coxa/trochanter, prefemur, base of femur; brush setae unbranched, tapering to blunt point. Pre-anal ring moderately setose; hypoproct subtrapezoidal; epiproct from above tapering smoothly to rounded tip, extending slightly past anal valves. Spinnerets in square array.

Gonopore on distomedial bulge of leg 2 coxa, protected by tall, thin cowl. Short brushes of setae on sternite between legpairs 4 and 5. Legs 6 and 7 bases (Fig. 2A)

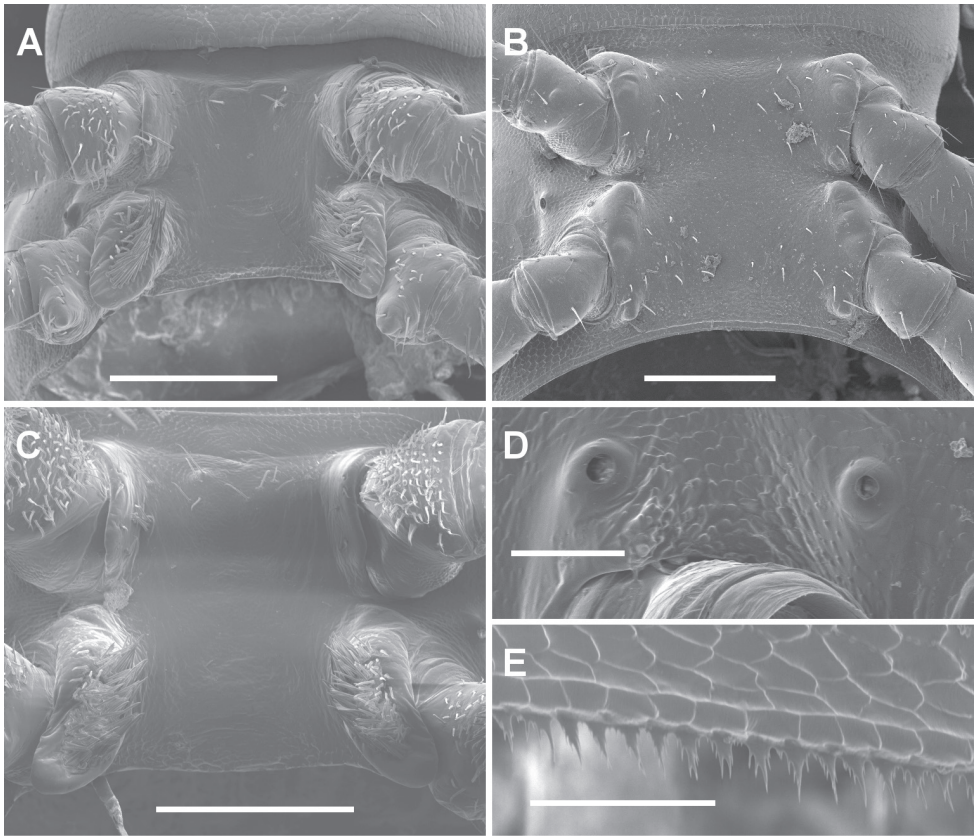


Figure 2. **A, D, E** *Tasmaniosoma anubis* sp. n., paratype ex QVM 23:53817 **B** *T. interfluminum* sp. n., paratype ex QVM 23:52247 **C** *T. nicolaus* sp. n., paratype ex QVM 23:53860 **A, B, C** Ventral views of male ring 6 **D** Left lateral view of midbody spiracles **E** Limbus on lateral portion of midbody ring. Scale bars: **A–C** = 0.25 mm, **D, E** = 0.05 mm.

well- and equally separated; no sternal tab by leg 6; tall, rounded sternal tab by leg 7 with medial brush of thick, rod-like, pointed setae; leg 7 coxa with short, rounded distomedial bulge.

Gonopod aperture ovoid, ca 1/2 as wide as ring 7 prozonite, posterolateral margin raised. Gonocoxa short, subcylindrical, slightly tapering distally. Telopodites (Fig. 3) almost straight, parallel; extending nearly to leg 6 bases when retracted. Telopodite straight, subcylindrical, divided at about 3/4 telopodite height into three major processes: (a) short, slightly helicoid, pointed solenomere posteromedially, directed distally; (b) large, wide, anteroposteriorly flattened central process with apex twisted and flattened mediolaterally with rounded apical margin and narrow bursa-like fold at apex base, and with medial margin of central process curving posteriorly as rounded tab; (c) long, rod-like, tapering, apically rounded lateral process directed distally and slightly laterally. Telopodite projecting posteriorly at base as thin shelf, concave distally. Anterior surface of telopodite at about 2/3 telopodite height with tapering, anteromedially directed tab,

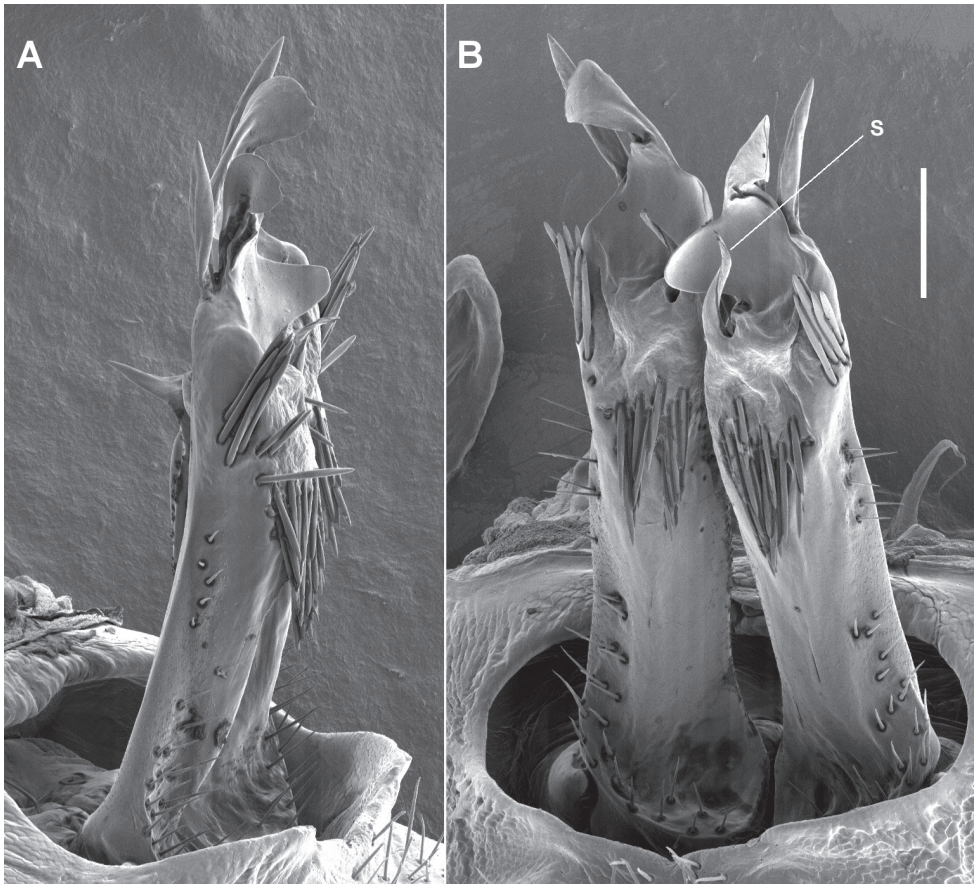


Figure 3. *Tasmaniosoma anubis* sp. n., paratype ex QVM 23:53817; right lateral **A** and posterior **B** views of gonopods in situ. **s** = solenomere. Scale bar = 0.1 mm.

longer than wide. Sparse, fine, mainly short setae on lateral and posterolateral surfaces to about 1/2 telopodite height, and on basal shelf. Two closely packed clusters of stout, rod-like, pointed setae: one (ca 12 setae) on posterior telopodite surface, arising just over 1/2 telopodite height and directed basally, the other (ca 10 setae) arising posterolaterally at level of solenomere base and directed distally and slightly posteriorly. Prostatic groove running more or less straight to base of solenomere on medial surface.

Female with legs more slender and prefemora and femora not swollen. Epigynum ca 1/3 width of ring 2, posterior margin produced medially as small, rounded triangle with irregular margin. Cyphopods not examined. (See also Remarks, below.)

Distribution. Eucalypt forest and woodland within a range envelope of <12 km in the city of Launceston, Tasmania, with a core habitat area of <6 km² (Figs 4A, 5A). Locally abundant in the core habitat area and readily found in bark litter at the bases of *Eucalyptus viminalis* trees (Fig. 4B). Co-occurs with *Tasmaniosoma armatum* and the introduced julid millipedes *Ommatoiulus moreleti* (Lucas, 1860) and *Cylindroiulus* spp.



Figure 4. **A** Museum specimen localities to 15 February 2015 of *Tasmaniosoma anubis* sp. n. (blue markers). Base map from <http://maps.thelist.tas.gov.au/listmap/app/list/map>; for general location see index map, Fig. 5A. **B** *T. anubis* sp. n. type locality, looking west to Lake Trevallyn. Accumulations of bark litter at the base of *Eucalyptus viminalis* (the tall, white-barked trees at top centre) are preferred shelters for *T. anubis* sp. n.

Name. Greek “Anubis”, a jackal-headed god of ancient Egypt; noun in apposition. The tip of the gonopod telopodite in posterolateral view resembles popular representations of the head of Anubis (Fig. 5B). The “snout” of the jackal corresponds to the medial tab of the central process, and the “ears” to the lateral process and the apical portion of the central process. This name was suggested by collector Lisa Clarkson.

Remarks. The core habitat area for *T. anubis* sp. n. includes the 440 ha Trevallyn Nature Recreation Area (TNRA; Fig. 4A), which is managed as urban parkland.

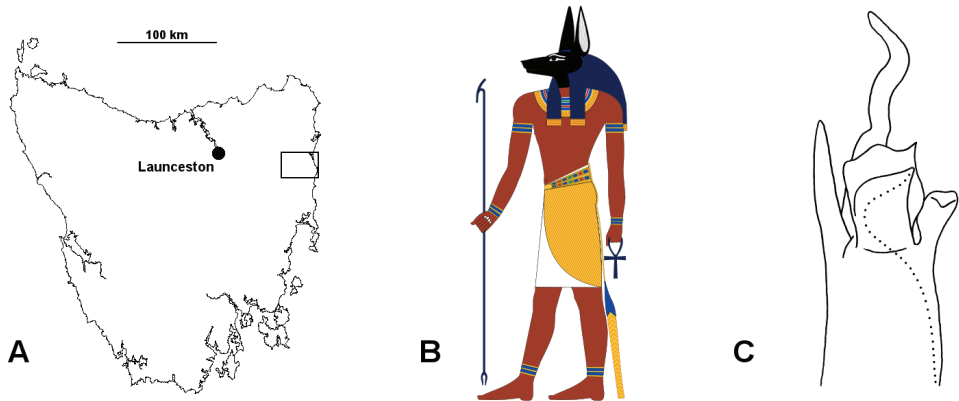


Figure 5. A The main island of Tasmania (Mercator projection) showing locations of Launceston (*T. anubis* sp. n. range) and the Nicholas Range area (rectangle; ranges of *T. interfluminum* sp. n. and *T. nicolaus* sp. n.) **B** Anubis, as illustrated by Jeff Dahl (Creative Commons Attribution-ShareAlike license, GNU Free Documentation License; http://commons.wikimedia.org/wiki/File:Anubis_standing.svg) **C** Posterior and slightly ventral view of distal portion of right gonopod of *T. interfluminum* sp. n., ex QVM 23:52262. Dotted line marks course of prostatic groove.

Large populations of *T. anubis* sp. n. can be found in grassy woodland adjacent to bitumenised roads in the TNRA.

T. anubis sp. n. has not been found more than ca 1.5 km from the South Esk River near its confluence with the Tamar River at Cataract Gorge in the city of Launceston (Fig. 4A). The land snail *Pasmaditta jungermanniae* (Petterd, 1879), the pseudoscorpion *Neopseudogarypus scutellatus* Morris, 1948 and the spider *Migas plomleyi* Raven & Churchill, 1989 are also believed to be restricted to the Cataract Gorge area, or to the Gorge area and small outlying localities (Fearn 2003). However, one possible male specimen of *T. anubis* sp. n., examined years ago and unfortunately now lost, and two possible female specimens (QVM 23:52256) have been collected in small, degraded remnants of native vegetation close to the South Esk River in the town of Evandale, ca 15 km southeast of Launceston. I suspect that *T. anubis* sp. n. was more widespread along the lower South Esk River in pre-European times, i.e. before the early 19th century. Millipede populations would have declined as sheep grazing degraded the local eucalypt woodlands, and would have disappeared over most of the Launceston area as woodlands were cleared for residential development.

Unlike the similar-sized, co-occurring dalodesmid *Atrophotergum pastorale* Mesibov, 2004 and unlike most *Tasmaniosoma* species, *T. anubis* sp. n. do not usually run away rapidly when disturbed, but remain “crouched” and stationary on the bark, leaf or wood pieces among which the animals are sheltering.

As with *Tasmaniosoma compitale* Mesibov, 2010 and *T. hickmanorum* Mesibov, 2010 (Mesibov 2010), most *T. anubis* sp. n. females are missing their second pair of legs and have plugs of sclerotised scar tissue where these legs have broken off.

***Tasmaniosoma interfluminum* sp. n.**

<http://zoobank.org/AD1A118D-F8C7-4DD6-A585-BAE4757AC6B5>

Figs 1B, E, 2B, 5C, 6

Holotype. Nicholas Range, Tas, -41.5417 148.0786 \pm 25 m (GPS), 570 m a.s.l., 14 May 2012, W. Clarkson and L. Clarkson, QVM 23:53867 (ex QVM 23:52247).

Paratypes. 3 males, details as for holotype, QVM 23:52247.

Other material. 21 males and 4 females (see Suppl. material 1 for details).

Diagnosis. Very similar to *T. decussatum*, but without a setose sternal tab adjoining leg 7, with the anterolateral telopodite process prominently notched, with the solenomere tabs curving posteriorly and less deeply separated, and with the medial process tongue-like and curving posterobasally, rather than forming a rounded, mediolaterally flattened, tab-like solenomere extension as in *T. decussatum*.

Description. Male/female approximate measurements: length 12/11 mm, mid-body paranota width 1.4/1.4 mm, maximum vertical diameter 1.1/1.1 mm. Live and freshly preserved adults with yellowish ground colour (Figs 1B, 1E), antennae and distal podomeres pale reddish brown, reddish brown transverse streaks or cellular margins anterior to transverse furrow and near posterior margin of metatergite, and laterally on prozonites and below paranota. Colouring fades in alcohol; long-preserved animals entirely decoloured or more or less uniformly pale yellowish white.

Non-gonopodal features in males mostly as for *T. anubis* sp. n., but head moderately setose; antennal sockets separated by ca 1.5 \times socket diameter; overall ring widths 6>5>(4,head)>2>3>collum; rings 8-16 distinctly elongated; ring 2 ventrally on either side with wide, shallow pit, the anterolateral margin well-defined; metatergites with indistinct low tubercles medially; midbody legs with tarsus ca 1.8 \times as long as femur; brush setae on coxa/trochanter, prefemur and femur of anterior legs; legs 6 and 7 bases (Fig. 2B) well- and equally separated; no setose sternal tab by leg 6 or leg 7, but sternite by leg 7 base slightly produced as rounded bumps.

Gonopod aperture ovoid, ca 1/2 as wide as ring 7 prozonite, posterolateral margin raised. Telopodites (Figs 5C, 6) almost straight, parallel; extending to leg 6 bases when retracted. Telopodite with shallow concavity over most of posterior surface, the margin continuing as posterior margin of posterobasal shelf; anterior surface strongly and broadly ridged. Telopodite divided at ca 2/3-3/4 height into four processes: (a) long, rod-like, tapering, apically rounded lateral process directed distally and slightly posteriorly; (b) large anterolateral process curving posteriorly with distinctive, V-shaped notch on anterior edge, S-shaped distal to notch with acuminate apex directed distally and slightly laterally; (c) posteromedial solenomere developed as parallel, subquadrangular, transverse tabs separated by narrow slit, curving posteriorly; (d) tongue-like medial process curving basally and directed slightly medially. Sparse setae posterolaterally to ca 1/2 telopodite height, with small, separate patch of fine, short setae on posterior surface ca 1/3-1/2 telopodite height. Prostatic groove running up medial surface of telopodite, curving laterally across posterior surface in slit between solenomere tabs,

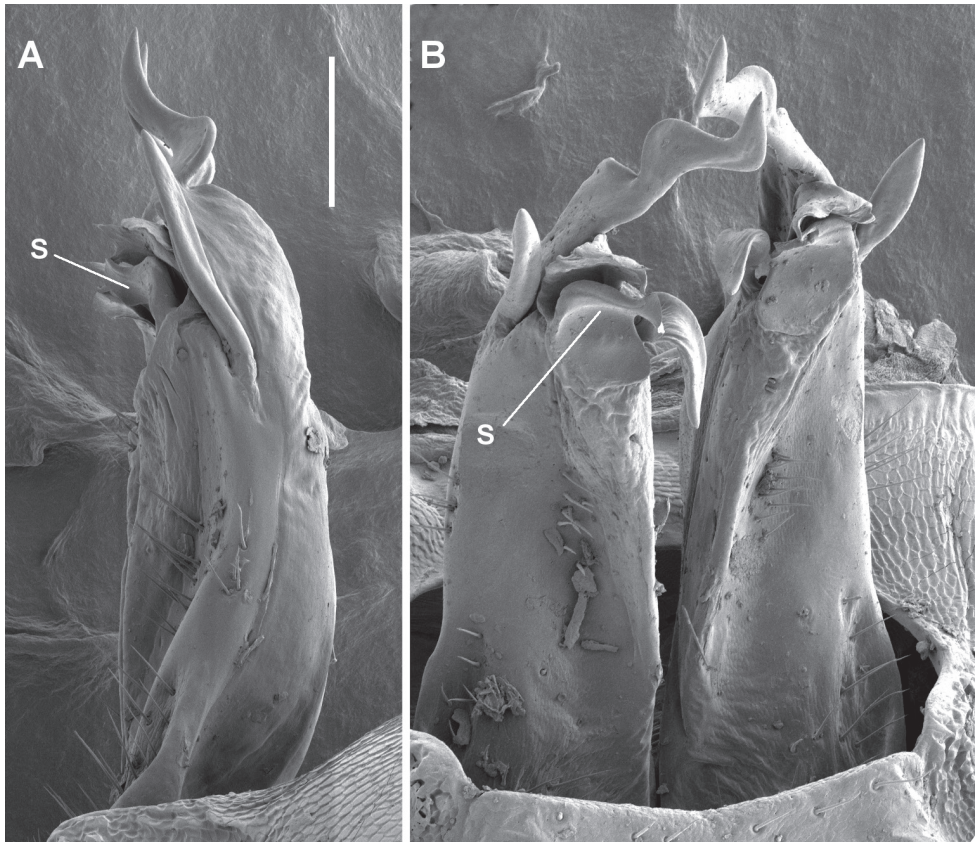


Figure 6. *Tasmaniosoma interfluminum* sp. n., paratype ex QVM 23:52247; left lateral **A** and posterior and slightly ventral **B** views of gonopods in situ. **s** = solenomere. Scale bar = 0.1 mm.

then running along lateral margin of more basal tab to open near medial corner of tab (Figs 5C, 6).

Female about as robust as male but shorter, with posterior rings not elongated; legs more slender and prefemora and femora not swollen. Epigynum ca 1/3 width of ring 2, posterior margin produced medially as low trapezoid with irregular margin. Cyphopods not examined.

Distribution. Eucalypt forest over ca 100 km² north and east of Fingal, Tasmania, with an outlying record near the town of Scamander on the east coast (Figs 5A, 7A). Co-occurs with *T. barbatulum*, *T. nicolaus* sp. n. and *T. orientale* in bark and leaf litter in the Nicholas Range.

Name. Latin *inter* (between) + *fluminum* (genitive plural of *flumen* = river); adjective. The largest populations of this species are found between the upper South Esk and Break O'Day Rivers.

Remarks. The gonopod telopodite structure of *T. interfluminum* sp. n. is remarkably similar to that of *T. decussatum*, the two differing only in the details noted above

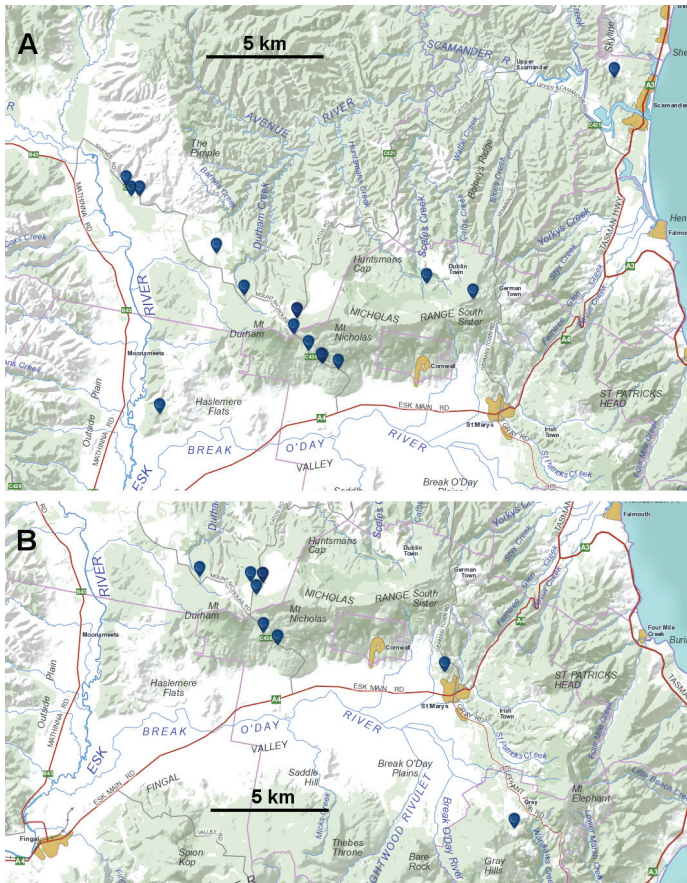


Figure 7. Known localities (blue markers) to 15 February 2015 of *Tasmaniosoma interfluvium* sp. n. (**A**) and *T. nicolaus* sp. n. (**B**). Base map from <http://maps.thelist.tas.gov.au/listmap/app/list/map>; for general location see index map, Fig. 5A.

in Diagnosis. Another difference is a setose sternal tab adjoining the base of leg 7: present in *T. decussatum*, absent in *T. interfluvium* sp. n. I am unable to distinguish the two species in the field.

***Tasmaniosoma nicolaus* sp. n.**

<http://zoobank.org/40D169CB-9D35-4A0A-BA36-F4DDDF4FD93FA>
Figs 1C, F, 2C, 8, 9A

Holotype. Male, Catos Road, Tas, -41.5350 148.0842 ±50 m (GPS), 520 m a.s.l., 9 February 2015, R. Mesibov, QVM 23:53864 (ex QVM 23:53860).

Paratypes. 18 males, details as for holotype, QVM 23:53860.

Other material. 5 males and 3 females (see Suppl. material 1 for details).

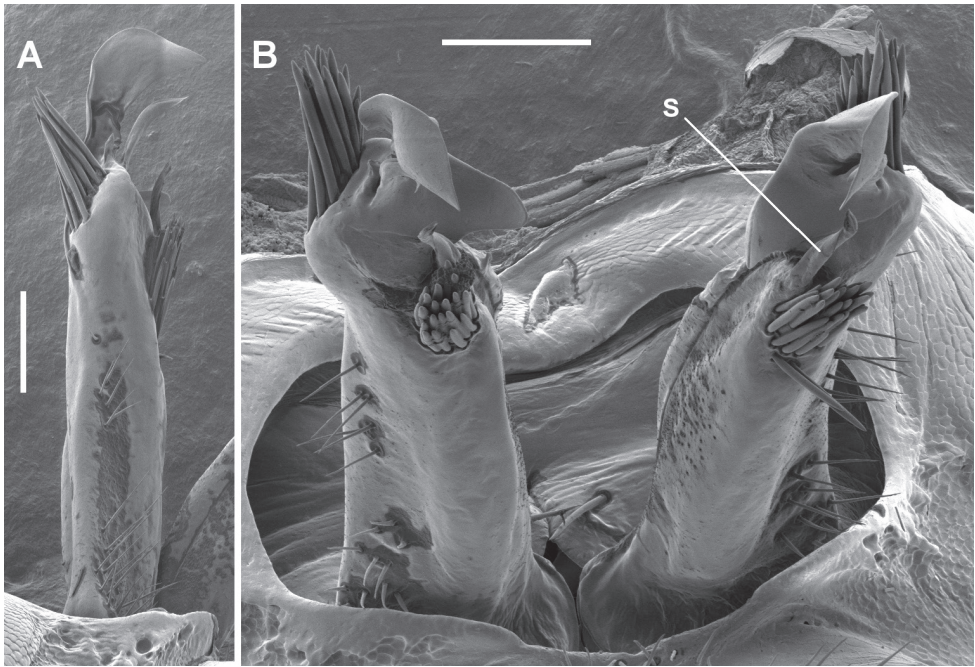


Figure 8. *Tasmaniosoma nicolaus* sp. n., paratype ex QVM 23:53860; lateral view of right gonopod (A) and posteroventral view of both gonopods (B) in situ. **s** = solenomere. Scale bars = 0.1 mm.

Diagnosis. Member of the “*anubis* group” within *Tasmaniosoma* (see Discussion); distinguished from *T. anubis* sp. n., *T. barbatulum* and *T. fragile* by the absence of a basally directed cluster of stout, rod-like setae on the posterior surface of the gonopod telopodite; from *T. clarksonorum*, *T. compitale* and *T. hickmanorum* by the absence of a lateral process on the telopodite apex; and from *T. fasciculum* by the telopodite apex extending as a mediolaterally flattened process in the shape of a bird’s head pointed posteriorly.

Description. Male/female approximate measurements: length 11/10 mm, mid-body paranota width 1.3/1.2 mm, maximum vertical diameter 1.0/1.0 mm. Live and freshly preserved adults (Figs 1C, F, 9A) with dark reddish brown head and antennae; body with yellowish ground colour, dark reddish brown on paranotal margins, dorso-laterally on prozonites, as cellular borders in patches laterally, and as diffuse streaks and cellular borders dorsomedially and as margin lines posteriorly on pro- and metazonites; legs darkening slightly distally. Long-preserved animals almost entirely decoloured.

Non-gonopodal features in males as for *T. anubis* sp. n., but overall ring widths $6 > 5 > (4, \text{head}) > (3, 2) > \text{collum}$; prefemoral swellings to about leg 20. Legs 6 and 7 bases (Fig. 2C) well- and equally separated; no sternal tab by leg 6; tall, rounded sternal tab by leg 7 with medial brush of thick, rod-like, pointed setae; leg 7 coxa without distomedial bulge.

Telopodites (Fig. 8) almost straight, parallel; extending nearly to leg 6 bases when retracted; without prominent posterobasal shelves. Telopodite straight, subcylindrical,



Figure 9. **A** *Tasmaniosoma nicolaus* sp. n., freshly killed male paratype ex QVM 23:53860 **B, C** *T. barbatus* Mesibov, 2010, freshly killed male ex QVM 23:53861; dorsal (**B** anterior to left) and right lateral (**C** anterior to right) views of midbody rings. Scale bars: **A** = 2.5 mm, **B, C** = 0.5 mm.

at about 3/4 telopodite height swelling distolaterally, centrally and medially projecting as large anteroposteriorly flattened process with apex twisted to be mediolaterally flattened, shaped like bird's head and pointed posteriorly; smaller sickle-shaped process arising at base of apex and directed posterodistally; and medial margin of large process curving posteriorly as thin tab with rounded margin. Solenomere short, slightly helioid, pointed, arising posterior to base of large process and directed distally. Sparse, fine, fairly long setae on lateral and posterolateral surfaces to about 1/2 telopodite

height. Two closely packed clusters of stout, rod-like, pointed setae: one (ca 12 setae) on anterolateral surface near base of large telopodite process and directed distally and slightly anteriorly, the other (ca 15 setae) arising posteromedially just posterior to solenomere base and directed distally and slightly posteriorly. Prostatic groove running more or less straight to base of solenomere on medial surface.

Female with legs more slender and prefemora and femora not swollen. Epigynum ca 1/3 width of ring 2, posterior margin produced medially as small, rounded triangle with irregular margin. Cyphopods not examined. (See also Remarks, below.)

Distribution. Eucalypt forest over <40 km² on the Nicholas Range and the Mt Elephant area at the eastern end of the Fingal Valley in northeast Tasmania, on both north- and south-facing slopes at ca 300–500 m a.s.l. (Figs 5A, 7B). Co-occurs with *T. barbatulum*, *T. interfluminum* sp. n. and *T. orientale* in bark and leaf litter.

Name. Latinised “Nicholas” for the Nicholas Range, type locality of this species; noun in apposition.

Remarks. All of the known *T. nicolaus* sp. n. collection sites are in forest patches with evidence of past logging and burning, and part of the known range of *T. nicolaus* sp. n. is within the ca 800 ha Nicholas Range Regional Reserve. Like *T. anubis* sp. n., *T. nicolaus* sp. n. can be locally abundant: I found most of the 19 type specimens in bark litter under two *Eucalyptus* trees.

My identification of three females as *T. nicolaus* sp. n. (QVM 23:53635) is tentative. Two of the three females are missing legs 2.

Note on *T. barbatulum*

Alcohol-preserved specimens of *T. barbatulum* are almost entirely decoloured, i.e. more or less uniformly pale white (Mesibov 2010). Live and freshly preserved specimens are coloured very similarly to *T. nicolaus* sp. n. (Fig. 9). Where the two species co-occur they can be hard to distinguish in the field, but *T. nicolaus* sp. n. is a little longer and distinctly more robust than *T. barbatulum*.

Discussion

The new species *Tasmaniosoma anubis* sp. n. and *T. nicolaus* sp. n. join *T. barbatulum*, *T. clarksonorum*, *T. compitale*, *T. fasciculum*, *T. hickmanorum* and probably *T. fragile* in a well-defined group within *Tasmaniosoma*, first recognised in Mesibov (2010) and here called “the *anubis* group”. Species in this group have complex but fugitive colouration; three rows of low, rounded, metatergal tubercles; a sternal tab with thick setae at the base of leg 7; and a gonopod telopodite with two or three tight clusters of stout, rod-like setae at or near the telopodite apex. The group occurs over most of Tasmania but has not yet been found in the far south or the southeast of the main island, or on islands in Bass Strait.

The relationships of *T. interfluminum* sp. n. are uncertain, but it is clearly very close to *T. decussatum* and the two species may be parapatric in northeast Tasmania.

Acknowledgements

Wade and Lisa Clarkson (Riverside, Tasmania) diligently searched for the new species described in this paper. I am very grateful to the Clarksons for their enthusiastic and voluntary efforts in the field, and to Julianne Waldock of the Western Australian Museum for the loan of a *T. anubis* sp. n. specimen. SEM images were acquired with the help of Sandrine Feig of the Central Science Laboratory, University of Tasmania. I thank reviewers Cathy Car and Sergei Golovatch for recommending improvements to the draft manuscript. This study was funded by the author.

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Supplementary material I

Specimen records of *Tasmaniosoma* species.

Authors: Robert Mesibov

Data type: Tab Separated Value File (tsv).

Explanation note: Specimen records of *Tasmaniosoma* species as of 15 February 2015.

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Subdivision of the tribe Oligaphorurini in the light of new and lesser known species from North-East Russia (Collembola, Onychiuridae, Onychiurinae)

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<http://zoobank.org/222F80DD-F7A3-444B-8A2A-7A25A6454FE8>

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Abstract

The paper is devoted to a taxonomic review of Oligaphorurini from the north-eastern part of Palaearctic. Two new species, i.e. *Oligaphorura ambigua* **sp. n.** and *O. duocellata* **sp. n.**, are described. Four species, *O. nataliae* (Fjellberg, 1987), *O. interrupta* (Fjellberg, 1987), *O. pingicola* (Fjellberg, 1987), and *Micraphorura alnus* (Fjellberg, 1987), are redescribed on base of the types and new material, and remarks on other species known for the region, *O. groenlandica* (Tullberg, 1876), *O. ursi* (Fjellberg, 1984), *O. aborigensis* (Fjellberg, 1987), and *M. absoloni* (Börner, 1901), are given to clarify their generic affiliation. Finally, merits and disadvantages of the current subdivision of the tribe are discussed and a key to the northern species of the tribe is provided.

Keywords

Taxonomy, new species, Oligaphorurini, north-eastern Asia

Introduction

Two undescribed species of the tribe Oligaphorurini from the upper reaches of Kolyma River (North-East Russia, Magadan region) do not fit the current generic subdivision of the tribe, which is mainly based on revisions made by Pomorski (1996) and Weiner (1996). Other east Palaearctic species, described by one of the authors (A. Fjellberg) from the same region, also need a critical review to fix their generic affiliation. Below, the new species are described, others are redescribed in more detail, and finally the current generic subdivision of the tribe is critically analyzed.

The current subdivision of Oligaphorurini

Bagnall (1949) was the first author to recognize Oligaphorurinae (as a subfamily of Onychiuridae). He split it into four genera: *Archaphorura*, *Micraphorura*, *Oligaphorura* and *Dimorphaphorura* based on five species only, the sixth species, described in the same paper, is now considered as a synonym. Since then many other species have been established, often in shifting generic associations. At present, according to the database of Collembola of the World (Bellinger et al. 1996–2014) approximately 50 species of the tribe are known. Using different approaches Weiner (1996) and Pomorski (1996) retained the four original genera described by Bagnall. One new genus, *Chribellphorura*, was established by Weiner (1996) for *Onychiurus allanae* Christiansen & Bellinger, 1980, displaying a unique set of characters. However, this generic framework bears internal contradictions and does not cope with the known morphodiversity of the species. Both Pomorski and Weiner (op. cit.) based their diagnoses on the gradual reduction of the furcal field on the sternum of the fourth abdominal segment. Pomorski examined the first instar juveniles, while Weiner used adults. Both authors studied a rather limited set of mainly European species. Table 1 summarizes the diagnostic characters separating the genera and which species were involved.

Recently Shvejonkova and Potapov (2011) described three new species of Oligaphorurini which did not possess anal spines, a feature which was characteristic only to the genus *Archaphorura*. Nevertheless the species were assigned to the genera *Oligaphorura* and *Micraphorura*, an action which brings the above diagnostic scheme to a state of collapse. However, the cited authors did not establish the synonyms which would have been a natural consequence.

In 2014 a complete revision of the genus *Dimorphaphorura* has been undertaken (Weiner and Kaprus' 2014). The authors of this revision described six new Palaearctic species of the genus, redescribed and clarified generic affiliation of a number of other known species, and defined diagnostic characteristics of the revised genus. According to the diagnosis provided, it differs from other genera of the tribe in the organization of the furcal area (see Table 1). As a result the majority of Palaearctic species previously treated as *Micraphorura* have been transferred to *Dimorphaphorura*. The two new species described below introduce further chaos in the existing generic system.

Table 1. Main diagnostic characters used for genus separation in Oligaphorurini.

	<i>Chribellphorura</i>	<i>Archaphorura</i>	<i>Microphorura</i>	<i>Oligaphorura</i>	<i>Dimorphaphorura</i>	
Weiner (1996)	Apical vesicle on <i>Ant</i> .4	present	absent			
	Tibiotarsal setae	clavate	pointed			
	Anal spines	present	absent	present		
	Furcal rudiment	finely granulated area	small pocket or finely granulated area	finely granulated area, some-times with a kind of pocket	cuticular fold or deep pocket	
	Dental setae	four in line	four in two rows	two in line	four in two rows	
	Manubrial setae	one row	two rows	two rows	two (seldom one) rows	
Pomorski (1996)	Unpaired setae on <i>Abd</i> .6	p_0	m_0	p_0 or a_0 and p_0	a_0 and p_0	
	Species involved	<i>allanae</i>	<i>serratotuberculata</i> and some species that have not yet been described	<i>absoloni</i> , <i>pieninensis</i>	<i>groenlandica</i> , <i>montana</i> , <i>unilica</i> , <i>judithae</i> , <i>koreana</i> , <i>lindene</i>	
	Anal spines		absent	present		
	Setae on <i>area funalis</i>		2+2 setulae + 2+2 setae	1+1 setulae + 1+1 setae	2+2 setulae + 2+2 setae	
	Species involved		<i>serratotuberculata</i>	<i>absoloni</i> , <i>pieninensis</i>	<i>groenlandica</i> , <i>judithae</i>	
	<i>AO</i>		in subapical position	normal		
Shyunkova and Potapov (2011)	Anal spines		absent	present or (rarely) absent	“So far the independence of <i>Dimorphaphorura</i> calls for further ground”	
	Distal tibiotarsal setae		11	11 or fewer		
	Furcal rudiment			cuticular furrow or finely granulated area		
	Dental setae			two or four in one row		four in two rows
	Manubrial setae			number of rows varied		
	<i>Abd</i> .5–6		fused	separated		
Weiner and Kaprus' (2014)	Anal spines		present	present or absent		
	Distal tibiotarsal setae			11	5–11	
	Furcal rudiment			cuticular furrow	cuticular fold	
	Dental setae			1+1	2+2	
	<i>ma</i> setae			2 (at a level with posterior row of dental setae)		
	<i>mm</i> setae			4–6	3–6	2
Weiner and Kaprus' (2014)	<i>mp</i> setae			4–5	4–7	4–6

Abbreviations

A, AB, AC and **ABC** – four types of labium in Onychiuridae in accordance with the presence of thickened and blunt-tipped setae on corresponding labial papillae (Fjellberg 1999)

ABD – the fifth type of labium in Onychiuridae (Shvejonkova and Potapov 2011)

Abd.1-6 – abdominal segments

A-B, T-setae, setae M and **Y** – tibiotarsal setae (Deharveng 1983)

Ant.1-4 – antennal subsegments

AO – antennal organ on *Ant.3*

a_0 , m_0 and **p_0** – unpaired axial setae on terga

CNC – Canadian National Collection (Ottawa)

d_0 – unpaired axial seta on *area frontalis* of the head

ma-, mm- and **mp-row** – anterior, medial and posterior rows of setae on manubrial field (Weiner 1996)

ms – microsensillum

MSPU – Moscow State Pedagogical University

PAO – postantennal organ

psa – pseudocellus(i)

psx – parapseudocellus(i)

q-setae – proximal setae on furcal field of Onychiuridae (Pomorski 1996)

Th.1-3 – tergal segments

Description of new species

Oligaphorura ambigua sp. n.

