

Pullimosina (Pullimosina) turfosa sp. nov. and other Sphaeroceridae (Diptera) from peat bogs in the North Caucasus (Russia)

Jindřich Roháček¹, Andrey A. Przhiboro²

1 Silesian Museum, Nádražní okruh 31, CZ-746 01 Opava, Czech Republic **2** Zoological Institute, Russian Academy of Sciences, St Petersburg, 199034 Russia

Corresponding author: Jindřich Roháček (rohacek@szm.cz)

Academic editor: Marc De Meyer | Received 7 September 2022 | Accepted 19 October 2022 | Published 25 November 2022

<https://zoobank.org/D0144E9F-A485-4450-B279-A813F3EF0AEF>

Citation: Roháček J, Przhiboro AA (2022) *Pullimosina (Pullimosina) turfosa* sp. nov. and other Sphaeroceridae (Diptera) from peat bogs in the North Caucasus (Russia). ZooKeys 1132: 1–49. <https://doi.org/10.3897/zookeys.1132.94579>

Abstract

The first data about Sphaeroceridae occurring on eight montane and foothill peat bogs of various types in the North Caucasus (Russia) are presented. A total of 38 species has been recorded and their affinity to peat-bog habitats is discussed. A single species is classified as a tyrphobiont, viz. the strongly brachypterous *Pullimosina (Pullimosina) turfosa* sp. nov. being strictly associated with *Sphagnum* hummocks in peat bogs. This new species is described and illustrated in detail and its relationships, biology, and wing reduction are discussed. Only three species are considered tyrphophilous or probably tyrphophilous, viz. *Ischiolepta nitida* (Duda, 1920), *Phthitia (Kimosina) longisetosa* (Dahl, 1909), and *Spelobia ibrida* Roháček, 1983. The majority of recorded species do not have close affinity to peat bogs and are treated as tyrphoneutral, and *Rachispoda hostica* (Villeneuve, 1917) is probably tyrphoxenous due to occasional occurrence in a peat bog. Species composition of Sphaeroceridae on Caucasian peat bogs is discussed in comparison to those known from peat bogs in other parts of Europe. Taxonomic notes are given on *Minilimosina (Svarciella)* species of the *M. vitripennis* group. Six species (including *P. turfosa* sp. nov.) are new additions to the fauna of Russia.

Keywords

biology, brachyptery, distribution, lesser dung flies, Limosininae, relationships, taxonomy, tyrphophily

Introduction

Sphaeroceridae or Lesser dung flies are a relatively large family of Acalyptratae, with more than 1,800 described (and at least 5,000 estimated) species in the world fauna of Diptera (Papp and Roháček 2021). The family is richly represented in all biogeographic regions except for extreme Arctic and Antarctic areas. The European fauna of Sphaeroceridae is diverse, with approximately 260 named and more than 270 presupposed species (Pape et al. 2015). Probably all species are saprophagous (more precisely, microsaprofagous) because both larvae and adults are feeding on liquids with microorganisms and decomposed organic substances from decaying animal (excrement, carrion), vegetal (dead plants and their remnants including forest litter), and fungal (sporocarps of macrofungi) organic matter (Richards 1930; Roháček 1998; Papp and Roháček 2021). This trophic strategy enables these flies to colonize very diverse habitats, including nutrient-poor (oligotrophic) and strongly acidic peat bogs.

Insect fauna of mires (peat bogs in a broad sense, i.e., peatlands where peat is currently being formed and accumulating) has been relatively well studied both in Europe and North America (for reviews, see Marshall et al. 1999; Keiper et al. 2002; Spitzer and Danks 2006; Batzer et al. 2016) but most of the published faunal and ecological studies are devoted to Lepidoptera and Coleoptera while even in most complex studies (e.g., Harnisch 1925; Peus 1928, 1932; Rabeler 1931; Pax 1937; Krogerus 1960; Nelson 1971; Coulson and Butterfield 1985; Drake et al. 1989; Boyce 2004; Spungis 2008; Sushko 2012; Anderson et al. 2017), as a rule, Diptera are treated only marginally, with faunal studies mostly devoted to selected families of this order (e.g., Rief 1996; Salmela 2004; Przhiboro and Paasivirta 2012). This is particularly true for Sphaeroceridae: the reliable data on the occurrence of sphaerocerid species on peat bogs are not very numerous and can mostly be found in studies published by specialists on this group, viz. Roháček (1984), Roháček and Barták (1999) (in the Czech Republic), Kuznetsova (1987) (in Latvia), Pitkin et al. (1985) and Holmes et al. (1992) (in Great Britain), and Marshall (1994, 1997) (in Canada). Additional data on Sphaeroceridae from peat bogs can be found in publications by other dipterists, e.g., Elberg (1969, 1971), Taillefer and Wheeler (2010, 2011), and Przhiboro (2012).

This study is devoted to Sphaeroceridae obtained from montane and submontane peat bogs in the North Caucasus by the second author. These mires are rare, mostly small and isolated habitats situated near the southernmost limit of the occurrence of this habitat type in Europe and the whole of the Palearctic Region. They are characterized by specific environmental conditions and distinctive composition of vegetation (Botch and Masing 1979, 1983) with relict taxa of originally Boreal flora. The knowledge of insects in these peat bogs is poor and the composition of the fauna of Diptera remains practically unknown apart from small recent contributions dealing with Tephritidae (Evstigneev and Przhiboro 2021; Evstigneev and Glukhova 2022) and Anthomyzidae (Roháček and Przhiboro 2022).

Materials and methods

Material

A total of 119 adults of Sphaeroceridae was collected in peat bogs together with other macroinvertebrates in the scope of faunal and ecological studies of these mires in early May 2016, late May to early June 2018, and in September 2018. Most of the examined material is deposited in Zoological Institute, Russian Academy of Sciences, St Petersburg, Russia (**ZISP**). Some duplicates are retained in Slezské zemské muzeum, Opava, Czech Republic (**SMOC**). Most specimens are preserved in 80% ethanol, only the type specimens and a few other voucher specimens (indicated in the list of material as “dry”) have been dried and mounted on pinned triangular cards to be deposited in dry collections of Diptera.

Collecting methods

On each mire, most sampling effort was focused on collecting macroinvertebrates from dry and wet habitats where *Sphagnum* mosses dominate or are abundant. The following main sampling techniques were used in each mire: sweep-netting with aerial net over grassy vegetation (in different daytime periods and weather), yellow pan traps, pitfall traps, sifting substrate of *Sphagnum* cushions or hummocks located in drier places, trampling *Sphagnum* cushions located in wet places (like shorelines of in-mire lakelets), sweep-netting with aquatic net in puddles and along shorelines of lakelets, and sampling the substrate (*Sphagnum*, other plants, turf, and litter). The latter samples were washed in sieves (the smallest 0.25 mm mesh), then macroinvertebrates were extracted by flotation in a strong solution of NaCl combined with hand-sorting of the coarse fraction. However, most Sphaeroceridae were collected by sweep-netting; only a few specimens were obtained by sifting, yellow pan traps, and from the samples of substrata (indicated below as “sample no.”).

Methods of preparation and study of postabdominal structures

Abdomens of some specimens were detached, cleared by boiling for several minutes in 10% solution of potassium hydroxide (KOH) in water, then neutralized in 10% solution of acetic acid (CH_3COOH) in water, washed in water and subsequently transferred to glycerin. Postabdominal structures were dissected and examined in a drop of glycerin under binocular microscopes (Reichert, Olympus). Detailed examinations of genital structures were performed with a compound microscope (Zeiss Jenaval). After examination, all dissected parts were put into small plastic tubes containing glycerin, sealed with hot forceps and pinned below the respective specimens. Specimens with abdomen removed and terminalia dissected are indicated in the list of material by the abbreviation “genit. prep.”

Drawing techniques and photography

Legs and details of the male and female genitalia were drawn by means of an Abbe's drawing apparatus on a compound microscope (Zeiss Jenaval) at magnification 130–500 \times . Wings were photographed on an Olympus BX51 compound microscope with an attached digital camera (Canon EOS 1200D). Whole adult (dry-mounted) specimens and heads were photographed by means of a Canon EOS 5D Mark III digital camera with a Nikon CFI Plan 10 \times /0.25NA 10.5mm WD objective attached to a Canon EF 70–200mm f/4L USM zoom lens. The specimen photographed by means of the latter equipment was repositioned upwards between each exposure using a Cognisys StackShot Macro Rail and the final photograph was compiled from multiple layers (~ 40) using Helicon Focus Pro 7.0.2. The final images were edited in Adobe Photoshop CS6. All morphological illustrations were prepared by the first author.

Measurements

Five characteristics of the new species were measured: body length (measured from anterior margin of head to end of cercus, thus excluding the antenna), index t_2 : mt_2 (= ratio of length of mid tibia: length of mid basitarsus), wing length (from wing base to wing tip), wing width (maximum width), Cs_1 : Cs_2 (= ratio of length of 1st costal sector: length of 2nd costal sector). All type specimens were measured.

Presentation of faunistic data

Label data of the type specimens are presented strictly verbatim including information on form and color of all associated labels. Locality data of other specimens examined are given in brief form because all other information is given under the descriptions of localities. Localities are listed in the same order as in their descriptions below. Biological information obtained from the material examined and literature are given in the Comments paragraph. General distribution of species recorded are based on Roháček et al. (2001) and Marshall et al. (2011) unless mentioned otherwise. Species recorded from Russia for the first time are marked by * preceding the species' name.

Assessment of the affinity of species to mire habitats

The affinity of a species to peat-bog habitat has been judged by the first author based on his knowledge of the biology, autecology and distribution of the species. Four categories are differentiated according to the degree of association with bog habitats following Peus (1928, 1932), Roháček and Máca (1982), and Spitzer and Danks (2006):

1. tyrphobiont (**TB**) – species strictly associated with peat-bog habitats (occur only in bogs),
2. tyrphophilous (**TPH**) – species preferably associated with peat-bog habitats (characteristic of bogs but not confined to them),

3. tyrphoneutral (**TN**) – species with a wide habitat tolerance (resident in bogs but also, often more successfully, in other habitats),
4. tyrphoxenous (**TX**) – species coincidentally encountered in peat-bog habitats (non-resident vagrants which cannot survive in bogs).

These categories can be compared with those more generally used in North Europe (e.g., by Krogerus 1960) as follows: tyrphobiont = eucoenic (euzön), tyrphophilous = tychocoenic (tychozön), tyrphoneutral = acoenic (azön), tyrphoxenous = xeno-coenic (xenzön).

Morphological terminology

Morphological terminology follows that used for Sphaeroceridae by Roháček (1998) in the Manual of Palaearctic Diptera including terms of the male hypopygium. The “hinge” hypothesis of the origin of the eremoneuran hypopygium, re-discovered and documented by Zatwarnicki (1996), has been accepted and, therefore, the following synonymous terms of the male genitalia (emanating from other hypotheses) need to be listed (terms used first): ejacapodeme = ejaculatory apodeme, epandrium = periandrium, medandrium = intraperiandrial sclerite, phallapodeme = aedeagal apodeme. Morphological terms of the male postabdomen and genitalia are depicted in Figs 23–30, those of the female postabdomen in Figs 33–39. Abbreviations of morphological terms used in text and illustrations are listed below.

Abbreviations of morphological terms used in text and/or figures

A₁	anal vein
ac	acrostichal (seta)
ads	additional (setulae) on frons
asc	additional sclerite
C	costa
ce	cercus
Cs₁, Cs₂	1 st , 2 nd costal sector
CuA₁	cubitus
cx₁	fore coxa
dc	dorsocentral (seta)
dp	distiphallus
ea	ejacapodeme
ep	epandrium
f₁, f₂, f₃	fore, mid, hind femur
g	genal (seta)
gs	gonostylus
h	humeral cross-vein
hu	humeral (= post-pronotal) (seta)
hy	hypandrium

ifr	interfrontal (seta)
M	media
ma	medandrium
mt₂, mt₃	mid, hind basitarsus
oc	ocellar (seta)
occe	outer occipital (seta)
occi	inner occipital (seta)
ors	fronto-orbital (seta)
pg	postgonite
pha	phallapodeme
pp	phallopore
prg	pregonite
pvt	postvertical (seta)
R₁	1 st branch of radius
R₂₊₃	2 nd branch of radius
R₄₊₅	3 rd branch of radius
S1–S10	abdominal sterna
sc	scutellar (seta)
stpl	sternopleural (= kat-episternal) (seta)
T1–T10	abdominal terga
t₁, t₂, t₃	fore, mid, hind tibia
va	ventroapical seta on t ₂
vi	vibrissa
vte	outer vertical (seta)
vti	inner vertical (seta)

Localities studied

For mire types and characteristics, we mostly follow the terminology and definitions adopted by Joosten et al. (2017). In general, they are in agreement with the terms used in recent entomological reviews on mires (Vitt 1994; Marshall et al. 1999; Keiper et al. 2002; Spitzer and Danks 2006, etc.).