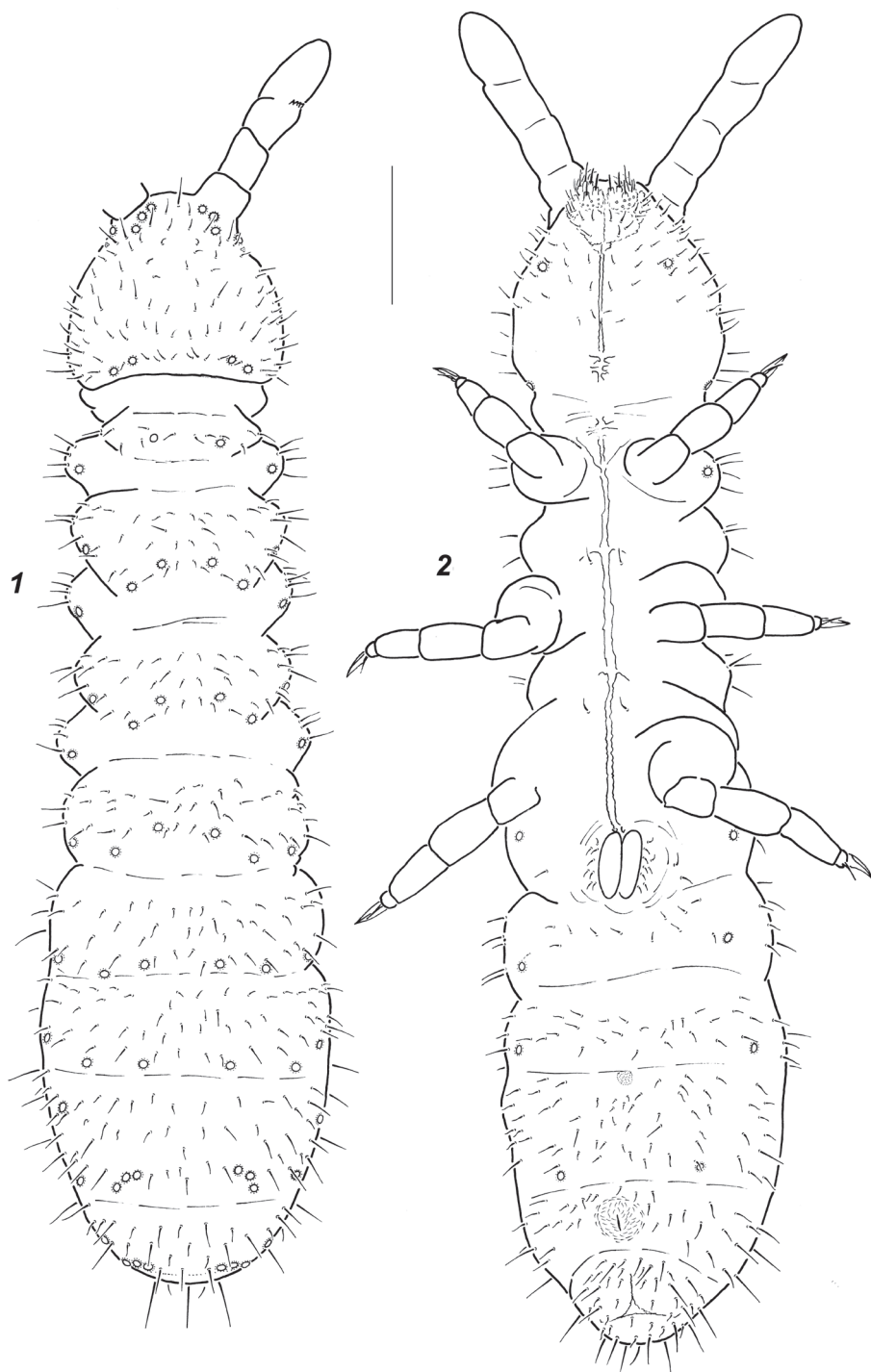
<http://zoobank.org/36FF3284-F55E-4F97-B85C-210D66A3CBC6>

Figs 1–9, 29–30

Material. Holotype ♂, Russia, Magadan District, upper reaches of Kolyma River, Bolshoi Annachag Mt. Range, field station “Aborigin” [61°56'N, 149°40'E], mountains above station, rather dry moss/lichen in rock crevices, 1600 m alt., 23 vii 1979, A. Fjellberg leg. (MSPU).

Paratypes 6♂, 5♀, and 4 juveniles, same data as holotype (MSPU); 1♂, 2♀, and 1 juveniles, same data but moss, lichens on rock, 1650 m alt., 23 vii 1979, A. Fjellberg leg. (MSPU).

Description. Colour white. Size of adults 0.73–0.92 mm. Body slender and elongated, *Abd.3-4* clearly widened, *Abd.6* short and hardly visible in dorsal view (Fig. 1), anal spines not developed (Fig. 3). Antennae about as long as head, *Ant.4* not wider than *Ant.3* (Fig. 5). *Ant.4* with spherical subapical organite surrounded by cuticular papillae (Fig. 6), basal microsensillum present on level with proximal whorl of setae (Fig. 5). *AO* consisting of 4 finger-like papillae, 2 sensory rods, 2 smooth sensory clubs clearly differing in shape



Figures 1–2. *Oligaphorura ambigua* sp. n. Chaetotaxy and *pso* position. **1** dorsal view **2** ventral view.
Scale bar: 0.1 mm.

(Fig. 7), 5 guard setae and a lateral microsillium (Fig. 5). *Ant.* 1 and 2 with (8)9 and 14–15 setae respectively. *PAO* smaller than nearest *psa*, usually with 3 subequal lobes (Fig. 8). Labrum with 7 setae and 4 prelabral ones. Apical part of labium with thick terminal setae on papillae *A*, *B* and *C* (*ABC*-type), 7 long and 4 spiniform guard setae, and 6 proximal setae (Fig. 4). Basal fields of labium (mentum and submentum) with 4 and 5 setae, hypostomal complex of usual shape. Maxillary palp simple, with 2 sublobal setae.

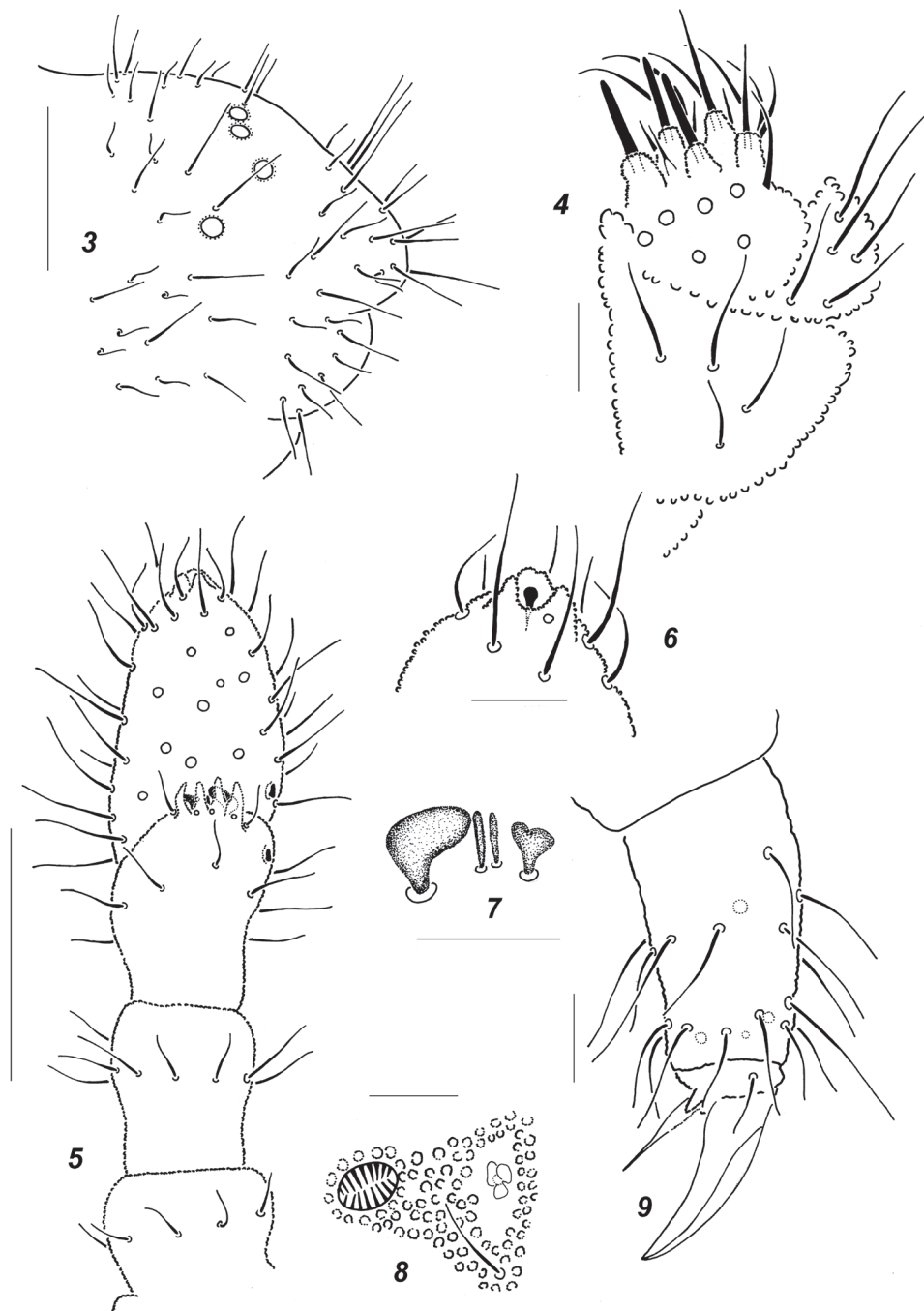
Pseudocellar formulas (*psa*) as follows, dorsal: 42/133/33354, ventral: 11/000/1111, parapseudocelli (*psx*) invisible. Each upper subcoxa with two *psa*, dorsal and ventral. Localization of *psa* as in Figs 1–2. Granulation fine and uniform, without areas of enlarged granules. Dorsal chaetotaxy more or less symmetrical, with frequent variations even in axial parts of terga. Setae smooth and clearly differentiated, especially on abdominal tip: meso- and macrosetae straight, thick and blunt, microsetae curved and pointed, sensory setae indistinct (Fig. 1). *Th.* 1 with 6+6 setae. Lateral *ms* present only on *Th.* 2. All terga from *Th.* 2 to *Abd.* 3 with 3+3 axial microsetae as a rule. Unpaired dorsal seta d_0 on head absent, *Abd.* 4–5 usually with meso- and macrosetae p_0 , *Abd.* 6 dorsally with 1–2 axial macrosetae. Thoracic sterna of *Th.* 2–3 with 1+1 setae along ventral line, rarely absent on one or both sterna, ventral chaetotaxy of abdomen as in Fig. 2. Furca reduced to a small area of fine granulation situated at contact with borders of *Abd.* 3–4 sterna, with 2+2 small posterior setae arranged in 2 rows and surrounded by several (age dependent) longer setae including two flank macrosetae in row *mp* (cf. Fig. 29 and Fig. 30). Ventral tube with (8)9+9 distal setae and 1(2) proximal ones at base. Upper subcoxae usually with 4–5–5, tibiotarsi with 20–21–20 setae as a rule. Distal whorl with 11 setae (7 *A* and 4 *T*-setae), whorl *B* with 7–7–6 setae, setae *M* and 1–2 setae of *C*-whorl present. Unguis simple, with neither inner nor lateral teeth, unguiculus without distinct basal lamella, clearly shorter than unguis (Fig. 9).

Affinities. This new species resembles two congeners recently described from the European part of Russia, namely *Oligaphorura humicola* Shvejonkova & Potapov, 2011 and *O. kremenitsai* Shvejonkova & Potapov, 2011. All three species lack anal spines and have no cuticular fold on the sternum of *Abd.* 4. Apart from this, the former is characterized by a set of *psa* on both dorsal and ventral sides on a body, as well as on upper subcoxae identical to that in *O. ambigua* sp. n., and also has no *ms* on *Th.* 3 and ventral *psx*. *O. kremenitsai* differs from both *O. ambigua* and *O. humicola* having more *psa* on *Th.* 2–3 (42/144/33354 as a whole). Some differences like the uncommon position of anterior *psa* on head and submedial ones on *Abd.* 4–5 in *O. humicola* and *O. kremenitsai* or their reduced tibiotarsal chaetotaxy may be a result of small body size (< 0.6 mm). Nevertheless, the palp structure (*ABD*-type) in *humicola/kremenitsai* and the loss of labial papilla *C* probably reflects a certain genetic distance.

The presence of only four papillae in *AO* is also an unusual condition in the tribe, shared only with *Micraphorura absoloni* (Börner, 1901), *Oligaphorura palissai* (Yosii, 1971) and *Dimorphaphorura sophyae* Weiner & Kaprus', 2014. The clear cuticular papillae on antennal tip are also quite characteristic.

Etymology. The name reflects the uncertain generic position of the new species.

Distribution. Known only from the type locality, the alpine belt in the upper reaches of Kolyma river.



Figures 3–9. *Oligaphorura ambigua* sp. n. **3** abdominal tip **4** labium **5** antennae **6** antennal tip with subapical organite **7** sensorial elements of AO **8** PAO and nearest *pro* **9** *Ti.3*. Scale bars: **3, 5** = 0.05 mm; **4, 6–9** = 0.01 mm.

***Oligaphorura duocellata* sp. n.**

<http://zoobank.org/D3CCBC1E-3F6C-4737-A999-13C07A501D45>

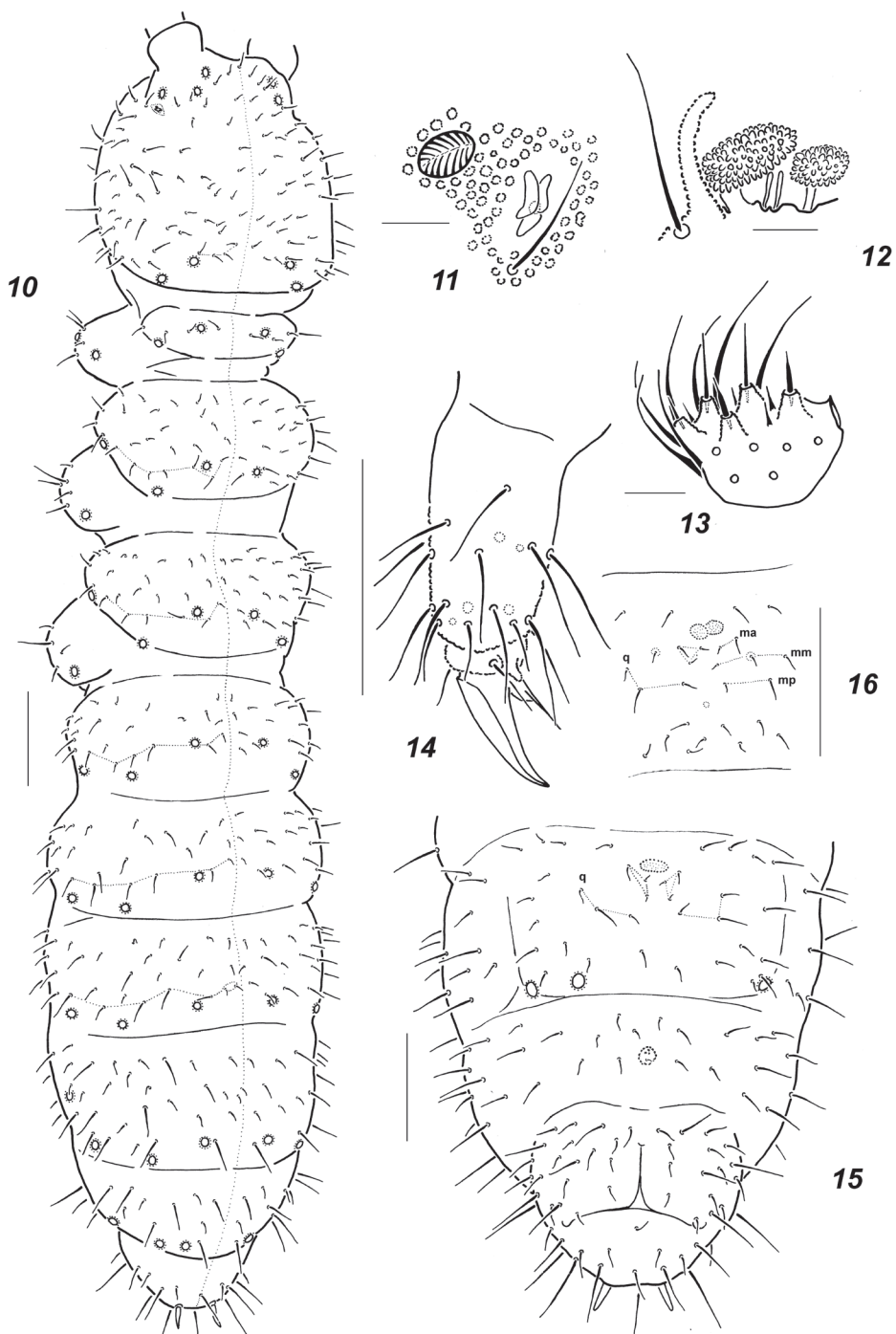
Figs 10–16

Material. Holotype ♂, Russia, Magadan District, upper reaches of Kolyma River, Bolshoi Annachag Mt. Range, field station “Aborigen” [61°56'N, 149°40'E], mosses on slope, 1400–1500 m alt., 27.vii.1979, leg. A. Fjellberg (MSPU).

Paratypes 1♂, 1♀, and 1 juvenile, same data as holotype (MSPU).

Description. Colour white. Size of adults 1.2–1.3 mm. Body slender and elongated. Antennae slightly shorter than head, club-like with *Ant.4* clearly wider than *Ant.3*. Subapical organite on *Ant.4* peg-like, basal microsensillum set on level with proximal whorl of setae. *AO* consisting of 5 long papillae, 2 sensory rods, 2 granulated sensory clubs clearly differing in shape (Fig. 12), 5 guard setae and a lateral microsensillum. *Ant.1* and 2 usually with 8 and 14 (15) setae, respectively. *PAO* about as long as nearest *ps*, usually with 3 elongated lobes (Fig. 11). Labrum with 9 setae and 4 prelabrals. Apical part of labium with thick terminal setae on papillae *A* and *C* (*AC*-type), terminal setae on all papillae rather short (Fig. 13), 7 long, usual 4 spiniform guard setae and 6 proximal setae present. Basal fields of labium (mentum and submentum) with 4 and 5 setae, hypostomal complex of usual shape. Maxillary palp simple, with 2 sublobal setae.

Pseudocellar formulas (*ps*) as follows, dorsal: 32/(1)233/33343, ventral: 11/000/1111(2), parapseudocelli (*psx*) hardly visible (probably due to long preservation), but *psx* on unpaired anal lobe present. Upper subcoxae with 2-(2)3-3 *ps*, one dorsal and 1-2 ventral. Localization of dorsal *ps* as in Fig. 10, submedial *ps* on *Abd.4* set far apart. Granulation fine and uniform, without areas of enlarged granules. Dorsal chaetotaxy more or less symmetrical, but with frequent variations even in axial parts of terga. Setae smooth and clearly differentiated only on abdominal tip: meso and macrosetae straight, thick and blunt, microsetae curved and pointed, sensory setae indistinct (Fig. 10). *Th.1* with few setae, (3)4+4 as a rule, even in full grown specimens. Both *Th.2* and 3 with lateral *ms*. All terga from *Th.2* to *Abd.3* with 3+3 axial microsetae as a rule. Setae *p*₁ set clearly in forward position comparing with *p*₂ setae on head and *Th.2-Abd.3*. Unpaired dorsal seta *d*₀ on head absent, *Abd.4 m*₁ setae fine and curved, much shorter than straight *a*₁ and *p*₁, *Abd.6* with axial macroseta *a*₀ almost subequal to *a*₂ setae. Thoracic sterna of *Th.2-3* without setae along ventral line. Furca reduced to a small area with fine granulation situated in some distance from anterior border of *Abd.4*, 2+2 setae arranged in 2 rows below furcal remnant are clearly shorter than surrounded ones and moved posteriorly (Fig. 16). In juveniles manubrial field with 3+3 setae between furcal remnant and *q*-setae (Fig. 15), adult with few additional setae in intermediate position (Fig. 16). Ventral tube with 7+7 distal setae and 1-2 proximal ones at base. Upper subcoxae usually with 3-4-(4)5 setae, tibiotarsi with more than 20-20-19 setae: distal whorl always with 11 setae (7 *A* and 4 *T*-setae), whorl *B* with 7-7-6 setae, setae *M* and variable *C*-whorl with one or two setae present. Unguis simple, with neither inner nor lateral teeth,



Figures 10–16. *Oligaphorura duocellata* sp. n. **10** dorsal chaetotaxy and *psa* position **11** *PAO* and nearest *psa* **12** sensorial elements of *AO* **13** labium **14** *Ti.2* **15** chaetotaxy of abdominal sterna, juvenile **16** *ibid*, adult. Scale bars: **10**, **16** = 0.1 mm; **32**, **15** = 0.05 mm; **11–13** = 0.01 mm.

unguiculus with wide basal lamella, clearly shorter than unguis (Fig. 14). Anal spines long and rather thin set without clear papillae.

Affinities. Several uncommon features, like 2+2 pseudocelli and few setae on *Th*.1, the presence of pseudocelli on several abdominal sterna, the absence of setae on thoracic sterna, and a furcal remnant in the form of a finely granulated area with 4 small setae behind it, permit easy identification of the new species. In addition to *O. duocellata* sp. n. nine known species of the tribe possess pseudocelli on several abdominal sterna. Three of them, *Archaphorura serratotuberculata* (Stach, 1933), *A. alavensis* Simón & Luciáñez, 1994, and *A. marcuzzii* (Cassagnau, 1968) are usually considered as representatives of the genus *Archaphorura* due to the absence of anal spines. The presence of ventral *ps*o in the former species is uncertain as specimens from Moscow vicinity contrary to those from Poland (see Pomorski 1998) have only ventral *ps*x on abdomen. The loss of anal spines also characterizes *O. humicola*, *O. kremenitsai* and *O. ambigua* sp. n.

The only known species of the tribe with *AS* and *ps*o on several abdominal sterna (*M. multiperforata* (Gruia, 1973), *M. uralica* (Khanislamova, 1986), are within *Micraphorura* on the www.collembola.org or treated as *Dimorphaphorura* (*D. olenae* Weiner & Kaprus', 2014). *M. multiperforata* is a unique species with dorsal *ps*o multiplication, whereas *M. uralica* seems to be the most similar to *O. duocellata* sp. n. having also more than 2 *ps*o on subcoxae (a unique character) and no setae on thoracic sterna, a character which is known only for species from eastern parts of Asia and North America, i.e. *Oligaphorura nuda* (Fjellberg, 1987), *O. judithae* (Weiner, 1994), *O. linderiae* (Weiner, 1994), *O. montana* Weiner, 1994, *O. pseudomontana* Sun & Wu, 2012, and *O. chan-kaensis* Sun & Wu, 2012.

Etymology. Named after the presence of 2+2 *ps*o on *Th*.1, a character previously unknown for the tribe.

Distribution. Known only from the type locality.

Redescription and remarks on other species of Oligaphorurini from north-east Russia

Micraphorura absoloni (Börner, 1901)

Aphorura absoloni Börner, 1901: 422.

Micraphorura absoloni (Börner): www.collembola.org

Remarks. Juveniles from Magadan (NE Russia) have a furcal field with 2+2 setae behind the cuticular furrow, followed by 3+3 *q*-setae (Fig. 27). This pattern is in a full accordance with what Pomorski (1996) reported from European populations. In adults a few additional setae (usually in asymmetric positions) may appear between the primary rows of the juvenile, obscuring the original pattern (Fig. 28). The formula of the parapseudocelli (*ps*x) in specimens from Magadan is also the same as Pomorski (1998) noticed from Europe: 0/000/1101, absent on subcoxae.

***Oligaphorura nataliae* (Fjellberg, 1987), comb. n.**

Onychiurus (*Archaphorura*) *nataliae* Fjellberg, 1987: 281.

Micraphorura nataliae (Fjellberg): www.collembola.org

Material. holotype, ♂, "USSR, Chukotka, Chaun Bay [68°44'N, 170°36'E], upland heath, soil, 13.viii 1977" (CNC 165046, type No 20114); paratypes: 1 juv. same data (CNC 165136, type No 20113); 3♀, same place, Loc. S-1, Sept. 1975 (CNC 165135, type No 20112), all S.F. MacLean leg.

Additional material. 15 specimens, Russia, Novosibirsk Islands, Kotel'nyi, Balyktakh river [75°03'N, 140°10'E], various habitats, vii 1994, A. Babenko leg.

Redescription. Colour white. Size 0.8–0.9 mm. Body shape cylindrical. Antennae about as long as head, *Ant.* 3–4 broad, club-like. *Ant.* 4 with subapical organite and microsensillum located in proximal row of setae. *AO* consists of 5 long and thin papillae, two sensory rods, two granulated sensory clubs (internal straight, external much bigger and bent), 5 guard setae, and a lateral microsensillum which is set below the organ. *Ant.* 1 and 2 with 8 and 14–15 setae, respectively. *PAO* with 3–4 lobes, slightly longer than nearest pseudocellus. Labrum with 4/5–2–2 setae but variations also seen. Apical part of labium with thick terminal setae on papillae *A* and *C*, usually complete number of long guard setae (7) and 4 spiniform ones, 6 proximal setae present. Basal fields of labium with 4+5(6) setae. Maxillary palp simple with two sublobal hairs. Maxillae not modified.

Pseudocellar formula (*pso*) as follows, dorsal: 32/033/33343, ventral: 2/000/0000, parapseudocelli (*psx*) invisible. Each subcoxa with one *pso*, *psx* invisible (absent?). Granulation fine, clearly coarser around pseudocelli on all segments. Dorsal chaetotaxy almost symmetrical, setae smooth, macrosetae clearly differentiated only on abdominal tip, sensory setae indistinct. *Th.* 1 with (5)6+6 setae. Lateral *ms* present only on *Th.* 2. On head p_1 clearly above p_2 , its position on *Th.* 2–*Abd.* 3 rather variable but usually more or less at a level with p_2 . *Abd.* 1–3 with setae p_4 present as a rule. *Abd.* 5 with m_1 curved, thinner and shorter than the straight a_1 and p_1 , the latter usually shorter than anterior macrosetae a_1 . Unpaired setae: d_0 absent, *Abd.* 5 often with seta p_0 present, *Abd.* 6 with two axial macrosetae, a_0 clearly shorter than a_2 . Thoracic sterna with 0, 1+1, 1+1 setae. Furca as small cuticular furrow in some distance from anterior border of sternum. Chaetotaxy of furcal field in juveniles as in Fig. 32: usual 3+3 proximal *q*-setae and 3+3 setae set in triangle below furrow; adults with few (1–2) additional setae in front of *q*-row (Fig. 31). Ventral tube usually with 6+6 distal and 2(1) proximal setae at base. Subcoxae with 3–5–(4)5 setae, tibiotarsi with 20–20–19 setae: each distal whorl (*A*+*T*) with 11 setae, whorl *B* with 7–7–6 setae, setae *M* and *Y* present on all tibiotarsi. Unguis simple, without inner or lateral teeth, unguiculus with small basal lamella, about 3/4 as long as unguis. Anal spines rather long and thin, almost straight and hardly constricted at base, set without papillae. Males present.

Remarks. Originally described as *Onychiurus* (*Archaphorura*) *nataliae*, the species is now listed under *Micraphorura* on www.collembola.org. Nevertheless the chaetotaxy of the manubrial field in juveniles of this species is identical with that found in north-

ern partenogenetic populations of *O. groenlandica* (Tullberg, 1876) (cf. Fig. 32 and Fig. 18). Adults usually have a pattern with four setal rows behind the cuticular furrow (Fig. 31), which considered being typical for *Oligaphorura*.

In the interactive key on www.collembola.org the species keys out with *Oligaphorura interrupta* (*Micraphorura* on www.collembola.org) which can easily be distinguished by higher number of abdominal *pso*, presence of *ms* on *Th.3* and absence of ventral setae on *Th.2*.

Five known species of the tribe possess the same number of dorsal and ventral pseudocelli as *nataliae*, i.e. *O. pingicola* (Fjellberg, 1987), *O. koreana* (Weiner, 1994), *Dimorphaphorura raxensis* (Gisin, 1961), *D. chatyrdagi* (Kaprus', Weiner & Pomorski, 2002), and *D. sanjiangensis* Sun & Wu, 2012. *O. nataliae* differs from the above *Oligaphorura* species (*O. pingicola* and *O. koreana*) in having no *ms* on *Th.3*. *D. raxensis* according to Weiner and Kaprus' (2014) has 9 distal setae on tibiotarsi and *ABC* type of labium. *D. chatyrdagi* can easily be distinguished due to strongly reduced tibiotarsal chaetotaxy (with 5 distal setae) and the presence of *ms* on *Th.3*. *D. sanjiangensis*, recently described from northern China, can be separated from *O. nataliae* due to different type of labium (*A* versus *AC* in *O. nataliae*), the presence of *psx* on abdominal sterna (0/000/122201+1^m), and identical number of tibiotarsal setae on all legs (20-20-20) which is very characteristic if it is correct. Apart of this, all three species of *Dimorphaphorura* should have no more than 5+5 setae in the manubrial field whereas even first instars of *O. nataliae* possess 6+6 setae.

The presence of 7 long guard setae of labium in such small species as *O. nataliae* is an uncommon character in the tribe and needs additional confirmation being seen in few specimens. Only five other Asiatic species, *D. sanjiangensis*, *Micraphorura changbaiensis* Sun & Wu, 2012, *O. aborigensis* (Fjellberg, 1987) and the two new *Oligaphorura* species described above, share this character with *O. nataliae* whereas 18 species of the tribe are known as having only 6 long guards.

***Micraphorura alnus* (Fjellberg, 1987), comb. n.**

Onychiurus (*Archaphorura*) *alnus* Fjellberg, 1987: 282.

Dimorphaphorura alna (Fjellberg): www.collembola.org

Dimorphaphorura alnus (Fjellberg): Weiner and Kaprus' 2014: 6.

Material. holotype, ♀, “USSR, Magadan Reg., Aborigen [field station, 61°56'N, 149°40'E], deep, moist *Pinus pumila* litter, 27 vii 1979” (CNC 165044, type No 20108); Paratypes, 5 ♀, same sample (CNC 165130, type No 20111); 1 ♀, same region, “*Alnus* litter in dense thickets, 25 vii 1979” (CNC 165129, type No 20110), all A. Fjellberg leg.; 9 specimens (in bad condition), “USSR, Chukotka, Chaun Bay [68°44'N, 170°36'E], Sept. 1975” (CNC 165128, type No 20109), S.F. MacLean leg.

Additional material. 1 ♂, Magadan District, Bolshoi Annachag Mts. Range, upper reaches of Kolyma River, field station “Aborigen”, valley bottom near station, moss

and litter of *Larix/Pinus* on slope, 25 vii 1979, A. Fjellberg leg.; 5♀ and 3♂, same region, deep moist litter in thickets of *Pinus pumila*, 1200 m alt., 27 vii 1979, A. Fjellberg leg.; 2 ♂, same region, stand of *Pinus pumila*, *Betula*, *Larix dahurica*, and *Alnus fruticosa*, 24 vii 1979, V. Behan leg.

Redescription. Colour white. Size 0.8-0.9 mm. Body shape cylindrical. Antennae about as long as head, *Ant.* 3-4 broad, club-like. *Ant.* 4 with subapical organite and microsensillum located in proximal row of setae. *AO* consists of 5 long and thin papillae, two sensory rods, two granulated sensory clubs (internal almost straight, external much larger and bent), 5 guard setae and a lateral microsensillum which is set below the organ. *Ant.* 1 with 8 setae, *Ant.* 2 with (12)13 setae. *PAO* with 3-4 lobes, slightly longer than nearest pseudocellus. Labrum with 4/3-2-2 setae. Apical part of labium with thick terminal setae on papillae *A* and *C*, 6 long guard setae and 6 proximal setae present, basal fields with 4+5 setae. Maxillary palp simple with two sublobal hairs.

Pseudocellar formula (*ps*) as follows, dorsal: 32/133/33343, ventral: 2/000/0001, parapseudocelli (*psx*) invisible. Each subcoxa with one *ps*, *psx* absent. Granulation rather coarse, especially around pseudocelli and on *Abd.* 6. Dorsal chaetotaxy almost symmetrical, setae smooth and fine, macrosetae poorly differentiated, sensory setae (2/011/222211) more or less distinct, *Th.* 1 usually with 6+6 setae, *Th.* 2-3 with lateral *ms*, *p*₁ on head and *Th.* 2-3 almost on level with other medial *p*-setae. *Abd.* 5 with *m*₁ longer than *a*₁, subequal to *p*₁. Unpaired setae: *d*₀ and axial seta on *Abd.* 5 absent, *Abd.* 6 with two axial setae, *a*₀ subequal to *a*₂. Thoracic sterna with 0-1(2)-1(2-3) setae on each side of ventral line. Upper subcoxae usually with 3-3-4 setae. Furca as a small area with fine granulation in middle section of sternum of *Abd.* 4, some setae present on sternum anteriorly to furcal remnant. In juveniles manubrial field with usual 3+3 proximal *q*-setae and 2+2 distal ones set in a row, in adults some additional setae sometimes present, especially in large specimens (Fig. 33). Ventral tube with (5)6+6 distal and (1)2 proximal setae at base. Subcoxae with 3-(3)4-(3)4 setae, tibiotarsi with 20-20-19 setae: each distal whorl (*A*+*T*) with 11 setae, whorl *B* with 7-7-6 setae, setae *M* and *Y* present on all tibiotarsi. Unguis simple, without inner or lateral teeth, unguiculus with clear basal lamella, about 3/4 as long as unguis. Anal spine bent, rather thick and constricted at base, set without papillae. Males present.

Remarks. The above redescription completely matches the original one, although Fjellberg (1987) did not mention ventral *ps* on *Abd.* 4. The species was recently redescribed by Weiner and Kaprus' (2014). The only clear difference with this description is the number of labral setae which states as being full (4/3-4-2). The authors treat the species as *Dimorphaphorura* because their specimens had no secondary setae in the manubrial field (only 5+5 setae in all). In our largest specimens from Magadan the manubrial field has several additional *mm*-setae (the holotype has 14 setae on the manubrial field in total) which illustrates the weak distinction between *Dimorphaphorura* and *Micraphorura*.

The set of dorsal pseudocelli displayed by *M. alnus* is shared with several other species in the genus. Among these only four species have ventral *ps* present on *Abd.* 4,

i.e. *M. alnus*, *M. pieninensis* Weiner, 1988, *Dimorphaphorura irinae* (Thibaud & Taraschuk, 1997), and *D. olenae*. *Micraphorura pieninensis* differs from both other species in having no *ms* on *Th.3*. *Dimorphaphorura irinae* can be distinguished by the reduced tibiotarsal chaetotaxy (only 2 *T*-setae present), a full number of labral setae (4/9) and different labial type (*ABC*) (Weiner and Kaprus' 2014). *Dimorphaphorura olenae* possesses ventral *pso* on all sterna from *Abd.1* to *Abd.4*, and two *pso* on subcoxae of leg.2-3.

***Oligaphorura interrupta* (Fjellberg, 1987), comb. n.**

Onychiurus (*Archaphorura*) *interruptus* Fjellberg, 1987: 282.

Micraphorura interrupta (Fjellberg): www.collembola.org

Material. holotype, ♀, “USSR, Magadan Reg., “Death Valley”, Magadan-Ust’ Umchug [road], 209 km from Magadan, moss, lichen, *Vaccinium*, 30 vii 1979” (CNC 165045, type No 20107); Paratypes, 9♀ and 1♂, same sample (CNC 165134, type No 20106), all A. Fjellberg leg.

Additional material. 1 specimen, Magadan District, Bolshoi Annachag Mts. Range, upper reaches of Kolyma River, field station “Aborigen” [61°56'N, 149°40'E], alpine study area (lichen, moss, *Dryas*, *Empetrum*), 26 vii 1979, V. Behan leg.; 11 specimens, same region, Butugychag (“Death Valley”) [61°18'N, 149°11'E], moist *Sphagnum*, litter *Betula nana*, *Alnus* thickets, 30 vii 1979, A. Fjellberg leg.; 10 specimens, Magadan vicinities, “Snow Valley”, rich meadow (*Veratrum*, *Angelica*), 20 viii 1979; ca. 15 specimens, Northern Yakutia, Shirokostan Peninsula, Ledyanoe lake [72°25'N, 141°00'E], various habitats, 1994, A. Babenko leg.; 1 ♀, North-Eastern Yakutia, delta of Indigirka river [71°26'N, 149°45'E], *Eriophorum vaginatum* tussock, 1994, A. Babenko leg.; ca. 30 specimens, Magadan District, upper reaches of Ola River [60°39'N, 151°16'E], various sites, viii 2011, A. Babenko leg.

Redescription. Colour white. Size 0.75 mm. Body shape cylindrical. Antennae about as long as head, *Ant.* 3–4 broad, club-like. *Ant.4* with a peg-like subapical organite, microsensillum located in proximal row of setae. *AO* consisting of 5 long and thin papillae, two sensory rods, two granulated sensory clubs (internal straight, external much bigger and bent), 5 guard setae and a lateral microsensillum set below the organ. *Ant.1* and 2 with 8 setae and 13–14 setae respectively. *PAO* with 3–4 lobes, longer than nearest pseudocellus. Labrum with 4/3–2–2 setae. Apical part of labium with thick terminal setae on papillae *A* and *C*, common number of guard setae (6 long and 4 spiniform ones), and 6 proximal setae. Basal fields with 4+5(6) setae. Maxillary palp simple with two sublobal hairs.