Eight montane and submontane mires (peat bogs) were studied, all situated in the central part of the northern slope of the Greater Caucasus Range (Fig. 1). Four mires (Fig. 1: localities 1–4) are located in Cherekskiy District of the Kabardino-Balkarian Republic (area of eastern Balkaria). The other four mires (Fig. 1: localities 5–8) are situated in the Republic of North Ossetia-Alania: Chifandzar and two bogs at Kubus Mountain in Irafskiy District (historical area of Western Digoria), and Tarskoe peatland in Prigorodnyy District (in Tarskaya Hollow).

The mires under study strongly differ in the size (0.0004 to ca. 0.5 km²), altitude (800 to 2290 m), trophic status (oligo- to eutrophic), origin, and type (*Sphagnum*-, *Carex-Sphagnum*- and *Carex*-dominated). Conditions of the study mires and previous publications about these mires were briefly reviewed in Prokin et al. (2019) and Prokina

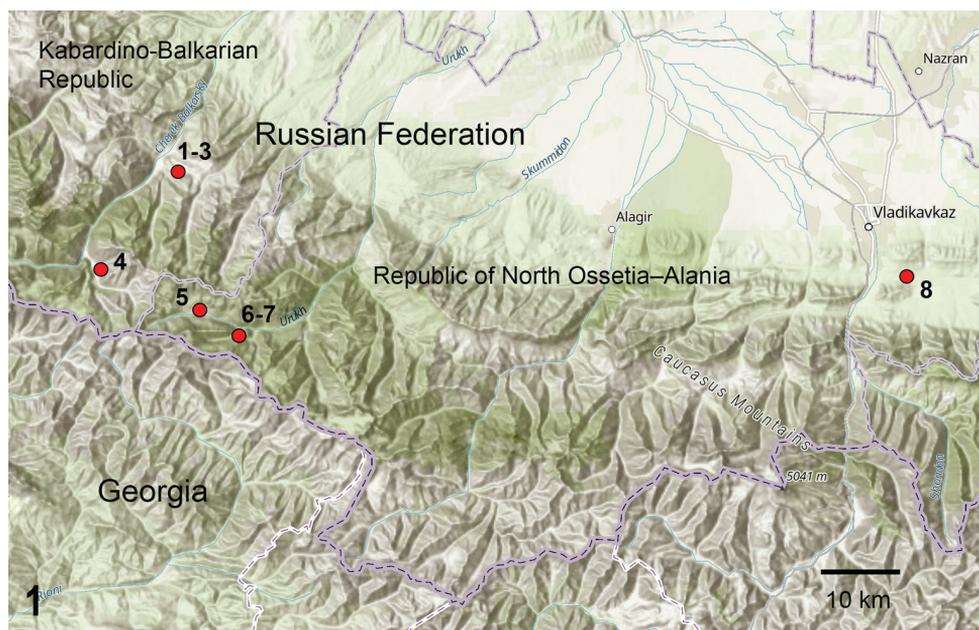


Figure 1. Map of the North Caucasus with position of mires under study. Localities on map; 1 Kurnoyatsu-1; 2 Kurnoyatsu-2; 3 Kurnoyatsu-3; 4 Ushtulu; 5 Chifandzar; 6 Kubus-larger; 7 Kubus-smaller; 8 Tarskoe. Map source: ArcGIS Online.

and Philippov (2019). The mires are briefly described below, with additional information given in Table 1. Photos of the mires under study (taken by the second author) are given as Figs 2–11. It should be said that in general the mires under study are ranging from a transitional mire to a rich fen; typical ombrotrophic bogs (i.e., fed solely on precipitation; raised or flat) are absent. Several mires are transient (mixed), i.e., include parts or sites which correspond to different hydromorphic and trophic types. All mires are unforested and flat.

Mires of the Kabardino-Balkarian Republic

Three small transitional mires called here Kurnoyatsu-1, Kurnoyatsu-2, and Kurnoyatsu-3 (having no official names) are situated on the slope at left bank of the Kurnoyatsu River, ca. 3 km SE of Verkhnyaya Balkaria Village. These mires are situated in the alpine zone near the forest edge, on small flat terraces at different heights, 200–500 m from each other. The mires are limnogenous; each has a lakelet in the middle, with swing moor at shoreline. Relief of hummocks is not developed. Kurnoyatsu-1 (Fig. 2) and Kurnoyatsu-2 (Figs 3, 4) are transient (mixed) mires, with the fen changing into a bog; they have a large, dry, mostly *Sphagnum*-dominated, bog area (apparently ombrotrophic in the second case) and a wet *Sphagnum*- and/or *Carex*-dominated fen area around the lakelet. In Kurnoyatsu-3 (Fig. 5), dry habitat is not developed.

Table 1. Characteristics of study mires.

Region (area within)	Bog name	Coordinates	Altitude (m)	Mire area (m ²)*	Trophic status	Habitats	Dominating species of <i>Sphagnum</i>	Dominating species of phanerogams
Kabardino-Balkaria (eastern Balkaria)	Kumoyatsu-1	43.10062°N, 43.48418°E	1776	2600	oligotrophic to meso-oligotrophic	dry	<i>S. magellanicum</i> -coll. (<i>S. divinum</i>)	<i>Molinia caerulea</i> , <i>Meryanthes trifoliata</i>
	Kumoyatsu-2	43.09834°N, 43.47776°E	1810	4000	oligotrophic to meso-oligotrophic	wet (near lake)	<i>S. squarrosum</i> , <i>S. teres</i> , <i>S. flexuosum</i> , <i>S. obtusum</i> , <i>S. fuscum</i>	<i>Carex rostrata</i> , <i>C. canescens</i> , <i>C. ?diandra</i> , <i>Meryanthes trifoliata</i> , <i>Rhododendron luteum</i> , <i>Empetrum nigrum</i> , <i>Carex rostrata</i>
	Kumoyatsu-3	43.09714°N, 43.47950°E	1836	1500	oligotrophic to meso-oligotrophic	wet (near lake)	<i>S. fallax</i> , <i>S. flexuosum</i>	<i>Carex rostrata</i> , <i>C. canescens</i> , <i>Calamagrostis</i> sp.
North Ossetia-Alania (western Digoria)	Ushrulu	42.97457°N, 43.33263°E	1995	180000	eutrophic	mostly wet	<i>S. fallax</i> , <i>S. flexuosum</i>	<i>Carex rostrata</i> , <i>Eriophorum angustifolium</i>
	Chifandzar	42.91867°N, 43.51493°E	2289	520000	eutrophic	dry (large hummocks)	<i>S. uarnstorffi</i> , <i>S. uarnstorffi</i> , <i>S. teres</i>	<i>Carex rostrata</i> , <i>Carex rostrata</i> , <i>Carex rostrata</i> , <i>C. sp.</i> , <i>Nardus stricta</i>
	Kubus-larger	42.89350°N, 43.57733°E	2077	2300	oligotrophic	wet	<i>S. subsecundatum</i>	<i>Carex rostrata</i> , <i>Nardus stricta</i>
North Ossetia-Alania (Tarskaya Hollow)	Kubus-smaller	42.89350°N, 43.57733°E	2080	400	oligotrophic	dry	<i>S. capillifolium</i>	<i>Molinia caerulea</i> , <i>Eriophorum angustifolium</i> , <i>Nardus stricta</i>
	Tarskoe	42.96311°N, 44.72636°E	800	62000	meso-oligotrophic	mostly wet	<i>S. subsecundatum</i>	<i>Carex rostrata</i> , <i>C. magellanic</i> , <i>C. lasiocarpa</i> , <i>Nardus stricta</i>
						dry	<i>S. magellanicum</i> -coll. (<i>S. divinum</i>), <i>S. centrale</i> , <i>S. subsecundatum</i>	<i>Molinia caerulea</i> , <i>Nardus stricta</i>

* Calculated from satellite images in SAS Planet software (Bing-Satellite, ArcGIS.Clarity, Google-Satellite, Yandex-Satellite) using the photos of study bogs taken in 2016–2018. Some values given for the same bogs in Prokin et al. (2019) are erroneous.



Figures 2, 3. Mires under study **2** Kurnoyatsu-1, 6 June 2018 **3** Kurnoyatsu-2, 22 September 2018.

Ushtulu mire (also called “Narzannoe”; Fig. 6) is situated in the valley of the Karasu River (right tributary of the Balkarskiy Cherek River in its upper reach), at its right bank, 17 km SW of Verkhnyaya Balkaria Village, above the timberline. It is a 700-m long eutrophic, mostly high *Carex*-dominated (partially *Carex-Sphagnum*-dominated) rich fen of spring origin, with emissions of mineral groundwater (mostly spring-fed), without distinct relief of hummocks. There are secondary in-mire lakes surrounded by wide wet areas including swing moor at their shorelines, and drier areas outside.



Figures 4, 5. Mires under study **4** Kurnoyatsu-2, 7 June 2018 (close-up view) **5** Kurnoyatsu-3, 7 June 2018.



Figures 6, 7. Mires under study **6** Ushtulu, 21 September 2018 **7** Chifandzar, 2 June 2018 (arrow indicates an area in which large *Sphagnum* hummocks are located).



Figures 8, 9. Mires under study **8** Chifandzar, 18 September 2018, a large *Sphagnum* hummock **9** Tarskoe, 11 September 2018.



Figures 10, 11. Mires under study **10** Kubus-larger, 4 June 2018 **11** Kubus-smaller, 12 September 2018.

Mires of the Republic of North Ossetia-Alania

Chifandzar mire (Fig. 8) is situated in the valley of the Kharesidon River (upper reach of the Uruk River) and occupies a wide and flat fluvial terrace at the left bank of the river. It is the highest and largest (ca. 2 km long) mire in the study area, situated in the alpine zone above the timberline. Chifandzar is a *Carex*-dominated poor fen; most of its area is wet, with small brooks and a well-developed relief consisting of small hummocks and moist interspaces between them. Most of the mire area is almost lacking *Sphagnum*. Dry habitat (Fig. 9) is represented by ~ 15 larger hummocks (with *Sphagnum teres* predominant) located in the eastern part of the mire.

Two small transitional mires of Kubus, Kubus-larger (Fig. 10) and Kubus-smaller (Fig. 11), are situated on a flat saddle at the Kubus Mountain, 1 km W of its top. These mires are less than 100 m from each other, each surrounded by mixed forest. The larger bog has also the name “Tana glade”. It is distinctly drier, while the smaller bog is wet. Both are *Sphagnum*-dominated and rather uniform, without distinct hummocks.

Tarskoe peatland (Fig. 9) is located in Tarskaya Hollow, ca. 2.5 km W of Tarskoe Village. It is a foothill transitional mire, the lowest, situated ca. 100 km E of the other studied mires. As distinct from the other mires, Tarskoe is strongly modified by drainage and peat extraction which started in 1939; the peatland is crossed by numerous artificial ditches. Grass mesophilic assemblages dominate over most of the peatland area, which has a well-developed relief consisting of hummocks. *Carex-Sphagnum*-dominated habitats are confined mostly to ditches and also occur as a few patches in drier areas beyond ditches.

Three Kurnoyatsu mires are occasionally used for grazing horses, while Chifandzar and Tarskoe mires, for grazing cattle. Chifandzar and Kubus mires are located within the Alania National Park; Tarskoe peatland has a formal protection status as a regional natural monument; Ushtulu mire is situated within the borders of the Kabardino-Balkaria State High-Mountain Reserve; Kurnoyatsu mires have no protection status.

Results

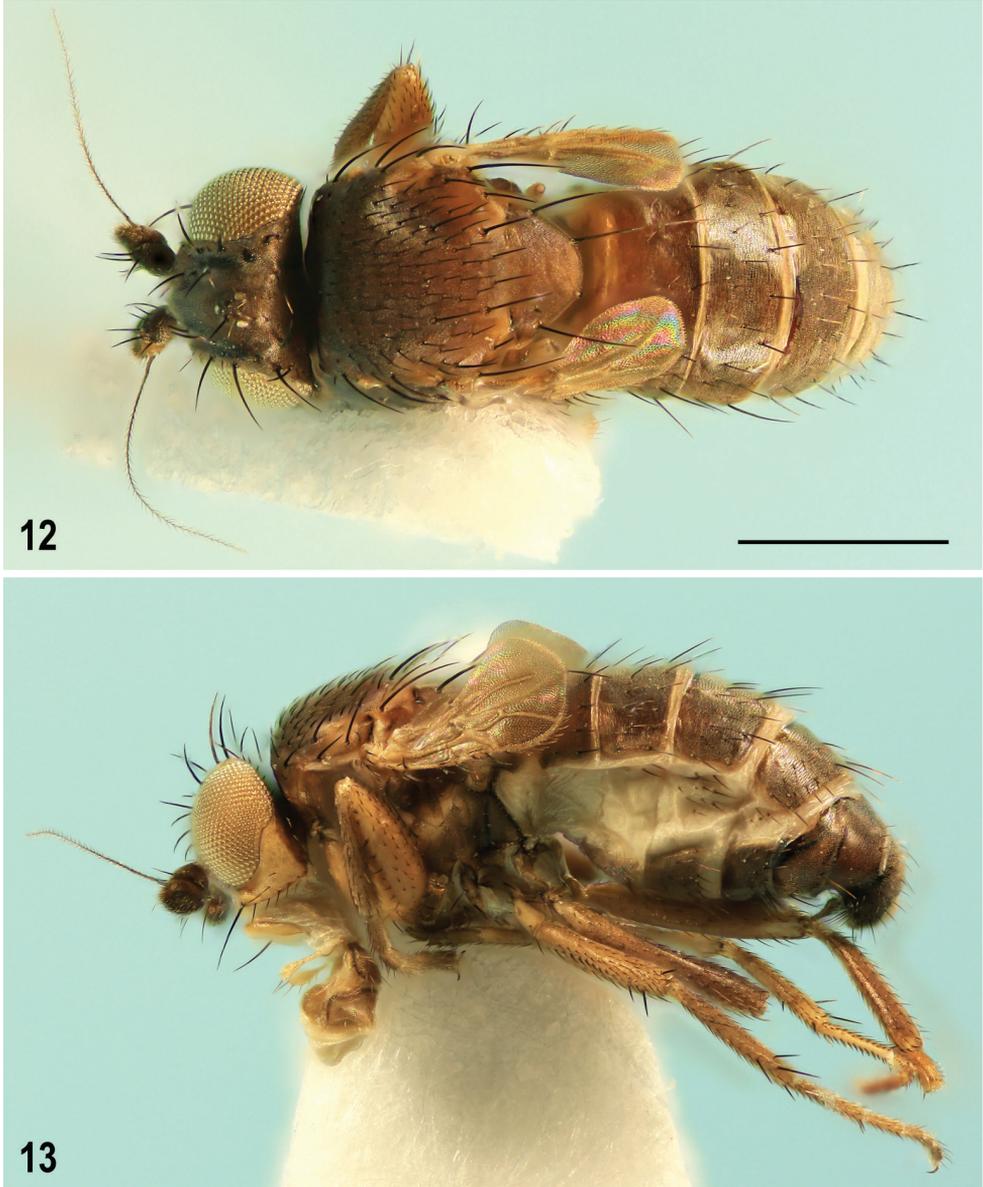
Pullimosina (Pullimosina) turfosa sp. nov.

<https://zoobank.org/3D55B25A-F2A7-4FAF-ACC2-D189349E7AFC>

Figs 12–39

Type material. *Holotype* ♂ labelled: “RUSSIA: N Ossetia, W Digoria, Chifandzar mire in Kharesidon River valley, 42.91867°N, 43.51493°E, 2289 m, sifting from *Sphagnum teres* hummocks, 18.ix.2018, A. Przhiboro leg.”; “Holotypus ♂ *Pullimosina (Pullimosina) turfosa* sp. n., J. Roháček det. 2022“ (red label). The specimen is dried from ethanol and mounted on pinned triangular card, intact (deposited in ZISP, Figs 12, 13).

Paratypes: 6♂ 5♀ with same locality labels but with “Paratypus [♂ or ♀], *Pullimosina (Pullimosina) turfosa* sp. n., J. Roháček det. 2022“ yellow labels; 3♂ 1♀ paratypes preserved in pinned microvial in glycerin, with abdomen detached, and terminalia dissected; others dry-mounted from ethanol and pinned as is the holotype; 1♂ 1♀ with wing



Figures 12, 13. *Pullimosina (Pullimosina) turfosa* sp. nov. (male holotype) **12** whole body, dorsally **13** ditto, laterally. Scale bar: 0.5 mm.

removed for photography and also preserved in glycerin in pinned plastic tube below the specimen (4♂ 3♀ in ZISP, 2♂ 2♀ in SMOC). Other paratypes: 1♀, same locality data, but with “Sample Ч 14 (*Sphagnum teres*), 17.ix.2018“; 1♀, same locality data, but with “Sample Ч 9 (*Sphagnum subsecundum*), 17.ix.2018“, both A. Przhiboro leg. (ZISP).

Etymology. This strongly brachypterous species is named *turfosa* (= peaty, Latin adjective) owing to its strict association with *Sphagnum* hummocks in the type locality.

Description. Male (Figs 12, 13). Total body length 1.27–1.64 (holotype 1.64) mm; general color brown to dark brown with greyish brown microtomentum, subshining dorsally (thorax, abdomen) and ventrally (abdomen), dull on thoracic pleuron.

Head (Figs 13, 14) higher than long (ca. 5:4), bicolorous, dorsally and posteriorly brown to pale brown, anteriorly and ventrally yellow to pale ochreous. Frons brown to pale brown, with anterior margin and orbits pale ochreous (Figs 14, 16), sparsely microtomentose and partly (mainly medially) shining; occiput dark brown with brownish grey microtomentum. Orbits, interfrontalia and ocellar triangle with paler greyish microtomentum; orbit separated from interfrontalia by dark brown dull stripe (shortened anteriorly, never reaching anterior margin of frons); frontal triangle indistinctly delimited but long, almost reaching anterior margin of frons, finely longitudinally microsculptured (Fig. 14), and more shining than rest of frons. Cephalic chaetotaxy (cf. Figs 12–14, 16): pvt present but reduced, hair-like but convergent and with apices almost meeting medially; occe and occi subequal (or occi slightly longer) and ca. two-thirds to three-fourths length of vti; vti normally thickest and longest of frontal setae; vte and oc only slightly shorter than vti; 2 ors, posterior almost as long as vte (or oc) and only slightly longer than anterior ors; 4 ifr, none markedly enlarged, middle 2 pairs usually longer than posterior pair, foremost pair small, about ca. half the length of the previous pair; 1 microseta in front of anterior margin of frons, lateral to foremost ifr; 4–6 minute ads inside and below ors; g small, ca. as long as foremost peristomal setula and 1 or 2 short setae behind it; vi robust, ca. as long as vti; peristomal setulae (5–6) slightly longer than those in single postocular row; 3 postgenal setae, all relatively strong and curved. Frontal lunule of moderate length, well-developed, yellow and sparsely whitish microtomentose, slightly paler than anterior margin of frons. Face yellow, sparsely whitish microtomentose but facial cavities below antennae relatively shining; medial carina small, most distinct dorsally, below frontal lunule. Parafacialia darker than face, ochreous brown. Gena yellow, somewhat darkened only at vibrissal angle and very narrowly on ventral margin, all sparsely whitish microtomentose and rather dull. Postgena brown, sharply delimited from gena. Mouthparts ochreous to brownish including clypeus. Palpus yellowish, slender but distinctly clavate (Fig. 14), with ca. 5 dark setae (subapical longest) along ventral margin. Eye broadly suboval (9:8), of moderate size, with longest diameter ~ 6.0× as long as smallest genal height. Antenna brown (1st flagellomere) to dark brown (scape and pedicel); 1st flagellomere ca. as long as scape + pedicel, ellipsoid, with short greyish ciliation on apex (not longer than cilia on arista). Arista ~ 3.5× as long as antenna, shortly but densely ciliate.

Thorax brown to pale brown (pleuron paler) and greyish brown microtomentose; mesonotum subshining, pleuron and scutellum more densely microtomentose and duller (Figs 12, 13). Mesonotum laterally (notopleural area) and posteriorly (in front of scutellum) paler, usually ochreous; scutellum also somewhat paler posteromedially. Thoracic pleuron with propleuron and sternopleuron largely pale brown to ochreous, other sclerites more or less ochreous margined. Scutellum large, transversely (8:5) rounded, trapezoidal, flat on disc. Thoracic chaetotaxy: mesonotal macrosetae relatively short and weak; 1 hu and 2 microsetae on humeral callus; 3 postsutural dc but the foremost very small (less



Figures 14–17. *Pullimosina (Pullimosina) turfosa* sp. nov. (holotype, paratypes) heads and wings **14** male head, frontally (holotype) **15** male right wing, dorsally (paratype) **16** female head, frontally (paratype) **17** female right wing, dorsally (paratype). Scale bars: 0.2 mm (**14, 16**); 0.1 mm (**15, 17**).

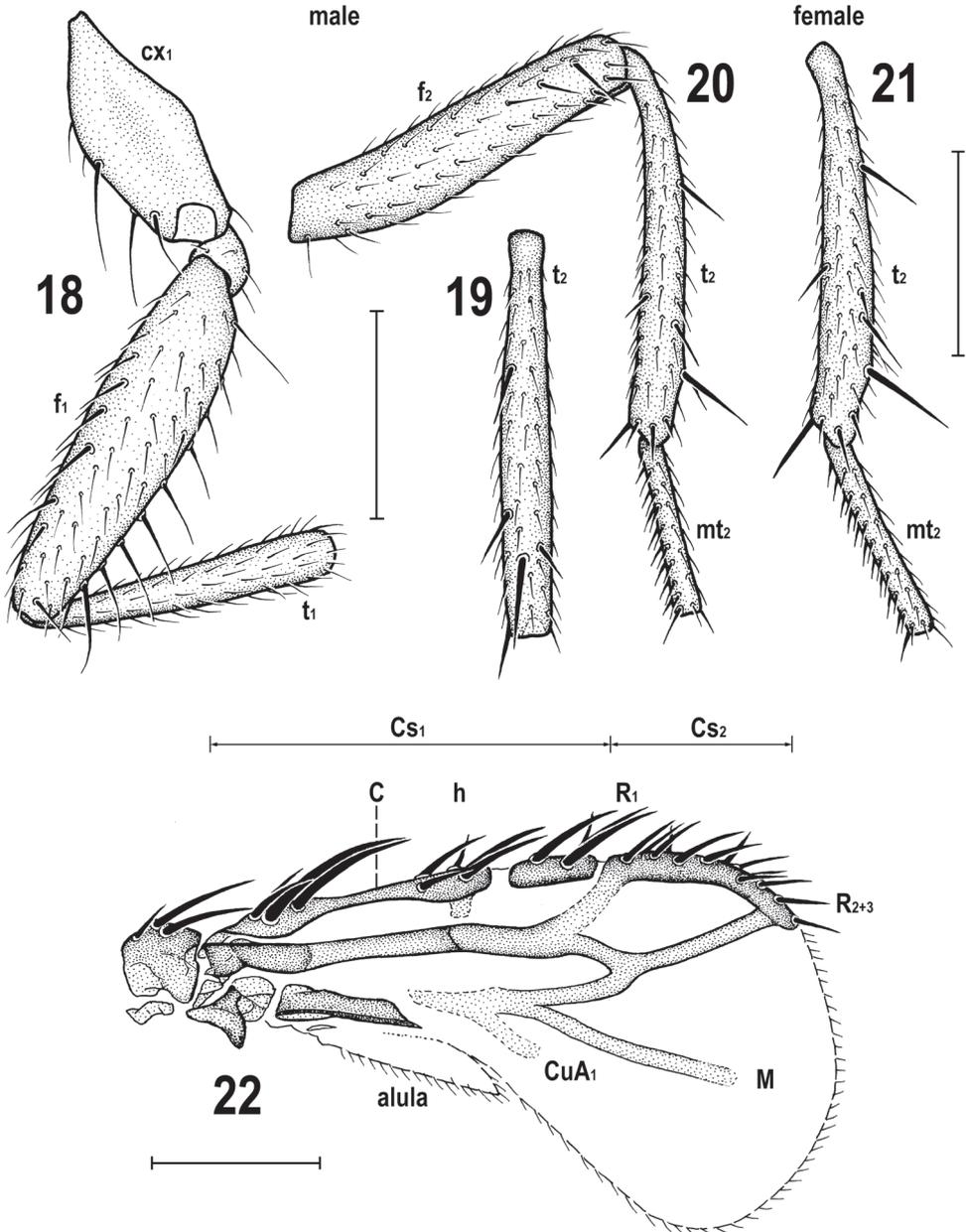
than twice as long as dc microseta in front of it), the middle dc weak, ca. half the length of posterior, the latter long, ca. as long as scutellum; 6 rows of ac microsetae on suture; medial prescutellar ac pair distinctly prolonged, only slightly shorter than middle dc; 2 long sc, laterobasal $\sim 1.3\times$ as long as scutellum, apical (longest thoracic seta) $\sim 1.4\times$ as long as laterobasal; 2 stpl but anterior reduced to very small setula, sometimes indistinct.