Most common dorsal pseudocellar formula (*pso*) as 32/033/33353, submedial *pso a* and *b* on *Abd.1–2* set close together (with *pso b* on level with setae *p3*). Variations are frequent and specimens with additional *pso* on some abdominal terga (usually asymmetrical) are seen. The whole formula may be expressed as follows, 32/033/3(4),3(4),3(4),(4)5,3(4). Ventral side of head with two *pso* as usual. Parapseudocelli (*psx*)

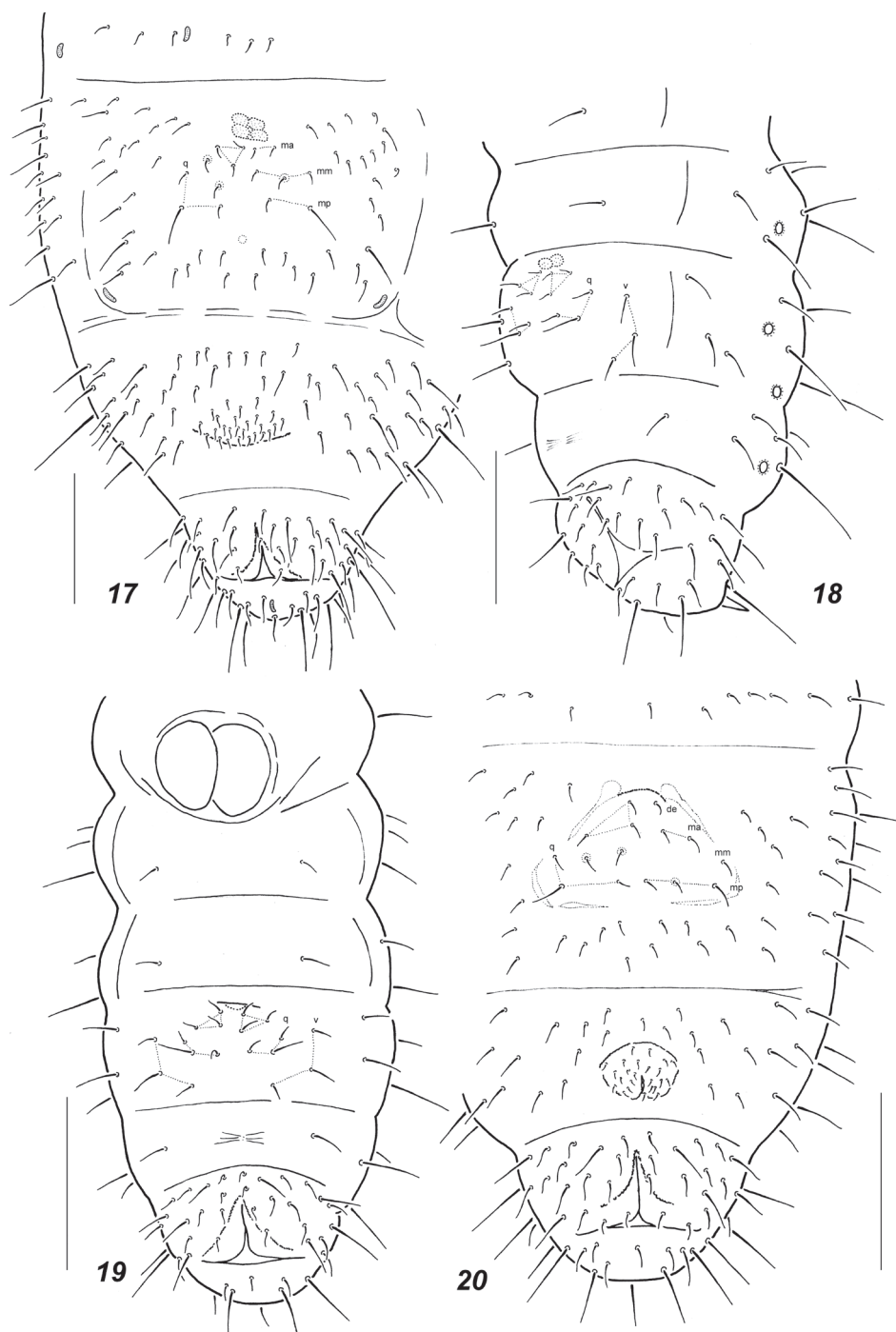
invisible. Each subcoxa with one *pso*. Granulation fine and uniform, sometimes clearly coarser around pseudocelli. Dorsal chaetotaxy almost symmetrical, setae smooth, macrosetae short, needle-like usually blunt at tip, sensory setae more or less distinct, usually 2/011/22211 in number, sensilla like, broaden seta usually present on lower *Scx*.3. *Th*.1 with 5–6 setae on each side. Both *Th*.2 and 3 with lateral *ms*, *p*₁ on head and *Th*.2–3 usually slightly in front of *p*₂, *Abd*.1–3 with setae *p*₄ usually present. *Abd*.5 with *m*₁ curved, thinner and shorter than the straight *a*₁ and *p*₁. Unpaired setae: *d*₀ absent, *p*₀ frequently present on *Abd*.5, *Abd*.6 with two axial setae, *a*₀ clearly shorter than *a*₂. Thoracic sterna 1–3 with 0–0–1 setae, sometimes setae completely absent. Furca remnant as a small fold in some distance from anterior border of *Abd*.4 sternum, chaetotaxy of manubrial field in juveniles as in Fig. 19, usually with 3+3 proximal *q*-setae and 3+3 setae in triangles between cuticular fold and *q*-setae. In adults 1–3 additional setae usually present in intermediate position (Fig. 20). Four irregular setal rows may be distinguished. Ventral tube with 6+6(7) distal and 2(1) proximal setae at base. Subcoxae usually with 3(4)–4(5)–4 setae, tibiotarsi with 20–20–19 setae: each distal whorl (*A*+*T*) with 11 setae, whorl *B* with 7–7–6 setae, setae *M* and *Y* present on all tibiotarsi. Unguis simple, without inner or lateral teeth, unguiculus with small basal lamella, about 3/4 as long as unguis. Anal spines short and thick, slightly bent and constricted at base, set without papillae.

Remarks. The number of pseudocelli in the species appears to be more variable than stated in the original description by Fjellberg (1987), even within the region of the type locality. That is why Nearctic *Oligaphorura nuda*, characterized by increased number of abdominal *pso*, appears to be hardly separable from *O. interrupta* despite their different generic positions on the www.collembola.org. Nevertheless the chaetotaxy of manubrial field in *O. interrupta* is identical to that of *Oligaphorura groenlandica* (cf. Figs 17–18 and Figs 19–20) and clearly differs from the pattern typical of *Micraphorura absoloni* (Figs 26–27). The structure of manubrial field in the *nuda* holotype (CNC 165047, type No 20103) also indicates its position within the genus *Oligaphorura*.

The presence of ventral setae on *Th*.3 in *O. interrupta* was used by Fjellberg (1987) as an additional diagnostic character to separate *O. interrupta* and *O. nuda* (setae absent). However, new material of *O. interrupta* from various regions of eastern Palaearctic shows this character to be invalid. Some specimens of *O. interrupta* may also be completely devoid of ventral setae on thorax. More material is evidently needed to clarify the real relationships between these two species.

Only one other known species of the tribe shares the absence of *pso* on *Th*.1 combined with presence of 5 *pso* on *Abd*.4 with *O. interrupta* and *O. nuda*: *Oligaphorura reversa* (Fjellberg, 1987). This characteristic species differs from the above-mentioned species in having an unusual position of the dorsal pseudocelli on *Abd*.1–3: the medial *pso a* is set in a posterior position, clearly behind submedial *pso b*.

The species listed as *O. sp. aff. nuda* in Babenko (2013) from Taimyr is another congener with a similar dorsal pseudocellar formula. It differs from both *O. interrupta* and *O. nuda* having 1+1 ventral *pso* on *Abd*.4.



Figures 17–20. Chaetotaxy of abdominal sterna. **17** *Oligaphorura groenlandica* (adult, Taimyr) **18** *Oligaphorura groenlandica* (I instar, Taimyr) **19** *O. interrupta* (I instar) **20** *O. interrupta* (adult). Secondary setae in adults circled. Scale bars: **17** = 0.1 mm, **18–20** = 0.05 mm.

Oligaphorura groenlandica* (Tullberg, 1876)Lipura groenlandica* Tullberg, 1876: 41.*Oligaphorura groenlandica* (Tullberg): www.collembola.org

Remarks. Pomorski's (1996) description of the furcal area of the first instar was as follows: ...*q*-chaetotaxy – 3 chaetae, area furcalis with 2+2 setulae below cuticular furrow and 2+2 setae at base [all together 4+4 setae]. It was based on a single specimen from a bisexual population from Wolin Island on the Polish shore of the Baltic Sea. Weiner's description (1996): ...*small, finely granulated cuticular fold or quite a deep pocket with 2 setae on its posterior edge, sometimes with 1+1 additional setae and two other dental setae posteriorly, with manubrial setae on both sides and with other manubrial setae usually in two rows* is more complicated. According to the interactive key on the www.collembola.org *Oligaphorura* should have two dental setae on the fold or posteriorly and three manubrial rows of setae behind them. In fact, the type species of the genus, *O. groenlandica* (or more correctly the most common parthenogenetic form of this species) has no cuticular fold or clear furrow, just an area with fine granulation in anterior third of the sternum of *Abd.4* (Fjellberg 1998). In adults, the position of setae of the furcal area is rather irregular due to weak polychaetosis (Fig. 17) and juveniles clearly differ from that described by Pomorski with only 3+3 setae in front of the 3+3 *q*-setae (Fig. 18).

Unfortunately, this parthenogenetic form is not the only one present in the northern areas of the Palaearctic. On Taimyr Peninsula and Novosibirsk Islands another bisexual form was found. Probably the same (or similar) form exists in southern Norway (Fjellberg 1998) and Poland (Pomorski 1998). Its furcal area is more similar to the described pattern for *O. groenlandica* by Pomorski (1996) with cuticular fold and 4+4 setae between the fold and *q*-setae in the first instar juveniles (Fig. 26). In adults, two “dental” setae set in front of three irregular manubrial rows of setae (Fig. 25). These two forms are very similar and apart from the furcal area, differ only in size (the parthenogenetic form is larger) and in differentiation of the medial setae on *Abd.5*: “microsetae” m_1 (thin and pointed) are much longer than macrosetae a_1 and p_1 (straight and truncate) in the true parthenogenetic *O. groenlandica*. Bisexual specimens usually have m_1 curved and short and a_1 and p_1 long and straight. There are also some differences in *psx* formulas: 10/000/222201+1^m, upper subcoxae with 2-2-2 *psx* in the bisexual form and 10/000/222101^m, subcoxae 1-1-2 in the parthenogenetic one. Unfortunately the number of *psx* in the latter form is not stable. Some specimens lack postlabial *psx* or one of *psx* on anterior abdominal sterna, others may have additional *psx* on *Abd.4* or on paired anal lobes; and anterior *psx* on subcoxae of fore and middle legs can be just invisible due to position. Pomorski (1998) gave slightly different formula for the Polish specimens: 1/000/122101^m. Thus several similar forms do exist in Palaearctic, but the real *O. groenlandica* described by Tullberg from Greenland and Svalbard probably belongs to the main parthenogenetic form with circumpolar distributional range lacking cuticular fold on the sternum of *Abd.4*.

***Oligaphorura ursi* (Fjellberg, 1984)**

Onychiurus ursi Fjellberg, 1984: 71.

Oligaphorura ursi (Fjellberg): www.collembola.org

Remarks. Contrary to *O. groenlandica*, *O. ursi*, another northern circumpolar species of the genus, is common in the Magadan region inhabiting different wet sites above the tree-line. Recently the species was redescribed on the basis of specimens from northern China (Sun and Wu 2012a). We have some doubts about the identity of the Chinese and northern populations. Northern specimens usually have 6 long and four spiniform guard setae on the labial palp [versus 11 in Chinese specimens], ventral *psx* 10/000/212201+1^m with frequent variations [versus 0/000/122200 in the Chinese ones] and at least one *psx* on each subcoxae, most usually 1-2-2 [versus completely absent]. Apart from this, it was said that the Chinese specimens had an identical number of setae on all tibiotarsi [versus 20-20-19 setae in northern populations].

***Oligaphorura aborigensis* (Fjellberg, 1987)**

Onychiurus (*Archaphorura*) *aborigensis* Fjellberg, 1987: 285.

Oligaphorura aborigensis (Fjellberg): www.collembola.org

Material. holotype, ♀, “USSR, Magadan Reg., Aborigen [67°57'N, 149°34'E], alpine snow fields, under stones, 27 vii 1979” (CNC 165043, type No 20102); paratypes, ♀ and juv., same sample (CNC 165127, type No 20101), all A. Fjellberg leg.

Unfortunately the types of the species were partly damaged and no additional specimens were found in the available material from the vicinity of Aborigen field station. So, only few additional details can be added to the original description.

Labium with thick terminal seta only on papilla *A*, 7 long guard setae and 6 proximal setae, basal fields with 4+6 setae. Tibiotarsi with complete set of setae (20-20-19): each distal whorl (*A*+*T*) with 11 setae, whorl *B* with 7-7-6 setae, setae *M* and *Y* present on all tibiotarsi. Furcal fold straight and comparatively small, situated in mid-section of *Abd.*4, furcal field in the only seen juvenile with 4+4 setae between proximal *q*-setae and the cuticular fold (as on Fig. 24), adults with some additional setae in intermediate position forming 4 more or less regular rows as typical for other *Oligaphorura*.

The species is well defined due to the absence of sublobal setae on the maxillary outer lobe (a unique character for the tribe or even for Onychiurinae), strong differentiation of dorsal setae and the pseudocellar formula (32/133/33353) which is not especially common for the tribe being shared with only *D. pseudoraxensis* (Nosek & Christian, 1983), *O. sabulosa* Babenko, 2008, and *D. jingyueensis* Sun & Wu, 2012. All of them have the usual two sublobals on the maxillary palp and the macrosetae being much shorter and finer than in *O. aborigensis*. Apart from this the two former species are characterized by the absence of *ms* on *Th.*3.

***Oligaphorura pingicola* (Fjellberg, 1987)**

Onychiurus (*Archaphorura*) *pingicolus* Fjellberg, 1987: 285.

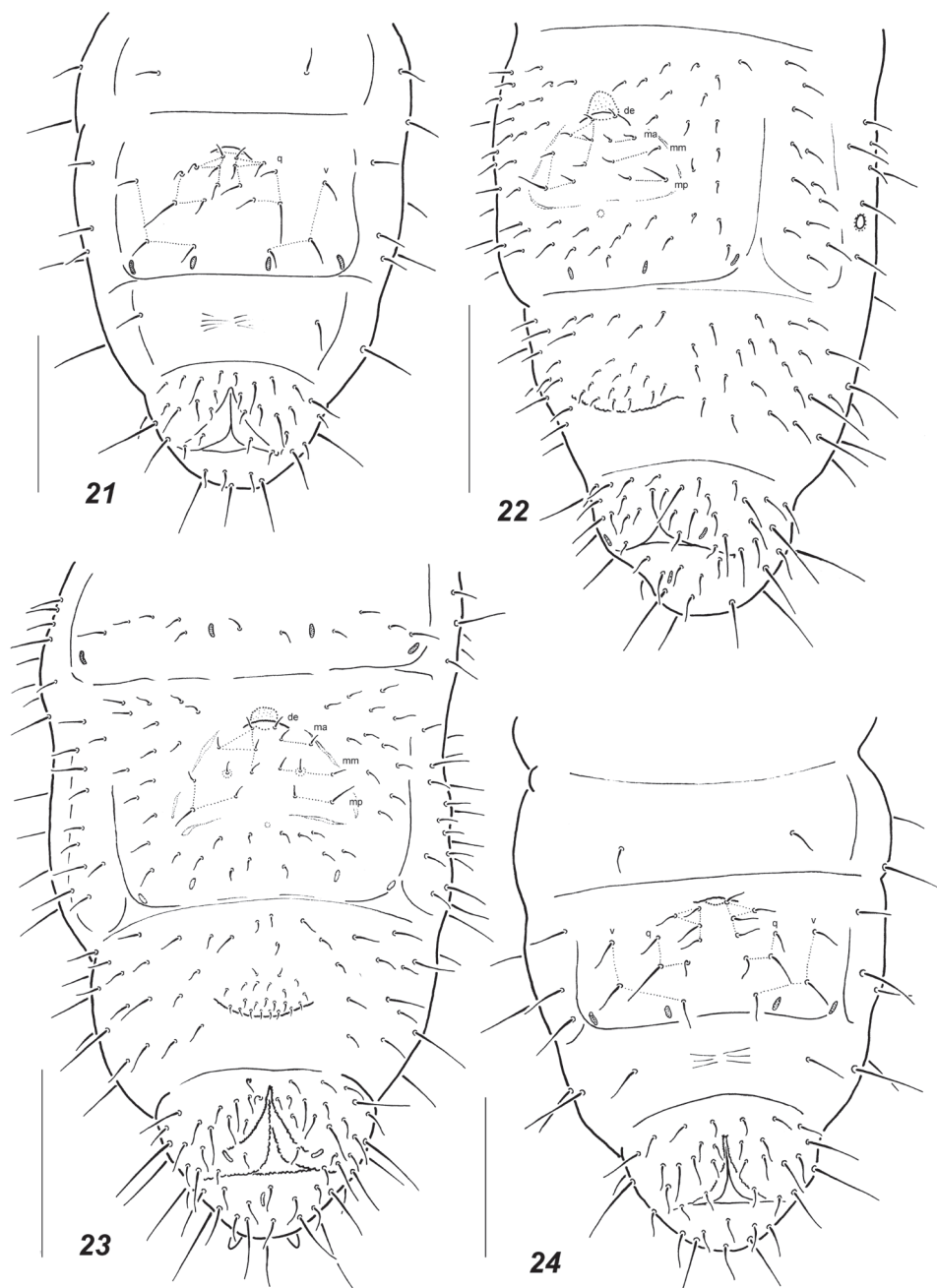
Oligaphorura pingicola (Fjellberg): www.collembola.org

Material. holotype, ♂, "Alaska, Prudhoe Bay, *Dryas*-turf on pingo, 16 viii 1976" (CNC 165048, type No 20099); paratypes, 5♀ and ♂, same sample (CNC 165139, type No 200100), all A. Fjellberg leg.

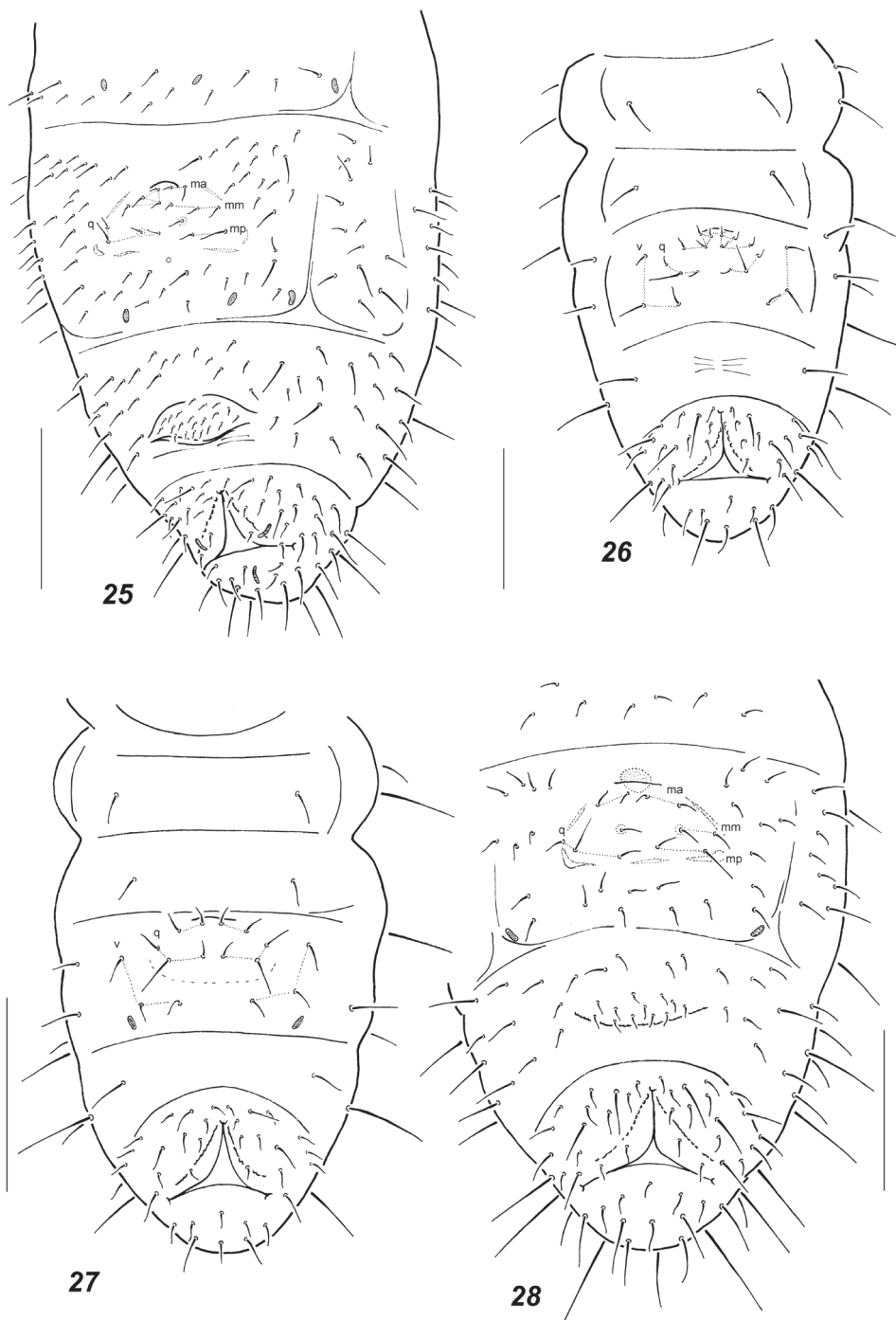
Additional material. 50 specimens, Russia, Yakutia (Sakha Republic), Suntar-Khayata Mt. Range, upper reaches of Kyubyume River [63°13'N, 139°32'E], various sites, viii 2002, O. Makarova leg.; 25 specimens, Magadan District, upper reaches of Ola River [60°39'N, 151°16'E], snow fields, 1100–1200 m alt., A. Babenko leg.; 4 specimens, Magadan District, Bolshoi Annachag Mts. Range, upper reaches of Kolyma River, field station "Aborigen" [61°56'N, 149°40'E], thick moss among rocks near snow field, 26 vii 1979, A. Fjellberg leg.; 4 specimens, same region, lichen/*Ledum* in northern slope, 28 vii 1979, A. Fjellberg leg.; 1 specimens, same region, *Pinus pumila* and lichen cover on hillside, 20 vii 1979, V. Behan leg.; 2 specimens, same region, alpine study area (lichen, moss, *Dryas*, *Empetrum*), 26 vii 1979, V. Behan leg.

Redescription. Colour white. Granulation distinctly enlarged on *Abd.*6 and on head. Size 1.0–1.1 mm. Body shape cylindrical. Antennae about as long as head, *Ant.* 3–4 broad, club-like. *Ant.*4 with a subapical spherical organite and a microsensillum located in proximal row of setae. *AO* consists of 5 long and thin papillae, two sensory rods, two granulated sensory clubs (internal almost straight, external much larger and bent), 5 guard setae and a lateral microsensillum which set below the organ. *Ant.*1 and 2 with 8–9 and 15–16 setae respectively. *PAO* with 2–3 elongated lobes, much longer than nearest pseudocellus. Labrum with 4/5–2–2 setae. Apical part of labium with thick terminal setae on papillae *A* and *C*, 6 long guard setae and 6 proximal setae present, basal fields with 4+(5)6 setae. Maxillary palp simple with two sublobal hairs.

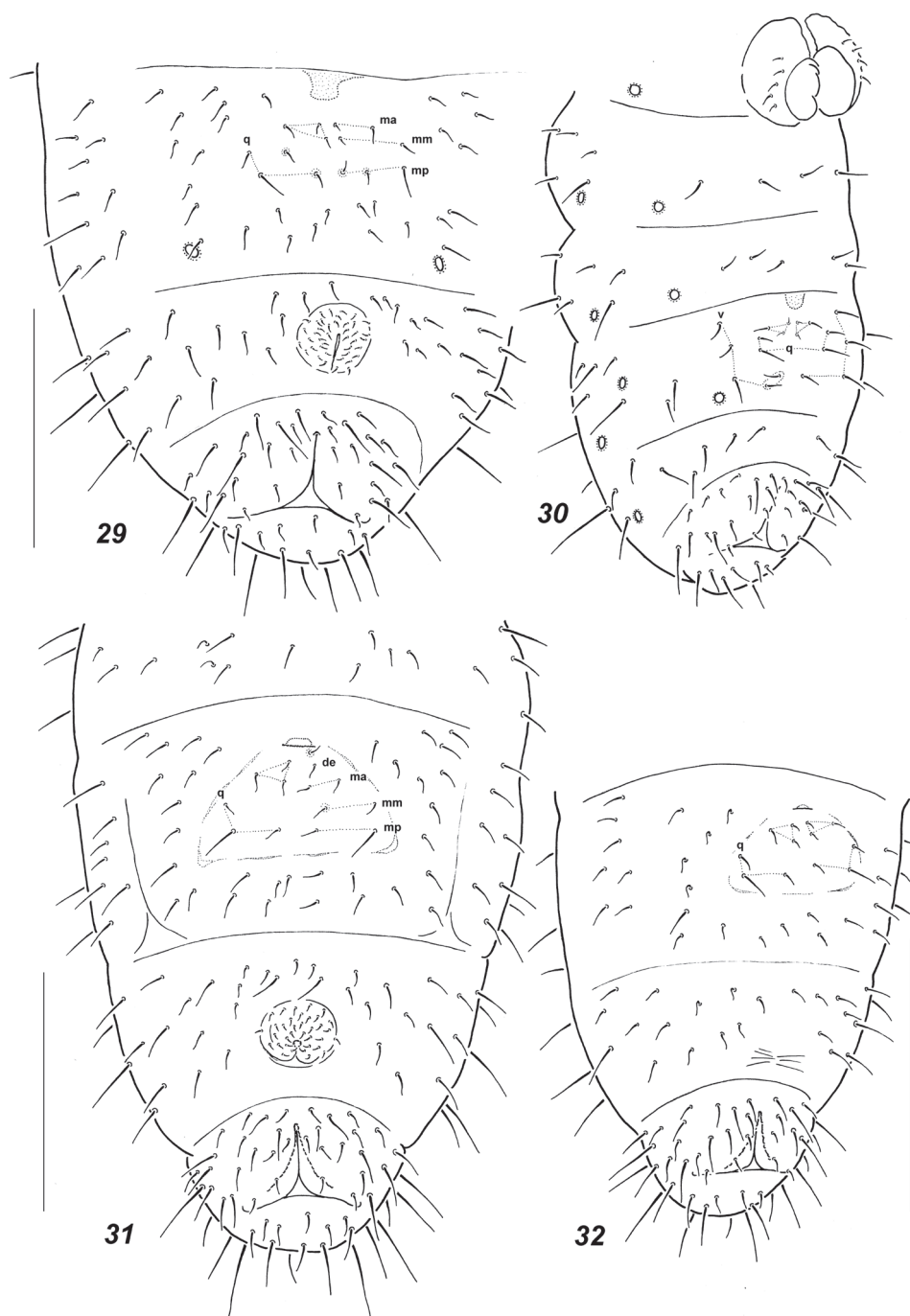
Pseudocellar formula (*pso*) as follows, dorsal: 32/033/33343, ventral: 2/000/0000, parapseudocelli (*psx*) 10/000/222201+1^m. Each subcoxa with one *pso* and one *psx*, *psx* present also on femora and on border between *Ant.*3–4. Granulation rather fine but clearly coarser around pseudocelli and on *Abd.*6. Dorsal chaetotaxy almost symmetrical, setae smooth and clearly differentiated, sensory setae more or less distinct, usually 2/011/222211. *Th.*1 with 7–8 setae on each side, both *Th.*2 and 3 with lateral *ms*, *p*₁ on head and *Th.*2–3 usually moved forward in relation to other medial *p*-setae. *Abd.*5 with microsetae *m*₁ thin and curved, clearly shorter than mesosetae *a*₁ and *p*₁. Unpaired seta *d*₀ on head absent, *Abd.*5 frequently with one unpaired axial seta in *p*-row, two axial setae present on *Abd.*6, *a*₀ shorter than *a*₂. Thoracic sterna of both *Th.*2 and 3 with 1+1 setae along ventral line. Furca shaped like a small fold in some distance from anterior border of *Abd.*4, in juveniles furcal field with 4+4 setae between proximal *q*-setae and the cuticular fold (Fig. 24), adults with some additional setae in intermediate position forming 4 more or less regular rows as typical for *Oligaphorura* (Fig. 23). Ventral tube with 8–9 distal and (1)2 proximal setae at base. Subcoxae with 4(5–6)–5(6)–5(6) setae, tibiotarsi



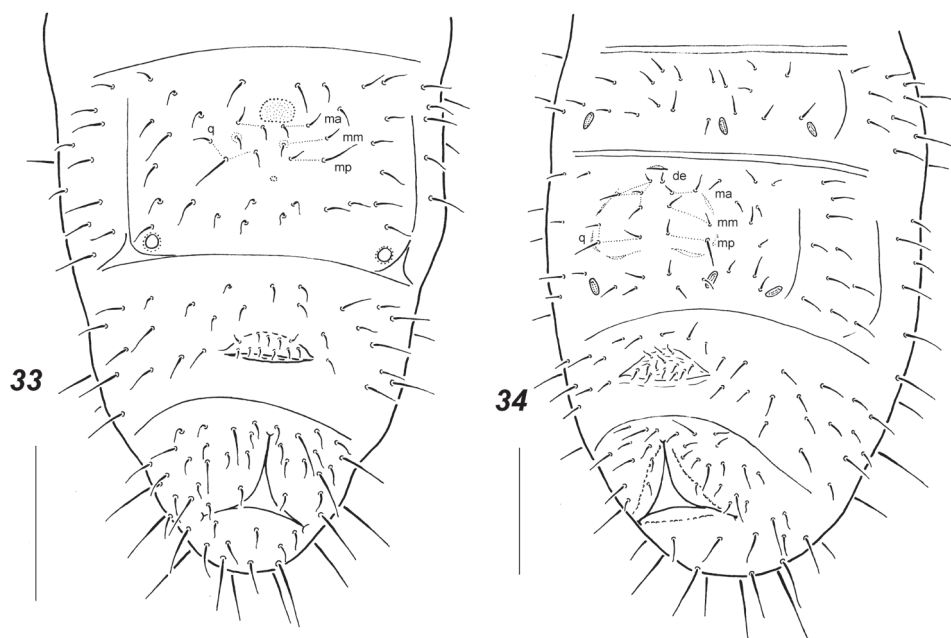
Figures 21–24. Chaetotaxy of abdominal sterna. **21** *Oligaphorura ursi* (I instar) **22** *Oligaphorura ursi* (adult) **23** *O. pingicola* (adult) **24** *O. pingicola* (I instar). Secondary setae in adults circled. Scale bars: **21, 24** = 0.05 mm, **22–23** = 0.1 mm.



Figures 25–28. Chaetotaxy of abdominal sterna. **25** *Oligaphorura* sp. aff. *groenlandica* (adult, Taimyr) **26** *Oligaphorura* sp. aff. *groenlandica* (I instar, Taimyr) **27** *Micraphorura absoloni* (I instar) **28** *Micraphorura absoloni* (adult). Secondary setae in adults circled. Scale bars: **9** = 0.1 mm, **10–12** = 0.05 mm.



Figures 29–32. Chaetotaxy of abdominal sterna. **29** *Oligaphorura ambigua* sp. n. (adult) **30** *Oligaphorura ambigua* sp. n. (juvenile) **31** *O. nataliae* (adult) **32** *O. nataliae* (juvenile). Secondary setae in adults circled. Scale bars: **29, 31–32** = 0.1 mm, **30** = 0.05 mm.



Figures 33–34. Chaetotaxy of abdominal sterna. **33** *Micraphorura alnus* (adult) **34** *Archaphorura serratotuberculata* (adult). Secondary setae circled. Scale bars: 0.05 mm.

with 20-20-19 setae: each distal whorl ($A+T$) with 11 setae, whorl B with 7-7-6 setae, setae M and Y present on all tibiotarsi. Unguis without inner tooth but usually with small and hardly visible lateral teeth present, unguiculus with small basal lamella about $3/4$ as long as unguis. Anal spines bent, rather thick, set on low papillae. Males present.

Remarks. The above redescription is in full accordance with the original one, adding a few details. While originally described from Alaska, Fjellberg (1987) also remarked that two specimens of the main form are also seen from alpine meadows at Aborigen, USSR (Magadan Reg.). In fact the species seems to be widespread and common not only in the Magadan Region but also in inner parts of the eastern Palaearctic (Suntar-Khayata Mts. Range, Yakutia). Fjellberg (1987) mentioned two distinct forms for Alaska differing in mutual position of setae on *Abd.5* and in level of granulation. Only the main form seems to be present in the eastern Palaearctic.

Oligaphorura pingicola shares the number of dorsal and ventral pseudocelli with at least five known species of the tribe, namely *O. koreana*, *O. nataliae*, *Dimorphaphorura raxensis*, *D. chatyrdagi*, and *D. sanjiangensis*. *O. koreana* is very similar to *O. pingicola*, differing by fewer tibiotarsal setae (19-19-18 versus 20-20-19) and by absence of *psx* ("indistinct"). The absence of *psx* is also characteristic for *O. nataliae* which differs from *O. pingicola* in having 7 long guard setae on labial palp and absence of *ms* on *Th.3*, as well as 2 setae of the proximal row on labrum (4/7 as a whole). *Dimorphaphorura raxensis* has 9 distal setae on tibiotarsi, full number of labral setae and *ABC* type of labium (Weiner and Kaprus' 2014). *Dimorphaphorura chatyrdagi* can easily be distinguished

due to reduced tibiotarsal chaetotaxy with only 5 distal setae, whereas *D. sanjiangensis* apart from the chaetotaxy of the sternum of *Abd.*4 differs in labium type (*A* versus *AC*) and identical number of tibiotarsal setae on all legs (20-20-20 versus 20-20-19).

Oligaphorura tottabetsuensis (Yosii, 1972), a species known from northern Japan, probably also belongs to the same group although the reported number of dorsal pseudocelli is slightly different (32/033/33333). The species is in need of redescription.

Discussion

The morphological characters being widely accepted as separating genera of Onychiuridae involve the shape of the postantennal organ (*PAO*), structures of the antennal organ (*AO*), tibiotarsal chaetotaxy, arrangement of the pseudocelli (*pso*), presence/absence of anal spines, distribution and shape of sensory setae on the body, and the gradual reduction of the furca. In our view a genus diagnosis based exclusively on reductional stages of the furca is dubious for at least two reasons: (1) similarity in reductional stage may represent a convergence achieved independently from distant phyletic lines, resulting in a polyphyletic or paraphyletic assemblage of species; (2) many collembolan genera (*Xenylla*, *Folsomia*, *Folsomides*, *Scutisetoma*, etc.) cover species with a wide range of furcal reduction, but are still accepted as natural genera which no one would split. In Collembola at least the initial stages of furcal reduction are clearly of adaptive nature, reflecting a shift from surface activity to life in deeper strata where jumping ability is restricted. Although the species under discussion have a furca which is no longer functional, the adaptive character of the reduction probably masks the underlying genetic relationships. Moreover, the practically identical furcal remnant of the Onychiuridae genera *Supraphorura* Stach, 1954 and *Psyllaphorura* Bagnall, 1948 is obviously not a good proof for any close relationship.

Bagnall's (1949) original diagnoses of four genera of Oligaphorurini were more species than genus diagnoses. Re-establishment of these genera by Weiner (1996) and Pomorski (1996) was based on other diagnostic characters and involved more species but created some taxonomic problems which are not yet solved. According to these authors the four principal genera may be recognized as follows: *Archaphorura* and *Oligaphorura* differ by absence of anal spines in the former, presence in the latter. Both have identical furcal fields, differing from the two other genera by an additional row of setae, even in the first instar juvenile. *Dimorphaphorura* has the same chaetotaxy of the furcal field as a juvenile *Micraphorura*, whereas adults of the latter have a few (1-4) additional intermediate setae. In practice juveniles of *Archaphorura* and *Oligaphorura* are easily separated, also from juveniles of *Dimorphaphorura* and *Micraphorura*, while juveniles of the two latter are inseparable by the furcal field. Sorting out the generic affiliation of adults is much more difficult.

On the www.collembola.org there is an interactive key which proposes the following characters for identification of Oligaphorurini genera.

Chribellphorura: antennal tip with a retractive papilla, tibiotarsi with clavate setae in distal whorl; *Archaphorura*: *Abd.*5-6 fused dorsally, *Ant.*3-4 fused, anal spines absent; *Dimorphaphorura*: furcal rudiment in a form of finely granulated area; *Oligaphorura*: furcal rudiment in a form of cuticular furrow or small fold; chaetotaxy: 2 dental setae on the fold or posteriorly and three manubrial rows of setae behind them; *Micraphorura*: similar to *Oligaphorura* but without 2 dental setae, so only three rows of setae can be distinguished, *mm*-row with 4-6 setae.

In summary, *Archaphorura* has a unique character combination, *Dimorphaphorura* has no furcal fold or furrow, and *Oligaphorura* has an additional row of the setae on manubrial field compared with *Micraphorura*. The monotypic genus *Chribellphorura* is unique and needs no further discussion to be distinguished.

This adequate but probably too simplified scheme was neglected by Shvejonkova and Potapov (2011) who included three new species without anal spines and furcal fold not in *Archaphorura* but in *Micraphorura* (*M. stojkoe*) and *Oligaphorura* (*O. kremenitsai* and *O. humicola*). As a result *Archaphorura* lost its main diagnostic feature (absence of anal spines), as did *Dimorphaphorura* (furcal rudiment in the form of a finely granulated area). The authors considered *Archaphorura* to be a good genus not due to the absence of AS, but because of the peculiar antennae (fused *Ant.*3 and 4, subapical position of AO and *ms* of *Ant.*4 hidden under long papillae) and the fused *Abd.*5-6. There is also one neglected diagnostic character state of *A. serratotuberculata*, the type species of the genus, namely the absence of *M*-setae on tibiotarsi. This very character was registered in two rather remote European regions, Fennoscandia (Fjellberg 1998) and Moscow vicinity (new data). In all other Oligaphorurini with known tibiotarsal chaetotaxy this seta is present. Unfortunately there is still a number of species in which tibiotarsal chaetotaxy is not completely known and the character may end up as non-diagnostic for *Archaphorura*. The exact definition of *A. serratotuberculata* is obscure (Shvejonkova and Potapov 2011) and several species may be involved.