Legs brown to pale brown, coxae, trochanters and knees ochreous to yellow; fore coxa and all trochanters lightest, dirty yellow. Chaetotaxy: f_1 with a posterodorsal row of 6 or 7 shorter setae and a posteroventral row of 7 or 8 longer setae in addition to ventrobasal fine seta (Fig. 18). f_2 ventrally uniformly setulose but with 3 anterodorsal setae in distal third, including longest subapical seta (Fig. 20). t_2 (as in most European

congeners) ventrally with 1 short and weak seta below middle (in distal two-fifths), 1 longer (but also relatively short) va seta and 1 small anteroapical seta (see Fig. 20); dorsally with only 4 setae, viz. 1 anterodorsal seta in proximal third, 1 anterodorsal seta in distal third, 1 long dorsal (most robust) seta in distal sixth and 1 small postero-dorsal seta in distal fifth (Fig. 19). Hind leg, including f_3 , uniformly setulose. Ratio t_2 : $mt_2 = 2.17$ – 2.30 (holotype 2.17).

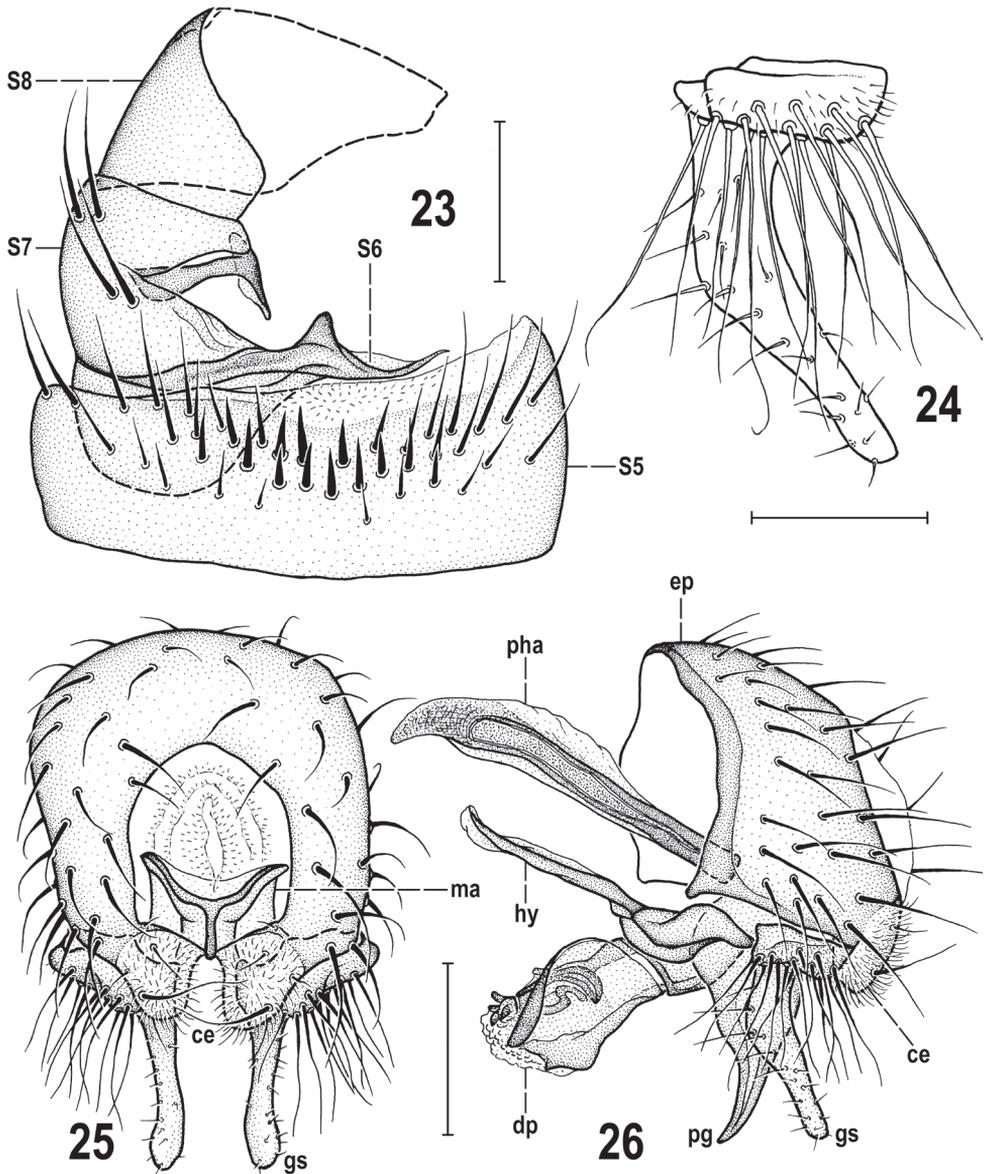
Wing (Figs 15, 22) strongly reduced, only ca. twice as long as scutellum, racket-shaped, with brownish membrane, most darkened around R_{2+3} and M; veins brown- to pale-pigmented. Distal radial and anal part of wing strongly reduced, thus R_{4+5} and A_1 entirely absent. Basal part of C (= Cs_1) well developed, including both breaks; distal part of C abbreviated (only Cs_2 developed) so that C only slightly produced beyond apex of R_{2+3} . Subcosta absent but presence of humeral (h) cross-vein indicated by darkened stump in front of humeral break (Fig. 22). Basal stem of radial veins robust but R_1 short, pale pigmented and poorly visible (Fig. 15); R_{2+3} dark brown, very slightly to distinctly upcurved to C. M present, dark brown, forming anterior remnant of discal cell (Figs 15, 22); CuA_1 strongly reduced, only indicated by a darkening near base of M. Anal lobe and hence also A_1 absent; alula distinct but very narrow. Wing measurements: length 0.36–0.52 (holotype 0.52) mm, width 0.18–0.26 (holotype 0.26) mm, Cs_1 : $Cs_2 = 1.80$ – 2.27 (holotype 1.80). Haltere present but strongly reduced (see Fig. 12), with knob entirely absent and stem shortened (length of haltere remnant 0.09–0.11 mm), dirty yellow.

Abdomen (Figs 12, 13) darker brown dorsally, paler (mainly anteriorly) brown ventrally. Preabdominal terga broad, transversely suboblong, and relatively shining because of sparse greyish brown microtomentum. T2–T5 sparsely but relatively long-setose, with longest setae in posterior corners and margins. T1+2 largest tergum, ~ 1.5× as long as T3, simply sclerotized (without medial depression) but original T1 pale brown to ochreous and distinctly delimited from original T2 (being dark brown) by a transverse wrinkle. T3–T5 subequal in length but becoming slightly narrower posteriorly, T5 smallest. Preabdominal sterna: S1+2 small, reduced to pale and bare poorly delimited sclerite; S3 and S4 subequal in length, relatively large and broad (becoming wider posteriorly), brown and well-sclerotized; both S3 and S4 transversely trapezoidal, narrower anteriorly, but S3 distinctly smaller than S4, the latter smaller and narrower than S5. S3 and S4 with shorter and finer setae than adjacent terga. S5 (Fig. 23) darker brown than S3 or S4, more transverse, slightly asymmetrical (longer on left), with short posterior submembranous, unpigmented and finely haired margin and with a transverse group of robust setae, those in the middle particularly thickened, spine-like. Postabdominal sclerites S6+7 and S8 forming a relatively long complex synsclerite situated left ventrolaterally to dorsolaterally (Fig. 23). S6+7 strongly asymmetrical, with various projections and placed ventrolaterally to laterally; S8 less asymmetrical and situated more dorsally. Synsclerite S6+7 with original S6 attenuated right ventrally and bearing a distinctive subtriangular posteromedial (in medial axis of abdomen) process (Fig. 23), left ventrally dilated, without setae; original S7 ventrolaterally incised and with unusual slender T-shaped projection arising near this incision and directed



Figures 18–22. *Pullimosina (Pullimosina) turfosa* sp. nov. (paratypes) **18** male fore leg without tarsus, posteriorly **19** male mid tibia, dorsally **20** male mid femur, tibia and basitarsus, anteriorly **21** female mid tibia and basitarsus, anteriorly **22** male right wing, dorsally. Scale bars: 0.2 mm (**18–21**); 0.1 mm (**22**).

right medially/internally (Fig. 23); left compact part of S7 with 2 pairs of relatively long and stout setae. S8 relatively simple, saddle-shaped, with only a few (3–5) shorter setae, mainly situated at posterior margin.



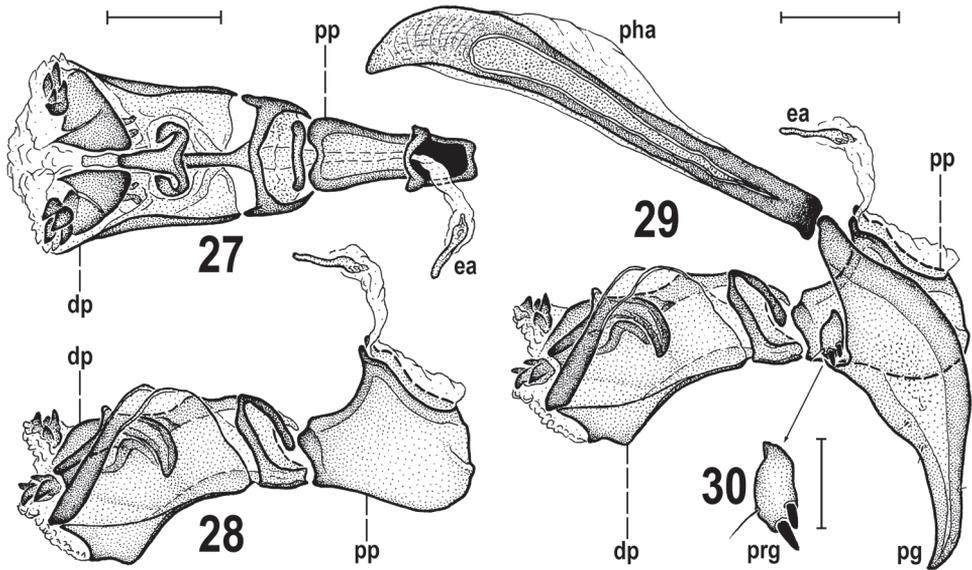
Figures 23–26. *Pullimosina (Pullimosina) turfosa* sp. nov. (male paratype) **23** S5 and postabdominal sclerites, ventrally **24** gonostylus, laterally **25** external genitalia, caudally **26** ditto, laterally. Scale bars: 0.1 mm (**23**, **25**, **26**); 0.05 mm (**24**). Abbreviations: ce – cercus, dp – distiphallus, ep – epandrium, gs – gonostylus, hy – hypandrium, ma – medandrium, pg – postgonite, pha – phallapodeme, S – sternum.

Genitalia: Epandrium (Figs 25, 26) of medium length and width, very slightly asymmetrical in caudal view (Fig. 25), rather uniformly setose (longest setae postero-ventrally but sometimes also 1 dorsolateral seta enlarged). Anal fissure not large,

roughly hexagonal, higher than wide (Fig. 25). Cerci short, fused with epandrium and medially forming subanal plate being ventromedially deeply narrowly incised (Fig. 25); each cercus with 1 longer and 2 or 3 short setae, micropubescent. Med-andrium subquadrate in caudal view but its posterior part Y-shaped, hence ventrally narrowed (Fig. 25), posteromedially fused with cerci and posteroventrally movably connected with gonostyli. Hypandrium roughly Y-shaped in dorsal view, with simple anteromedial rod-like apodeme, relatively robust paired lateral sclerites, and more medially with small sclerites connecting hypandrium with postgonites via remnants of pregonites. Gonostylus (Figs 24–26) very distinctive, of unusual (in *Pullimosina*) shape: dorsally with small and low lateral part overgrown with a tuft of long sinuous setae and some micropubescent; anteroventrally (and more medially) protruding into a slender and long, slightly bent, apically blunt and shortly setulose projection. Aedeagal complex (Figs 27–30). Phallapodeme distinctly longer and more robust than hypandrial apodeme, with well-developed dorsal keel. Aedeagus composed of compact, laterally flattened phalophore (Figs 27, 28) and relatively short distiphallus. Distiphallus basally with slender arcuate sclerite bent on lateral sides (Figs 27, 28) and dilated ventrally; the latter dorsally connected with slender sclerite projecting anteriorly where bearing small wing-like processes and longer medial projection almost reaching apex of distiphallus (Fig. 27); distal part of distiphallus formed by large trough-like lateroventral sclerite and by a pair of apical dorsal sclerites, each of which having a group of 4 or 5 short dark spines attached laterally (Figs 27, 28). Postgonite (Fig. 29) relatively large (somewhat longer than distiphallus) but simple, wider proximally and gradually tapered distally, slightly bent and with acute apex, with only 2 or 3 microsetae anteriorly and posteriorly in distal half and fourth, respectively. Remnant of pregonite (Figs 29, 30) forming small but distinct and separate sclerite situated in anterodorsal emargination of postgonite, possessing distally 2 short blunt spines and 1 setula (see Fig. 30). Ejacapodeme reduced, represented by small and very slender, rod-like but proximally somewhat dilated, sclerite (Figs 27, 30).