The recent revision of the Palaearctic species of *Dimorphaphorura* by Weiner and Kaprus' (2014) defined the genus more legibly and added a further criterion distinguishing *Dimorphaphorura* from other genera of the tribe – the absence of so called “dental” setae. In our view this character is rather subjective as setae set just below cuticular trace of furca differ (in size or sockets) from other sternal setae on *Abd.*4 only occasionally even in *M. absoloni*, can hardly represent a reliable criterion. The two new species described in the present paper further complicate the situation as one of them lacks AS but has long, not club-like, antenna and both have “furca” in the form of a “finely granulated area” (typical of *Dimorphaphorura*) but with 2+2 small setae in two rows below it as in *Oligaphorura* (Figs 15–16, 29–30).

In fact the diversity of manubrial chaetotaxy patterns in Oligaphorurini seems to be much higher than postulated so far, which obscures the current generic subdivisions. Thus four different patterns were found in juveniles of the northern species of the tribe: apart from 3+3 proximal *q*-setae the furcal field may have 2+2 setae (*alnus*, *absoloni*, Fig. 27), 3+3 (*groenlandica*, *nataliae*, *interrupta*, Figs 18–19, 32) or 4+4 setae (most studied *Oli-*

gaphorura, Figs 21, 24). In the latter case there are at least two patterns with a different mutual position of setae (cf. Fig. 21 and Fig. 26). The fifth variant with only 1+1 setae is known for the first instar of *Dimorphaphorura daii* (Pomorski et al., 1998). The number of secondary setae appearing during ontogenesis on the furcal field is surprisingly low, usually 1-3, rarely more. Nevertheless, the position and the number of these secondary setae are not stable within a species. We have probably never seen any adult specimens with completely symmetrical chaetotaxy of furcal field when there are any secondary setae present.

The present generic framework for Oligaphorurini is probably unique – difficult to use and hardly reflecting real relationships. There is great temptation to return to a single genus *Archaphorura* as Christiansen and Bellinger (1980, 1998) and Fjellberg (1987) had done. Nevertheless we realize that such a pooling of all species of the tribe within a single unit obviously contradicts recent taxonomic traditions. Despite being unsatisfactory the most realistic alternative is to keep the current “five genera” system, admitting that this solution is clearly provisional and does not fully reflect a natural generic affiliations of the species pool. Hopefully future genetic studies (barcoding) may contribute to solve these problems.

Key to the northern species of the Oligaphorurini tribe

- | | | |
|---|--|----------------------------------|
| 1 | <i>Th</i> .1 without <i>pso</i> | 2 |
| – | <i>Th</i> .1 with <i>pso</i> | 6 |
| 2 | Only <i>Th</i> .2 with lateral <i>ms</i> | <i>O. nataliae</i> (Fjellberg) |
| – | Both <i>Th</i> .2 and <i>Th</i> .3 with lateral <i>ms</i> | 3 |
| 3 | <i>Abd</i> .4 with 4 dorsal <i>pso</i> [totally 32/033/33343] | <i>O. pingicola</i> (Fjellberg) |
| – | <i>Abd</i> .4 with 5 dorsal <i>pso</i> including 3 in submedial group | 4 |
| 4 | <i>Th</i> .2 with at least 1+1 ventral setae. <i>Abd</i> .1-3 with <i>pso b</i> moved forward above medial <i>pso a</i> . Dorsal <i>pso</i> formula as 32/033/44454..... | <i>O. reversa</i> (Fjellberg) |
| – | <i>Th</i> .2 without ventral setae. <i>Abd</i> . 1-3 with <i>pso b</i> set behind medial <i>pso a</i> | 5 |
| 5 | <i>Th</i> .3 at least sometimes with 1+1 ventral setae | <i>O. interrupta</i> (Fjellberg) |
| – | <i>Th</i> .3 without ventral setae | <i>O. nuda</i> (Fjellberg) |
| 6 | <i>Th</i> .1 with 2+2 <i>pso</i> and with only 4+4 setae present in adults. Thoracic sterna without setae..... | <i>O. duocellata</i> sp. n. |
| – | <i>Th</i> .1 with only 1+1 <i>pso</i> and more than 4+4 setae in adults. <i>Th</i> .2-3 as a rule with ventral setae | 7 |
| 7 | Only <i>Th</i> .2 with lateral <i>ms</i> | 8 |
| – | Both <i>Th</i> .2 and <i>Th</i> .3 with lateral <i>ms</i> | 11 |
| 8 | <i>AO</i> with 4 papillae..... | 9 |
| – | <i>AO</i> with 5 papillae..... | 10 |
| 9 | Anal spines present. Upper subcoxae with 1-1-1 <i>pso</i> . Labrum with 9 setae. Labium of <i>AC</i> type | <i>M. absoloni</i> (Börner) |
| – | Anal spines absent. Upper subcoxae with 2-(2)3-3 <i>pso</i> . Labrum with 7 setae. Labium of <i>ABC</i> type | <i>O. ambigua</i> sp. n. |

- 10 *Abd.*4 with 4 dorsal *ps*o [totally 32/133/33343]. Labium *A*-type ***O. ursi* (Fjellberg, 1984)**
- *Abd.*4 with 5 dorsal *ps*o [totally 32/133/33353]. Labium *AC*-type ***O. sabulosa* Babenko, 2008**
- 11 Maxillary outer lobe without sublobals. Formula of dorsal *ps*o as follows 32/133/33353 ***O. aborigensis* (Fjellberg)**
- Maxillary outer lobe with 2 sublobals. Formula of dorsal *ps*o as follows 32/133/33343 **12**
- 12 Labium of *A*-type ***O. schoetti* (Lie-Pettersen)**
- Labium of *AC* type **13**
- 13 *Abd.*4 with ventral *ps*o. Labrum with 7 setae ***M. alnus* (Fjellberg)**
- *Abd.*4 without ventral *ps*o. Labrum with 9 setae ***O. groenlandica* (Tullberg)**

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Five new Lamiinae (Coleoptera, Cerambycidae) from Bolivia in honor of James E. Wappes

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Abstract

Five new species of Lamiinae are described from Bolivia, all named after James E. Wappes: *Xenofrea wappesi* (Xenofreini); *Anobrium wappesi* (Pteropliini); *Cotycicuiara wappesi*, *Nesozineus wappesi*, and *Psapharochrus wappesi* (Acanthoderini). *Anobrium wappesi*, *C. wappesi*, and *N. wappesi* are included in known keys. A short note on the name and date of *Anobrium oberthueri* Belon, 1903 is provided.

Keywords

Keys, South America, Taxonomy

Introduction

During recent years, particularly in the last ten years, James E. Wappes has sent a large number of longhorn beetles to the MZSP (see below) for identification. Most of the specimens have come from Bolivia, where he has concentrated his collection efforts. New species have often been found and named after James. In this work, we describe five new species which are named after him. Thus, the species described have the same etymology.

The Cerambycidae fauna of Bolivia (Monné 2014, cat.) continues to surprise researchers with incredible numbers of new species found there. The five new species

of Cerambycidae described in this work are only a small portion of the species from Bolivia that remain undescribed.

Materials and methods

Photographs were taken with Canon EOS Rebel T3i DSLR camera, Canon MP-E 65mm f/2.8 1–5X macro lens, controlled by Zerene Stacker AutoMontage software.

The acronyms used in the text are as follows:

ACMT	American Coleoptera Museum (James E. Wappes), San Antonio, Texas, USA.
MNKM	Museo de Historia Natural Noel Kempff Mercado, Santa Cruz, Bolivia.
MZSP	Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil.

Taxonomy

Xenofreini Aurivillius, 1923

Xenofrea wappesi sp. n.

<http://zoobank.org/74C4E719-FABE-4FB3-8CD1-EF49985A98C0>

Figs 1–3

Description. *Holotype male.* Color. Integument dark brown, almost black, except for scape, distal third of pedicel, distal quarter of antennomeres III–IV, basal two-thirds of antennomeres V–VII, basal third of antennomere VIII, most of gumentum, most of peduncle of meso- and metafemora, and basal half of tibiae which are brown; basal three-quarters of antennomeres III–IV reddish-brown.

Head. Frons trapezoidal; finely, densely punctate, interspersed with coarse, sparse punctures; with white pubescence, not completely concealing integument. Area between antennal tubercles and upper eye lobes concave; moderately coarsely, abundantly punctate; pubescence white, mixed with yellowish white pubescence. Antennal tubercles finely, abundantly punctate; with white pubescence mixed with yellowish white pubescence. Dorsal area between eyes and anterior edge of prothorax coarsely punctate; pubescence very sparse, slightly more conspicuous around coronal suture. Coronal suture distinct from clypeus to anterior edge of prothorax. Area behind eyes with white pubescence (more yellowish depending on angle of incidence of light). Genae with yellowish white pubescence, sparser under lower eye lobe. Distance between upper eye lobes, in frontal view, equal to 0.45 times length of scape; distance between lower eye lobes equal to 0.80 times length of scape. Antennae as long as 1.7 times elytral length, reaching elytral apex at apex of antennomere VIII; scape, pedicel and lighter areas of antennomeres III–VIII with white pubescence, not obliterating integument; antennal formula based on antennomere III: scape = 0.59;

pedicel = 0.22; IV = 0.94; V = 0.59; VI = 0.54; VII = 0.50; VIII = 0.44; IX = 0.42; X = 0.37; XI = 0.35.

Thorax. Prothorax transverse, largest width 1.4 times central length. Pronotum, moderately finely, abundantly punctate; anterior and posterior transverse sulcus wide, moderately deep; central pubescence white, very sparse; wide lateral band of yellowish brown pubescence mixed with white, not reaching anterior and posterior margin, adjacent to wide band of white pubescence. Lateral sides of prothorax with punctures denser than on pronotum; with long, sparse, dark setae on basal half; pubescence whitish, distinctly not concealing integument. Ventral surface with whitish pubescence, not obliterating integument; on metasternum, in front of mesocoxal cavities and mesosternal process, narrow band of white, dense pubescence. Scutellum with sparse white and yellowish brown pubescence. Elytra. Moderately coarsely, abundantly punctate; elongate, with lateral sides sub-parallel at basal two-thirds; apex narrow, individually rounded; short, elongate band of yellowish brown pubescence on each side of scutellum, internally margined with white; above humeri, small spot of yellowish brown pubescence; remaining surface of basal two-thirds with white pubescence, forming designs (Fig. 1), but mostly glabrous; distal third with sinuous, wide band of yellowish brown pubescence, margined with white pubescence (Fig. 1).

Abdomen. Urosternites finely, densely punctate; pubescence whitish, not obliterating integument; on urosternite I, between metacoxal cavities, narrow, dense, V-shaped band of white pubescence. Legs. Femora and tibiae with white, not dense pubescence. Club of metafemora not notably enlarged.

Dimensions in mm (male/female). Total length, 6.05/7.05; length of prothorax at center, 1.30/1.60; anterior width of prothorax, 1.50/1.90; posterior width of prothorax, 1.55/1.80; humeral width, 2.25/2.75; elytral length, 4.55/5.25.

Variability. Paratype female. Peduncle of meso- and metafemora dark-brown. Antennae as long as 1.6 times elytral length; reaching elytral apex at apex of antennomere IX.

Type material. Holotype male from BOLIVIA, *Santa Cruz*: Florida (4 km N Bermejo; Refugio los Volcanes; 18°06'S / 63°36'W; 1045–1350 m), 4–9.XII.2013, Wappes & Skillman col. (MNKM). Paratype female, same data as holotype, except for: (1000–1200 m), 29.X.2011, Skillman & Wappes col. (ACMT).

Remarks. *Xenofrea wappesi* differs from *X. areolata* Bates, 1885, *X. ocellata* Tavakilian & Néouze, 2006, and *X. punctata* Galileo & Martins, 2005 as follows: body distinctly narrower; central area of pronotum with sparse, white pubescence; basal two-thirds of elytra mostly with white, narrow bands of pubescence. In *X. areolata* and *X. punctata* the body is wider (mainly in *X. areolata*), the central area of pronotum has a band of orange pubescence, and the basal two-thirds of elytra has wide bands of orange pubescence. *Xenofrea wappesi* also differs from *X. punctata* and *X. ocellata* by the punctures on elytra distinctly smaller. It can be distinguished from *X. basitriangularis* Néouze & Tavakilian, 2005, *X. berkovae* Néouze & Tavakilian, 2005, *X. morvanae* Néouze & Tavakilian, 2005, and *X. murina* Néouze & Tavakilian, 2005 mainly by the antennae, which are distinctly shorter (in males, surpassing the elytral apex by two segments). In males of *X. basitriangularis*, *X. berkovae*, *X. morvanae* and *X. murina*, the antennae surpass the elytral apex by more than three segments.

Pteropliini Thomson, 1860***Anobrium wappesi* sp. n.**

<http://zoobank.org/E5546F1D-64CB-4BD7-835A-E7788F1E1943>

Figs 4–6

Description. *Holotype female.* Color. Integument dark-brown; scape, pedicel, antennomeres III–V, and tarsi brown.

Head. Frons coarsely, abundantly punctate; with short, sparse, white setae, interspersed with long, sparse, yellowish setae. Area between antennal tubercles and posterior edge of upper eye lobes coarsely punctate (punctures confluent towards frons); setae as on frons. Area between upper eye lobes and anterior edge of prothorax finely, sparsely punctate, with very short, sparse white setae. Coronal suture distinct from clypeus to anterior edge of prothorax. Area behind lower eye lobes microsculptured, with long, sparse, yellowish setae close to eye. Distance between upper eye lobes, in frontal view, equal to 0.35 times length of scape; distance between lower eye lobes equal to 0.70 times length of scape. Antennae as long as 1.25 times elytral length; reaching distal sixth of elytra; scape and pedicel with short, sparse white setae, interspersed with long, yellowish setae, mainly ventrally; antennomeres III–VII with short, sparse white setae, interspersed with long, yellowish and brownish setae; antennomeres VIII–XI with short brownish setae, interspersed with long brownish setae; antennal formula based on antennomere III: scape = 0.85; pedicel = 0.26; IV = 0.79; V = 0.70; VI = 0.68; VII = 0.62; VIII = 0.56; IX = 0.53; X = 0.53; XI = 0.56.

Thorax. Prothorax cylindrical, approximately equally long as wide; lateral sides slightly rounded, without tubercles. Pronotum coarsely, moderately abundantly punctate; centrally, from base to apex, with band of white, short setae, with wide band of very sparse, white setae on each side; laterally with short, moderately abundant white setae; whole surface with long, sparse, yellowish setae. Lateral sides of prothorax with moderately sparse, white setae interspersed with long, sparse yellowish setae. Pro- and mesosternum with short, sparse, white setae interspersed with long, sparse yellowish setae. Metasternum with moderately abundant, white setae, interspersed with long, sparse, white and yellowish setae. Elytra. Moderately coarsely, abundantly punctate (punctures finer, sparser towards apex); with moderately abundant, white setae interspersed with long, yellowish setae; apices together rounded.

Abdomen. Urosternites shallowly, sparsely punctate; with sparse, white setae interspersed with long, yellowish setae; apex of urosternite V emarginate.

Legs. Femora with sparse, white setae interspersed with long, yellowish setae. Tibiae with moderately abundant, long, yellowish setae (mainly towards apex), sparse, short, white setae at base.

Dimensions in mm (female). Total length, 6.20; length of prothorax at center, 1.20; anterior width of prothorax, 1.00; posterior width of prothorax, 1.10; humeral width, 1.65; elytral length, 4.50.



Figures 1–6. 1–3 *Xenofrea wappesi*, holotype male: 1 dorsal habitus 2 ventral habitus 3 lateral habitus 4–6 *Anobrium wappesi*, holotype female: 4 dorsal habitus 5 ventral habitus 6 lateral habitus.

Type material. Holotype female from BOLIVIA, *Santa Cruz*: Potrerillo del Guenda (Snake farm; 400m; 17°40'S / 63°27'W; 370–400 m), 14–16.X.2011, Skillman & Wappes col. (MNKM).

Remarks. *Anobrium wappesi* differs from all other species in the genus by the absence of a tubercle at the lateral sides of the prothorax. It differs from *A. fraterculum* Galileo & Martins, 2012 by the pronotum not microsculptured (pronotum distinctly

microsculptured in *A. fraterculum*). It can be distinguished from *A. oberthueri* Belon, 1903 by the distinctly more abundant elytral pubescence (sparser in *A. oberthueri*), dark-brown elytra, femora, and tibiae (reddish-brown in *A. oberthueri*), and prothorax about as long as wide (distinctly longer than wide in *A. oberthueri*).

Although the general appearance of *Anobrium wappesi* be more similar to that of *A. fasciatum* Galileo & Martins, 2002, it can be included in the alternative of couplet “7”, from Galileo and Martins (2002) (translated; modified):

- 7(6) Vertex and pronotum without haloed punctures; center of pronotum without microsculpture. Bolivia, Brazil (Rondônia, Pará, Mato Grosso, Minas Gerais ***Anobrium oberthueri* Belon, 1903**
- Vertex and pronotum with haloed punctures; center of pronotum microsculptured.....7’
- 7’(7) Lateral sides of prothorax with distinct tubercle. Brazil (São Paulo, Rio Grande do Sul) ***Anobrium fraterculum* Galileo & Martins, 2002**
- Lateral sides of prothorax unarmed. Bolivia (Santa Cruz)..... ***Anobrium wappesi* sp. n.**

Note. Belon (1903) described his species of *Anobrium* as *A. oberthüri*. The specific epithet was emended to *A. oberthuri* by Monné (1993). However, according to ICZN (1999: Article 32.5.2.1), the correct spelling of the name should be *A. oberthueri*. Moreover, the species description has been cited as having been published in 1902. However, according to the Bulletin de la Société Entomologique de France, issue number 20 (“Dates d’apparition des numéros du Bulletin de 1902”), in which the species was described, was distributed on 22nd January 1903.

Acanthoderini Thomson, 1860

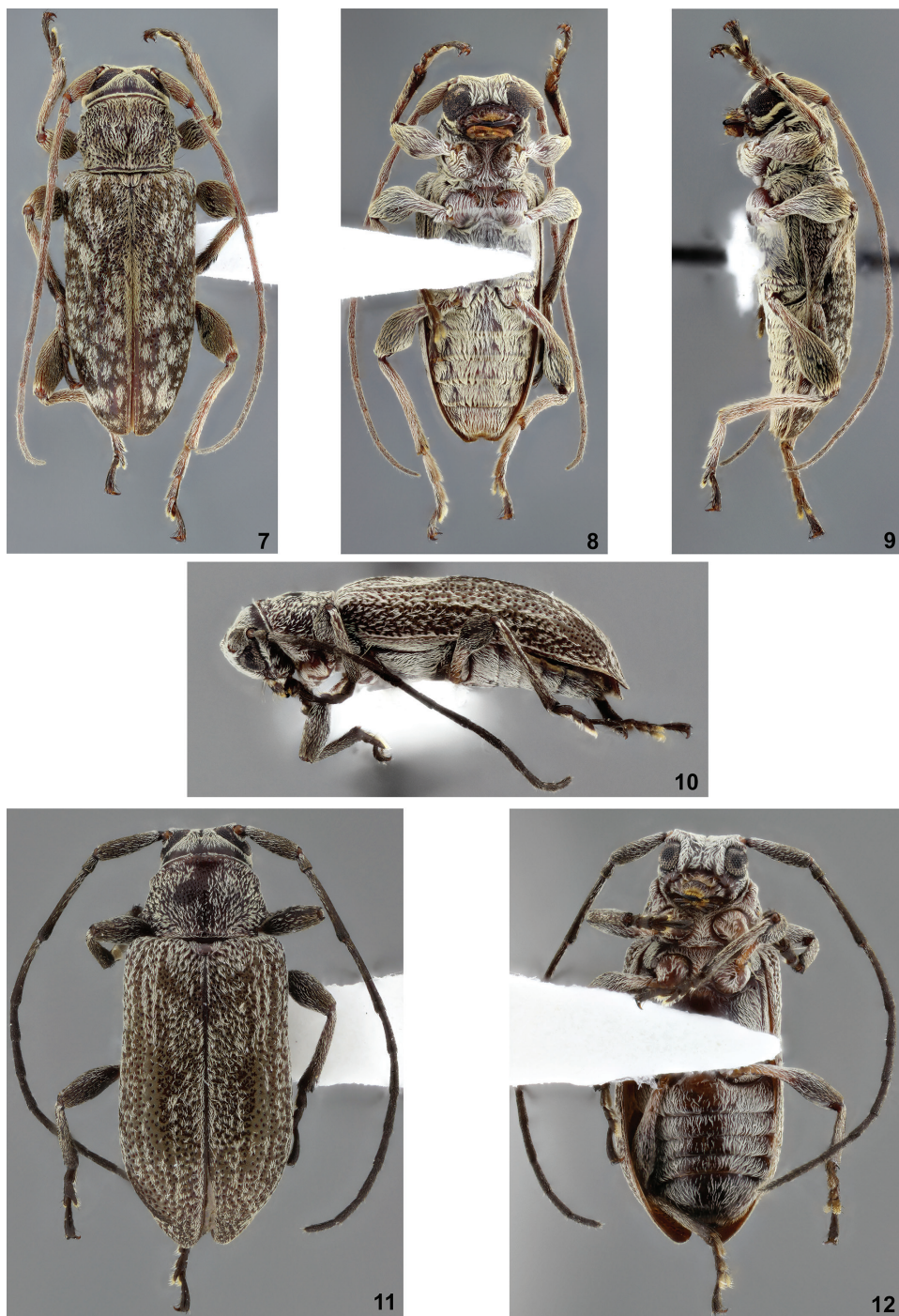
Cotycicuiara wappesi sp. n.

<http://zoobank.org/D9340A3F-9482-4824-9855-6B8CC6C3D454>

Figs. 7–9

Description. *Holotype male*. Color. Integument dark-brown; approximately distal half of labrum and palpi reddish-brown.

Head. Frons, vertex and antennal tubercles finely, abundantly punctate; pubescence yellowish white (more whitish depending on angle of incidence of light), almost obliterating integument; with some long, dark setae close to lower eye lobes. Coronal suture distinct from clypeus to approximately middle of upper eye lobes. Area between eyes and antennal socket with narrow, dense, yellowish white band of pubescence. Area behind upper eye lobes finely, densely punctate; with dense band of yellowish white pubescence close to eyes, less dense towards prothoracic margin. Area behind lower eye



Figures 7–12. 7–9 *Cotyciciara wappesi*, holotype male: 7 dorsal habitus 8 ventral habitus 9 lateral habitus 10–12 *Nesozineus wappesi*, holotype female: 10 lateral habitus 11 dorsal habitus 12 ventral habitus.

lobes finely, abundantly punctate; with band of yellowish white pubescence close to eyes, enlarged towards gena, glabrous towards prothoracic margin. Genae with dense yellowish white pubescence, except for narrow distal band and area under lower eye lobes with sparse pubescence; with sparse, long, dark setae. Distance between upper eye lobes equal to 0.15 times length of scape; distance between lower eye lobes equal to 0.65 times length of scape. Antennae as long as 1.8 times elytral length; reaching elytral apex at apex of antennomere VIII; scape, pedicel and antennomeres III–VIII with yellowish white pubescence, not obliterating integument; antennal formula based on antennomere III: scape = 0.79; pedicel = 0.28; IV = 1.01; V = 0.82; VI = 0.73; VII = 0.66; VIII = 0.57; IX = 0.58; X = 0.54; XI = 0.47.

Thorax. Pronotum moderately coarsely, abundantly punctate; pubescence yellowish white, mixed with yellowish brown pubescence; with very sparse, long, dark setae near posterolateral angles. Lateral sides of prothorax with conical tubercle at about middle; pubescence (somewhat denser close to anterior margin) and sculpture as on pronotum. Ventral surface with yellowish white pubescence (more whitish depending on angle of incidence of light), not obliterating integument, denser in narrow band on metasternum close to mesocoxal cavities and apex of mesosternal process. Scutellum with yellowish white pubescence. Elytra. Moderately coarsely, abundantly punctate on basal third, gradually sparser towards apex; pubescence (Fig. 7) whitish, mixed with brownish pubescence; on basal two-thirds, moderately wide band of yellowish brown pubescence around suture; on each side of basal quarter, well-marked, slightly raised gibbosity, adjacent to transverse, slightly marked depression; elytral apex sub-truncate.

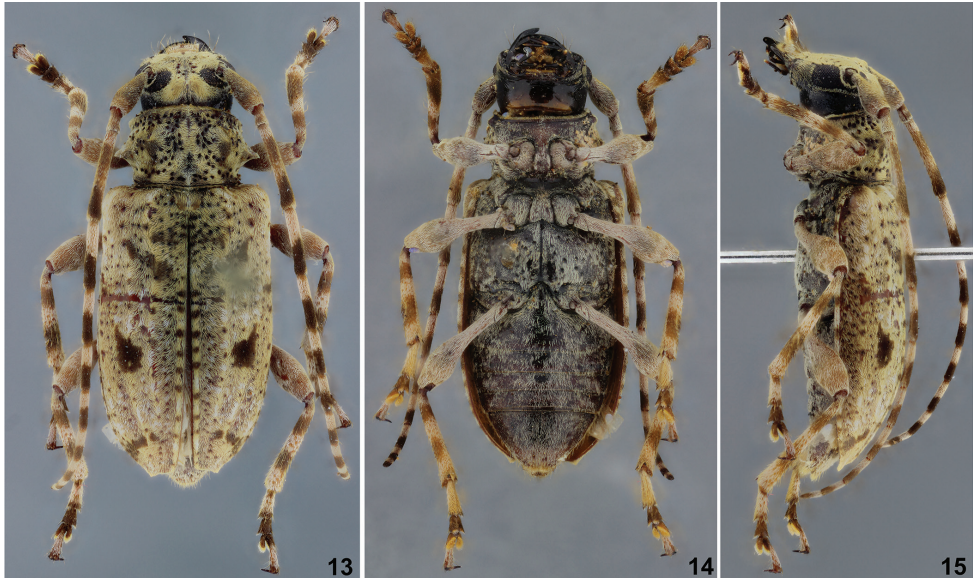
Abdomen. Urosternites with dense, yellowish white pubescence (more whitish depending on angle of incidence of light), almost obliterating integument. Legs. Femora and tibiae with yellowish white pubescence; length of metatarsomere V equal to 0.75 times II–III together.

Dimensions in mm (holotype/male). Total length, 8.40/8.35–8.50; length of prothorax at center, 1.75/1.55–1.60; anterior width of prothorax, 1.80/1.85–2.05; posterior width of prothorax, 1.95/1.95–1.95; largest width of prothorax, 2.4/2.20–2.50; humeral width, 2.95/3.00–3.10; elytral length, 6.10/6.20–6.20.

Type material. Holotype male from BOLIVIA, *Santa Cruz*: Potrerillo del Guenda (Snake farm; 17° 40' 15" S; 63° 27' 26" W 400 m), 14-23-30.X.2013, Wappes & Kuckartz col. (MNKM). Paratypes – BOLIVIA, *Santa Cruz*: 83 km N Camiri (900 m, Road to Itai, 6–8 km E Highway 9; 19° 19' S; 63°25'W), 2 males, 4–5.XII.2012, Skillman, Wappes & Bonaso col. (ACMT, MZSP).

Remarks. *Cotycuiara wappesi* differs from *C. acuminata* Galileo & Martins, 2012 as follows: elytral apex sub-truncate (distinctly acuminate in *C. acuminata*); pronotum abundantly punctate (mostly impunctate in *C. acuminata*); elytra with whitish pubescence occupying large areas (mostly yellowish brown in *C. acuminata*). It can be distinguished from *C. chionea* Martins & Galileo, 2010 by its humeral width, equal to approximately 1.2 times the largest width of head (approximately 1.7 times the largest width of the head in *C. chionea*), and elytral pubescence not forming notably dense spots (which occur in *C. chionea*).

Cotycuiara wappesi can be included in the alternative of couplet "10", from Martins and Galileo (2010):



Figures 13–15. *Psapharochrus wappesi*, holotype female: **13** dorsal habitus **14** ventral habitus **15** lateral habitus.

- 10'(9) Elytral pubescence uniformly distributed on basal and distal half. Bolivia.....
 *C. wappesi* sp. n.
 – Elytral pubescence denser on basal half than on distal half..... **10**
 10(10') Pronotum with wide central longitudinal band of yellowish pubescence and
 sides with white pubescence; anterior half of elytra covered by white pubes-
 cence, except on contrasting punctures; posterior half with several spots of
 white pubescence. Brazil (Minas Gerais, Espírito Santo)
 *Cotycicuiara nivaria* Martins & Galileo, 2010
 – Pronotum completely covered with white pubescence; elytra with a narrow
 white basal area, bordered posteriorly by a transverse less pubescent area, and
 with irregular white spots on the remaining surface. Brazil (Minas Gerais, Rio
 de Janeiro) *Cotycicuiara chionea* Martins & Galileo, 2010

***Nesozineus wappesi* sp. n.**

<http://zoobank.org/B76DAACE-DFA4-4961-A1AC-19978DBBFD30>

Figs. 10–12

Description. *Holotype female.* Color. Integument black; peduncle of femora partially dark-brown; pro- and mesosternal process brown; basal projection of urosternite I reddish-brown. General pubescence grayish-white.

Head. Frons, vertex and antennal tubercles microsculptured; pubescence abundant but not obliterating integument. Coronal suture distinct from clypeus to anterior edge of prothorax. Area behind eyes microsculptured; pubescence denser close to eyes than towards

prothoracic margin. Genae microsculptured, sparsely pubescent. Distance between upper eye lobes equal to 0.35 times length of scape; distance between lower eye lobes, in frontal view, equal to 0.65 times length of scape. Antennae as long as 1.65 times elytral length; reaching elytral apex at middle of antennomere IX; scape, pedicel and basal half of antennomeres III–IV with sparse, grayish-white pubescence; antennomeres III–IV enlarged at distal inner side; antennal formula based on antennomere III: scape = 0.82; pedicel = 0.22; IV = 0.98; V = 0.52; VI = 0.50; VII = 0.47; VIII = 0.47; IX = 0.42; X = 0.45; XI = 0.50.

Thorax. Pronotum finely, abundantly punctate; pubescence moderately abundant, not obliterating integument; disc slightly convex, slightly depressed on each side of basal quarter. Sides of prothorax with distinct, conical tubercle at basal half; tumid close to lateroanterior angles; punctures closer than on pronotum; pubescence dense in wide band close to anterior margin, sparser towards posterior margin. Ventral side with moderately dense pubescence, not totally obliterating integument. Scutellum laterally pubescent, glabrous in wide central area. Elytra. Coarse, abundantly punctate; with wide, curve depression from near humerus to apex of middle third (deep on basal third), together on elytra forming X-like; discal sides at distal third tumid (not reaching apex), and the vertical lateral side somewhat depressed; apex moderately narrow, individually rounded; pubescence laterally sub-aligned in rows.

Abdomen. Urosternites laterally pubescent, centrally with pubescence distinctly sparser. Legs. Femora and tibiae with pubescence not dense; meso- and metafemoral club not notably enlarged.

Dimensions in mm (female). Total length, 4.85; length of prothorax at center, 1.00; anterior width of prothorax, 1.25; posterior width of prothorax, 1.25; largest width of prothorax, 1.55; humeral width, 1.75; elytral length, 3.55.

Type material. Holotype female from BOLIVIA, Santa Cruz: Cordillera Province (Road to Itai, 83 km N Camiri; 19°20'S / 63°28'W; 890 m), 17–18.XII.2011, Wap-pes, Lingafelter and Woodley col. (MNKM).

Remarks. *Nesozineus wappesi* differs from *N. unicolor* Martins et al., 2009 by its thicker dorsal pubescence, coarser and sparser elytral punctures, and elytral surface with depressed areas (uniform in *N. unicolor*). It differs from *N. lineolatus* Galileo & Martins, 1996 by its distinctly more robust body and the lateral tubercle of prothorax not spiny and shorter.

Nesozineus wappesi can be included in the alternative of couplet “4”, from Galileo and Martins (1996) (translated):

- | | | |
|-------|--|---|
| 4'(3) | Scape shorter than antennomere III; elytra as long as twice humeral width. Bolivia | <i>Nesozineus wappesi</i> sp. n. |
| – | Scape as long as antennomere III; elytra longer than twice humeral width | 4 |
| 4(3') | Elytral pubescence uniformly distributed. Venezuela, Bolivia, Brazil (Maranhão, Piauí). | <i>Nesozineus apharus</i> Galileo & Martins, 1996 |
| – | Elytral pubescence more concentrated on four narrow, longitudinal rows at basal two-thirds. Brazil (Maranhão, Alagoas, Sergipe, Mato Grosso do Sul), Paraguay..... | <i>Nesozineus lineolatus</i> Galileo & Martins, 1996 |

***Psapharochrus wappesi* sp. n.**

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Figs 13–15

Description. *Holotype female.* Color. Integument dark-brown; base of gula yellowish brown; apex of last maxillary and labial palpomere yellowish; tibiae brown.

Head. Frons coarsely, sparsely punctate; pubescence dense, mostly yellowish brown, laterally more yellowish, obliterating integument. Antennal tubercles impunctate, with yellowish brown pubescence obliterating integument. Area between antennal tubercles and middle of upper eye lobes somewhat flat, coarsely, partially confluent punctate; pubescence centrally yellowish brown, laterally yellowish, not obliterating punctures. Vertex distinctly raised from middle of upper eye lobes; moderately finely, sparsely punctate; pubescence mostly yellowish, distinctly less dense around coronal suture and close to anterior edge of prothorax, with wide spot of yellowish brown pubescence on each side of coronal suture. Coronal suture distinct from clypeus to anterior edge of prothorax. Area behind upper eye lobes finely, rugose-punctate close to eyes, moderately abundantly punctate towards prothorax; with band of yellowish pubescence, not totally obliterating integument, gradually narrowed towards lower eye lobes. Area behind lower eye lobes fine, abundantly punctate, gradually sparser towards gula; with narrow band of yellowish pubescence close to eyes, almost glabrous on the remaining surface. Gula with yellowish pubescence, not obliterating integument. Submentum with short, yellowish pubescence on area near mentum. Distance between upper eye lobes equal to 0.45 times length of scape; distance between lower eye lobes, in frontal view, equal to length of scape. Antennae as long as 1.65 times elytral length; reaching elytral apex at basal quarter of antennomere IX; antennomere III with ring with whitish pubescence on base, followed by wide ring with brown-yellowish pubescence, central ring with whitish pubescence mixed with brown-yellowish pubescence, with wide ring with dark-brown pubescence, and narrow apical band of whitish pubescence; antennomeres IV–XI with whitish pubescence on basal half, and dark-brown pubescence on distal half; antennal formula based on antennomere III: scape = 0.65; pedicel = 0.23; IV = 0.73; V = 0.58; VI = 0.48; VII = 0.45; VIII = 0.43; IX = 0.35; X = 0.27; XI = 0.25.

Thorax. Lateral tubercles of prothorax large, conical, apex slightly directed upwards and backwards. Lateral tubercles on pronotal disc large, raised, apex not acute; central tubercle carina-like, from basal quarter to near apex; surface among tubercles coarsely, deeply, moderately abundantly punctate; central pubescence yellowish between lateral tubercles; with weakly defined band of yellowish brown pubescence crossing lateral tubercles, from base to apex; laterally with yellowish pubescence. Lateral sides of prothorax coarsely, deeply, moderately abundantly punctate; pubescence as on lateral of pronotum. Prosternum with short, not dense (laterally slightly denser), pale yellow pubescence (more whitish depending on angle of incidence of light). Prosternal process with lateral sides raised about middle; pubescence as on center of prosternum, slightly denser on transverse band in middle and laterally on distal half. Mesosternum and mesosternal process with pubescence slightly denser than on center of prosternum (shorter, sparser on basal center of mesosternum). Metasternum coarsely, deeply, sparsely punctate; pu-

bescence as on mesosternal process. Scutellum with yellowish pubescence in center, yellowish brown on sides. Elytra. Moderately coarsely, sparsely punctate; each elytron with two distinct carinae from near base to near apex; pubescence (Fig. 13) mostly yellowish; with oblique band with brown pubescence on basal third, not reaching lateral side and suture; large spot of brown pubescence immediately adjacent to center; on distal quarter, oblique band with brown pubescence, starting at lateral margin, not reaching suture; close to suture, on distal two-thirds, small spots of brown pubescence, smaller, sparser towards apex; apex slightly obliquely truncate, with outer angle projected.

Abdomen. Pubescence pale yellow (more whitish depending on angle of incidence of light), not obliterating integument. Legs. Tibiae with yellowish pubescence, with wide ring of brownish pubescence on each half. Tarsomere I with yellowish pubescence, except for narrow apical band with dark-brown pubescence; tarsomeres II–IV with dark-brown pubescence; tarsomere V with yellowish pubescence, sparser near apex.

Dimensions in mm (female). Total length, 11.5; length of prothorax at center, 2.1; anterior width of prothorax, 2.9; posterior width of prothorax, 2.7; largest width of prothorax, 3.7; humeral width, 4.2; elytral length, 7.6.

Type material. Holotype female from BOLIVIA, *Tarija*: 5 km W of Villamontes (Foothill Chaco Forest; 21°17'S / 63°28'W; ca. 500 m), 13.I.2008, R. Clarke & S. Zamalloa col. (MNKM).

Remarks. *Psapharochrus wappesi* differs from *P. piraiuba* Martins & Galileo, 2003 as follows: elytra with distinct spots of brown pubescence (absent in *P. piraiuba*); pronotal punctures sparser (denser in *P. piraiuba*); antennae in female surpassing the elytral apex (not reaching the elytral apex in *P. piraiuba*); and tibiae with distinct rings of pubescence (not present in *P. piraiuba*). *Psapharochrus wappesi* differs from *P. ridleyi* (Waterhouse, 1894) by the sub-parallel elytral margins from their base to the base of their distal third (uniformly narrowed from base to apex in *P. ridleyi*), antennae in female distinctly surpassing the elytral apex (at most, slightly surpassing elytral apex in *P. ridleyi*), and flatter body (distinctly convex in *P. ridleyi*).