Female (Figs 31, 32). Similar to male unless mentioned otherwise below. Total body length 1.27–1.67 mm. Foremost ifr more robust, often almost as long as other ifr setae. t_2 with all macrosetae relatively longer, both ventrally (cf. ventroapical seta on Figs 20 and 21) and dorsally. mt_2 relatively (compared to t_2) longer (Fig. 21). Ratio $t_2: mt_2 = 1.92\text{--}2.09$. Wing (Fig. 17) slightly shorter on the average and often with more cut apex. Remnant of haltere also shorter, only 0.06–0.08 mm long. Wing measurements: length 0.36–0.43 mm, width 0.19–0.25 mm, $Cs_1: Cs_2 = 2.14\text{--}3.00$. Preabdominal terga somewhat shorter and more transverse (Fig. 32); T1+2 only slightly shorter than T3; T3–T5 becoming distinctly narrower posteriorly but similarly setose as in male. Preabdominal sterna S3–S5 sparsely and shortly setose, subequal in length and width. S5 unmodified, transversely suboblong, subequal to S4; preabdominal sterna S3–S5 brown, well sclerotized but paler than adjacent terga.

Postabdomen (Figs 34–36) relatively short and broad, with sparsely setose sclerites, narrower than preabdomen at 5th segment. T6 markedly narrower and only ca. half the length of T5, transverse, only slightly wider than S6, with both lateral and



Figures 27–30. *Pullimosina (Pullimosina) turfosa* sp. nov. (male paratype) **27** aedeagus (phallus) dorsally **28** ditto, laterally **29** aedeagal complex, laterally **30** pregonite (enlarged), laterally. Scale bars 0.05 mm (27–29), 0.02 mm (30). Abbreviations: dp – distiphallus, ea – ejacapodeme, pg – postgonite, pha – phallopodeme, pp – phallophore, prg – pregonite.

posterior margins pale and setose in posterior half (Fig. 34), setae at posterior margin long; T7 transversely suboblong, slightly shorter and seemingly narrower than T6 because bent farther onto lateral side (see Fig. 36), with pale posterior margin and 8 setae in single row of setae in front of it. T8 dorsomedially narrowly interrupted to form two lateral sclerites (Fig. 34), each dorsally shortened but ventrally expanded and longer than other postabdominal sclerites (Fig. 36) and bearing 1 long and a few short to small setae. T10 transversely pentagonal, distinctly wider than long, pale-pigmented, finely sparsely micropubescent and with a pair of relatively distant setae (see Fig. 34). S6 slightly narrower but distinctly ($0.7\times$ as long as) shorter than S5, and only slightly wider and more setulose than S7 (Fig. 35). S7 simple, transversely suboblong (as is S6), slightly wider than T6, with setae only at pale posterior margin. S8 (Figs 35, 37) transversely subellipsoid, much larger than S10 (in largest extension view, see Fig. 37), somewhat convex in the middle, posteriorly more rounded than anteriorly, with only 4 or 6 short setae centrally but with distinctive micropubescent. Additional sclerite unusual, situated behind and partly under S8 (its anterior part overlapped by S8, cf. Fig. 36, asc), narrowly trapezoidal but anteriorly membranous and hence its anterior margin undefined, largely bare, with only 4 setulae at posterior margin (Fig. 37). S10 slightly more than half length of S8, transversely pentagonal, pale pigmented, micropubescent and setulose only in posterior third, posteromedially with a pair of longer setae (Fig. 35). Spectacles-shaped sclerite



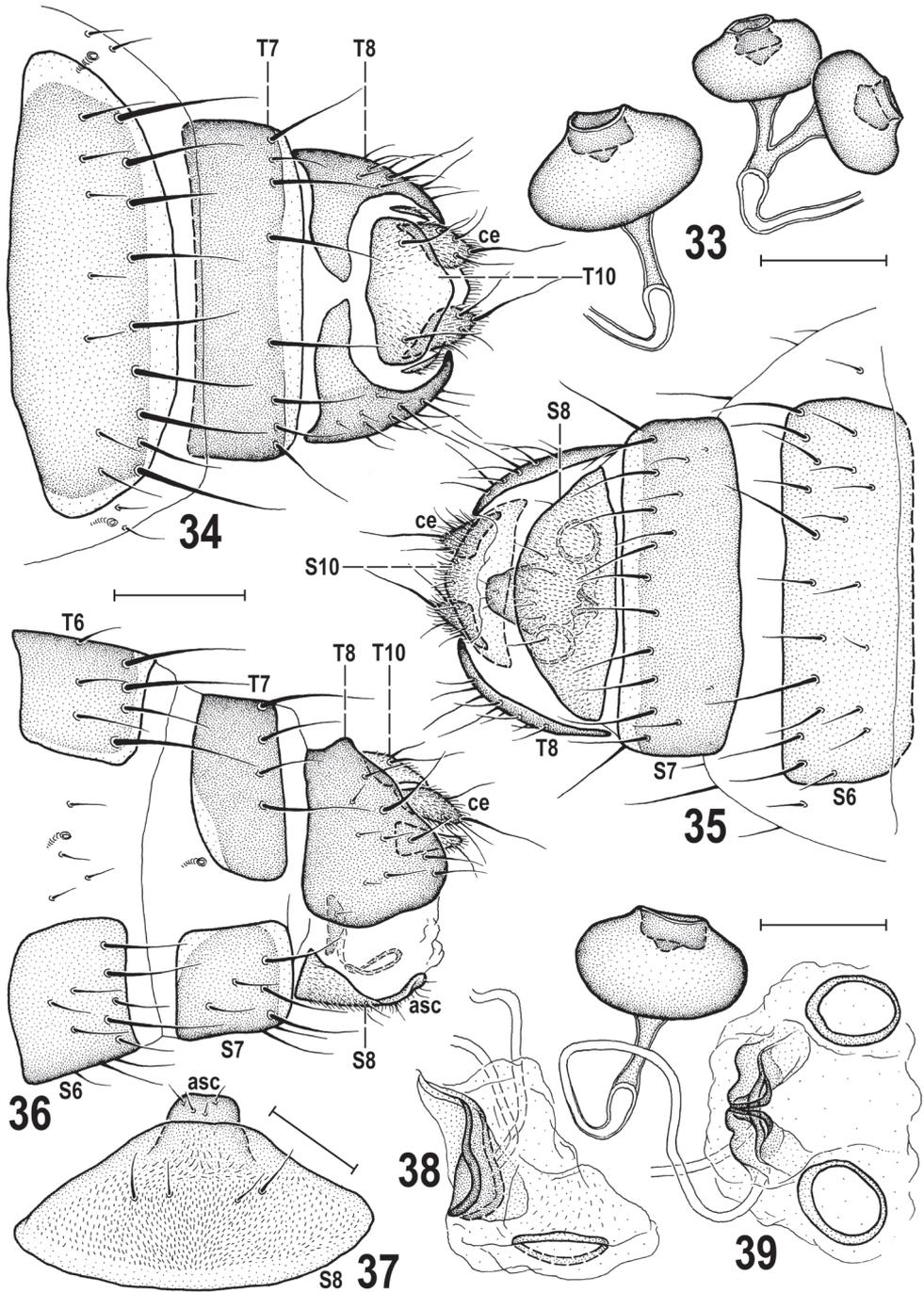
Figures 31–32. *Pullimosina (Pullimosina) turfosa* sp. nov. (female paratype) **31** whole body, dorsally **32** ditto, laterally. Scale bar: 0.5 mm.

(= sclerotization of female genital chamber) oriented rather vertically (Fig. 38, see in situ, Fig. 36), with rings of moderate size and its medial anterior sclerotization relatively complex (Fig. 39). Spermathecae 2+1 (Figs 33, 39), blackish brown; body

of single spermatheca distinctly larger than those of paired ones; each spermatheca of relatively robust tyre-shaped form, most resembling those of *P. moesta* (Villeneuve, 1918), with plain surface, terminal invagination somewhat widened internally and terminal parts of ducts well-sclerotized, slightly conically dilated towards insertion and ca. as long as body of spermatheca. Cerci (Figs 34–36) short but not robust, tapered both towards base and terminal seta, micropubescent, each with 4 or 5 setae, apical one longest (slightly longer than cercus) and sinuate as also is the shorter dorsopreapical seta.

Remarks. Despite a number of peculiarities in the male and female terminalia and unusual reduction of wing venation, *Pullimosina turfosa* sp. nov. clearly is a representative of the subgenus *Pullimosina* s. str. (Roháček 1983; Marshall 1986). However, it proved not to be closely related to any other described European (or Palaearctic) species of this subgenus (cf. Papp 1973; Roháček 1983; Hayashi 2006; Su 2011; Su et al. 2013; Roháček 2019). Based on structures of its male and female terminalia it surely belongs to the *Pullimosina antennata* group (as defined by Marshall 1986). Note: this group should be re-named to *P. moesta* group because *P. antennata* (Duda, 1918) is a junior synonym of *P. moesta* (Villeneuve, 1918), see Roháček (2001) and Roháček et al. (2001). *Pullimosina turfosa* shares all synapomorphic characters defining this group (cf. Marshall 1986: fig. 100), viz. the densely and long setose gonostylus, the distiphallus with spinose or toothed distal sclerites and a well-developed additional sclerite between female S8 and S10, except for his character 11 (middle interfrontal setae cruciate). Surprisingly, *P. turfosa* appears to have the male terminalia most similar to those of the macropterous Nearctic species *P. vockerothi* Marshall, 1986. The shared characters include (1) male S6 with a ventromedial process (Fig. 23, cf. Marshall 1986: fig. 79), (2) the gonostylus with long and slender anteroventral projection (Fig. 24, cf. Marshall 1986: fig. 77), and (3) similar shape of postgonite (Fig. 30, cf. Marshall 1986: fig. 78). The former two features (1, 2) could be considered synapomorphic and demonstrating a closer relationship of these species. Additionally, the female T8 and the spectacles-shaped sclerite seem to be similarly formed in *P. vockerothi* and *P. turfosa* (Figs 34, 39, cf. Marshall 1986: figs 38, 40) but T8 in *P. vockerothi* has a small medial strip-like sclerite in addition to large lateral sclerites and the female S8 and additional (acs) sclerite are markedly different in the shape and chaetotaxy (Fig. 37, cf. Marshall 1986: fig. 39). There are also distinct differences in the armature of the male S5 (Fig. 23, cf. Marshall 1986: fig. 79), shape of the gonostylus (having basal part very small and anteroventral projection simple in *P. turfosa*: Fig. 24, cf. Marshall 1986: fig. 77) and detailed structure of the distiphallus (Fig. 28, cf. Marshall 1986: fig. 78).

Pullimosina turfosa can be most easily recognized from all Holarctic *Pullimosina* species by its strongly abbreviated wings with very characteristic venation (Figs 15, 22). As for European species, the brachypterous form of the wing-polymorphic *P. meijerei* (Duda, 1918) externally most resembles this new species (cf. Roháček 2012: figs 3, 4) including coloration of the head but the wings of *P. meijerei* are less shortened,



Figures 33–39. *Pullimosina (Pullimosina) turfosa* sp. nov. (female paratype) **33** spermathecae **34** post-abdomen, dorsally **35** ditto, ventrally **36** ditto, laterally **37** S8 and additional sclerite, ventrally **38** spectacles-shaped sclerite, laterally **39** ditto and single spermatheca, ventrally. Scale bars: 0.1 mm (**34–36**); 0.05 mm (**33, 37–39**). Abbreviations: asc – additional sclerite, ce – cercus, S – sternum, T – tergum.

more elongate and with more complete venation (Roháček 2012: figs 24–27) not to mention very dissimilar structures of the male and female postabdomen (cf. Roháček 1985: figs 792–802).

The peculiar reduction of the wing and its veins in *P. turfosa* (Fig. 22) needs a special comment. It differs from all other cases of brachyptery known in West Palaearctic Sphaeroceridae (Roháček 2012) in having the distal part of wing strongly abbreviated while its basal part (up to subcostal break) is almost normal, R_{4+5} is completely absent (in this somewhat resembling the wing venation of *Aptilotus anapterus* (Papp & Roháček, 1981) from La Palma, Canary Is, which, however, has a small basal remnant of this vein retained) but simultaneously with M present. Thus, the reduction of veins in *P. turfosa* is somewhat intermediate between stages 5 and 6 as recognized by Roháček (2012: figs 39, 40).