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Two new species of the genus *Diostracus* Loew from Tibet, with a key to the Himalayan fauna (Diptera, Dolichopodidae)

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Abstract

Previously only one species of the genus *Diostracus* was known to occur in Tibet. Here the following two new species are added to the fauna of Tibet: *Diostracus acutatus* **sp. n.** and *D. tibetensis* **sp. n.** Their relationships with similar species are discussed. A key to the species of *Diostracus* from the Himalayas is presented.

Keywords

Diptera, Dolichopodidae, *Diostracus*, new species, Tibet

Introduction

The genus *Diostracus* is a large genus in the subfamily Hydrophorinae and includes dolichopodids living on wet rocks and stones in mountain streams (Saigusa et al. 1997). It is distributed in the Holarctic and Oriental regions with 83 known species. Among them, three species are known to occur in the Nearctic region, 21 in the Palearctic and 59 in the Oriental (Yang et al. 2006). The major references dealing with this genus are as fol-

lows: Takagi (1968, 1972), Negrobov (1980), Saigusa (1984), Saigusa et al. (1997), Yang (1998), Masunaga (2000) and Yang et al. (2011). Up to now, 23 species are recorded from China (Takagi 1968; Wei and Liu 1996; Yang 1998, 1999; Yang and Saigusa 2000; Zhang et al. 2003; Yang et al. 2011). The Chinese species were revised by Yang et al. (2011).

Only one species, *Diostracus nebulosus* Takagi, of the genus *Diostracus* was known to occur in Tibet (Yang et al. 2011). Here two new species are added to the fauna of Tibet, based on material collected by Dr. Zhaohui Pan and the junior author with Malaise traps (Map 1). Nine species groups for the species of *Diostracus* from the Himalayas were proposed by Saigusa (1984), and the three species from Tibet are placed within these groups. A key to the species of *Diostracus* from the Himalayas is presented.

Material and methods

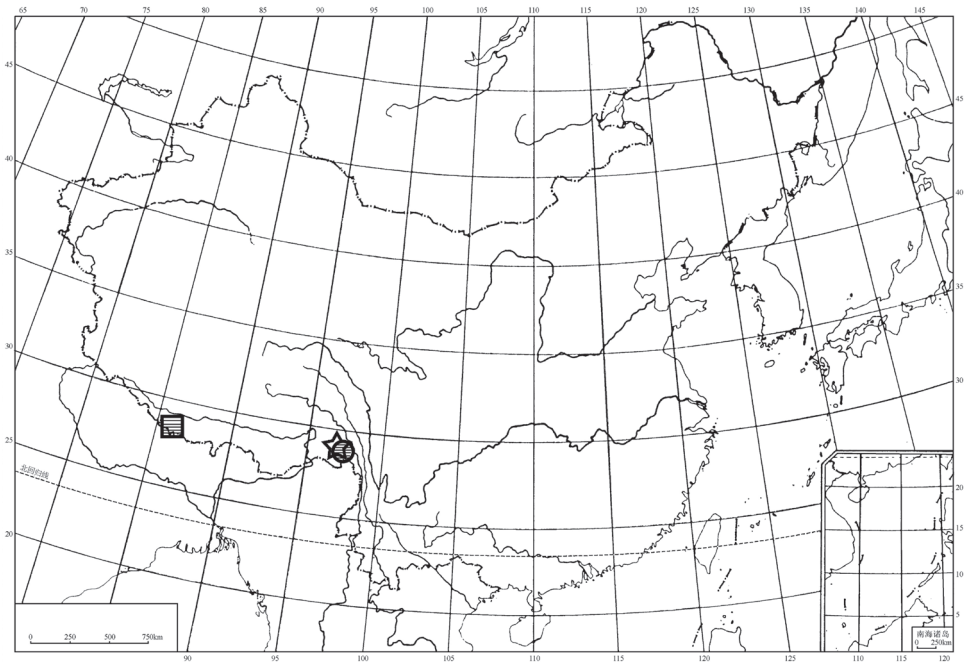
Type specimens are deposited in the Entomological Museum of China Agricultural University (CAU), Beijing. Morphological terminology generally follows McAlpine (1981) and Cumming and Wood (2009). The following abbreviations are used for bristles: acr–acrostichal, ad–anterodorsal, av–anteroventral, dc–dorsocentral, h–humeral, LI–fore leg, LII–mid leg, LIII–hind leg, npl–notopleural, oc–ocellar, pd–posterodorsal, ph–posthumeral, psa–postalar, pv–posteroventral, pvt–postvertical, sa–supraalar, sc–scutellar, vt–vertical.

Taxonomy

Key to the species (males) of *Diostracus* from the Himalayas

(modified from Saigusa 1984)

- | | | |
|---|--|---|
| 1 | Only posterior npl present, anterior npl absent (<i>unisetosus</i> -group)..... | 2 |
| – | Anterior and posterior npl present | 4 |
| 2 | Discal cell with 1-2 accessory cellulae at anterodistal corner (Saigusa 1984, fig. 2; Saigusa 1995, fig. 3)..... | 3 |
| – | Discal cell without accessory cellulae at anterodistal corner (Saigusa 1984, fig. 1)..... | <i>Diostracus unisetosus</i> Saigusa |
| 3 | 6 dc; mid femur without spine-like av | <i>Diostracus nigrilineatus</i> Saigusa |
| – | 5 dc; mid femur with 3-5 spine-like av at basal 1/4..... | |
| | | <i>Diostracus bisinuatus</i> Saigusa |
| 4 | Empodium and pulvilli reduced into minute protuberance (<i>fenestratus</i> -group)..... | 5 |
| – | At least empodium well developed, hair-like and ventrally ciliated..... | 14 |
| 5 | ph near transverse suture; vt absent (<i>fenestratus</i> -subgroup)..... | 6 |
| – | ph near h; vt present | 8 |



Map I. Distribution map of *Diostracus* in Tibet. ☆ *Diostracus acutatus* sp. n.; □ *Diostracus nebulosus* Takagi; ○ *Diostracus tibetensis* sp. n.

- 6 Mid and hind femora without long hairs and bristles; mid tibia long ciliated.... 7
- Mid femur with thick clump of erect golden yellow pv hairs between basal 1/3 and 1/2, hind femur with row of erect av except basal and apical 1/4; mid tibia simple *Diostracus ramulosus* Takagi
- 7 Jet-black nodule of discal crossvein about 5 times as long as wide; 5 accessory cellulae formed at anterodistal corner of discal cell; cercus uniformly short yellow haired *Diostracus reticulatus* Saigusa
- Jet-black nodule of discal crossvein about 2.6 times as long as wide; 3 accessory cellulae formed at anterodistal corner of discal cell; cercus with long golden hairs apically..... *Diostracus fenestratus* Saigusa
- 8 Discal crossvein strongly sinuate, S-shaped; anterodistal corner of discal cell with an accessory cellula (*pulchripennis*-subgroup) 9
- Discal crossvein nearly straight; anterodistal corner of discal cell without accessory cellula (*flex*-subgroup) 11
- 9 Lateral portion of abdominal tergite 5 projected into an elongate process; mid tibia without row of erect fine posterior bristles 10
- Lateral portion of abdominal tergite 5 expanded into a broad triangular lobe; mid tibia with row of erect fine posterior bristles *Diostracus pretiosus* Saigusa
- 10 Mid femur ventrally weakly raised subbasally, with modified hairs and bristles *Diostracus emotoi* Saigusa

–	Mid femur evenly flattened ventrally throughout and nearly bare	
 <i>Diostracus pulchripennis</i> Saigusa	
11	Wing shape normal, without finger-like lobe at posterior margin.....	12
–	Wing shape anomalous, with a finger-like lobe at posterior margin (Saigusa 1984, fig. 5)	<i>Diostracus pennilobatus</i> Saigusa
12	Fore tarsomere 1 with an obtuse apicoventral corner, fore tarsomere 2 without finger-like process near extreme base (Saigusa 1984, figs 7–8).....	13
–	Fore tarsomere 1 with a nearly acute apicoventral process, fore tarsomere 2 with a short finger-like ventral process near extreme base (figs 2, 5)	
 <i>Diostracus acutatus</i> sp. n.	
13	Fore tarsomere 1 with apicoventral corner rounded (Saigusa 1984, fig. 7); mid tibia ventrally not swollen near base.....	<i>Diostracus flexus</i> Saigusa
–	Fore tarsomere 1 with apicoventral corner angulated (Saigusa 1984, fig. 8); mid tibia ventrally weakly swollen near base	
 <i>Diostracus nishidai</i> Saigusa	
14	Pulvilli atrophied, bare (<i>impulvillatus</i> -group)	15
–	Pulvilli well developed, pad-like, pilose	19
15	Fore tarsomere 1 not furcate apically, fore tarsomere 2 shorter than tarsomere 1 (Saigusa 1984, figs 15–17).....	16
–	Fore tarsomere 1 furcate apically, fore tarsomere 2 much longer than tarsomere 1 (Saigusa 1984, fig. 18).....	<i>Diostracus angustipalpis</i> Saigusa
16	Wing without dark spot at discal crossvein; fore tarsomere 1 swollen apically (Saigusa 1984, figs 16–17)	17
–	Wing with a circular grayish spot at discal crossvein; fore tarsomere 1 not swollen apically (Saigusa 1984, fig. 15)	<i>Diostracus longiunguis</i> Saigusa
17	Fore tarsomere 1 weakly dilated apically, 1.5 times thicker than its base (Saigusa 1984, fig. 17)	18
–	Fore tarsomere 1 strongly dilated apically, 3 times thicker than its base (Saigusa 1984, fig. 16)	<i>Diostracus chaetodactylus</i> Saigusa
18	Cercus 3 times as long as wide, parallel-sided (Saigusa 1984, fig. 13)	
 <i>Diostracus impulvillatus</i> Saigusa	
–	Cercus about 1.5 times as long as wide, rather wide with narrow base (Saigusa 1984, fig. 14)	<i>Diostracus fulvispinatus</i> Saigusa
19	Only 4 dc (<i>quadrisetosus</i> -group).....	20
–	5–6 dc	28
20	Leg mostly yellowish.....	21
–	Legs darkened, at most trochanters and knees tinged yellow	23
21	vt absent; fore tarsomere 1 without short erect av (Saigusa 1984, fig. 26)	22
–	vt present; fore tarsomere 1 with row of short erect av (Saigusa 1984, fig. 27).....	<i>Diostracus parvus</i> Saigusa
22	Anterior npl absent	<i>Diostracus janssonorum</i> Saigusa
–	Anterior npl present.....	<i>Diostracus simplicipes</i> Saigusa
23	Fore coxa subapically raised at anterior surface.....	24

–	Fore coxa normal	25
24	Fore femur not strongly swollen basally (Saigusa 1984, fig. 21); fore tarsomere 1 nearly straight	<i>Diostracus auripalpis</i> Saigusa
–	Fore femur strongly swollen basally (Saigusa 1984, fig. 22); fore tarsomere 1 distinctly sinuate	<i>Diostracus femoratus</i> Saigusa
25	Face without grayish median stripe	26
–	Face with a narrow grayish median stripe	<i>Diostracus makiharai</i> Saigusa
26	R_{4+5} distinctly thicker than R_{2+3} ; palpus at most 0.9 times as long as eye height	27
–	R_{4+5} thinner than R_{2+3} ; palpus 1.1–1.2 times as long as eye height	<i>Diostracus magnipalpis</i> Saigusa
27	Palpus enlarged, about 3/4 as long as eye height (Saigusa 1984, fig. 20)	<i>Diostracus aurifer</i> Saigusa
–	Palpus not enlarged, about 1/3 as long as eye height	<i>Diostracus quadrisetosus</i> Saigusa
28	Lower postocular bristles including posteroventral hairs on head yellow ...	29
–	Hairs and bristles on head wholly black (<i>nigripilosus</i> -group)	<i>Diostracus nigripilosus</i> Saigusa
29	First flagellomere triangular; arista subbasal	30
–	First flagellomere not triangular; arista apical, subapical or dorsal	31
30	vt much shorter and thinner than pvt; wing broadly darkened along veins; fore tarsomere 1 slender (Saigusa 1984, fig. 28) (<i>umbrinervis</i> -group)	<i>Diostracus umbrinervis</i> Saigusa
–	vt almost as strong as pvt; wing not broadly darkened along veins; fore tarsomere 1 distinctly thickened apically (Saigusa 1984, fig. 29) (<i>tangalensis</i> -group)	<i>Diostracus tangalensis</i> Saigusa
31	Discal crossvein straight, without jet-black nodule or stripe (<i>nebulosus</i> -group)	32
–	Discal crossvein bent, with a jet-black nodule or stripe	33
32	Mid and hind femora without ventral bristles; cercus long finger-like in lateral view (Saigusa 1984, fig. 4A)	<i>Diostracus burmanicus</i> Saigusa
–	Mid and hind femora with ventral bristles; cercus short, subtriangular in lateral view (Yang et al. 2011, fig. 199d)	<i>Diostracus nebulosus</i> Takagi
33	5 dc	34
–	At least 6 dc (<i>unipunctatus</i> -group)	35
34	M without dark cloud, discal crossvein with narrow jet-black nodule (Saigusa 1984, fig. 31)	<i>Diostracus alticola</i> Saigusa
–	M with a dark cloud, discal crossvein with rounded jet-black nodule (Saigusa 1984, fig. 30)	<i>Diostracus shimai</i> Saigusa
35	First flagellomere short circular, nearly as long as wide (Saigusa 1984, figs 38–39)	36
–	First flagellomere distinctly or strongly elongated, distinctly longer than wide (Saigusa 1984, figs 32–35)	37

- 36 Mid femur without very long yellow ventral bristles at base; first flagellomere with somewhat tapering apex (Saigusa 1984, fig. 39) *Diostracus unipunctatus* Saigusa
- Mid femur with several very long yellow ventral bristles at base (Saigusa 1984, fig. 45); first flagellomere with wide apex (Saigusa 1984, fig. 38) *Diostracus rotundicornis* Saigusa
- 37 First flagellomere 1 apically strongly narrowed, not trapezoid 38
- First flagellomere 1 nearly trapezoid 39
- 38 Arista nearly apical (Saigusa 1984, fig. 32); scutellum with strong sc *Diostracus nepalensis* Saigusa
- Arista subapical (Saigusa 1984, fig. 33); scutellum without strong sc *Diostracus gymnoscutellatus* Saigusa
- 39 First flagellomere much elongated, about 2 times longer than wide (Saigusa 1984, figs 34, 36) 40
- First flagellomere 1.3–1.5 times longer than wide (Saigusa 1984, figs 35, 37) 41
- 40 Arista located at dorsoapical corner of first flagellomere (Saigusa 1984, fig. 34) *Diostracus auripilosus* Saigusa
- Arista dorsal (Saigusa 1984, fig. 36) *Diostracus longicornis* Saigusa
- 41 Arista subapical (Fig. 9; Saigusa 1984, fig. 35); vt distinctly longer than diameter of lateral ocellus 42
- Arista dorsal; vt extremely reduced, as long as diameter of lateral ocellus *Diostracus malaisei* Saigusa
- 42 vt as strong as pvt; first flagellomere 1.5 times longer than wide (Saigusa 1984, fig. 35); abdominal tergite 5 with long yellow lateral hairs *Diostracus parvipunctatus* Saigusa
- vt shorter and weaker than pvt; first flagellomere 1.3 times longer than wide (Fig. 9); abdominal tergite 5 with short lateral hairs. *Diostracus tibetensis* sp. n.

***Diostracus acutatus* sp. n.**

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Figs 1–3, 4–6

Diagnosis. vt rather short, 0.5 times as long as oc. First flagellomere somewhat triangular, 1.5 times longer than wide; arista apical (Fig. 4). Fore tarsomere 1 distinctly shortened, thickened, concave ventrally, and with a nearly acute apicoventral process; tarsomere 2 basally bent, concave ventrally, and with a short finger-like ventral process near extreme base (Figs 2, 5). Crossvein m-cu much elongated, strongly bent (Fig. 3).

Description. Male. Body length 8.0 mm; wing length 8.5 mm.

Head metallic green with pale gray pollen. Eyes widely separated; face widened towards clypeus. Hairs and bristles on head black; lower postocular bristles including posteroventral hairs pale, mostly very long. Ocellar tubercle distinct, with pair of long



Figures 1–3. *Diostracus acutatus* sp. n. (male). **1** adult, lateral view **2** fore leg, posterior view **3** wing. Scale bar = 1 mm.

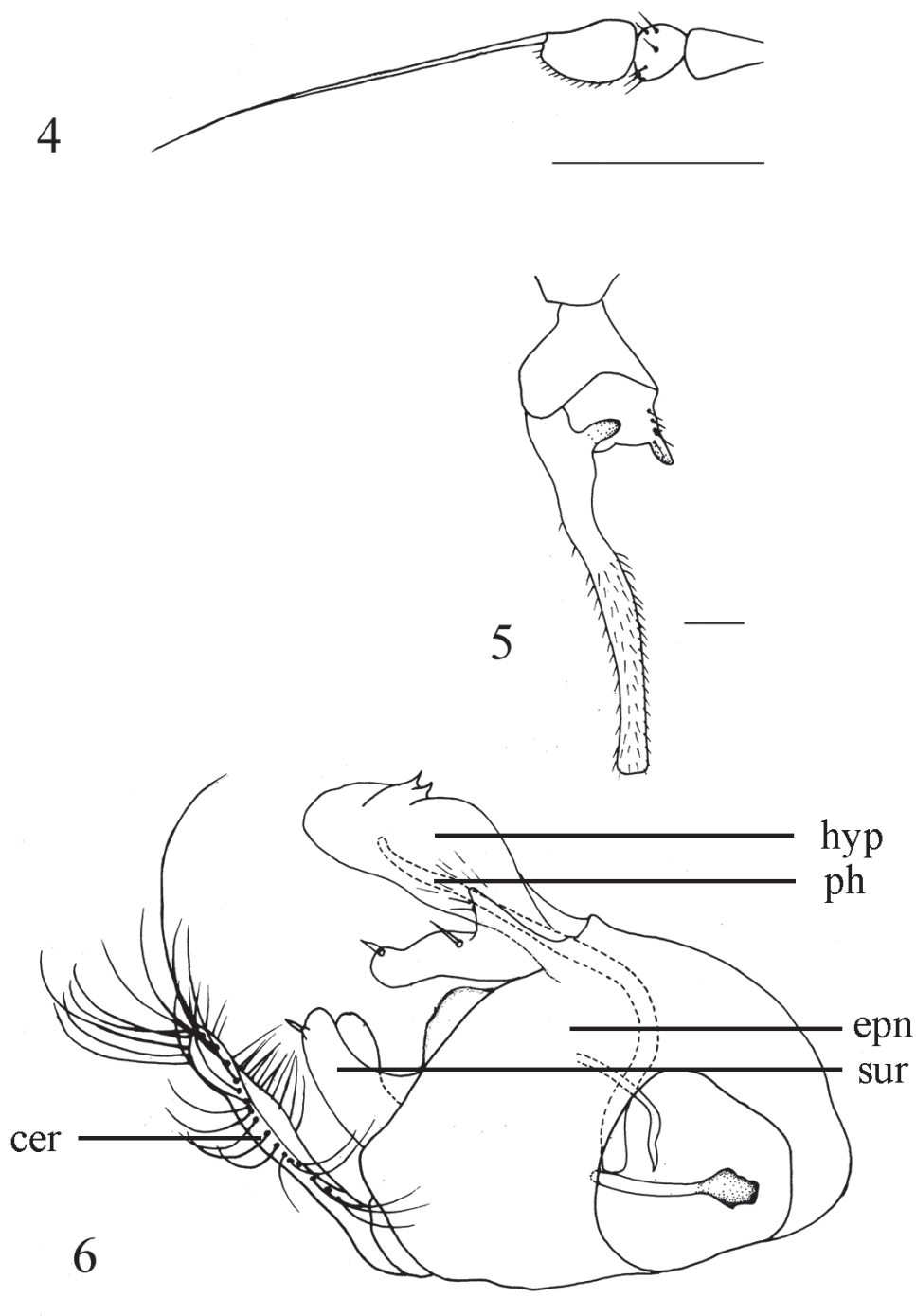
strong oc, without posterior hairs; vt rather short, 0.5 times as long as oc, nearly as long as pvt. Antenna (Fig. 4) black; scape without any dorsal hairs; first flagellomere subtriangular, 1.5 times longer than wide; arista apical, 4 times as long as first flagellomere, nearly bare. Proboscis blackish with pale hairs; palpus lobate, 3.5 times as long as broad, produced far beyond apex of proboscis, blackish with a purple luster, and with black hairs.

Thorax metallic green with pale gray pollen; mesoscutum with two pairs of dark brown longitudinal spots (middle pair strip-like). Hairs and bristles on thorax black; 6 mostly hair-like dc except posteriormost 1 dc longest and thick; acr absent; 1 h and 1 very short hair, 1 ph, 2 npl, 1 sa, 1 psa; scutellum with pair of long sc. Propleuron with short pale hairs on upper portion and long pale hairs on lower portion. Legs nearly entirely black except fore trochanter dark yellow; claws well developed, empodium and pulvilli reduced. Fore trochanter elongated, with hook-like posterior process (Fig. 2). Fore femur distinctly thickened (Fig. 2). Mid femur slightly bent, somewhat flattened dorsoventrally. Fore tibia slightly thickened, weakly curved (Fig. 2). Fore tarsomere 1 distinctly shortened, thickened, concave ventrally, and with a nearly acute apicoventral process; tarsomere 2 basally bent, concave ventrally, and with a short finger-like ventral process near extreme base (Figs 2, 5). Hairs and bristles on legs black except those on coxae pale; fore coxa with group of long pale anterior hairs at base; hind coxa apically with 2 brownish anterior bristles. All femora somewhat bare ventrally, with only very short, sparse pale ventral hairs, except fore femur with 3 distinct pale av hairs basally. Mid femur with 3 anterior bristles on apical 1/3. Fore tibia with 4–5 ad and 1 posterior bristle at apical 1/3. Mid tibia with 3 pd, and with very long posterior hairs on apical 1/5 somewhat curved; apically with 1 short spine-like av. Hind tibia with 5 ad and 4 pd; apically with 1 ad. Relative lengths of tibia and five tarsomeres: LI 3.7 : 0.7 : 2.2 : 1.35 : 0.7 : 0.75; LII 7.1 : 3.7 : 1.4 : 0.9 : 0.45 : 0.65; LIII 7.6 : 3.6 : 2.1 : 1.1 : 0.5 : 0.7. Wing (Fig. 3) hyaline, indistinctly tinged grayish; veins dark brown, R_{4+5} and M convergent apically; crossvein m-cu much elongated, strongly bent, margined with black on long anterior portion, and with blackish spot at short posterior portion. Squama brown with pale hairs. Halter brown.

Abdomen distinctly longer than head and thorax combined, metallic green with pale gray pollen. Abdomen with pale pubescence. Tergite 5 with lateral portion slightly extended downward. Sternite 1 with a nearly acute process at middle; sternite 4 medially with an obtuse anterior process and 2 short thin, contiguous posterior processes bearing bundle of brown hairs. Hypandrium not distinctly swollen.

Male genitalia (Fig. 6): Epandrium slightly longer than wide. Epandrial lobe short thick, finger-like, weakly bent, with an acute basal process; 1 slightly long bristle present at middle and 1 short thick bristle at tip. Surstylus short thick, apically furcated, with 1 very short apical denticle bearing 1 very short spine-like bristle. Hypandrium short thick, apically with a shallow, V-shaped apical incision, subapically with 2 small acute processes. Cercus slightly bent, nearly finger-like in lateral view, with long dark yellow hairs.

Female. Unknown.



Figures 4–6. *Diostracus acutatus* sp. n. (male). **4** antenna, lateral view **5** fore tarsomeres 1–2, posterior view **6** genitalia, lateral view. Abbreviations: cer = cercus; epn = epandrium; hyp = hypandrium; sur = surstylus; ph = phallus. Scale bar = 0.2 mm.

Type material. Holotype: male, China: Tibet, Nyingchi (N29°38'18", E94°21'46"), Sejlashan Mountain, Zhongshan Station, 4200 m, 20.VI.–10.VII. 2014, Malaise trap, leg. Baohai Wang and Zhaohui Pan (CAU).

Distribution. China (Tibet).

Remarks. The new species belongs to the *flexus*-subgroup of the *fenestratus*-group. It may be separated from *D. flexus* Takagi and *D. nishidai* Saigusa from Nepal by the fore tarsomere 1 with a nearly acute apicoventral process and fore tarsomere 2 with a short finger-like ventral process near the extreme base (Figs 2, 5). In *D. flexus* and *D. nishidai*, the fore tarsomere 1 has an obtuse apicoventral corner, and the fore tarsomere 2 has no finger-like process near the extreme base (Saigusa 1984, figs 7–8).

Etymology. The specific name refers to the fore tarsomere 1 with a nearly acute apicoventral process.

Diostracus nebulosus Takagi, 1972

Diagnosis. First flagellomere (Yang et al. 2011, fig. 199b) 1.3 times longer than wide, obtuse apically; arista dorsal. Wing (Yang et al. 2011, fig. 199a) with an obscure spot at anteroapical corner of discal cell; crossvein m-cu straight. Male cercus (Yang et al. 2011, fig. 199d) short, subtriangular.

Distribution. China (Tibet), Nepal.

Remarks. This species belongs to the *nebulosus*-group.

Diostracus tibetensis sp. n.

<http://zoobank.org/227A5CD2-DAE4-48A8-88FF-036F31E41D3F>

Figs 7–8, 9–10

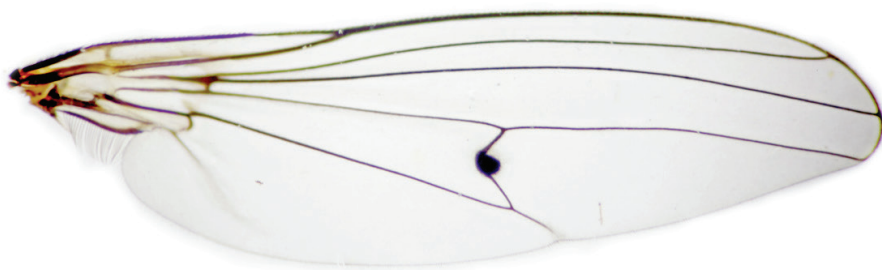
Diagnosis. vt rather short and weak, 0.4 times as long as oc. First flagellomere somewhat quadrate, 1.3 times longer than wide; arista subapical (Fig. 9). Wing (Fig. 8) hyaline; crossvein m-cu medially distinctly bent with small round black nodule located at middle of crossvein. Fore coxa with bundle of short dense black anterior hairs bristle-like at extreme tip. Mid and hind femora with very long pale ventral hairs (longest ones about 3 times as long as femur thickness). Abdominal tergites 4–5 with lateral portion slightly extended downwards, only tergite 4 with very long lateral hairs.

Description. Male. Body length 6.4 mm; wing length 7.6 mm.

Head metallic green with pale gray pollen. Eyes widely separated; face widened towards clypeus. Hairs and bristles on head black; lower postocular bristles including posteroventral hairs pale, mostly very long. Ocellar tubercle distinct, with pair of strong oc, without posterior hairs; vt rather short and weak, 0.4 times as long as oc, 0.7 times as long as pvt. Antenna (Fig. 9) black; scape without any dorsal hairs; first flagellomere short, somewhat quadrate, 1.3 times longer than wide; arista subapical, 3.9 times as long as first flagellomere, nearly bare. Proboscis blackish with pale hairs; palpus lobate, smoky black with black hairs.



7



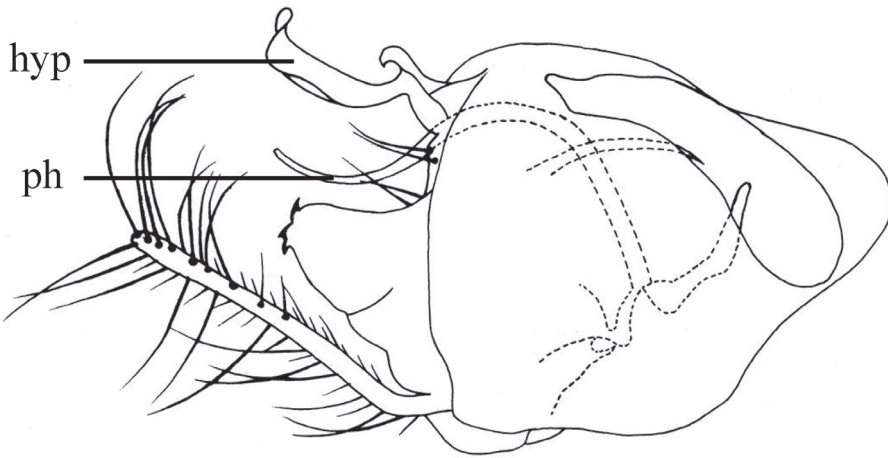
8

Figures 7–8. *Diostracus tibetensis* sp. n. (male). **7** adult, lateral view **8** wing. Scale bar = 1 mm.

Thorax metallic green with pale gray pollen; mesoscutum with two pairs of dark brown longitudinal spots (middle pair strip-like). Hairs and bristles on thorax black; 6 slightly long dc, posteriormost dc longest; acr bristles absent; 1 h and 1 short bristle, 1 ph, 2 npl, 1 sa, 1 psa; scutellum with pair of long sc and 4 very short marginal hairs



9



10

Figures 9–10. *Diostracus tibetensis* sp. n. (male). **9** antenna, lateral view **10** genitalia, lateral view. Scale bar = 0.2 mm.

(2 hairs between 2 sc). Propleuron with short pale hairs on upper portion and mostly long pale hairs on lower portion. Legs entirely black; claws well developed, empodium and pulvilli distinct. Hairs and bristles on legs black except those on coxae pale; fore coxa with bundle of short dense black anterior hairs bristle-like at extreme tip; hind coxa apically with 4 long blackish anterior hairs bristle-like. Mid and hind femora with some pale ventral hairs. Fore femur with two rows of black ventral bristles (longest ones slightly shorter than femur thickness), and with 3 long posterior bristles at extreme base. Mid femur basally with nearly two close rows of long pale ventral hairs (longest ones about 3 times as long as femur thickness), subbasally with 4 black short thick av. Hind femur with about two close rows of long pale ventral hairs (longest ones about 3 times as long as femur thickness) and with 5 black short thick av. Fore tibia

with 4 ad and 4 pv on apical half; apically with 3 bristles. Mid tibia with 3 ad and 2 pd; apically with 3 bristles. Hind tibia with 4 ad, 5 pd, 3 av and 6 pv; apically with 3 bristles. Fore tarsomere 1 with row of short dense erect av spines and one row of dense thin pv (longer than av). Relative lengths of tibia and five tarsomeres: LI 3.3 : 1.6 : 1.6 : 0.8 : 0.55 : 0.7; LII 5.8 : 2.9 : 1.1 : 0.75 : 0.5 : 0.75; LIII 7.1 : 3.2 : 1.9 : 1.2 : 0.6 : 0.8. Wing (Fig. 8) hyaline; veins dark brown, R_{4+5} and M convergent apically; crossvein m-cu medially distinctly bent with small round black nodule located at middle of crossvein. Squama brown with pale hairs. Halter brown to dark brown.

Abdomen rather short, nearly as long as head and thorax combined, metallic green with pale gray pollen. Abdomen with pale pubescence except dorsum with some black hairs at middle. Tergites 4 distinctly and tergite 5 weakly with lateral portion extended downward; lateral portion of tergite 4 with very long hairs apically bent, slightly shorter than those on sternite 3, but lateral portion of tergite 5 only with short hairs.

Male genitalia (Fig. 10): Epandrium relatively short, slightly longer than wide. Epandrial lobe weak, with 2 long bristles. Surstylus enlarged, with three acute denticles at apical margin. Hypandrium narrowed, bent; apically with a shallow, V-shaped apical incision and lateral lobe curled; basally with a hook-like process. Cercus straight, long finger-like, with long yellow hairs.

Female. Unknown.

Type material. Holotype: male, China: Tibet, Nyingchi (N29°38'18", E94°21'46"), Sejilashan Mountain, Zhongshan Station, 4200 m, 20.VI.-10.VII. 2014, Malaise trap, leg. Baohai Wang and Zhaohui Pan (CAU).

Distribution. China (Tibet).

Remarks. The new species belongs to the *unipunctatus*-group. It is somewhat similar to *D. parvipunctatus* Saigusa from Nepal in the shape of the first flagellomere and fore and mid femora with long ventral hairs, but may be separated from the latter in the following points: vt is shorter and weaker than pvt; the first flagellomere is shorter, 1.3 times longer than wide, and the abdominal tergite 5 has the short lateral hairs. In *D. parvipunctatus*, vt is as strong as pvt or stronger; the first flagellomere is 1.5 times longer than wide (Saigusa 1984, fig. 35), and the abdominal tergites 4–5 has the long yellow lateral hairs (Saigusa 1984).

Etymology. The specific name refers to the type locality Tibet.

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Phylogenetic utility of ribosomal genes for reconstructing the phylogeny of five Chinese satyrine tribes (Lepidoptera, Nymphalidae)

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Abstract

Satyrinae is one of twelve subfamilies of the butterfly family Nymphalidae, which currently includes nine tribes. However, phylogenetic relationships among them remain largely unresolved, though different researches have been conducted based on both morphological and molecular data. However, ribosomal genes have never been used in tribe level phylogenetic analyses of Satyrinae. In this study we investigate for the first time the phylogenetic relationships among the tribes Elymniini, Amathusiini, Zetherini and Melanitini which are indicated to be a monophyletic group, and the Satyrini, using two ribosomal genes (*28s rDNA* and *16s rDNA*) and four protein-coding genes (*EF-1a*, *COI*, *COII* and *Cytb*). We mainly aim to assess the phylogenetic informativeness of the ribosomal genes as well as clarify the relationships among different tribes. Our results show the two ribosomal genes generally have the same high phylogenetic informativeness compared with *EF-1a*; and we infer the *28s rDNA* would show better informativeness if the *28s rDNA* sequence data for each sampling taxon are obtained in this study. The placement of the monotypic genus *Callarge* Leech in Zetherini is confirmed for the first time based on molecular evidence. In addition, our maximum likelihood (ML) and Bayesian inference (BI) trees consistently show that the involved Satyrinae including the Amathusiini is monophyletic with high support values. Although the relationships among the five tribes are identical among ML and BI analyses and are mostly strongly-supported in BI analysis, those in ML analysis are lowly- or moderately- supported. Therefore, the relationships among the related five tribes recovered herein need further verification based on more sampling taxa.

Keywords

Butterfly, molecular systematics, Bayesian inference, Satyrinae

Introduction

The butterfly subfamily Satyrinae, comprising approximately 2,500 described extant species, is amongst the most diverse groups in insects (Ackery et al. 1999). Recently, Marín et al. (2011) summarized the findings of systematic studies on this group (Peña et al. 2006; Peña and Wahlberg 2008; Wahlberg et al. 2009), proposing that the Satyrinae could be divided into nine tribes. However, phylogenetic relationships among them remain mostly unresolved despite they are assigned to four groups (Marín et al. 2011): group one consisting of two Neotropical Morphini and Brassolini; group two including Elymniini, Amathusiini, Zetherini, Dirini and Melanitini; group three including only the Neotropical Haeterini; and group four comprising the speciose Satyrini distributed worldwide. Regarding the group two, phylogenetic relationships of its five tribes remain unresolved except for the well-defined sister relationship of Dirini and Melanitini (Peña et al. 2006; Peña and Wahlberg 2008; Wahlberg et al. 2009; Price et al. 2011; see the figure 1 in Marín et al. 2011). The phylogenetic uncertainty among them can be mainly exhibited in two aspects: one is the weakly supported nodes bearing them; and another is the unstable topologies of trees conducted by different analysis methods (Peña et al. 2006; Peña and Wahlberg 2008; Wahlberg et al. 2009).

It is widely accepted that selecting suitable genetic markers is of great importance in study of molecular systematics. In previous phylogenetic studies on the tribe level relationships of Satyrinae, the protein-coding genes (e.g., mitochondrial *COI*, and a number of nuclear genes) have been the main source of phylogenetic information (Peña et al. 2006; Peña and Wahlberg 2008; Wahlberg et al. 2009; Price et al. 2011). However, the ribosomal genes, to date have been never considered. The ribosomal genes have already been proven to be informative for phylogenetic analyses in other butterfly groups (e.g., *16s rDNA* in Kim et al. 2010; *28s rDNA* and *18s rDNA* in Jiang et al. 2013).

In order to test the phylogenetic utility of the ribosome genes for constructing the tribe level relationships of Satyrinae which have not been resolved based on morphological and protein-coding sequence data, two ribosomal genes (*16s rDNA* and *28s rDNA*) as well as four additional protein-coding genes (*COII*, *Cytb*, *COI* and *EF-1a*) are used in our study to reconstruct the phylogeny of the Elymniini, Amathusiini, Zetherini, Melanitini and Satyrini which represent all the major lineages of Chinese satyrines. Besides, we further clarify the taxonomic placement of the *Callarge* Leech, a satyrine genus which has never been included in previous molecular studies.

Materials and methods

Taxon sampling

A total of 30 species were included in the analyses (Table 1). Of these, the 21 in-group species represent all the five satyrine tribes occurring in China. In consideration of

Table 1. Samples used for molecular analyses in this study together with relevant information.

Subfamily	Tribe	Species	Specimen voucher	Collecting locality	GenBank accession number				
					COI	COII	Cytb	16S rDNA	EF-1a
Libytheinae		<i>Libythea myrrha</i>	limyr1	China: Yunnan, Jinghong	KC158418*	KJ777775	KJ805831	KJ777730	KJ805856
		<i>Danaua genutia</i>	dagen1	China: Yunnan, Hekou	KF226386*	KJ777776	KJ805832	KJ777731	KJ805857
		<i>Panantica sita</i>	pasit1	China: Yunnan, Rili	NC_024412*	KJ777777	KJ805833	KJ777732	KJ805858
Danainae		<i>Euploea mulciber</i>	eumul	China: Yunnan, Lincang	NC_016720*	KJ777778	KJ805834	KJ777733	KJ805859
		<i>Apatura ilia</i>	apili1	China: Hunan, Zhangjiajie	NC_016062*	KJ777779	KJ805835	KJ777734	KJ805860
		<i>Ariadne merione</i>	armer1	China: Yunnan, Lincang	KC755827*	KJ777780	KJ805836	KJ777735	KJ805861
Calinaginae	Biblidini	<i>Calinaga davidis</i>	cadav1	China: Sichuan, Mt. Qingchengshan	NC_015480*	KJ777781	KJ805837	KJ777736	KJ805862
		<i>Charaxes bernardus</i>	chber1	China: Yunnan, Hekou	EF534101*	KJ777782	KJ805838	KJ777737	KJ805863
		<i>Polyura eudamippus</i>	poeud1	China: Sichuan, Pinwu	AB855881*	KJ777783	KJ805839	KJ777738	KJ805864
Charaxinae		<i>Melanitis leda</i>	meled1	China: Yunnan, Hekou	KM111608	KJ777784	KJ805840	KJ777739	KJ805865
		<i>Melanitis phedima</i>	mephe1	China: Fujian, Dehua	KM111609	KJ777785	KJ805841	KJ777740	KJ805866
		<i>Elymnias hypermnestra</i>	elhyp1	China: Yunnan, Hekou	KM111610	KJ777786	KJ805842	KJ777741	KJ805867
Elymniini		<i>Elymnias malelas</i>	elmal1	China: Xizang, Motuo	KM111611	KJ777787	KJ805843	KJ777742	KJ805868
		<i>Callarge sagittia</i>	casag1	China: Gansu, Wenxian	KM111612	KJ777788	KJ805844	KJ777743	KJ805869
		<i>Ethopea noirei</i>	NW121-7	Vietnam	DQ338773*	n.a.	n.a.	n.a.	DQ338915*
Zetherini		<i>Penthema adelma</i>	peade1	China: Gansu, Wenxian	EF534103*	KJ777789	KJ805845	KJ777744	KJ805870
		<i>Penthema darlisa</i>	CP-B02	Vietnam	DQ338775*	n.a.	n.a.	n.a.	DQ338917*
		<i>Lopinga achine</i>	loach1	China: Shaanxi, Baoji	KM111631	KJ777792	KJ805848	KJ777748	KJ805874
Satyrinae		<i>Hipparchia autonoe</i>	hiaut1	China: Qinghai, Huzhu	KM111644	KJ777794	KJ805850	KJ777750	KJ805876
		<i>Ninguchia schrenkii</i>	nisch1	China: Shaanxi, Huodiang	KM111641	KJ777793	KJ805849	KJ777749	KJ805875
		<i>Lethe albolineata</i>	lealb1	China: Yunnan, Jinghong	KM111634	KJ777795	KJ805851	KJ777751	KJ805877
		<i>Tatinga tibetana</i>	tatib1	China: Shaanxi, Baoji	KM111633	KJ777796	KJ805852	KJ777752	KJ805878
		<i>Neope pulaha</i>	nepul1	China: Sichuan, Pingwu	KM111640	KJ777797	KJ805853	KJ777753	KJ805879
		<i>Mycalis mamerta</i>	mymam1	China: Yunnan, Jinping	KM111627	KJ777798	KJ805854	KJ777754	KJ805880
		<i>Minois dryas</i>	midry1	China: Shaanxi, Baoji	KM111645	KJ777799	KJ805855	KJ777755	KJ805881

Subfamily	Tribe	Species	Specimen voucher	Collecting locality	GenBank accession number					
					COI	COII	Cytb	16s rDNA	EF-1α	28s rDNA
	Amathusiini	<i>Stichopphalmus bouqua</i>	sthwl1	China: Yunnan, Hekou	AY218250*	KJ777790	n.a.	KJ777745	KJ805871	n.a.
		<i>Faunis aerepe</i>	faer1	China: Zhejiang, Danxi	n.a.	KJ777791	KJ805846	KJ777746	KJ805872	n.a.
		<i>Amathusia phidippus</i>	NW114-17	Indonesia	DQ018956*	n.a.	n.a.	n.a.	DQ018923*	n.a.
		<i>Thauria latbyi</i>	tlat1	China: Yunnan, Jinghong	KM111613	n.a.	KJ805847	KJ777747	KJ805873	KJ777766
		<i>Discophora necho</i>	NW101-6	Indonesia	DQ338747*	n.a.	n.a.	n.a.	DQ338887*	n.a.

Note: * indicates the sequence downloaded from GenBank; n.a. indicates the corresponding gene fragment is not available.

previous studies (Freitas and Brown 2004; Peña et al. 2006), other nine species of six subfamilies (Libytheinae, Danainae, Apaturinae, Biblidinae, Calinaginae and Charaxinae) of the family Nymphalidae were selected as outgroup taxa. Among them, *Libythea myrrha* Fruhstorfer of Libytheinae was used to root the resulting phylogenetic trees, since Libytheinae is widely accepted as the sister group to the rest Nymphalidae (e.g., Ackery et al. 1999; Freitas and Brown 2004; Peña et al. 2006; Peña and Wahlberg 2008). The butterflies studied stem from the specimens in Entomological Museum of Northwest A&F University (NWAUFU), Yangling, China. Details of the sampling are presented in Table 1.

DNA extraction, amplification and sequencing

Genomic DNA was extracted from 95–100% ethanol-preserved muscle tissue of two adult butterfly legs, using an EasyPure Genomic DNA Kit according to the manufacturer's instructions (TransGen Biotech Co., Ltd., Beijing, China). Extracted genomic DNA was eventually dissolved in 80 μ L ddH₂O and kept in a freezer (–20 °C) until it was used for polymerase chain reaction (PCR). Sequences of six nuclear and mitochondrial genes (*EF-1 α* , *28s rDNA*, *COI*, *COII*, *Cytb* and *16s rDNA*) were amplified through PCR in a total volume of 25 μ L. The volume consisted of 12.5 μ L CWBIO 2 \times Taq MasterMix, 8.5 μ L sterile distilled H₂O, 2.0 μ L genomic DNA template and 1.0 μ L 10 μ M each primer. The primers used and corresponding annealing temperature in PCR as well as references are listed in Table 2. After electrophoretic analysis to ensure the amplification products were the target fragments we needed, the PCR products were subsequently sent to Sunny Biotechnology Co., Ltd. (Shanghai, China) for sequencing with the same primers used in the PCR. All sequences gathered in this study have been deposited in the GenBank.

Sequence analysis and phylogenetic inference

Sequence chromatogram was checked carefully using Chromas Pro software (Technelysium Pty Ltd., Tewantin, Australia). Each protein-coding sequence was translated for confirmation and assignment of codon positions in Primer Premier version 5.00 software (Premier Biosoft International, Palo Alto, CA). Multiple sequences were aligned using MAFFT version 7.037 with the auto strategy (Katoh and Standley 2013) and, if necessary, manual adjustment was made in MEGA version 6.06 (Tamura et al. 2013). Base frequency and the number of variable and parsimony informative sites were calculated in MEGA version 6.06 (Tamura et al. 2013). We investigated the chi-square of homogeneity of base frequencies across taxa for each gene with the program PAUP4.0b10 (Swofford 2002). The aligned ambiguous regions of two non-coding ribosomal genes (i.e. *16s rDNA* and *28s rDNA*) were retained because these positions might contain some information that is potentially useful

Table 2. Primers in PCRs for multiple genes used in this study.

Gene	Primer name (forward or reverse reading)	Sequence	Annealing temperature	References
<i>COI</i>	LCO1490 (f)	GGT CAA CAA ATC ATA AAG ATA TTG G	51 °C	Folmer et al. (1994)
	HCO2198 (r)	TAA ACT TCA GGG TGA CCA AAA AAT CA		Folmer et al. (1994)
<i>COII</i>	EVA (f)	GAG ACC ATT ACT TGC TTT CAG TCA CT	53 °C	Caterino and Sperling (1999)
	PATRICK (r)	CTA ATA TGG CAG ATT ATA TGT ATT GG		Caterino and Sperling (1999)
<i>Cytb</i>	CB-N3665 (f)	GTC CTA CCA TGA GGT CAA ATA TC	50 °C	Simon et al. (2006)
	CB-N11526 (r)	TTC AAC TGG TCG TGC TCC AAT TCA		Simon et al. (2006)
<i>16s rDNA</i>	LR-J-12887 (f)	CCG GTT TGA ACT CAG ATC ACG T	49 °C	Simon et al. (1994)
	LR-N-13398 (r)	CGC CTG TTT ATC AAA AAC AT		Simon et al. (1994)
<i>EF-1a</i>	ELF2F (f)	AAA ATG CCC TGG TTC AAG GGA	52 °C–57 °C	Wan et al. (2013)
	ef51.9 (f)	CAR GAC GTA TAC AAA ATC GG		Monteiro and Pierce (2001)
	efrcM4 (r)	ACA GCV ACK GTY TGY CTC ATR TC		Monteiro and Pierce (2001)
<i>28s rDNA</i>	rD3.2a (f)	AGT ACG TGA AAC CGT TCA SGG GT	58.8 °C	Whiting (2002)
	Rd4.2b (r)	CCT TGG TCC GTG TTT CAA GAC GG		Whiting (2002)

for phylogenetic reconstruction (Aagesen 2004; Redelings and Suchard 2009). As proposed by Xia et al. (2003), we performed tests of substitutional saturation based on the *I*_{ss} (i.e. index of substitutional saturation) statistic for different partitioned dataset with DAMBE version 5.3.74 (Xia 2013). For this method, if *I*_{ss} is smaller than *I*_{ss.c} (i.e. critical *I*_{ss}), we can infer that the sequences have experienced little substitutional saturation (Xia and Lemey 2009).

Maximum likelihood (ML) analysis was performed using the raxmlGUI version 1.3 interface (Silvestro and Michalak 2012) of RAxML version 7.2.6 (Stamatakis 2006). The best-fit substitution model for each gene partition was determined by jModelTest version 2.1.4 (Darriba et al. 2012) under the Akaike Information Criterion (AIC) (Akaike 1974). Clade supports were assessed using the ML + rapid bootstrap algorithm with 1000 bootstrap iterations.

Bayesian inference (BI) analyses were conducted in MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003). The best-fit partitioning schemes and partition-specific substitution models, defined from 16 subsets formed by gene and codon position of the six genes used, were tested using the ‘greed’ algorithm of program PartitionFinder v1.1

(Lanfear et al. 2012) under the Bayesian information criterion (BIC). Two independent MCMC runs were performed either for 300,000 generations or until the average standard deviation of split frequencies fell below 0.01. The sampling frequency was set as every 100 generations. After the first 25% of the yielded trees were discarded as burn-in, a 50% majority-rule consensus tree with the posterior probability (PP) values was constructed by summarizing the remaining trees. For BI analyses, two different datasets, the full six-gene-dataset and the non-*COI* + *Cytb* + *COII*-3rds-dataset (with 3rd positions removed), were used to examine the phylogenetic utility of the 3rd sites of *COI* + *Cytb* + *COII*, because these sites have suffered substantial saturation (see the results).

Phylogenetic informativeness

We used phylogenetic informativeness (PI) profiles to quantify the relative contribution of each partition to the resulted tree. The peak of the PI distribution is suggested to predict the maximum phylogenetic informativeness for corresponding partition (Owen et al. 2014). The PI profiles were generated with the PhyDesign (Townsend 2007; Lopez-Giraldez and Townsend 2011). For this, the aligned sequences and an ultrametric tree are needed as input files. In the sequence file, the eight partition schemes identified by PartitionFinder v1.1 (Lanfear et al. 2012) were applied. The ultrametric tree was generated with the BEAST version 1.7.5 (Drummond et al. 2012) using the eight partitions and corresponding models determined by PartitionFinder v1.1 (Lanfear et al. 2012) as well.

Results

Sequence characterization

One hundred and fifty-four sequences of the six genes were obtained for 30 species (Tables 1, 3). The final alignment yields 3,402 bp of the combined sequence data, of which 1,312 are variable and 1,053 are parsimony informative. The Chi-square test reveals no significant base composition heterogeneity among the taxa for any gene fragment, even for the 28s *rDNA* showing a high level of CG base composition ($p = 0.138$). In the case of the saturation test, all observed values of *I_{ss}* are smaller than the *I_{ss.c}* values for both symmetrical and asymmetrical topologies in all gene fragments. However, when the analysis was taken for each of the three codon positions of coding gene fragments separately, values of *I_{ss}* for the third codons of all the *COI*, *COII* and *Cytb* genes are smaller than the *I_{ss.c}* values in both symmetrical and asymmetrical topologies, indicating some of these sites have suffered substantial saturation.

Table 3. Sequence statistics for the six gene regions.

	<i>COI</i>	<i>COII</i>	<i>Cytb</i>	<i>16s rDNA</i>	<i>EF-1a</i>	<i>28s rDNA</i>
Number of sequences	29	25	25	26	30	19
Alignment length (bp)	621	690	591	530	510	460
Percentage A(%)	29.6	34.9	31.7	37.7	25.5	15.5
Percentage T(%)	39.5	41.6	43.3	41.6	26.1	18.2
Percentage C(%)	16.7	13.4	16.0	12.8	25.9	33.8
Percentage G(%)	14.2	10.1	9.0	7.9	22.5	32.5
Number of variable sites	233	288	275	167	165	184
Number of parsimony informative sites	203	222	226	125	139	138
Chi-square test of base frequency	$p = 1.000$	$p = 1.000$	$p = 0.998$	$p = 1.000$	$p = 0.999$	$p = 0.138$

Table 4. The best-fit partitioning schemes and corresponding partition models used in BI analysis.

Partitioned dataset	Nucleotide model under BIC	Implemented parameters in BI analysis
1) <i>COI</i> 1st + <i>COII</i> 1st + <i>Cytb</i> 1st	GTR + I + G	nst = 6, rates = invgamma
2) <i>COI</i> 2nd + <i>COII</i> 2nd + <i>Cytb</i> 2nd	HKY + I + G	nst = 2, rates = invgamma
3) <i>COI</i> 3rd + <i>COII</i> 3rd + <i>Cytb</i> 3rd	HKY + G	nst = 2, rates = gamma
4) <i>16s rDNA</i>	GTR + I + G	nst = 6, rates = invgamma
5) <i>28s rDNA</i>	GTR + G	nst = 6, rates = gamma
6) <i>EF-1a</i> 1st	TtN + I	nst = 6, rates = inv
7) <i>EF-1a</i> 2nd	JC	nst = 1
8) <i>EF-1a</i> 3rd	GTR + G	nst = 6, rates = gamma

Model selection and phylogenetic reconstruction

Each gene partition shows the GTR + I + G for its best-fit substitution model except the *28s rDNA* being the GTR + G, but we imposed the GTR + G for all gene partitions in ML analysis as recommended by Zahiri et al. (2011). For BI analysis, the best partitioning scheme includes eight partitions. Each partition and corresponding parameters used in BI analyses are summarized in Table 4.

The ML and BI trees based on the full six-gene-dataset show generally identical topologies (summarized in Figure 1). All tribes included with two or more taxa examined in this study are recovered to be monophyletic mostly with strong support values. The traditional “satyrine” clade consisting of Calinaginae, Charaxinae and Satyrinae is well-recovered by strong bootstrap value (BV) 100 and PP 1.00. The five tribes of Chinese satyrines constitute the Satyrinae clade with BV 93 and PP 1.00. Within this clade, the Satyrini is consistently recovered as sister of others. Then, Amathusiini branches off, and the Zetherini is sister to the sister group (Melanitini + Elymniini), but the relationship between Melanitini and Elymniini is poorly supported by both ML and BI analyses (BV = 42, PP = 0.71). The genus *Callarge* is nested into the Zetherini, forming a sister group with *PentHEMA* Westwood.

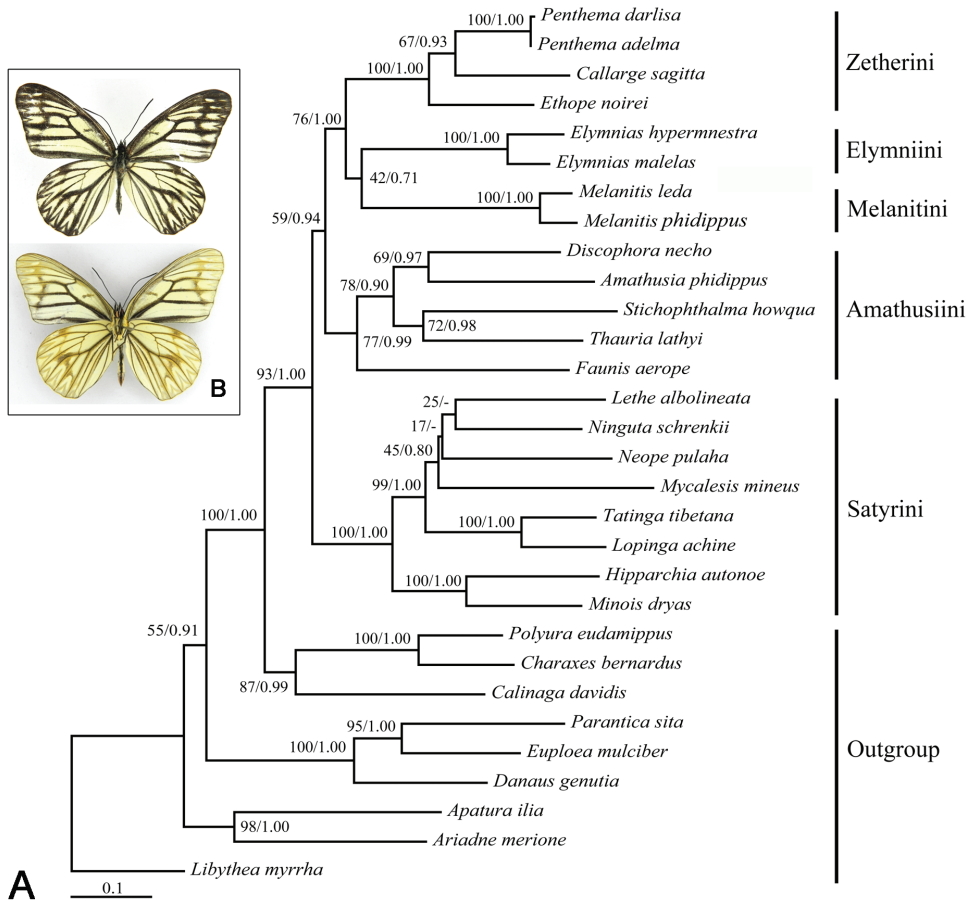


Figure 1. A Bipartitions tree obtained from maximum likelihood (ML) analysis based on the full six-gene-dataset; numbers separated by a slash on node are bootstrap value (BV) and posterior probability (PP) **B** *Callarge sagitta* (Leech), habitus, dorsal view on the above and ventral view on the below.

The trees constructed based on the non-*COI* + *Cytb* + *COII*-3rds-dataset is shown in Figure 2. The tree shows generally same topology with that based on the full six-gene-dataset, but some nodes especially that describing the terminal taxa are less resolved. This indicates that the 3rd sites of *COI* + *Cytb* + *COII* provided poor supports for the tribe level relationships.

Phylogenetic informativeness

As shown in Figure 3, the 3rd codon positions of the combined *COI*, *Cytb* and *COII* has the highest phylogenetic signal at all taxonomic levels, and a peak of the PI distribution can be recognized at about the 1/3 position of the tree near the terminal branches. Followed are the 1st codon positions of the combined *COI*, *Cytb* and *COII*.

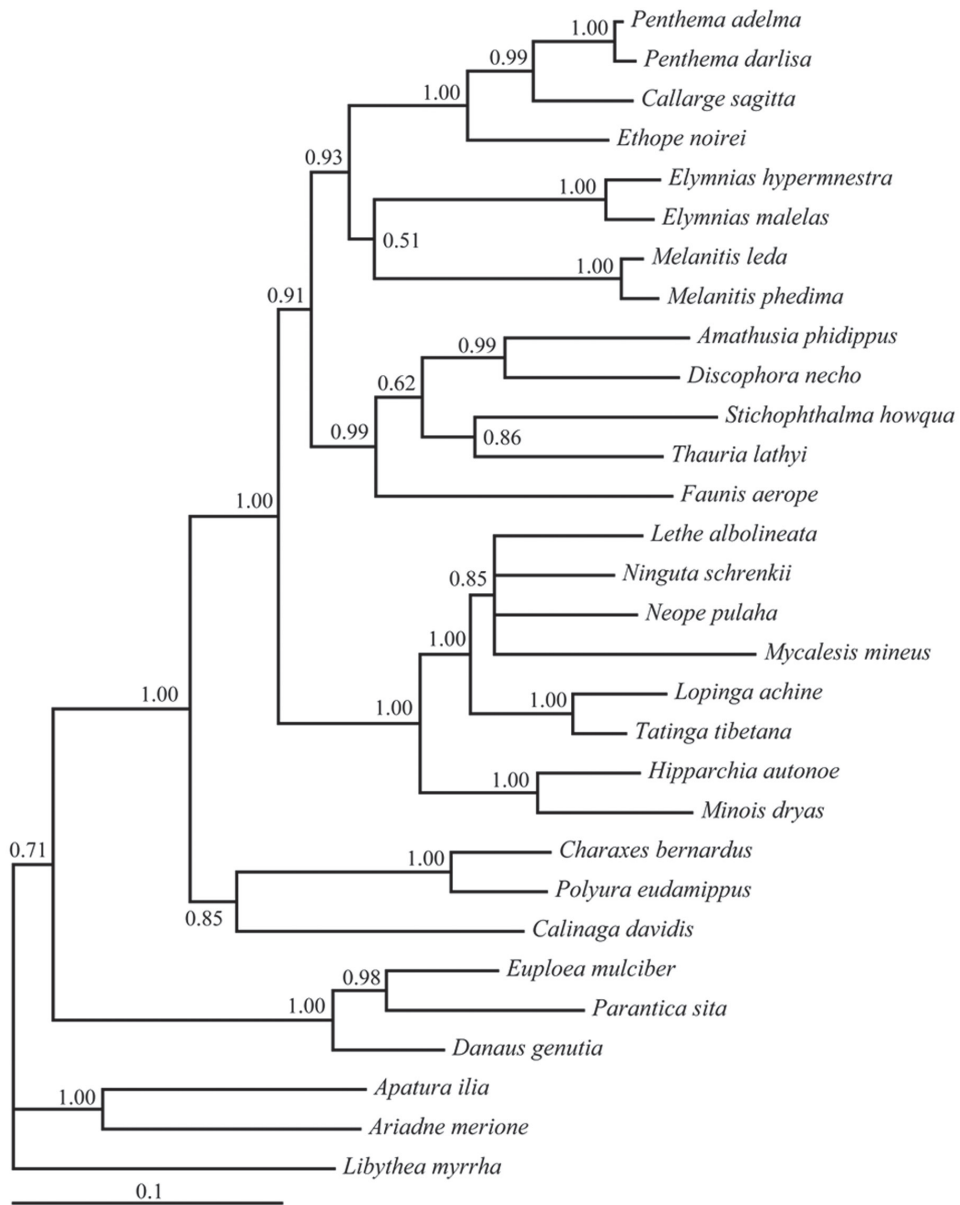


Figure 2. 50% majority-rule trees obtained from Bayesian inference (BI) analyses based on the non-*COI* + *Cytb* + *COII*-3rds-dataset. Numbers on nodes are the posterior probabilities (PP).

The ribosomal 16s and 28s DNA generally show the same phylogenetic informativeness with the 3rd codon positions of *EF-1a*, especially on the zone of tree showing the tribe level relationships of the Satyrinae. The remaining 2nd codon positions of the combined *COI*, *Cytb* and *COII*, the 1st and 2nd codon positions of *EF-1a* show relatively limited phylogenetic signals.

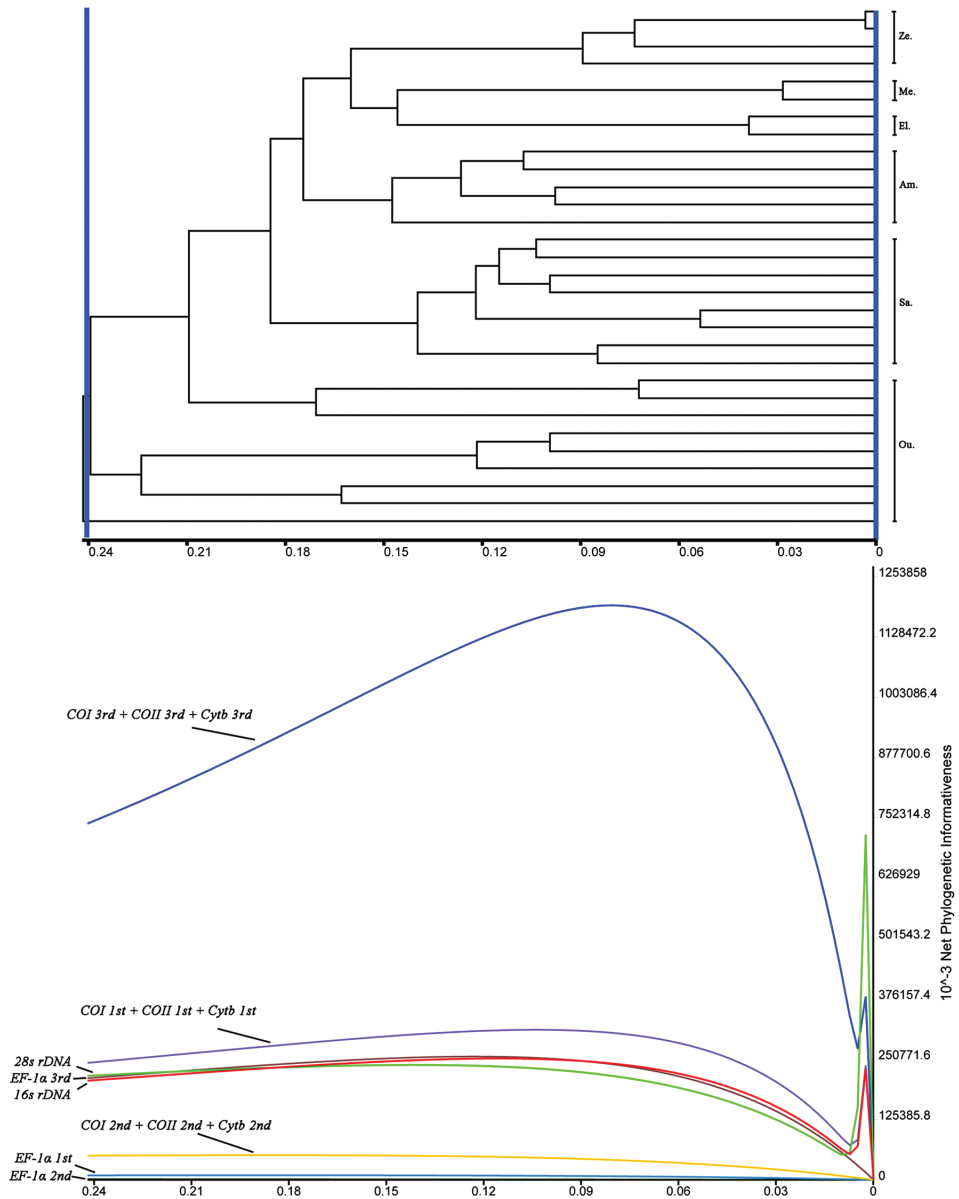


Figure 3. Phylogenetic informative profiles for all subsets used in this study. **Ze.** Zetherini; **El.** Elymniini; **Me.** Melanitini; **Am.** Amathusiini; **Sa.** Satyrini.

Discussion

Phylogenetic informativeness of related genes

The studies of molecular systematics have been increasingly accessible because more genetic markers have been developed with the advances of sequencing technology.

However, how to make informed choice to these markers confuses many systematics (Danforth et al. 2005). In high level systematics of Satyrinae, *EF-1a* was commonly used and proven to be quite informative in all previous studies (Peña et al. 2006; Peña and Wahlberg 2008; Wahlberg et al. 2009). Our results show the two ribosomal genes (i.e. *16s rDNA* and *28s rDNA*) have generally the same phylogenetic informativeness with *EF-1a* (Figure 3), which indicates that the former two genes also contribute well in constructing the tribe level relationships. Moreover, we infer the *28s rDNA* would show better informativeness if the *28s rDNA* sequence data for each sampling taxon had been obtained in this study. The consistency between the *28s rDNA* and *EF-1a* in phylogenetic utility supports the findings of Danforth et al. (2005) who suggested that the nuclear ribosomal and protein-coding genes should be combined in phylogenetic practices after comparing the substitution patterns between them in other groups of insects. The *16s rDNA* have been proven to be informative in high level systematics (e.g. Nazari et al. 2007) and was even recommended as standard marker for insect phylogenetics (Caterino et al. 2000). The high phylogenetic utility of *16s rDNA* examined in this study provides support for these proposals. However, this result does not support that mitochondrial gene datasets should not be applied on the deep divergences due to their substantial variation (Lin and Danforth 2004; Danforth et al. 2005).

We do not recommend the use of the 3rd positions of combined *COI*, *Cytb* and *COII* in high level systematics of Satyrinae, although these sites show higher phylogenetic signals than other partitions (Figure 3). On the one hand, our saturation tests show some sites of the 3rd positions of combined *COI*, *Cytb* and *COII* have suffered substantial saturation. These sites may positively contribute to the tip nodes of trees, but for the nodes after the PI profile peak they may become the source of noise deep in the tree and cause homoplasy (Owen et al. 2014). On the other hand, the deep branch pattern of BI tree (Figure 2) generally not change when excluding the 3rd positions of combined *COI*, *Cytb* and *COII*. This result indicates that the 3rd positions of combined *COI*, *Cytb* and *COII* contribute poorly to the tribe level relationships of the trees based on the full six-gene-dataset.

Phylogenetic relationships among related tribes of Satyrinae

In this study, we present the first use of the ribosomal genes in reconstructing the tribe level relationships of the Satyrinae. The “satyrine” clade consisting of Calinaginae, Charaxinae and Satyrinae defined by Peña and Wahlberg (2008) and Wahlberg et al. (2009) are well-supported by our results. Moreover, monophyly of involved Satyrinae with the Amathusiini included is highly supported by all ML and BI analyses based on multiple outgroup taxa, which confirms, at least partially, the findings of Peña et al. (2006) who noted Satyrinae is monophyletic with inclusion of the tribes Morphini, Brassolini and Amathusiini of Morphinae (*sensu* Ackery et al. 1999) (Peña and Wahlberg 2008; Wahlberg et al. 2009).

Among the five tribes of Satyrinae analyzed, our results recover the Satyrini as the basal lineage with a long-branch split from the rest four tribes, in agreement with the findings of Peña et al. (2006) and Peña and Wahlberg (2008). However, relationships among the remaining four tribes are incongruent with other related studies regardless of the Dirini not included herein. Our results recover their relationships as Amathusiini + (Zetherini + (Elymniini + Melanitini)); whereas other related studies concluded the following relationships: (Elymniini + Melanitini) + (Zetherini + Amathusiini) in both ML and BI analyses of Wahlberg et al. (2009), the Elymniini + Melanitini + Zetherini + Amathusiini in MP analysis of Wahlberg et al. (2009), and the Melanitini + (Zetherini + (Elymniini + Amathusiini)) in BI analysis of Peña and Wahlberg (2008). Although ribosomal genes were used for the first time in our study, and both the ML and BI trees based on the full six-gene-dataset show identical topology, it should be noticed that the nodes in ML analysis describing the tribe level relationships are lowly- or moderately-supported. Therefore, the relationships among the related five tribes recovered herein need further verification based on more sampling taxa.

The monotypic genus *Callarge* is distributed restrictedly in China and on the northern border of Vietnam. Morphologically, this genus has marked black veins and lacks eyespots on wings. It is currently placed in Zetherini of Satyrinae (Chou 1999; Yuan et al. 2008) by the presence of hairless eyes, the wings without striking eyespots, and the forewing with basal part of vein Sc, posterior vein of discal cell and vein 2A not swollen (Chou 1998). For the first time, we verify the status of the genus based on molecular phylogenetic analyses, and reveal that it is sister to the *Penthema* in the present study.

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A genus-level taxonomic review of primitively segmented spiders (Mesothelae, Liphistiidae)

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Abstract

The spider suborder Mesothelae, containing a single extant family Liphistiidae, represents a species-poor and ancient lineage. These are conspicuous spiders that primitively retain a segmented abdomen and appendage-like spinnerets. While their classification history is nearly devoid of phylogenetic hypotheses, we here revise liphistiid genus level taxonomy based on original sampling throughout their Asian range, and on the evidence from a novel molecular phylogeny. By combining morphological and natural history evidence with phylogenetic relationships in the companion paper, we provide strong support for the monophyly of Liphistiidae, and the two subfamilies Liphistiinae and Heptathelinae. While the former only contains *Liphistius* Schiödte, 1849, a genus distributed in Indonesia (Sumatra), Laos, Malaysia, Myanmar, Thailand, we recognize and diagnose seven heptatheline genera, all but three removed from the synonymy of *Heptathela*: i) *Ganthela* Xu & Kuntner, **gen. n.** with the type species *G. yundingensis* Xu, **sp. n.** is known from Fujian and Jiangxi, China; ii) a rediagnosed *Heptathela* Kishida, 1923 is confined to the Japanese islands (Kyushu and Okinawa); iii) *Qionghela* Xu & Kuntner, **gen. n.** with the type species *Q. baishensis* Xu, **sp. n.** is distributed disjunctly in Hainan, China and Vietnam; iv) *Ryuthela* Haupt, 1983 is confined to the Ryukyu archipelago (Japan); v) *Sinothela* Haupt, 2003 inhabits Chinese areas north of Yangtze; vi) *Songthela* Ono, 2000 inhabits southwest China and northern Vietnam; and vii) *Vinathela* Ono, 2000 (*Abcathela* Ono, 2000, **syn. n.**; *Nanthela* Haupt, 2003, **syn. n.**) is known from southeast China and Vietnam.

Keywords

East Asia, Southeast Asia, biogeography, classification, trapdoor spiders, living fossils

Introduction

The only extant family within the spider suborder Mesothelae, the family Liphistiidae consists of only 88 extant species-level taxa currently grouped in three genera, and displays an interesting geographical distribution confined to Southeast and East Asia (World Spider Catalog 2015). Liphistiids are relatively large, extremely long-lived (5–18 years), ground-dwelling spiders that build trapdoor burrows used for prey capture, shelter and protection (Bristowe 1976, Coddington and Levi 1991, Haupt 2003a). Despite being large and morphologically distinct, they are rarely encountered, making it difficult to secure taxonomically meaningful samples. Their natural history also suggests that liphistiids are confined to their burrows and that the spiders rarely move around, and phylogenetic and biogeographic analyses confirm that they are dispersal-limited and highly genetically structured (Xu et al. in press).

Since their discovery (Schödte 1849), much attention has been paid to taxonomy, and most authors (e.g. Schwendinger and Ono 2011) divide Liphistiidae into two distinct subfamilies, Liphistiinae Thorell, 1869 and Heptathelinae Kishida, 1923. Liphistiinae contains a single genus, *Liphistius* Schödte, 1849 with 50 species-level taxa. Their genital morphology is quite distinct from the 38 currently known species of Heptathelinae, the latter including two currently valid genera, *Heptathela* Kishida, 1923 and *Ryuthela* Haupt, 1983 (World Spider Catalog 2015). Liphistiines are also geographically separated from heptathelines, since *Liphistius* occurs in Southeast Asia (Indonesia (Sumatra), Laos, Malaysia, Myanmar, Thailand), whereas the heptathelines *Heptathela* and *Ryuthela* are confined to East Asia (China, Japan and Vietnam), and Japanese Ryukyu Islands, respectively (World Spider Catalog 2015). Non-taxonomic studies of these spiders have focused on genital evolution (Osaki 1969, Kraus 1978, 1984, Haupt 1983, Yin et al. 1983, 1988, Yin 2001), life history (Yoshikura 1954, 1955, Haupt 1979, 1983, 1984, 1986, 1991, 2003a, Platnick and Sedgwick 1984, Schwendinger 1990), prey-capture (Haupt 1979, 1992, 2003a, Chen et al. 1981, Klingel 1967), mating behaviour (Murphy and Platnick 1981; Haupt 1977, 1979, 1983, 1984, 1992, 2003a, Haupt and Traue 1986, Schwendinger 1990), ecology (Murakami 1934, Klingel 1967, Bristowe 1976, Kikuya 1980, 1982, 1994, Schwendinger 1987, 1988, 1990, 1993, Schwendinger and Pape 2000, Haupt 2003a), zoogeography (Paik 1953, Ono 2000, Haupt 2003a, 2003b) and silk biology (Marples 1967, Haupt 1979, 1983, 1991, 1992, 2003a, Küchler 1987, Haupt and Kovoov 1993, Craig 1997, 2003, Vollrath and Selden 2007, Swanson et al. 2009, Starrett et al. 2012).

All existing classification schemes for Mesothelae and Liphistiidae were dominated by a few selected characters and opinion rather than phylogenetic analyses. Schödte (1849) described the first species of the genus *Liphistius* (*Liphistius desultor*) and Thorell (1869) placed it in Liphistioidae (sic). Simon (1903) nominated a new genus

Anadiasthothela, but the species *A. thorelli* was a synonym of *Liphistius sumatranus* Thorell, 1890 (see Bristowe 1932). Kishida (1923) erected a new genus *Heptathela* (based on *Liphistius kimurai* Kishida, 1920), and divided the family Liphistiidae into two subfamilies, Liphistiinae (including the tribes Liphistiiae and Heptatheleae) and Anadiasthothelinae (*Anadiasthothele* Simon, 1903) based on details on spinnerets. In 1939, Petrunkevitch raised *Heptathela* to the family rank (Heptathelidae) to include Japanese and Chinese species. This classification system was retained until Haupt (1983, 1990) proposed dividing the group into three genera and two families (Liphistiidae (*Liphistius*), Heptathelidae (*Heptathela* and *Ryuthela*)). Ono's (2000) scheme treated the groups as two subfamilies: Liphistiinae and Heptathelinae. To *Heptathela* and *Ryuthela*, Ono (2000) added three new heptatheline genera, *Abcathela*, *Songthela* and *Vinathela*, solely based on the female genital morphology. However, Haupt (2003a) continued to prefer his two-family system (Haupt 1984, 1990), rejected *Abcathela* and *Vinathela*, considered *Songthela* as a synonym of *Sinothela* Haupt, 2003, and erected *Nanthela* Haupt, 2003. In the most recent classification scheme of the family, Schwendinger and Ono (2011) rejected all but three genera: *Liphistius* (Liphistiinae), *Heptathela* (Heptathelinae) and *Ryuthela* (Heptathelinae). However, they expressed some doubt at the validity of the genus *Heptathela*, with no fewer than 33 nominal taxa. According to these authors, *Heptathela* may need to be split again if a comprehensive revision and/or phylogeny was to suggest this.