Distribution. The species is known only from its type locality in Russia, North Ossetia (Caucasus Mts).

Biology. All specimens of the new species were collected on 17 and 18 August 2018 in a high-montane Chifandzar mire (Fig. 7), which is the highest (2289 m) and the largest (ca. 0.5 km²) of the mires under study. This mire is much more open and windier compared to the others.

All type specimens but one were collected from large *Sphagnum* hummocks (Fig. 8). This habitat is distinctive and represented only by nearly 15 hummocks all of which are located in the eastern part of the mire (Fig. 7: arrow). The hummocks are scattered over an area of ca. 100 × 50 m. Each hummock is 0.15–0.3 m high and 0.5–2 m wide. It consists mostly of loose thick cushion of *Sphagnum* (*S. teres* is predominant; *S. centrale* and *S. squarrosum* are common), with sparse shoots of *Carex* spp. and *Nardus stricta* and abundant remains of monocotyledons. The substrate of hummocks is dry to slightly wet, as distinct from moist or water-logged substrate on flat areas surrounding the hummocks and in other parts of the mire.

Most specimens were collected by means of sifting substrata of hummocks. Two females were collected by washing and subsequent flotation of substrate in NaCl solution: one specimen was sampled from the same habitat, and another one, from moist substrate beyond the hummocks, with predominating *Sphagnum subsecundum* and *Carex rostrata*. Hence, most individuals of *P. turfosa* concentrate in hummocks but some flies may also occur at some distance from them. No specimens were collected in early summer (2–3 June), suggesting that the adults of *P. turfosa* appear later.

Due to exclusive association of *P. turfosa* with the sphagnetum habitat, particularly with hummocks, we consider it a tyrphobiont (= eucoenic to peat-bog habitat) sphagnicolous species. Interestingly, no specimens of *P. turfosa* were collected from similar substrata in other bogs using the same techniques (sifting and washing/flotation). It is possible that the new peculiar species is confined to high montane bogs or even endemic to Chifandzar, considering that the montane bogs of the North Caucasus are rare and isolated island ecosystems.

Sphaeroceridae recorded from montane peat bogs in the North Caucasus

COPROMYZINAE (6 species)

- Borborillus uncinatus* (Duda, 1923)
Borborillus vitripennis (Meigen, 1830)
Copromyza equina Fallén, 1820
Lotophila atra (Meigen, 1830)
Norrbomia costalis (Zetterstedt, 1847)
Norrbomia sordida (Zetterstedt, 1847)

SPHAEROCERINAE (1 species)

- Ischiolepta nitida* (Duda, 1920)

LIMOSININAE (31 species)

- Chaetopodella scutellaris* (Haliday, 1836)
Coproica acutangula (Zetterstedt, 1847)
Coproica ferruginata (Stenhammar, 1855)
Coproica lugubris (Haliday, 1836)
Eulimosina ochripes (Meigen, 1830)
Gonioneura spinipennis (Haliday, 1836)
Leptocera fontinalis (Fallén, 1826)
Leptocera nigra Olivier, 1813
Leptocera oldenbergi (Duda, 1918)
Minilimosina (Minilimosina) fungicola (Haliday, 1836)
Minilimosina (Minilimosina) gemella Roháček, 1983
Minilimosina (Minilimosina) sp.
Minilimosina (Svarciella) pujadei Carles-Tolrá, 2001
Minilimosina (Svarciella) vitripennis (Zetterstedt, 1847)
Opacifrons coxata (Stenhammar, 1855)
Opalimosina (Opalimosina) mirabilis (Collin, 1902)
Opalimosina (Pappiella) liliputana (Rondani, 1880)
Phthitia (Kimosina) longisetosa (Dahl, 1909)
Pseudocollinella (Spinotarsella) humida (Haliday, 1836)
Pullimosina (Pullimosina) heteroneura (Haliday, 1836)
Pullimosina (Pullimosina) turfosa sp. nov.
Rachispoda hostica (Villeneuve, 1917)
Rachispoda lutoidea (Duda, 1938)
Spelobia clunipes (Meigen, 1830)
Spelobia czizeki (Duda, 1918)

Spelobia ibrida Roháček, 1983
Spelobia luteilabris (Rondani, 1880)
Spelobia parapusio (Dahl, 1909)
Spelobia rufilabris (Stenhammar, 1855)
Spelobia talparum (Richards, 1927)
Terrilimosina schmitzi (Duda, 1918)

Synopsis of species

COPROMYZINAE

Borborillus uncinatus (Duda, 1923) – TN

Material. Kubus-larger, sweep-netting, 9.v.2016, 1♂.

Comments. A largely coprophagous species, widespread in temperate and northern belt of the Palaearctic Region. Its occurrence on a peat bog is surely occasional due to attraction to some mammal excrement. There is a single previous record from two bogs in Wales (Holmes et al. 1992)

Borborillus vitripennis (Meigen, 1830) – TN

Material. Kubus-larger, sweep-netting, 9.v.2016, 1♂.

Comments. A coprophagous Palaearctic species, mainly associated with horse dung on pastures. There are only scarce records from peat bogs in England (Drake et al. 1989) and Estonia (Elberg 1971). It was captured together with the above species for the same reason.

Copromyza equina Fallén, 1820 – TN

Material. Kurnoyatsu-1, wet habitat (lake margin), sweep-netting, 6.vi.2018, 2♂.

Comments. A subcosmopolitan coprophagous species, occurring on (preferably horse) dung on pastures but also on manure. Also known to sometimes occur on peat bogs in Great Britain (Nelson 1971, 1981, 1982; Pitkin et al. 1985; Drake et al. 1989; Holmes et al. 1992) and Estonia (Elberg 1971), and was found on red-deer excrement on mires in the Czech Republic (Roháček 1984).

Lotophila atra (Meigen, 1830) – TN

Material. Kurnoyatsu-2, dry habitat (*Sphagnum fuscum*), sweep-netting, 7.vi.2018, 1♀; wet habitat (lake margin), 7.vi.2018, 1♀. Tarskoe, sweep-netting, 10.v.2016, 1♀; same but 1.vi.2018, 1♂; same but 11.ix.2018, 2♂.

Comments. A Holarctic, predominantly coprophagous, species, common on various animal dung. Although repeatedly recorded from several peat bogs in Europe (e.g., Peus 1928; Elberg 1969, 1971; Nelson 1971, 1981, 1982; Roháček 1984; Pitkin et al. 1985; Kuznetsova 1987; Drake et al. 1989; Holmes et al. 1992; Roháček and Barták 1999; Stuke and Roháček 2019) it has no closer affinity to peat-bog habitats because it is only attracted to various excrement, including droppings of voles (Roháček 1984).

Norrbomia costalis (Zetterstedt, 1847) – TN

Material. Chifandzar, sweep-netting 2 (daytime/sun), 18.vi.2018, 1 specimen (damaged, without abdomen); sweep-netting 1 (evening/rain), 17.ix.2018, 1♂ 1♀ (1♂ dry, genit. prep.).

Comments. A West Palaearctic coprophagous species, associated with (preferably horse) excrement on pastures. Formerly only recorded from a peat bog in Wales (Holmes et al. 1992).

Norrbomia sordida (Zetterstedt, 1847) – TN

Material. Tarskoe, sweep-netting, 10.v.2016, 1♂ (dry, genit. prep.).

Comments. Originally a Holarctic (introduced to Neotropical, Oriental, and Oceanian Regions) coprophagous species, mainly occurring on dung of hoofed animals. There is no previous record from peat bogs.

SPHAEROCERINAE

Ischiolepta nitida (Duda, 1920) – TPH?

Material. Kurnoyatsu-2, wet habitat (lake margin), sweep-netting, 7.vi.2018, 1♂ (genit. prep.).

Comments. A Palaearctic saprophagous (mainly coprophagous) species preferentially occurring in humid places in open and woodland habitats at higher altitudes. It seems to have distinct affinity to bog habitats and was recorded from peat bogs in England (Nelson 1971), Central Europe (Pax 1937; Roháček 1984; Roháček and Barták 1999), and Latvia (Kuznetsova 1987). It was classified as a tyrphophilous species by Roháček (1984) and Roháček and Barták (1999).

LIMOSININAE

Chaetopodella scutellaris (Haliday, 1836) – TN

Material. Tarskoe, sweep-netting, 11.ix.2018, 1♂.

Comments. A common, largely coprophagous species, widespread in the Palaearctic Region, most common on dung on pastures. Although it is known to occur on various peat bogs (Peus 1928; Rabeler 1931; Pitkin et al. 1985; Holmes et al. 1992; Roháček and Barták 1999), often on red-deer droppings (Roháček 1984) it was treated as a tyrphoneutral species both by Roháček (1984) and Roháček and Barták (1999).

Coproica acutangula (Zetterstedt, 1847) – TN

Material. Kurnoyatsu-1, dry habitat (*Sphagnum magellanicum*), sweep-netting, 6.vi.2018, 1♀; same but 22.ix.2018, 2♀.

Comments. A widespread (subcosmopolitan) coprophagous species associated with (mainly horse) dung on pastures. Records from bog habitats are very sporadic (Holmes et al. 1992; Stuke and Roháček 2019).

Coproica ferruginata (Stenhammar, 1855) – TN

Material. Kurnoyatsu-2, wet habitat (lake margin), sweep-netting, 7.vi.2018, 1♂.

Comments. A cosmopolitan coprophagous species, very common on dung. Although repeatedly recorded from peat bogs and similar mire habitats in Europe (e.g., Nelson 1971; Doskočil 1973; Roháček 1984; Pitkin et al. 1985; Holmes et al. 1992; Roháček and Barták 1999; Stuke and Roháček 2019) it is classified as tyrphoneutral (Roháček 1984) because it is ubiquitous, occurring in any habitat with dung and other decaying matter.

Coproica lugubris (Haliday, 1836) – TN

Material. Tarskoe, sweep-netting, 1.vi.2018, 1♀.

Comments. Another widespread (in the Palaearctic and Oriental Regions) coprophagous species, common on dung in pastures. It has been only occasionally recorded from peat bogs in Europe (Roháček 1984; Holmes et al. 1992; Roháček and Barták 1999; Stuke and Roháček 2019), mainly on excrement of ungulates.

Eulimosina ochripes (Meigen, 1830) – TN

Material. Kurnoyatsu-2, wet habitat (lake margin), sweep-netting, 7.vi.2018, 1♀. Tarskoe, sweep-netting, 11.ix.2018, 1♀.

Comments. A Holarctic phytosaprophagous species, mainly living on meadows. There are records from lagg meadows of peat bogs in England (Nelson 1981), Wales

(Holmes et al. 1992), Central Europe (Doskočil 1973; Roháček 1984), and Estonia (Elberg 1971), and, therefore, Roháček (1984) classified it as a tyrphoneutral species.

Gonioneura spinipennis (Haliday, 1836) – TN

Material. Kurnoyatsu-1, dry habitat (*Sphagnum magellanicum*), sweep-netting, 6.vi.2018, 1♀; same habitat, yellow pan traps, 6-8.vi.2018, 1♂; wet habitat (lake margin), sweep-netting, 6.vi.2018, 1♂; same but 7.vi.2018, 1♂. Kurnoyatsu-2, wet habitat (lake margin), sweep-netting, 7.vi.2018, 1♂. Chifandzar, wet habitat (*Sphagnum subsecundum*), sample Ч 2, 3.vi.2018, 1♀. Tarskoe, sweep-netting, 10.v.2016, 1♂ 1♀.

Comments. A common Holarctic polysaprophagous species, mainly living on dung. In Central Europe it is relatively frequent on peat bogs (Doskočil 1973; Roháček 1984; Roháček and Barták 1999; Stuke and Roháček 2019) but was found on mires also in Britain (Nelson 1971; Pitkin et al. 1985; Holmes et al. 1992). This ubiquitous species is classified as tyrphoneutral (see also Roháček 1984).

Leptocera fontinalis (Fallén, 1826) – TN

Material. Kurnoyatsu-1, dry habitat (*Sphagnum magellanicum*), sweep-netting, 6.vi.2018, 1♀; wet habitat (lake margin), sweep-netting, 6.vi.2018, 2♀. Kubus-smaller, sweep-netting (2), 14.ix.2018, 1♀.

Comments. A Holarctic saprophagous species, occurring in various humid habitat, mainly on decaying vegetation. Only Rabeler (1931); Nelson (1971); Pitkin et al. (1985); Drake et al. (1989), and Holmes et al. (1992) recorded it from peat bogs in Europe.

Leptocera nigra Olivier, 1813 – TN

Material. Kurnoyatsu-2, wet habitat (lake margin), sweep-netting, 7.vi.2018, 1♂. Ushtulu, sweep-netting, 21.ix.2018, 1♀. Kubus-larger, sweep-netting, 4.vi.2018, 1♂; same but 14.ix.2018, 3♂ 2♀. Kubus-smaller, sweep-netting, 4.vi.2018, 1♂; same but 12.ix.2018, 2♂.