A modern, species-level phylogeny of liphistiid spiders necessary for addressing taxonomic, evolutionary, and biogeographic questions has been long overdue. In a sister paper (Xu et al. in press), we used molecular data from our original extensive sampling to test the monophyly of the family Liphistiidae and the genera within. Based on a species-level multi-locus phylogeny reported in that paper, and on morphological and natural history diagnostic characters provided here, we revise below the higher level systematics of the family.

Materials and methods

In order to secure a comparative sample of these seemingly rare spiders, we sampled liphistiids through China, Japan and Vietnam both at type locations and in areas with suitable habitat. We collected adults and immature spiders by excavating them from their subterranean burrows, then reared juveniles to adulthood in the laboratory. Since we primarily focused on heptathelines (the liphistiids of East Asia), our sample is biased toward China, Japan, and Vietnam (Figure 1).

Specimens were studied using an Olympus SZX16 stereomicroscope, and anatomical details were examined and photographed with Leica M205C stereomicroscope and Olympus BX51 compound microscope. Genitalia were cleared in boiling KOH for a few minutes to dissolve soft tissues. Unless otherwise noted left palps were depicted. All measurements are in millimeters. Leg and palp measurements are given in the following order: total length (femur + patella + tibia + metatarsus + tarsus).



Figure 1. Map showing the sampling localities of liphistiid spider specimens across Southeast and East Asia.

Abbreviations used are: ALE = anterior lateral eyes, AME = anterior median eyes, BK = book lung, BL = body length, CL = carapace length, Co = conductor, CT = contrategulum, CW = carapace width, D = depression, E = embolus, OL = opisthosoma length, OW = opisthosoma width, PC = paracymbium, PLE = posterior lateral eyes, PME = posterior median eyes, PP = poreplate, RC = receptacular cluster, S = spinneret, SE = sternite, ST = sternum, T = tegulum, TG = tergite, TiA = tibial apophysis.

Results

In three years we accumulated 1,455 specimens (786 females, 118 males and 551 juveniles) from 145 localities in China, Japan, Laos, Malaysia and Vietnam. These vouchers, deposited at the Centre for Behavioural Ecology and Evolution (CBEE), College of Life Sciences, Hubei University, Wuhan, China, were the basis for our morphological examinations (reported here) and for molecular analyses (Xu et al. in press). Examined and illustrated specimens were labelled with unique codes (Appendix 1; see also Figure legends), which will be reused in the upcoming genus-level revisions. All designated type specimens were deposited at the National Zoological Museum of China (NZMC), Institute of Zoology, Chinese Academy of Sciences, Beijing, China.

Our trips to chosen sampling points based on the known records were highly successful, and we found heptathelines at most type localities except for *Ryuthela iheyana* from Ihayajima, Japan, *Sinothela sinensis* (Bishop & Crosby, 1932), comb. n. from the type locality, Jinan City, Shandong Province, *Sinothela schensiensis* (Schenkel, 1953), comb. n. from Tongyuan County, Shannxi Province, *Songthela hunanensis* (Song & Haupt, 1984), comb. n. from Qianyang County, Hunan Province, *Songthela yunnanensis* (Song & Haupt, 1984), comb. n. from Kunming, Yunnan Province. We did not sample *Qionghela nui* (Schwendinger & Ono, 2011), comb. n. and *Qionghela australis* (Ono, 2002), comb. n. from Lam Dong Province. Most of the field expeditions into previously unsampled areas in China were also successful. New liphistiid localities include Chongqing, Fujian (Putian, Quanzhou and Xiamen), Guizhou (Chishui and Yanhe), Hainan, Hebei (Yongnian), Hubei (Badong, Enshi, Jianshi, Lichuan and Yichang), Jiangxi (Ji'an), Yunan (Dali, Kunming, Mojiang and Yuanjian), and Shandong (Zhangqiu and Yiyuan) Provinces.

In a concurrent paper (Xu et al. in press), we report on phylogenetic analyses using original five-gene nucleotide data for 75 species. These results, summarized in Figure 2, form the phylogenetic basis for a revised classification of the family. The family and subfamily monophyly were well supported in all phylogenetic analyses (for details, see Xu et al. in press). The current classification of Liphistiidae, based on morphological features, treats as valid three genera (see World Spider Catalog 2015): *Heptathela* s.l., *Liphistius* and *Ryuthela*. Our phylogenetic results strongly support the monophyly of *Liphistius* and *Ryuthela*, but not of *Heptathela* s.l., and thus require substantial taxonomic emendations. Below, we classify the species currently in paraphyletic *Heptathela* s.l. in six genera—the monophyly of each strongly supported (for details, see Xu et al. in press)—of which two are new, describe two new species that become the type for the new genera, and propose further synonymies.

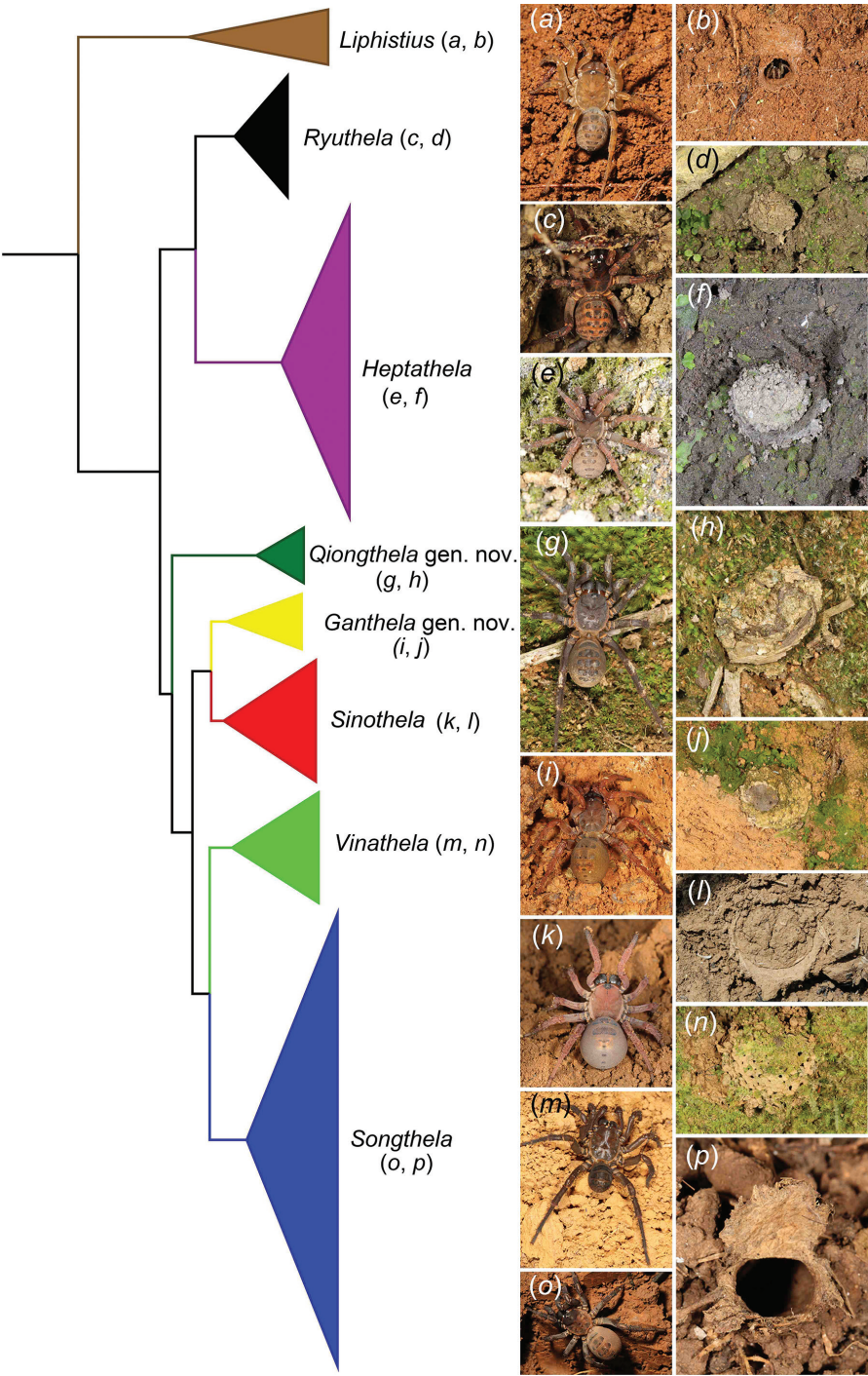


Figure 2. A simplified genus level phylogeny derived from the summary tree in the accompanying paper (Xu et al. submitted), as the basis for newly proposed classification. Images on the right depict typical generic characteristics (female habitus and trapdoor).

Taxonomy

Suborder Mesothelae Pocock, 1892

Phylogenetic definition (for details, see Xu et al. in press). In the analysis of divergence times, we treated Mesothelae as a stem group leading from the root of all spiders to the node-based clade Liphistiidae. Therefore, Mesothelae accommodates the fossil genus *Palaeothele* Selden, 2000, which does not share one of the synapomorphies of Liphistiidae (single row of teeth on cheliceral fang groove). Although the morphological diagnosis resembles that of Liphistiidae, Mesothelae is inclusive of Liphistiidae but the two groups are phylogenetically not identical.

Composition. Mesothelae includes the crown group Liphistiidae with extant species from East and Southeast Asia, and the fossil *Palaeothele montceauensis* (Selden 1996a, b) from the Upper Carboniferous of Montceau-les-Mines, France around 295 Ma.

Family Liphistiidae Thorell, 1869

Diagnosis. Unlike all other extant spiders, Liphistiidae possess tergites on all abdominal segments (Figure 3), their spinnerets are located in the middle of abdominal venter (Figure 4), and in addition to a narrow sternum they also possess another narrow ventral plate, the sternite, located adjacent to coxae IV (Figure 4).

Description. Medium to large sized ground dwelling and burrowing spiders, chelicerae with a single row of teeth, two pairs of book lungs (Figure 4), tibial spurs specialized as sense organs. Their ground burrows are closed with trapdoors, with or without additional concentric signal lines (Figure 2b, d, f, h, j, l, n, p).

Composition. *Ganthela* Xu & Kuntner, gen. n., *Heptathela* Kishida, 1923, *Liphistius* Schiödte, 1849, *Qionghela* Xu & Kuntner, gen. n., *Ryuthela* Haupt, 1983, *Sinothela* Haupt, 2003a, *Songthela* Ono, 2000, and *Vinathela* Ono, 2000.

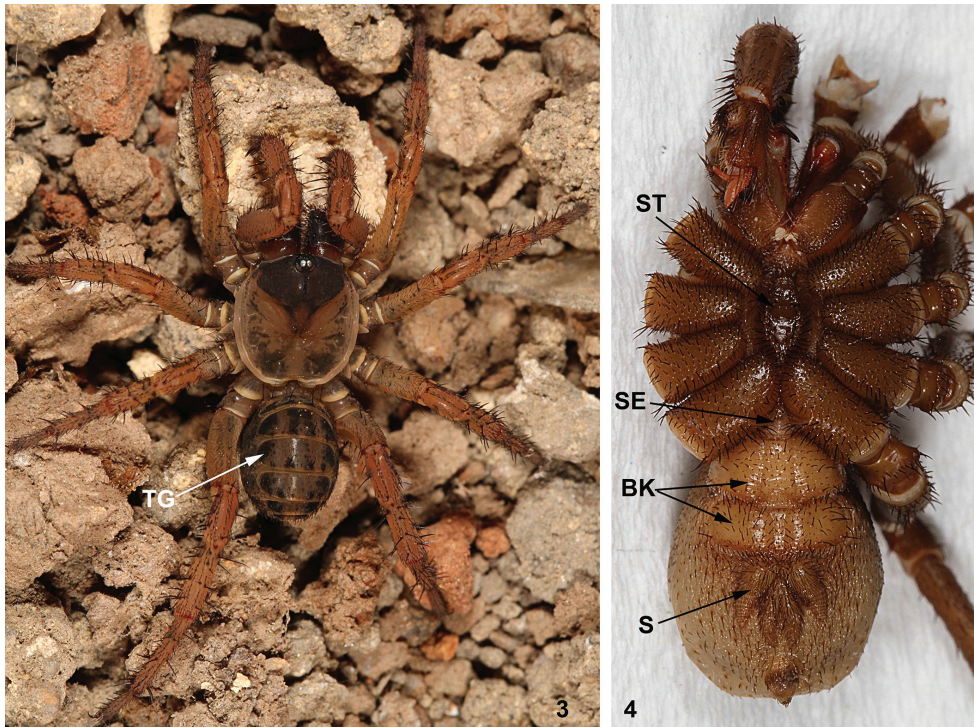
Distribution. China, Indonesia (Sumatra), Japan, Laos, Malaysia, Myanmar, Thailand and Vietnam.

Subfamily Liphistiinae Thorell, 1869

Diagnosis. In contrast to the members of the subfamily Heptathelinae, Liphistiinae spiders construct signal lines radiating from the burrow entrance (Figure 2b), the male palp possesses a tibial apophysis (Figures 5–7), and the female genitals have a poreplate and unpaired receptacular clusters (Figures 8–9). Platnick and Sedgwick (1984) also report the unique presence of clavate trichobothria on the tarsi and metatarsi of all legs and on the palpal tarsi.

Composition. *Liphistius* Schiödte, 1849.

Distribution. Indonesia (Sumatra), Laos, Malaysia, Myanmar, Thailand.



Figures 3–4. General somatic morphology of Liphistiidae. **3** Female *Heptathela yanbaruensis* Haupt, 1983 (XUX-2014–038A) **4** Male *Qionghela baishensis* sp. n. (XUX-2012–087). BK = book lung, S = spinneret, SE = sternite, ST = sternum, TG = tergite.

Genus *Liphistius* Schiödte, 1849

Figures 5–9

Liphistius Schiödte, 1849, type species *Liphistius desultor* Schiödte, 1849, P. 621.

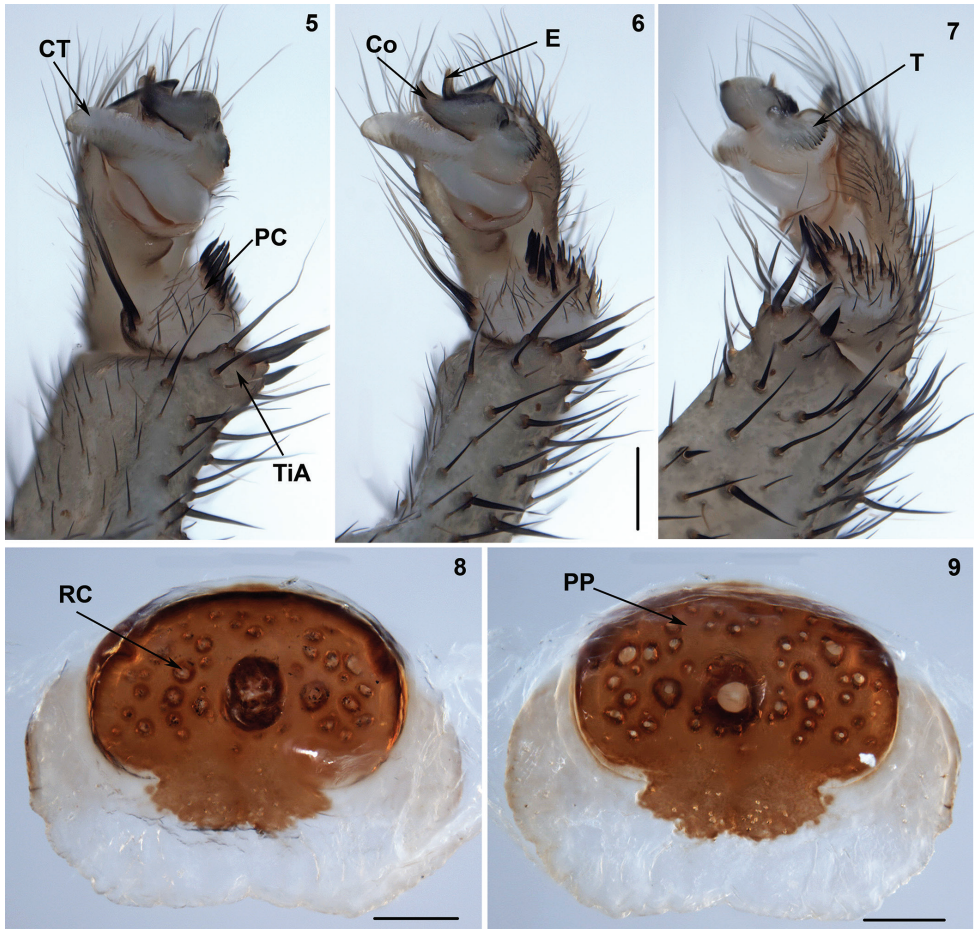
Anadiastothele Simon, 1903, type species by original designation *Anadiastothele thorelli*

Simon, 1903 = *Liphistius sumatranus* Thorell, 1890, P. 875; first synonymised by Bristowe, 1932, P. 1022.

Diagnosis. See Liphistiinae.

Description. Total length (excluding chelicerae) = 9–37 mm (Platnick and Sedgwick 1984); male palp with retrolateral tibial apophysis bearing strong apical spines and with a spinose paracymbium; female genitalia with a poreplate and unpaired receptacular clusters.

Species composition. *Liphistius albipes* Schwendinger, 1995; *L. batuensis* Abraham, 1923; *L. bicoloripes* Ono, 1988; *L. birmanicus* Thorell, 1897; *L. bristowei* Platnick & Sedgwick, 1984; *L. castaneus* Schwendinger, 1995; *L. dangrek* Schwendinger, 1996; *L. desultor* Schiödte, 1849; *L. endau* Sedgwick & Platnick, 1987; *L. erawan* Schwendinger, 1996; *L. fuscus* Schwendinger, 1995; *L. isan* Schwendinger, 1998;



Figures 5–9. Male (XUX-2013–267) and female (XUX-2013–256) genital anatomy of *Liphistius laoticus* Schwendinger, 2013. **5** palp prolateral view **6** palp ventral view **7** palp retrolateral view **8** vulva ventral view **9** vulva dorsal view. Scales **3–5**: 0.5 mm, **6–7**: 0.1 mm. Co = conductor, CT = contrategulum, E = embolus, PC = paracymbium, PP = poreplate, RC = receptacular cluster, T = tegulum, TiA = tibial apophysis.

L. jarujini Ono, 1988; *L. johore* Platnick & Sedgwick, 1984; *L. kanthan* Platnick, 1997; *L. lahu* Schwendinger, 1998; *L. langkawi* Platnick & Sedgwick, 1984; *L. lannaianus* Schwendinger, 1990; *L. laoticus* Schwendinger, 2013; *L. laruticus* Schwendinger, 1997; *L. lordae* Platnick & Sedgwick, 1984; *L. malayanus* Abraham, 1923; *L. malayanus cameroni* Haupt, 1983; *L. marginatus* Schwendinger, 1990; *L. murphyorum* Platnick & Sedgwick, 1984; *L. nesioticus* Schwendinger, 1996; *L. niphanae* Ono, 1988; *L. ochraceus* Ono & Schwendinger, 1990; *L. onoi* Schwendinger, 1996; *L. ornatus* Ono & Schwendinger, 1990; *L. owadai* Ono & Schwendinger, 1990; *L. panching* Platnick & Sedgwick, 1984; *L. phileion* Schwendinger, 1998; *L. phuketensis* Schwendinger, 1998; *L. pusohm* Schwendinger, 1996; *L. rufipes* Schwendinger, 1995; *L. sayam* Schwendinger, 1998; *L. schwendingeri* Ono, 1988; *L. sumatranus* Thorell, 1890;

L. suwat Schwendinger, 1996; *L. tempurung* Platnick, 1997; *L. tenuis* Schwendinger, 1996; *L. thaleban* Schwendinger, 1990; *L. thaleri* Schwendinger, 2009; *L. tham* Sedgwick & Schwendinger, 1990; *L. thoranie* Schwendinger, 1996; *L. tioman* Platnick & Sedgwick, 1984; *L. trang* Platnick & Sedgwick, 1984; *L. yamasakii* Ono, 1988; *L. yangae* Platnick & Sedgwick, 1984.

Distribution. Indonesia (Sumatra), Laos, Malaysia, Myanmar, Thailand.

Remarks. *Liphistius* always possess eight spinnerets, unlike all the remaining liphistiid genera in which the number is variable (either seven or eight). Therefore, the number of spinnerets is not a criterion for discriminating genera and species (Haupt 1983).

Subfamily Heptathelinae Kishida, 1923

Diagnosis. In contrast to the members of the subfamily Liphistiinae, the representatives of Heptathelinae lack signal lines radiating from the burrow entrance (Figure 2d, f, h, j, l, n, p), the male palp lacks a tibial apophysis (Figures 10–12, 15–17, 20–22, 26–28, 31–33, 36–38, 41–43), and the female genitals have paired or unpaired receptacular clusters on the bursa copulatrix with or without stalks (Figures 13–14, 18–19, 25, 34–35, 39–40, 44–45).

Composition. *Ganthela* Xu & Kuntner, gen. n., *Heptathela* Kishida, 1923, *Qionghela* Xu & Kuntner, gen. n., *Ryuthela* Haupt, 1983, *Sinothela* Haupt, 2003a, *Songthela* Ono, 2000, and *Vinathela* Ono, 2000.

Distribution. China, Japan and Vietnam.

Genus *Ganthela* Xu & Kuntner, gen. n.

<http://zoobank.org/F70E24D5-C13B-4195-825C-A69A684AB893>

Figures 10–14

Liphistius: Wang 1989, P. 30, description of *Liphistius cipingensis* (= *Ganthela cipingensis*).

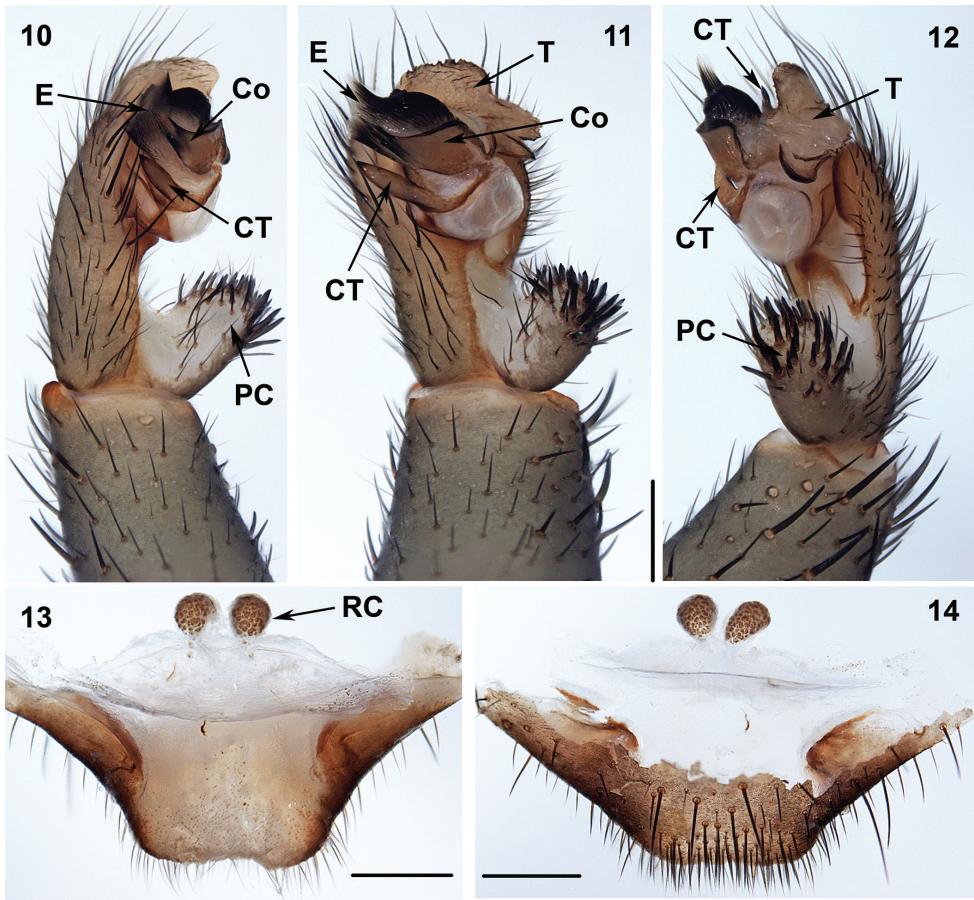
Songthela: Ono 2000, P. 150, transferred *Liphistius cipingensis* to *Songthela cipingensis* (= *Ganthela cipingensis*).

Heptathela: Platnick 1993, P. 77, transferred *Liphistius cipingensis* to *Heptathela cipingensis* (= *Ganthela cipingensis*).

Type species. *Ganthela yundingensis* sp. n.

Etymology. The genera of heptathelines contain in their name the word ‘thela’ referring to spinnerets as the Greek word *thele* means nipple-like protuberance (Ono 2000). We continue this tradition, but name the genus to start with Gan-, which refers to Jiangxi Province.

Diagnosis. Males of *Ganthela* differs from all other Heptathelinae genera by a smooth conductor with a distal spiniform apex (Figures 10–11), a flat opening embolus and scale-like contrategulum (Figures 10–11), females can be identified by a single pair of similar receptacular clusters (Figures 13–14).



Figures 10–14. Male (XUX-2013–136) and female (XUX-2013–135) genital anatomy of *Ganthela yundingensis* sp. n. **10** palp prolateral view **11** palp ventral view **12** palp retrolateral view **13** vulva dorsal view **14** vulva ventral view. Scales 0.5 mm. RC = receptacular cluster.

Description. Total length (excluding chelicerae) = 8–15 mm (N = 35); male palpal conductor smooth, wide, leaf-shaped, with a spiniform apex (Figures 10–11); spinose paracymbium relative short (Figures 10, 12); embolus with a flat opening (Figures 10–11); contrategulum scale-like with a smooth margin (Figures 10–11); female genitalia with paired receptacular clusters of similar size, situated at the anterior margin of the bursa copulatrix with tubular stems (Figures 13–14).

Species composition. *Ganthela cipingensis* (Wang, 1989), comb. n. (7♀), male is unknown, *Ganthela yundingensis* Xu, sp. n. (1♂1♀), one undescribed species from Jiangxi Province, China (11♀), and four undescribed species from Fujian Province, China (1♀, 1♂11♀, 1♀, and 3♀, respectively).

Distribution. China (Fujian, Jiangxi).

Remarks. Wang (1989) placed *G. cipingensis* in *Liphistius* based on the presence of eight spinnerets. Our collections from the type locality contain specimens with seven spinnerets. The number of spinnerets thus varies intraspecifically.

***Ganthela yundingensis* Xu, sp. n.**

<http://zoobank.org/4F54A057-613A-4E8E-ADB4-B1B0AA0BB579>

Figures 10–14

Types. Male holotype (XUX-2013–136) and female paratype from Mt. Yunding, Tingxi Town, Tong'an District, Xiamen City, Fujian Province, China; 24.87°N, 118.16°E, 631 m; 8 July 2013; collected by F. Liu, X. Xu and Z. Zhang, deposited at NZMC, Institute of Zoology, Chinese Academy of Sciences, Beijing, China.

Etymology. 'Yunding' refers to the type locality of this species, Mt. Yunding.

Diagnosis. Females can be distinguished from *G. cipingensis* and the five undescribed *Ganthela* species we are aware of by lacking genital stalks (Figures 13–14), and the males, uniquely among heptathelines, possess the contrategulum with two marginal apophyses (Figures 11–12), the prolateral one being scale-like (Figure 11).

Description. Male (holotype). Carapace and opisthosoma light brown; tergites dark brown; sternum narrow, twice as long as wide; a few long pointed hairs running over ocular mound in a longitudinal row; chelicerae robust with promargin of cheliceral groove with 10 denticles of variable size; legs with strong hairs and spines; opisthosoma with 12 tergites, the first 2–5 larger than others and the fourth largest, the first four close to each other; 7 spinnerets. Measurements: BL 9.80, CL 4.48, CW 4.03, OL 4.98, OW 3.75; ALE > PLE > PME > AME; leg I 13.60 (4.03 + 1.48 + 2.90 + 3.41 + 1.78), leg II 13.80 (3.81 + 1.70 + 2.91 + 3.48 + 1.90), leg III 16.01 (4.02 + 1.71 + 3.28 + 4.58 + 2.42), leg IV 20.60 (5.20 + 1.89 + 3.90 + 6.50 + 3.11).

Palp: Cymbium with a projection; prolateral side of paracymbium unpigmented and unsclerotised, numerous setae and spines at the tip of paracymbium (Figures 10–12). Contrategulum has two marginal apophyses, the first one scale-like with a smooth margin (Figures 10–11). Tegulum with a dentate edge (Figures 11–12). Conductor wide leaf-shaped, with spiniform apex, parallel to embolus (Figures 10–11). Embolus largely sclerotized, with a flat opening (Figures 10–11).

Female. Colouration of carapace and opisthosoma as in male; chelicerae robust with promargin of cheliceral groove with 12 strong denticles of variable size; legs with strong hairs and spines; opisthosoma with 12 tergites, as in male; 7 spinnerets. Measurements: BL 13.23, CL 5.96, CW 5.18, OL 7.28, OW 4.90; ALE > PLE > PME > AME; palp 9.64 (3.26 + 1.61 + 2.15 + 2.62), leg I 11.46 (3.33 + 2.08 + 2.17 + 2.30 + 1.58), leg II 11.82 (3.56 + 2.11 + 2.13 + 2.42 + 1.60), leg III 13.18 (3.71 + 2.20 + 2.33 + 3.02 + 1.92), leg IV 17.59 (4.03 + 2.40 + 3.30 + 5.19 + 2.67).

Female genitalia: The posterior part of the genital area rectangular (Figure 13–14), a pair of receptacular clusters close to each other, without stalks (Figures 13–14).

Genus *Heptathela* Kishida, 1923

Figures 15–21

Heptathela Kishida, 1923, type species *Liphistius kimurai* Kishida, 1920, P. 235.

Diagnosis. *Heptathela* males differ from all other Heptathelinae genera by a leaf-shaped conductor (Figures 18–19), a thumb-shaped embolus (Figures 15, 18) and a wide tegulum with a rugate margin (Figures 16, 18–19). *Heptathela* females can be distinguished from all other Heptathelinae genera by a single paired depression on the ventro-lateral part of genital atrium (Figure 20), and by the one pair of main receptacular cluster and secondary, lateral, irregular receptacular clusters (Figures 20–21).

Description. Total length (excluding chelicerae) = 7–17 mm (N = 229); male palp with a leaf-shaped conductor with spiniform apex or dentate edge, rugate (Figures 18–19); spinose paracymbium long, nearly the length of the cymbium (Figures 15–16); embolus thumb-shape (Figures 15, 18); tegulum wide, with a rugate margin (Figures 16, 18–19); female genitalia with a paired depression on the ventro-lateral part of the genital atrium (Figure 20); with a pair of main receptacular cluster at the anterior margin of the bursa copulatrix and separated from each other, and with secondary, lateral, irregular receptacular clusters (Figures 20–21).

Species composition. *Heptathela amamiensis* Haupt, 1983; *H. higoensis* Haupt, 1983; *H. kanenoi* Ono, 1996; *H. kikuyai* Ono, 1998; *H. kimurai* (Kishida, 1920); *H. nishikawai* Ono, 1998; *H. yaginumai* Ono, 1998; *H. yakushimaensis* Ono, 1998; *H. yanbaruensis* Haupt, 1983.

Distribution. Japan (Kyushu and Okinawa).

Genus *Qionghela* Xu & Kuntner, gen. n.

<http://zoobank.org/BA103085-F5FB-4DF1-81C7-CA5CDE26E65E>

Figures 22–27

Type species. *Qionghela baishensis* sp. n.

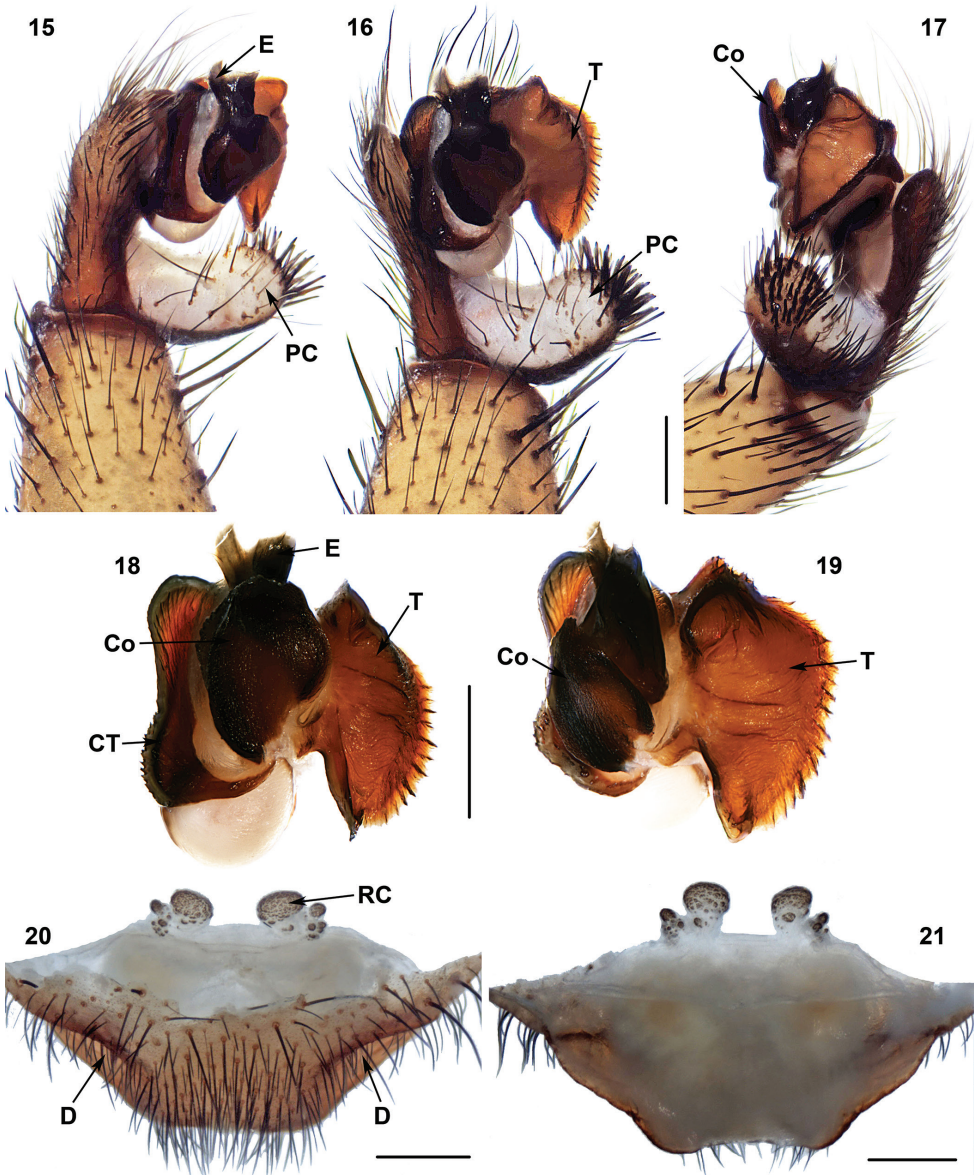
Etymology. The genera of heptathelines contain in their name the word ‘thela’ referring to spinnerets as the Greek word *thele* means nipple-like protuberance (Ono 2000). We continue this tradition, but name the genus to start with Qiong-, referring to Hainan Province, China.

Diagnosis. *Qionghela* males differ from all other Heptathelinae genera by the conductor with a narrow, blade-like, slightly hooked apex (Figures 22, 25–26), and by tegulum with two apophyses (Figures 23, 25–26). *Qionghela* females can be distinguished from all other Heptathelinae by two paired receptacular clusters located at the anterior margin of the bursa copulatrix (Figure 27).

Description. Total length (excluding chelicerae) = 13–31 mm (N = 14); male palp with a distally free conductor, narrow, blade-like with slightly hook-like apex, (Figures 22, 25–26); tegulum with two margins, spinose paracymbium (Figures 23, 25–26); female genitalia with two paired receptacular clusters, all situated at the anterior margin of the bursa copulatrix with more or less distinct tubular stems (Figure 27).

Species composition. *Q. australis* (Ono, 2002), comb. n., *Q. nui* (Schwendinger & Ono, 2011), comb. n., *Q. baishensis* sp. n. (3♂2♀), and three undescribed species (6♂8♀, 1♀ and 1♂1♀, respectively) from Hainan, China.

Distribution. Hainan (China) and Vietnam.



Figures 15–21. Male (XUX-2013–389) and female (XUX-2013–351) genital anatomy of *Heptathela higoensis* Haupt, 1983 and *Heptathela kimurai* (Kishida, 1920), respectively. **15** palp prolateral view **16** palp ventral view **17** palp retrolateral view **18** contrategulum, conductor and embolus, ventral view **19** contrategulum, conductor and embolus, retrolateral view **20** vulva ventral view **21** vulva dorsal view; Scales 0.5 mm. D = depression.

Remarks. Based on morphological descriptions, but not on phylogenetic analyses, we include two species from Vietnam in this genus, originally described as *Songthela australis* Ono, 2002 and *Heptathela nui* Schwendinger & Ono, 2011.

***Qionghela baishensis* Xu, sp. n.**

<http://zoobank.org/5C0F3DB2-3A07-4FC6-83B5-3E286F1493F1>

Figures 22–27

Types. Male holotype (XUX-2012–087, matured 10 October 2012 at CBEE, College of Life Sciences, Hubei University) and two male and two female paratypes from Nangaoing Forest Plantation, Baisha County, Hainan Province, China; 19.24°N, 109.38°E, 463 m, collected 18 July 2012 by D. Li, F. Liu and X. Xu, deposited at NZMC, Institute of Zoology, Chinese Academy of Sciences, Beijing, China.

Etymology. The species epithet refers to Baisha, the species type locality.