Comments. A very common species, widespread in the Old World but also introduced to Venezuela in the Neotropical Region (Buck and Marshall 2009). Polysaprophagous, associated with open habitats. Roháček (1984) considered it tyrphoxenous but later on it has been recorded from several peat bogs in Central Europe (Roháček and Barták 1999; Stuke and Roháček 2019) and Great Britain (Holmes et al. 1992); therefore, it has been re-classified as tyrphoneutral (cf. Roháček and Barták 1999).

****Leptocera oldenbergi* (Duda, 1918) – TN**

Material. Kurnoyatsu-1, dry habitat (*Sphagnum magellanicum*), sweep-netting, 6.vi.2018, 1♀ (genit. prep.). Kurnoyatsu-2, wet habitat (lake margin), sweep-netting, 7.vi.2018, 1♀.

Comments. A rare species known from temperate Europe (Belgium, Czech Republic, Denmark, Germany, Great Britain, Hungary, Ireland, Latvia, Netherlands, Slovakia, Sweden, Switzerland) but also recorded from Georgia (Roháček et al. 2001; Marshall et al. 2011). It is recorded for the first time from Russia. The species is usually found in undisturbed woodland habitats, often in runs of small mammals (Roháček 1982a) but hitherto unrecorded from peat bogs. Its surprising occurrence in Caucasian montane peat bogs could be due to presence of burrows of small mammals in bogs under study.

****Minilimosina (Minilimosina) fungicola* (Haliday, 1836) – TN**

Material. Kurnoyatsu-3, *Sphagnum*/sedge floating shores of lake, sweep-netting, 7.vi.2018, 2♀ (genit. prep.).

Comments. A Holarctic polysaprophagous species, habitat- and altitude-tolerant. It was recorded from mire habitats in England (Nelson 1971; Pitkin et al. 1985), Wales (Holmes et al. 1992), Central Europe (Roháček 1984; Roháček and Barták 1999; Stuke and Roháček 2019), and Latvia (Kuznetsova 1987). The above records seem to be the first from Russia (cf. Marshall et al. 2011).

****Minilimosina (Minilimosina) gemella* Roháček, 1983 – TN?**

Material. Kurnoyatsu-2, dry habitat (*Sphagnum fuscum*), sweep-netting, 7.vi.2018, 1♂ 1♀ (genit. prep.).

Comments. Also Holarctic, but essentially a Boreo-montane species, with a few records from Europe (cf. Marshall et al. 2011). First record from Russia. Although probably polysaprophagous as a larva, there is only a single previous record from peat bogs in Central Europe, viz. from the montane raised bog at Keprník-Vozka in the Hrubý Jeseník Mts, Czech Republic (Roháček 1984) but Pitkin et al. (1985) and Holmes et al. (1992) reported it from several bogs in England and Wales respectively.

Minilimosina (Minilimosina) sp.

Material. Chifandzar, sweep-netting 2, 18.vi.2018, 1♀ (genit. prep.).

Comments. Based on structures of the female postabdomen, this specimen cannot be associated with any of *Minilimosina* (s. str.) species known from Europe. It could

either be conspecific with some of the poorly characterized species described by Papp (1973, 1974) from Mongolia or belongs to an undescribed species. More material is necessary to solve the identity of this species.

****Minilimosina (Svarciella) pujadei* Carles-Tolrá, 2001 – TN?**

Material. Kubus-larger, sweep-netting, 9.v.2016, 1♂ (dry, genit. prep.).

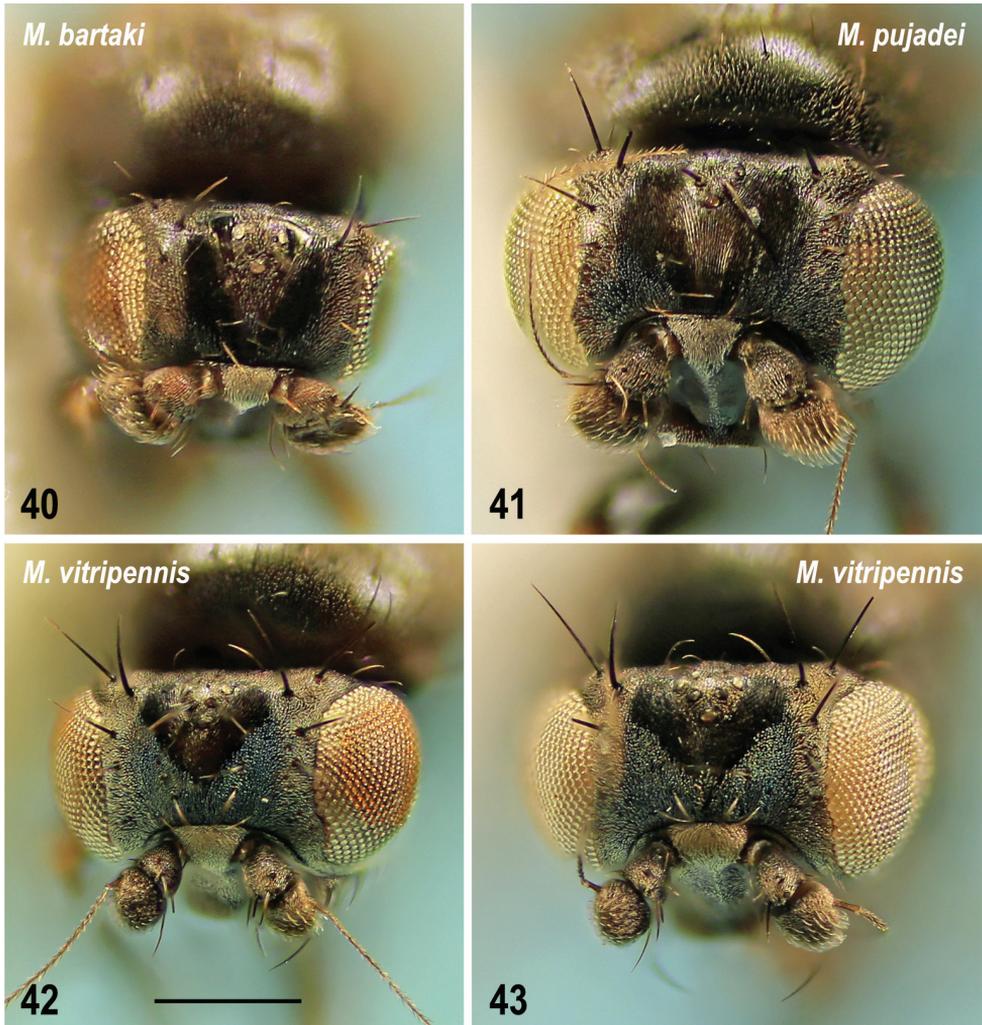
Comments. Apart from the above new *Pullimosina* species, this species is the most surprising finding from the Caucasian peat bogs. It was described from a single male captured in a Malaise trap near a forest and a river at 1050 m in Andorra (Carles-Tolrá 2001) and subsequently recorded from the Podyjí National Park (Czech Republic: South Moravia), where another male was collected in pan traps installed in a forest-steppe habitat at only ca. 340 m (Roháček et al. 2005). The above finding (of a third known specimen) is the first from Russia and a new easternmost record of the species. Biology of *M. pujadei* remains unknown but considering the diversity of the recorded habitats (montane forest, forest-steppe, peat bog, Fig. 10) it seems to be an eurytopic, albeit extremely rare, species.

Taxonomic notes. Owing to this surprising record, the Caucasian specimen has been compared to a male of *M. pujadei* from the Czech Republic (redescribed by Roháček 2010) including terminalia and pattern of frons. Conspecificity of both specimens has been confirmed. The heads of all three European species of the *M. (S.) vitripennis* group have been photographed to demonstrate distinct differences in their frontal microtomentose pattern. *Minilimosina pujadei* has the frons more similarly microtomentose to that of *M. bartaki* Roháček, 2010 while that of *M. vitripennis* differs from both these species in having frontal triangle smaller, forming a glabrous cordate spot surrounded by bluish silvery grey microtomentum (Figs 42, 43). *Minilimosina pujadei* (Fig. 41) can be distinguished from *M. bartaki* (cf. Fig. 40) by some bluish silvery grey microtomentum laterally at the anterior frontal margin and by fine longitudinal microsculpture medially in front of ocellar triangle (Fig. 41). Moreover, it also differs in having some microtomentum on the face (at least on medial carina and at ventral margin) while the face of *M. bartaki* is bare and shining.

***Minilimosina (Svarciella) vitripennis* (Zetterstedt, 1847) – TN**

Material. Kurnoyatsu-1, wet habitat (lake margin), sweep-netting, 6.vi.2018, 1♀ (dry, genit. prep.). Kurnoyatsu-2, dry habitat (*Sphagnum fuscum*), sweep-netting, 7.vi.2018, 1♂ (genit. prep.); same habitat, yellow pan traps, 7-8.vi.2018, 1♂ (genit. prep.). Kurnoyatsu-3, *Sphagnum*/sedge floating shores of lake, sweep-netting, 7.vi.2018, 1♂. Kubus-larger, sweep-netting, 4.vi.2018, 1♂ 2♀.

Comments. A Holarctic polysaprophagous species associated with various, mainly open, habitats (meadows, pastures etc.). There are also a few records from mire habitats



Figures 40–43. Heads of *Minilimosina* (*Svarciella*) species, frontally **40** *M. (S.) bartaki* Roháček, 2010, male paratype (Czech Republic) **41** *M. (S.) pujadei* Carles-Tolrá, 2001, male (Caucasus) **42** *M. (S.) vitripennis* (Zetterstedt, 1847), female (Czech Republic) **43** Ditto, female (Caucasus). Scale bar 0.2 mm.

in England (Nelson 1971, as *Leptocera fungicola*, Pitkin et al. 1985), Wales (Holmes et al. 1992), and Central Europe (Roháček 1984; Roháček and Barták 1999; Stuke and Roháček 2019).

Taxonomic notes. A female with enlarged glabrous frontal triangle (Fig. 43) similar to that described for the holotype of *Limosina paravitripennis* Papp, 1973 (Mongolia), has been also studied for postabdominal structures and compared to those of typical specimens of *M. (S.) vitripennis* from other parts of Europe. This examination resulted in finding that although this female from the Caucasus surely is conspecific (see below) with other European specimens, the ventral postabdominal sclerites (S8

and S10 in particular) seem to differ from those figured for this species in the revision by Roháček (1982b: fig. 190). The latter illustration proved to be somewhat simplified and, therefore, the postabdominal sterna of *M. vitripennis* are here newly illustrated and described for both Caucasian (Fig. 45) and the Czech specimens (Fig. 44): S8 is distinctly transversely darkened at posterior margin (Figs 44, 45) while its large anterior part is pale-pigmented; S10 (subanal plate) (Figs 44, 45) is distinguished by angularly separated and darkened anterolateral areas, while its main (posterior) part is posteriorly rounded and densely micropubescent; this micropubescent is also expanded anteromedially, between darkened anterolateral areas; S10 is otherwise with several marginal setae, 2 pairs of them are long, often longer than the longest setae on S7 and S8. True, the female from the Caucasus has S10 more angular anterolaterally (Fig. 45) but this aberration is considered to fall within the variability of *M. vitripennis* as is its enlarged frontal triangle. Roháček and Marshall (1988) reached the same conclusion when they synonymized *Limosina paravitripennis* Papp, 1973 with *M. (S.) vitripennis*.

Opacifrons coxata (Stenhammar, 1855) – TN

Material. Kurnoyatsu-1, wet habitat (lake margin), sweep-netting, 6.vi.2018, 1♀; same habitat, yellow pan traps, 6-8.vi.2018, 1♂. Kurnoyatsu-2, wet habitat (lake margin), sweep-netting, 7.vi.2018, 1♀. Ushtulu, sweep-netting, 21.ix.2018, 1♂.

Comments. A common Palaearctic species associated with mud on shores of water bodies and in marshland habitats. It is eurytopic and, therefore, able to live on peat mud in mires (see Rabeler 1931; Doskočil 1973; Roháček 1984; Pitkin et al. 1985; Kuznetsova 1987; Drake et al. 1989; Holmes et al. 1992; Roháček and Barták 1999; Stuke and Roháček 2019). Due to its occurrence in various muddy habitats it is considered a typhlophagous species.