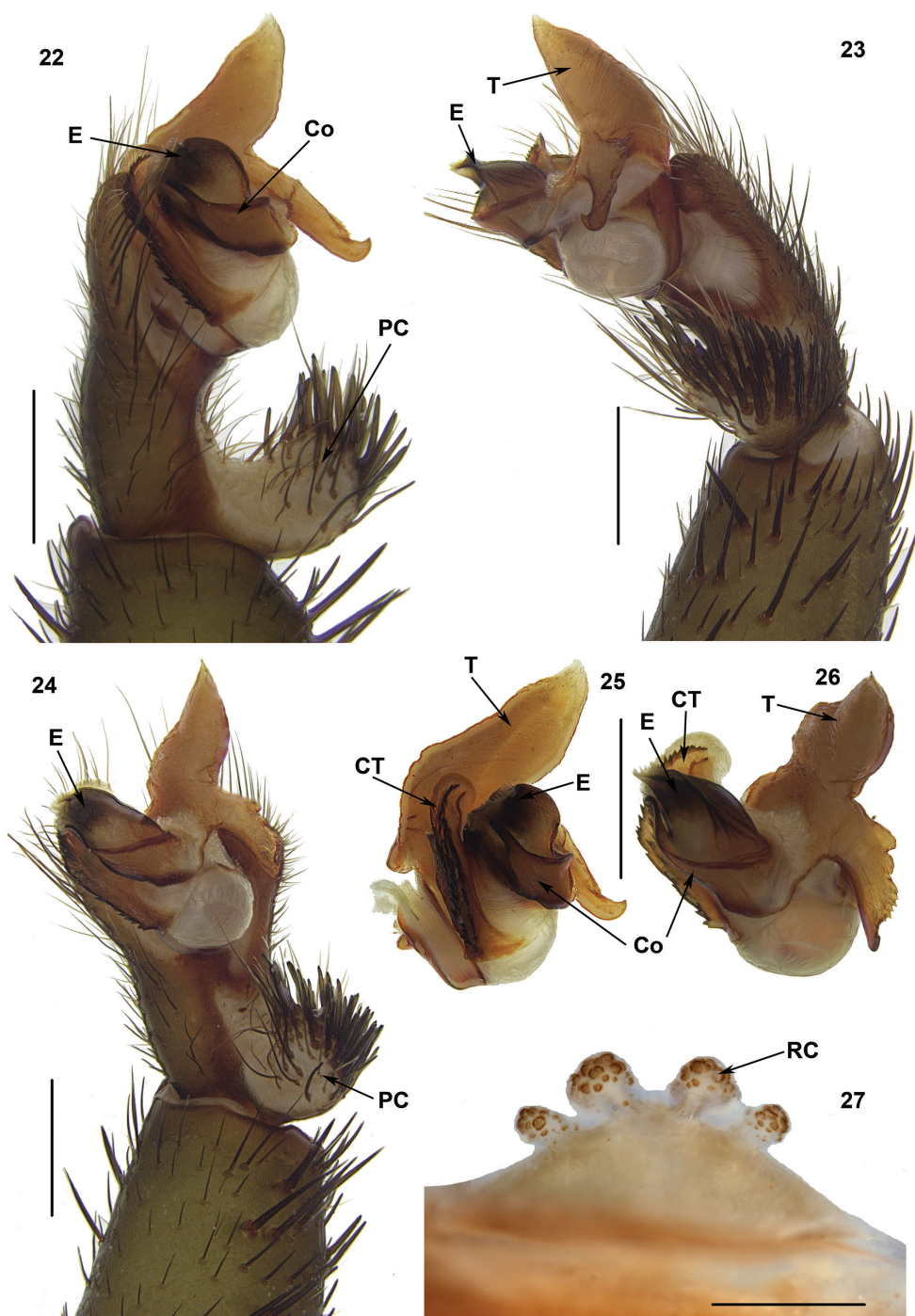
Diagnosis. Unlike other *Qionghela* species, males of *Q. baishensis* possess three parallel serrated distal edges of the contrategulum (Figures 25, 26), and females have two pairs of receptacular clusters, the median pair larger than the lateral one, with very short or no stalks (Figure 27).

Description. Male (holotype). Carapace and opisthosoma light brown; tergites darker; with a clear fovea; sternum narrow, nearly twice as long as wide; a few long pointed hairs running over ocular mound in a longitudinal row; chelicerae robust with promargin of cheliceral groove containing 10 denticles of variable size; legs with strong hairs and spines; opisthosoma with 12 tergites, the first 2–7 distinctly larger and the fifth largest; 7 spinnerets. Measurements: BL 16.75, CL 6.70, CW 6.65, OL 9.90, OW 7.45; ALE > PLE > PME > AME; leg I 19.76 (6.15 + 2.55 + 4.35 + 4.35 + 2.36), leg II 20.70 (5.59 + 2.67 + 4.24 + 5.45 + 2.75), leg III 21.16 (5.25 + 2.13 + 4.12 + 6.45 + 3.21), leg IV 26.03 (7.38 + 2.75 + 5.78 + 7.05 + 3.07).

Palp: Cymbium with a projection; prolateral side of paracymbium unpigmented and unsclerotised, numerous setae and spines at the tip of paracymbium (Figures 22, 24). Contrategulum with three parallel distal edges, row of denticles on inner edge running down to ventro-proximal margin of contrategulum and the outer row forming a sharp edge without denticles (Figures 22, 25–26). Tegulum with a very long, wide base, pointed, distally directed marginal apophysis with a sharp edge, and retrolaterally with a proximally directed terminal apophysis with a slightly short dentate row and continuously narrowing to a rounded, hooked apex (Figures 22–26). Conductor situated ventro-proximally on embolus, with a bent apex (Figures 22, 25–26). Embolus largely sclerotised, prolaterally with numerous longitudinal ribs (Figures 22–26).

Female (paratype). Colouration as in male; promargin of robust chelicerae with 9 strong denticles variable in size; legs and opisthosoma as in the male; 7 spinnerets. Measurements: BL 13.30–14.15, CL 4.51–6.23, CW 4.63–5.82, OL 7.20–7.45, OW 4.33–5.08; ALE > PLE > PME > AME; palp 10.25 (3.65 + 1.55 + 2.30 + 2.75), leg I 12.48 (4.25 + 1.95 + 2.53 + 2.55 + 1.20), leg II 12.15 (3.75 + 2.07 + 2.25 + 2.65 + 1.43), leg III 12.42 (3.55 + 2.12 + 2.03 + 3.07 + 1.65), leg IV 19.20 (5.45 + 2.65 + 3.45 + 5.10 + 2.55).

Female genitalia: Two pairs of receptacular clusters along the anterior margin of bursa copulatrix, the median pair larger than the lateral one, with very short or no stalks (Figure 27).



Figures 22–27. Male (XUX-2012–087) and female (XUX-2012–086) genital anatomy of *Qionghela baishensis* sp. n. 22 palp prolateral view 23 palp retrolateral view 24 palp ventral view 25–26 contrategulum, conductor and embolus, distal view 27 vulva dorsal view. Scales 18–20: 1 mm, 21–23: 0.5 mm.

Genus *Ryuthela* Haupt, 1983

Figures 28–34

Ryuthela Haupt, 1983, type species *Heptathela nishihirai* Haupt, 1979, P. 286.

Diagnosis. *Ryuthela* males differ from all other Heptathelinae genera by lacking the conductor and by the contrategulum with an elongate spine (Figures 28, 30). The females differ from *Heptathela*, *Qionghela*, *Sinothela*, *Songthela* and *Vinathela* by one paired receptacular cluster close to each other (Figures 31–32), located at the anterior margin of the bursa copulatrix, and from *Ganthela* by receptacular clusters without stems that may or may not be fused (Figures 31–34).

Description. Total length (excluding chelicerae) = 7–15 mm (N = 151); male palp with denticulate contrategulum and ventral portion with an elongate spine (Figures 28, 30); spinose paracymbium relatively short (Figures 28–30); female genitalia usually with one paired receptacular clusters, except in some specimens, notably in *R. sasakii*, where receptacular clusters are unpaired and without stalks (Figures 31–34).

Species composition. *Ryuthela iheyana* Ono, 2002; *R. ishigakiensis* Haupt, 1983; *R. nishihirai* (Haupt, 1979); *R. sasakii* Ono, 1997; *R. tanikawai* Ono, 1997.

Distribution. Ryukyu Island (Japan).

Remarks. In *Ryuthela*, female genital anatomy shows considerable intraspecific variation, therefore the structure of the male palp appears more reliable for diagnostics and identification.

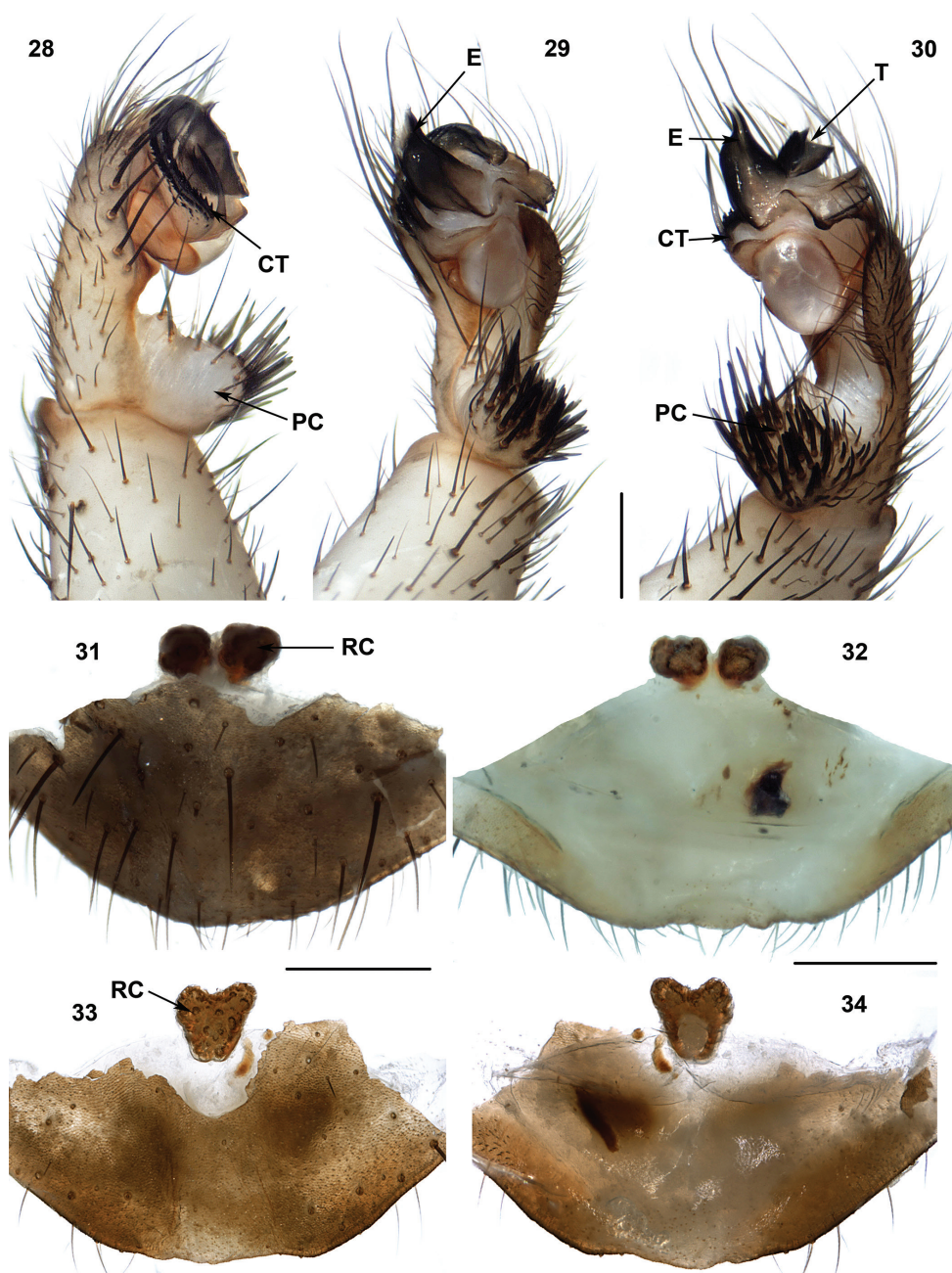
Genus *Sinothela* Haupt, 2003

Figures 35–39

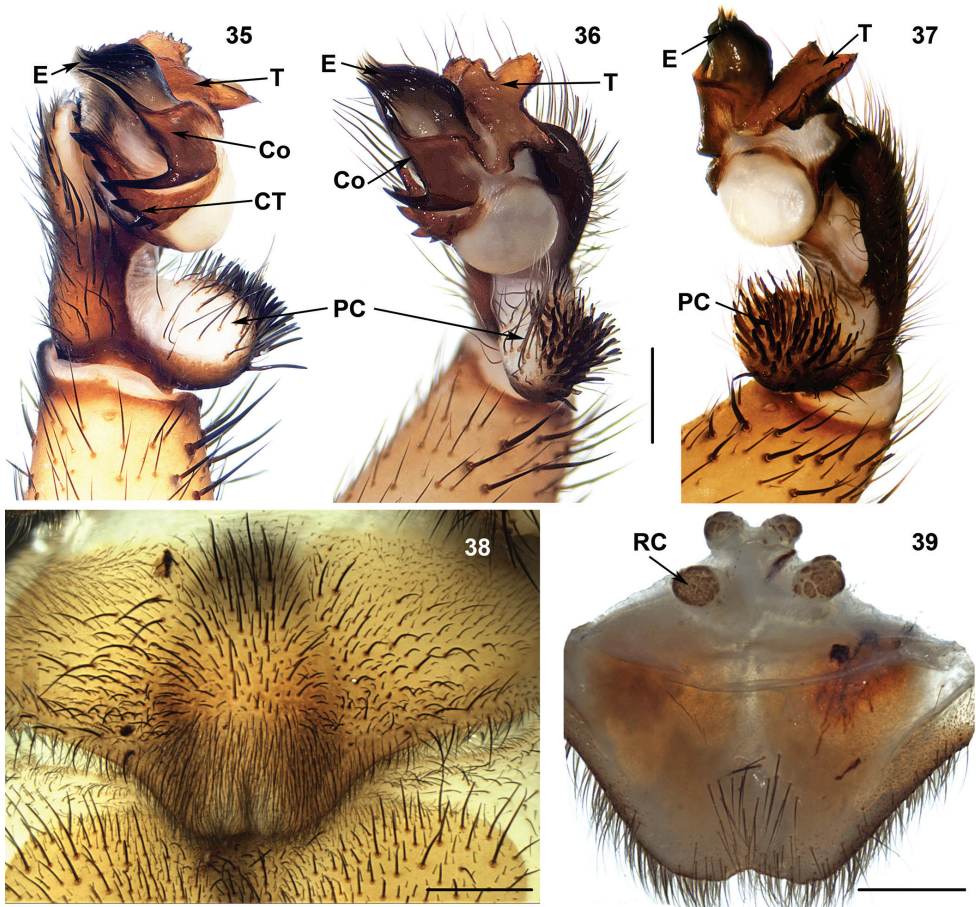
Sinothela Haupt, 2003a, type species *Heptathela sinensis* Bishop & Crosby, 1932; synonymized with *Songthela* by Platnick, 2011; synonymized with *Heptathela* by Schwendinger & Ono, 2011, P. 601. Herein removed from synonymy of *Heptathela*.

Diagnosis. *Sinothela* males differ from all other Heptathelinae genera by the conductor with a smooth surface, its proximal portion being fairly wide, and its distal portion with more than one apical spine (Figures 35–36), and by the contrategulum with large serrations (Figure 35). *Sinothela* females differ from all other Heptathelinae genera by two paired receptacular clusters with the median pair close to each other situated at the basal bursa copulatrix with tubular stem, lateral ones situated on dorsal side (Figure 39).

Description. Total length (excluding chelicerae) = 13–28 mm (N = 71); male palpal conductor smooth, proximally fairly wide, distally with more than one spine tip (Figures 35–36); contrategulum with a serrated edge (Figure 35); tegulum with three apophyses (Figures 35–37); spinose paracymbium relatively short (Figures 35–37);



Figures 28–34. Male (XUX-2013–228) and female (**31–32** XUX-2012–302 and **33–34** XUX-2012–364) genital anatomy of *Ryuthela ishigakiensis* Haupt, 1983, *Ryuthela nishihirai* (Haupt, 1979), and *Ryuthela sasakii* Ono, 1997, respectively. **28** palp prolateral view **29** palp ventral view **30** palp retrolateral view **31, 33** vulva ventral view **32, 34** vulva dorsal view. Scales 0.5 mm.

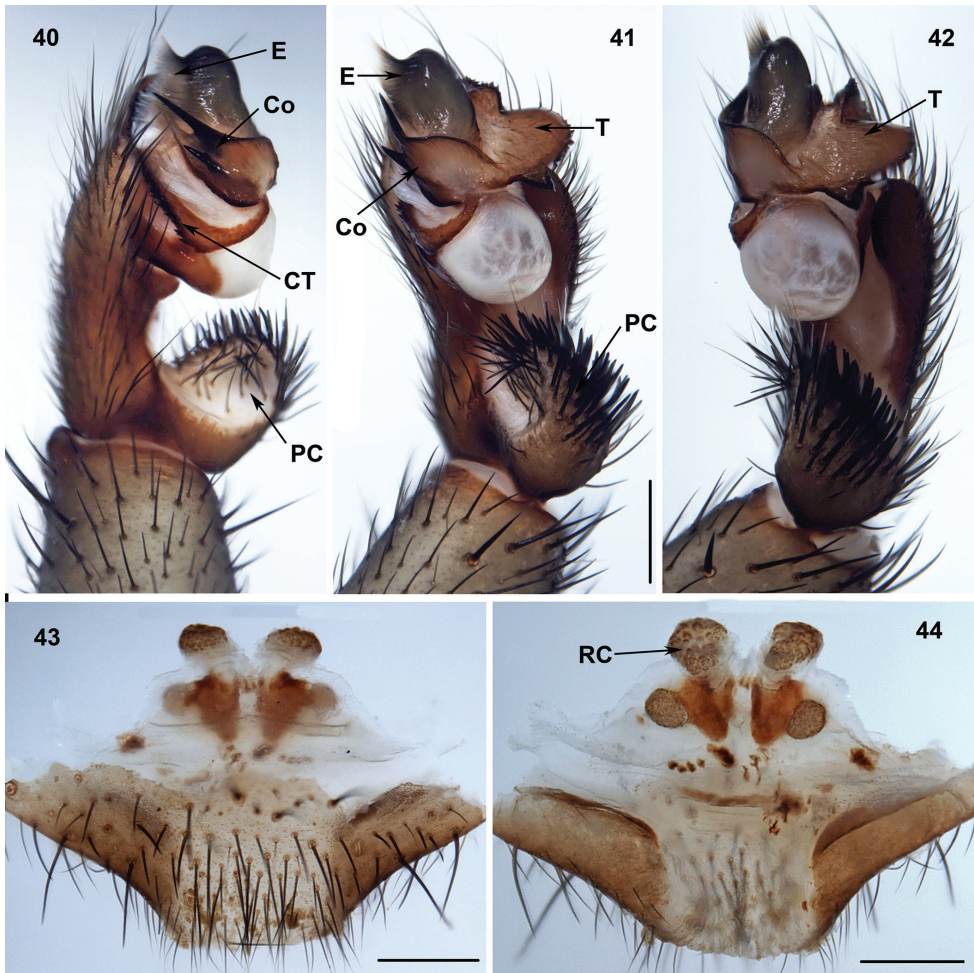


Figures 35–39. Male (XUX-2012–045) and female (XUX-2012–035) genital anatomy of *Sinothela sinensis* (Bishop & Crosby, 1932), comb. n. **35** palp prolateral view **36** palp ventral view **37** palp retro-lateral view **38** vulva ventral view **39** vulva dorsal view. Scales 0.5 mm.

female genitalia with two paired receptacular clusters, median pair close to each other situated at the basal bursa copulatrix with tubular stem, lateral ones situated more dorsally (Figure 39).

Species composition. *Sinothela heyangensis* (Zhu & Wang, 1984), comb. n. (8♂25♀; male previously unknown), *S. luotianensis* (Yin et al., 2002), comb. n. (3♀), *S. schensiensis* (Schenkel, 1953), comb. n., *S. sinensis* (Bishop & Crosby, 1932), comb. n. (2♂9♀).

Distribution. China north of Yangzi River (Hebei, Henan, Hubei, Shandong, Shaanxi, and Shanxi).



Figures 40–44. Male (XUX-2013–175) and female (XUX-2013–170) genital anatomy of *Songthela hangzhouensis* (Chen, Zhang & Zhu, 1981), comb. n. **40** palp prolateral view **41** palp ventral view **42** palp retrolateral view **43** vulva ventral view **44** vulva dorsal view. Scales 0.5 mm.

Genus *Songthela* Ono, 2000

Figures 40–48

Songthela Ono, 2000, type species *Heptathela hangzhouensis* Chen, Zhang & Zhu, 1981; synonymized with *Sinothela* by Haupt, 2003a, P. 71; synonymized with *Heptathela* by Schwendinger & Ono, 2011, P. 601. Herein removed from synonymy of *Heptathela*.

Type species. *Heptathela hangzhouensis* Chen, Zhang & Zhu, 1981.

Diagnosis. *Songthela* males differ from all other heptatheline genera by the conductor with a smooth surface and with the proximal portion relatively narrow, the distal portion with more than one apical spine (Figures 40–41, 45–46), and by the embolus with a flat opening (Figures 40–41, 45–46). *Songthela* females differ from all other heptatheline genera by two paired receptacular clusters, all four of similar size or median ones larger than laterals, median pair with tubular stems situated at the anterior margin of bursa copulatrix, lateral ones situated more dorsally (Figures 43–44, 47).

Description. Total length (excluding chelicerae) = 8–21 mm (N = 304); male palpal conductor with one or two distal spines: the long one nearly reaching the embolus edge, the shorter one positioned at the middle part of conductor (Figures 40–41, 45–46); embolus with a wide, flat opening (Figures 40, 45–46); tegulum with serrated margin (Figures 41–42, 46); spinose paracymbium relatively short (Figures 40–41, 45); female genitalia as diagnosed (Figures 43–44, 47).

Species composition. *Songthela bristowei* (Gertsch, 1967), comb. n. (2♂10♀), *S. ciliensis* (Yin, Tang & Xu, 2003), comb. n., *S. goulouensis* (Yin, 2001), comb. n. (8♂41♀; male previously unknown), *S. hangzhouensis* (Chen, Zhang & Zhu, 1981), comb. n. (4♂10♀), *S. jianganensis* (Chen et al., 1988), comb. n. (11♀), *S. mangshan* (Bao, Yin & Xu, 2003), comb. n., *S. sapana* (Ono, 2010), comb. n. (4♀), *S. shei* (Xu & Yin, 2001), comb. n. (3♂4♀; male previously unknown), *S. wosanensis* (Wang & Jiao, 1995), comb. n. (2♂7♀; male previously unknown), *S. xianningensis* (Yin et al., 2002), comb. n. (1♂23♀; male previously unknown), *S. yunnanensis* (Song & Haupt, 1984), comb. n.

Distribution. China (Chongqing, Guizhou, Hubei, Hunan, Jiangxi, Sichuan, Zhejiang, and Yunnan) and northern Vietnam.

Genus *Vinathela* Ono, 2000

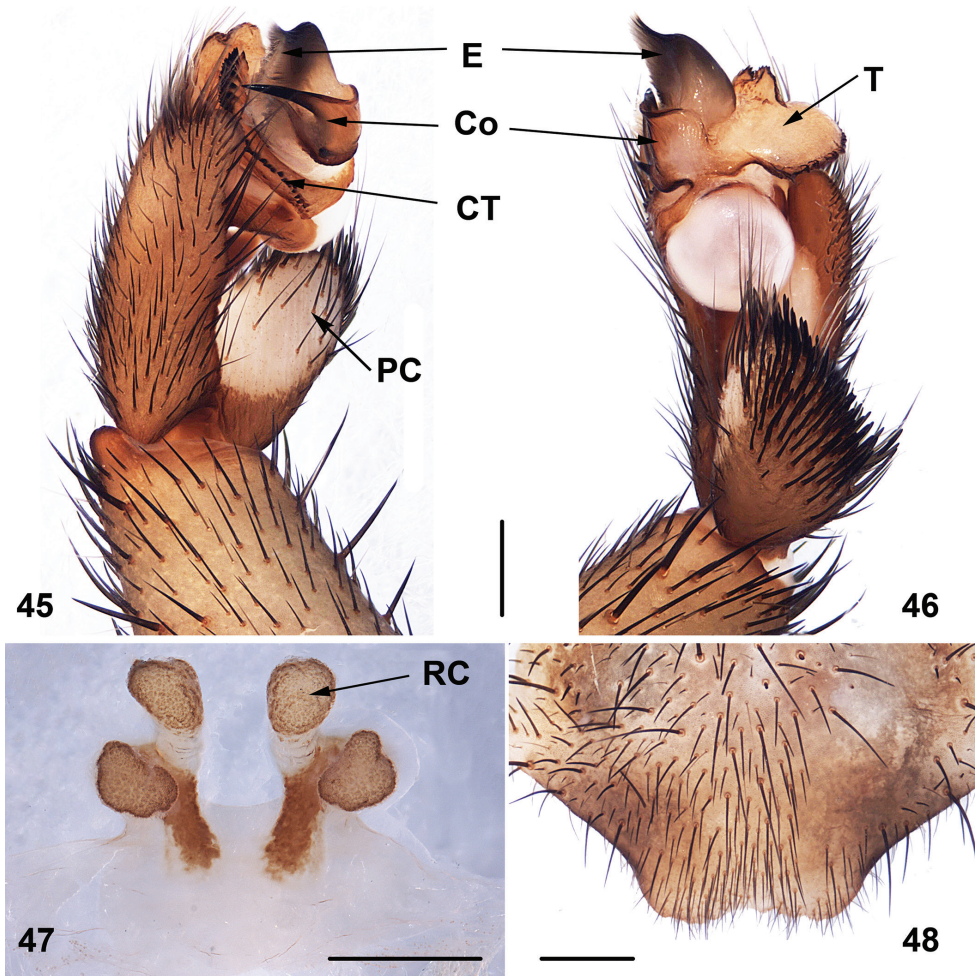
Figures 49–55

Vinathela Ono, 2000, type species *Heptathela cucphuongensis* Ono, 1999; synonymized with *Heptathela* by Haupt, 2003a: P. 91. Herein removed from synonymy of *Heptathela*.

Abcathela Ono, 2000, type species *Heptathela abca* Ono, 1999, P. 149; placed in the synonymy of *Heptathela* by Haupt, 2003a, P. 71, 79; **syn. n.**

Nanthela Haupt, 2003a, type species *Liphistius tonkinensis* Bristowe in Bristowe and Millot 1933; placed in the synonymy of *Heptathela* by Schwendinger and Ono 2011, P. 601; **syn. n.**

Diagnosis. Males of *Vinathela* differ from all other Heptathelinae genera by a wide proximal portion of the conductor, its distal portion being bent (Figure 50), and embolus with two peaks (Figures 49–50); females of *Vinathela* can be distinguished from all other Heptathelinae by three or four receptacular clusters situated at the anterior margin of bursa copulatrix, three of the same size or median pair small and lateral pair large (Figures 52–55).

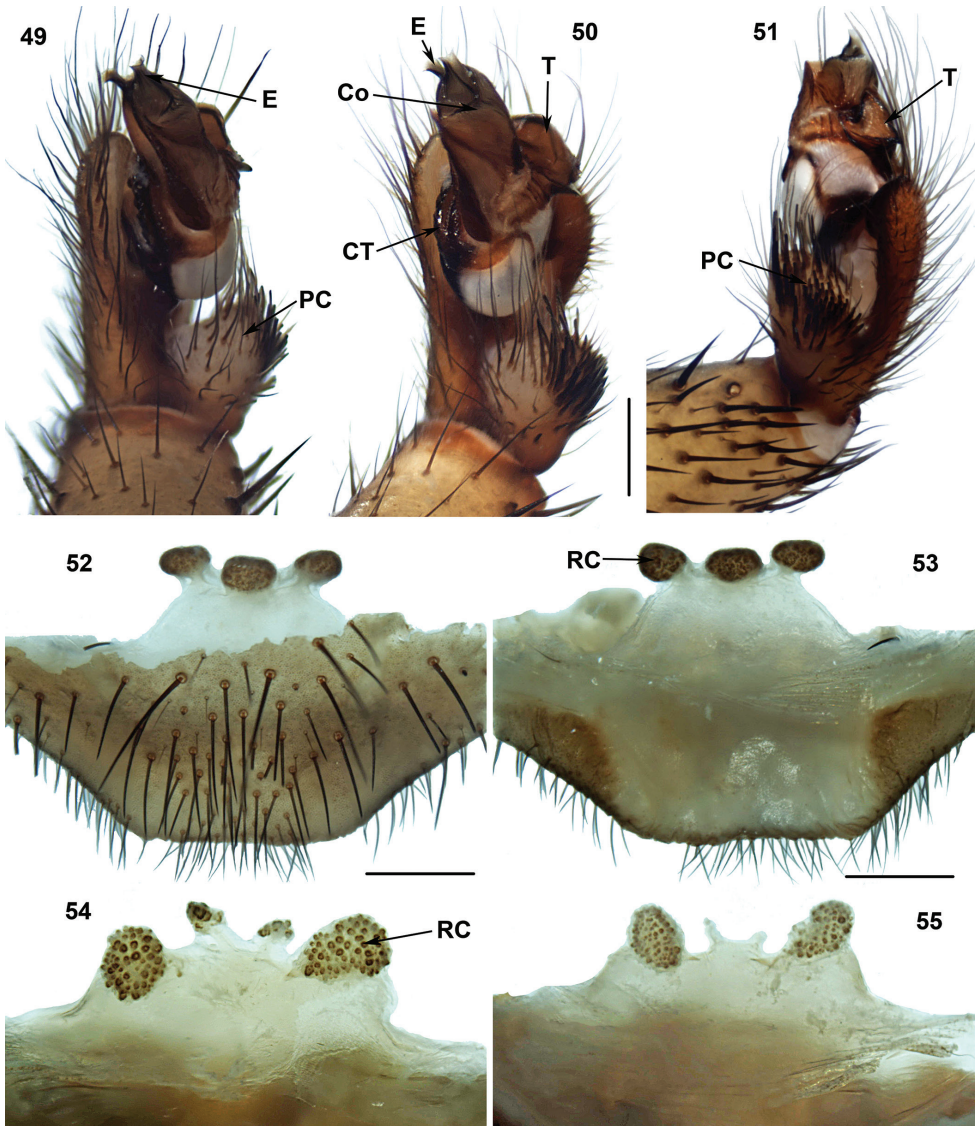


Figures 45–48. Male (XUX-2011-078) and female (XUX-2011-043) genital anatomy of *Songthela goulouensis* (Yin, 2001), comb. n. **45** palp prolateral view **46** palp retrolateral view **47** vulva ventral view **48** vulva dorsal view. Scales 0.5 mm.

Description. Total length (excluding chelicerae) = 9–22 mm (N = 71); male palp with long conductor, proximal portion wide, distal portion bent (Figure 50); tegulum thick (Figures 50–51); spinose paracymbium short (Figures 49–51); female genitalia as diagnosed (Figures 52–55).

Species composition. *Vinathela abca* (Ono, 1999), comb. n. (1♂7♀; male previously unknown), *V. cucphuongensis* (Ono, 1999), comb. n. (2♂7♀; male previously unknown), *V. hongkong* (Song & Wu, 1997), comb. n. (3♂19♀; female previously unknown), *V. hunanensis* (Song & Haupt, 1984), comb. n., *V. tomokunii* (Ono, 1997), comb. n. (6♀), *V. tonkinensis* (Bristowe, 1933), comb. n. (1♂4♀; female previously unknown).

Distribution. China (Hong Kong, Hunan and Jiangxi) and Vietnam.



Figures 49–55. Male (XUX-2013–007) and female genital anatomy of *Vinathela cucphuongsensis* (Ono, 1999), comb. n. (52–53: XUX-2013–006) and *Vinathela abca* (Ono, 1999), comb. n. (54: XUX-2013–049; 55: XUX-2013–048) 49 palp prolateral view 50 palp ventral view 51 palp retrolateral view 52 vulva ventral view 53–55 vulva dorsal view. Scales 0.5 mm.

Remarks. *Vinathela* Ono, 2000 has priority over *Nanthela* Haupt, 2003a. We chose *Vinathela* Ono, 2000 over *Abcathela* Ono, 2000 (from the same publication) since the latter also contains species from northern China.

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Appendix I

Specimens used in this study. Asterisks mark the previously unknown males.

Species	Specimen code	Sex	Locality	Coordinates	Collectors
<i>Ganthela yundingsensis</i> sp. n.	XUX-2013-136	male	Mt. Yunding, Tingxi Town, Tong'an District, Xiamen City, Fujian Province, China	24.87827°N; 118.16172°E	Fengxiang Liu, Zengtao Zhang, Xin Xu
	XUX-2013-135	female	Mt. Yunding, Tingxi Town, Tong'an District, Xiamen City, Fujian Province, China	24.87924°N; 118.16194°E	Fengxiang Liu, Zengtao Zhang, Xin Xu
	XUX-2013-389	male	Kozomo 1-chome, Higashi-ku, Kumamoto-shi, Kumamoto-ken, Japan	32.83685°N; 130.78337°E	Daiqin Li, Bo Wu
<i>Heptathela higoensis</i> Haupt, 1983					
<i>Heptathela kimurai</i> (Kishida, 1920)	XUX-2013-351	female	Shiroyama Park, Shiroyama-cho, Kagoshima-shi, Kagoshima-Ken, Japan	31.59704°N; 130.55087°E	Daiqin Li, Bo Wu
<i>Heptathela yanbaruensis</i> Haupt, 1983	XUX-2014-038A	female	Genka, Nago-shi, Okinawa, Japan	26.62753°N; 128.06044°E	Daiqin Li, Bo Wu
<i>Liphistius laoticus</i> Schwendinger, 2013	XUX-2013-267	male	Tad Fane Waterfall, Pakse-Paksong Road, Champasak, Laos	15.18264°N; 106.12713°E	Daiqin Li, Fengxiang Liu, Xin Xu
	XUX-2013-256	female	Tad E-Tu Waterfall, Pakse-Paksong Road, Champasak, Laos	15.19408°N; 106.10161°E	Daiqin Li, Fengxiang Liu, Xin Xu
	XUX-2012-087	male	Nangaoling Forest Plantation, Baisha County, Hainan Province, China	19.24934°N; 109.38940°E	Daiqin Li, Fengxiang Liu, Xin Xu
<i>Qionghela baishensis</i> sp. n.	XUX-2012-089	male	Nangaoling Forest Plantation, Baisha County, Hainan Province, China	19.24934°N; 109.38940°E	Daiqin Li, Fengxiang Liu, Xin Xu
	XUX-2012-092	male	Nangaoling Forest Plantation, Baisha County, Hainan Province, China	19.24940°N; 109.38934°E	Daiqin Li, Fengxiang Liu, Xin Xu
	XUX-2012-086	female	Nangaoling Forest Plantation, Baisha County, Hainan Province, China	19.24934°N; 109.3894°E	Daiqin Li, Fengxiang Liu, Xin Xu
<i>Ryuthela nishihirai</i> (Haupt, 1979)	XUX-2012-085A	female	Nangaoling Forest Plantation, Baisha County, Hainan Province, China	19.24934°N; 109.3894°E	Daiqin Li, Fengxiang Liu, Xin Xu
	XUX-2012-302	female	Sheyoshi Park, Shuri, Naha, Okinawa Prefecture, Japan	26.22731°N; 127.71532°E	Hirotsugu Ono, Daiqin Li, Fengxiang Liu, Xin Xu
	XUX-2013-228	male	Hirakubo River, Ishigaki island, Okinawa, Japan	24.58864°N; 124.31858°E	Daiqin Li, Bo Wu

Species	Specimen code	Sex	Locality	Coordinates	Collectors
<i>Ryuthela sasakii</i> Ono, 1997	XUX-2012-364	female	Maja, Nakazato-son, Kumejima Island, Okinawa, Japan	26.35823°N; 126.80168°E	Daiqin Li, Fengxiang Liu, Xin Xu
<i>Sinothela sinensis</i> (Bishop & Crosby, 1932), comb. n.	XUX-2012-045	male	Shiqiao Village, Shiqiao Town Yiyuan County, Shandong Province, China	36.15213°N; 118.33400°E	Fengxiang Liu, Zeliang Liu, Xin Xu
	XUX-2012-035	female	Caojia Village, Puji Town, Zhangqiu City, Shandong province, China	36.72776°N; 117.61112°E	Fengxiang Liu, Zeliang Liu, Xin Xu
<i>Songthela hangzhouensis</i> (Chen, Zhang & Zhu, 1981), comb. n.	XUX-2013-175	male	Wengjia Village, Mt. Shifeng, Lingyin District, Hangzhou City, Zhejiang Province, China	30.22069°N; 120.11679°E	Daiqin Li, Fengxiang Liu, Zengtao Zhang, Xin Xu
	XUX-2013-170	female	Wengjia Village, Mt. Shifeng, Lingyin District, Hangzhou City, Zhejiang Province, China	30.22074°N; 120.11555°E	Daiqin Li, Fengxiang Liu, Zengtao Zhang, Xin Xu
<i>Songthela goulouensis</i> (Yin, 2001), comb. n.	XUX-2011-078*	male	Zizhu Taoist Temple, Hengshan, Hunan Province, China	27.27707°N; 112.70016°E	Fengxiang Liu, Rong Xiao, Xin Xu
	XUX-2011-043	female	Zhongleici, Hengshan, Henyang, Hunan Province, China	27.27074°N; 112.71507°E	Fengxiang Liu, Rong Xiao, Xin Xu
<i>Vinathela abca</i> (Ono, 1999), comb. n.	XUX-2013-048	female	9 KM QL 4D, Coc San, Bat Xat District, Lao Cai Province, Vietnam	22.44414°N; 103.93818°E	Daiqin Li, Fengxiang Liu, Xin Xu
	XUX-2013-049	female	9 KM QL 4D, Coc San, Bat Xat District, Lao Cai Province, Vietnam	22.44414°N; 103.93818°E	Daiqin Li, Fengxiang Liu, Xin Xu
<i>Vinathela cucphuongensis</i> (Ono, 1999), comb. n.	XUX-2013-007*	male	Cuc Phuong National Park, Nho Quan, Ninh Binh Province, Vietnam	20.26831°N; 105.69324°E	Daiqin Li, Fengxiang Liu, Xin Xu
	XUX-2013-006	female	Cuc Phuong National Park, Nho Quan, Ninh Binh Province, Vietnam	20.26831°N; 105.69324°E	Daiqin Li, Fengxiang Liu, Xin Xu