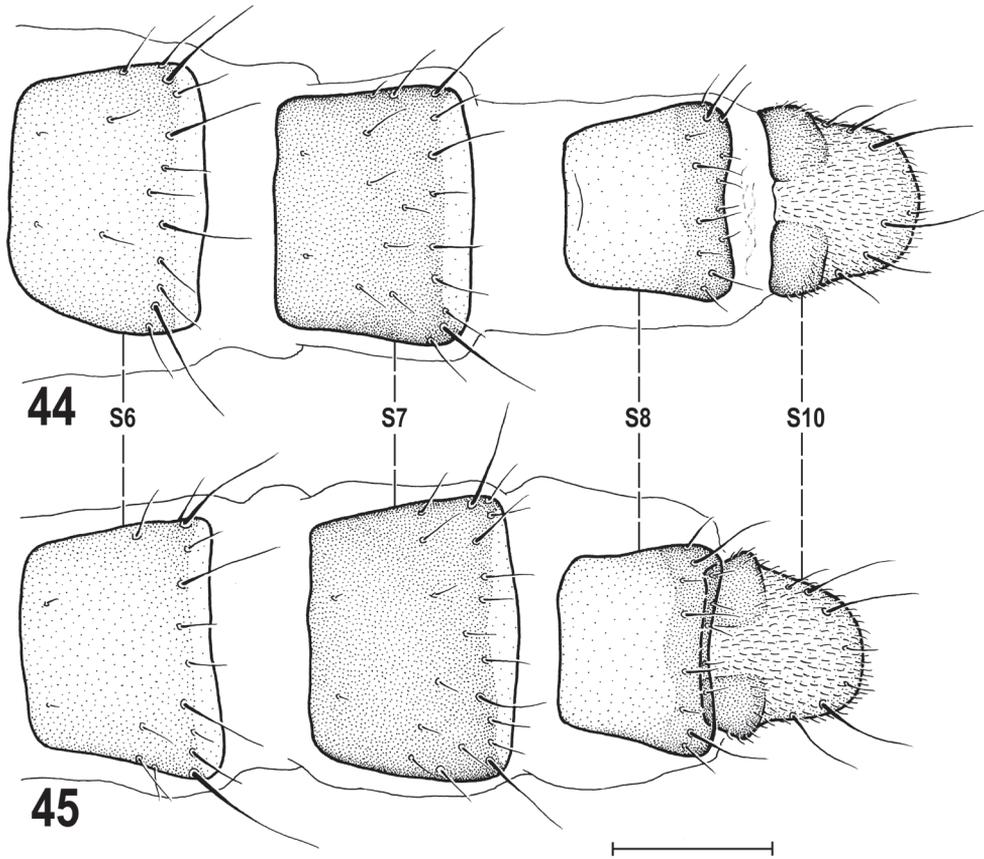
Opalimosina (Opalimosina) mirabilis (Collin, 1902) – TN

Material. Kurnoyatsu-2, wet habitat (lake margin), sweep-netting, 7.vi.2018, 1♀.

Comments. A subcosmopolitan ubiquitous, predominantly coprophagous species. It is extremely habitat-tolerant and, therefore, can also occur on various excrement on peat bogs; see e.g., Nelson (1971); Doskočil (1973); Roháček (1984); Holmes et al. (1992); Roháček and Barták (1999), and Stuke and Roháček (2019).

Opalimosina (Pappiella) liliputana (Rondani, 1880) – TN

Material. Kurnoyatsu-1, wet habitat (lake margin), sweep-netting, 6.vi.2018, 1♂ 1♀ (genit. prep.). Kurnoyatsu-2, dry habitat (*Sphagnum fuscum*), sweep-netting, 7.vi.2018, 1♂.



Figures 44–45. *Minilimosina (Svarciella) vitripennis* (Zetterstedt, 1847), female postabdominal sterna, ventrally **44** female from the Czech Republic **45** female from the Caucasus. Scale bar 0.1 mm. Abbreviations: S – sternum.

Comments. A Holarctic and widely habitat-tolerant species developing in various decaying substrates. In Europe, it was sporadically recorded also from mire habitats, viz. by Nelson (1971); Roháček (1984); Pitkin et al. (1985); Holmes et al. (1992), and Roháček and Barták (1999).

***Phthitia (Kimosina) longisetosa* (Dahl, 1909) – TPH?**

Material. Chifandzar, dry habitat (*Sphagnum teres* hummocks), sifting, 18.ix.2018, 1♀ (genit. prep.).

Comments. A rather rare West Palearctic species with poorly known biology, usually occurring in damp meadows, fens and humid forests, sometimes in burrows of small mammals (cf. Roháček 1983), in Russia only known from an old record from West Siberia (Duda 1938). Interestingly, the species was described from a single female

captured in “Torfmoos” (= peat moss) in a raised bog in Germany (Dahl 1909). Peus (1928, 1932) and Stuke and Roháček (2019) also recorded it from raised peat bogs in Germany, Pitkin et al. (1985) from peatlands in England and Holmes et al. (1992) found it fairly frequent in Welsh peatlands. Consequently, although hitherto unknown from peat bogs in the Czech Republic (Roháček 1984; Roháček and Barták 1999), this species may have a distinct affinity to bog habitats (as suggested by Peus 1932). The above specimen (peculiar for its unusually small size: body length only 1.5 mm) has been sifted from *Sphagnum teres* hummocks together with the type series of *Pullimosina turfosa* sp. nov.

***Pseudocollinella (Spinotarsella) humida* (Haliday, 1836) – TN**

Material. Kurnoyatsu-2, wet habitat (lake margin), sweep-netting, 24.ix.2018, 1♀. Kubus-smaller, sweep-netting, 4.vi.2018, 1♀.

Comments. A common paludicolous species, widespread in the Palaearctic Region. It is associated with muddy habitats and is also known to live on peat bogs in Europe (Elberg 1971; Nelson 1982; Nelson and Theaker 1982; Roháček 1984; Drake et al. 1989; Holmes et al. 1992; Roháček and Barták 1999; Stuke and Roháček 2019) although peat mud surely is not its preferred habitat.

***Pullimosina (Pullimosina) heteroneura* (Haliday, 1836) – TN**

Material. Kurnoyatsu-1, wet habitat (lake margin), sweep-netting, 6.vi.2018, 1♂. Tar-skoe, 10.v.2016, sweep-netting, 1♀.

Comments. A cosmopolitan, eurytopic polysaprophagous species, common on various rotting substrates but records (of only single specimens) from peat bogs are scarce (Roháček 1984; Pitkin et al. 1985; Holmes et al. 1992; Roháček and Barták 1999; Stuke and Roháček 2019).

****Pullimosina (Pullimosina) turfosa* sp. nov. – TB**

Material. Chifandzar, dry habitat (*Sphagnum teres* hummocks), sample Ч 14, 17.ix.2018, 1♀; same habitat, sifting, 18.ix.2018, 6♂ 5♀; wet habitat (*Sphagnum subsecundum*), sample Ч 9, 17.ix.2018, 1♀ (see also type material above; some with genit. prep.)

Comments. This new terricolous and strongly brachypterous species (described above) is surely tyrphobiont, i.e., exclusively associated with peat-bog habitat, because living in *Sphagnum* hummocks (Fig. 8). Its habitat is thus very similar to that of the circumboreal Boreo-montane tyrphobiont species *Pullimosina (Dablimosina) dabli* (Duda, 1918) (cf. Roháček 1984, Roháček and Barták 1999). Because the latter species nor any other tyrphobiont species of Sphaeroceridae known from

Europe (see Roháček and Barták 1999) have been found in the peat bogs under study, *P. turfosa* sp. nov. is currently the only true tyrphobiont sphaerocerid recorded from the Caucasus.

***Rachispoda hostica* (Villeneuve, 1917) – TX?**

Material. Kurnoyatsu-2, wet habitat (lake margin), sweep-netting, 7.vi.2018, 1♀ (genit. prep.).

Comments. An uncommon Palaearctic species (but unrecorded from most of Western Europe and North Africa) with easternmost records from Mongolia (Roháček 1991) and known from the Caucasus (Papp 1979). Adults occur on mud on shores or in marshy habitats (also in mountains) but there is no previous record from peat bogs. Consequently, we consider the above record rather exceptional.

***Rachispoda lutosoidea* (Duda, 1938) – TN**

Material. Tarskoe, sweep-netting, 30.v.2018, 1♂.

Comments. A common West Palaearctic species (also recorded from the Caucasus, cf. Roháček 1991) living on mud in various open and woodland habitats. In contrast to related and more eurytopic *R. lutosa* (Stenhammar, 1855) it seems to occur on peat mud rarely: there is only one previous record from a montane peat bog in the Czech Republic (Roháček 1984, 1991).

***Spelobia clunipes* (Meigen, 1830) – TN**

Material. Kurnoyatsu-1, wet habitat (lake margin), sweep-netting, 6.vi.2018, 2♀. Kurnoyatsu-2, dry habitat (*Sphagnum fuscum*), sweep-netting, 7.vi.2018, 3♀; wet habitat (lake margin), sweep-netting, 7.vi.2018, 2♀; wet *Sphagnum* habitat (lake margin), yellow pan traps, 7-8.vi.2018, 2♂. Kurnoyatsu-3, *Sphagnum*/sedge floating shores of lake, sweep-netting, 7.vi.2018, 1♂ 2♀ (genit. prep.). Kubus-larger, sweep-netting, 4.vi.2018, 2♂; sweep-netting (2), 14.ix.2018, 1♀. Tarskoe, sweep-netting, 10.v.2016, 6♂ 5♀ (genit. prep.).

Comments. A very common, eurytopic and polysaprophagous Holarctic species. Because of its wide habitat and trophic tolerance, it was often recorded from peat bogs in Europe (e.g., Krogerus 1960; Nelson 1971; Doskočil 1973; Roháček 1984; Pitkin et al. 1985; Drake et al. 1989; Holmes et al. 1992; Roháček and Barták 1999; Stuke and Roháček 2019). It has also been frequently encountered in peat bogs in the Caucasus.

***Spelobia czizeki* (Duda, 1918) – TN**

Material. Kurnoyatsu-1, dry habitat (*Sphagnum magellanicum*), sweep-netting, 6.vi.2018, 1♂ (genit. prep.). Kurnoyatsu-3, *Sphagnum*/sedge floating shores of lake, sweep-netting, 7.vi.2018, 1♀.

Comments. A rather uncommon polysaprophagous Palaearctic species associated with various subterranean habitats (Roháček 1983). It has not been previously recorded from peat bogs. Its finding in the Caucasian peat bogs is surely due to the presence of burrows of small mammals in the localities listed above.

****Spelobia ibrida* Roháček, 1983 – TPH**

Material. Kubus-larger, sweep-netting, 14.ix.2018, 1♀. Kubus-smaller, sweep-netting, 14.ix.2018, 1♂ (genit. prep.).

Comments. An uncommon phytosaprophagous species known from montane regions of Central and South Europe (Roháček et al. 2001) but also reported from peatlands in Canada (Marshall 1994). First records from Russia. The species was recorded from wet montane forests (Roháček 1983) and from a few peat bogs (Roháček 1983, 1984; Roháček and Barták 1999) in the Czech Republic and is, therefore, treated as tyrphophilous by the latter authors.

***Spelobia luteilabris* (Rondani, 1880) – TN**

Material. Kurnoyatsu-2, dry habitat (*Sphagnum fuscum*), sweep-netting, 7.vi.2018, 1♂ (genit. prep.).

Comments. A polysaprophagous, habitat- and altitude-tolerant, originally Holarctic species. It is also known from some European peat bogs (Nelson 1971; Doskočil 1973; Roháček 1984; Pitkin et al. 1985; Holmes et al. 1992; Roháček and Barták 1999).

***Spelobia parapusio* (Dahl, 1909) – TN**

Material. Kurnoyatsu-2, dry habitat (*Sphagnum fuscum*), yellow pan traps, 22–24.ix.2018, 1♂ (genit. prep.). Kubus-smaller, yellow pan traps, 12–14.ix.2018, 1♂. Tarskoe, sweep-netting, 11.ix.2018, 1♂.

Comments. An originally Palaearctic mycophagous species developing in sporocarps of various terrestrial macrofungi, mainly in woodland. It is parthenogenetic in Central and North Europe but bisexual in southern parts of the Palaearctic Region. *Spelobia parapusio* was described from 1♀ collected in *Sphagnum* on a raised bog in Germany (Dahl 1909) and subsequently recorded from several peat bogs (mostly on

fungi) in the Czech Republic (Roháček 1984; Roháček and Barták 1999) and Latvia (Kuznetsova 1987). It is peculiar that in the Caucasian peat bogs under study only males have been captured.

***Spelobia rufilabris* (Stenhammar, 1855) – TN**

Material. Kubus-smaller, sweep-netting (1), 12.ix.2018, 1♀; same bog, yellow pan traps, 12–14.ix.2018, 1♂ (genit. prep.).

Comments. A phytosaprophagous Palaearctic species living mainly in colder and humid montane forests but (less frequently) also occurring on peat bogs (Elberg 1969, 1971; Nelson 1971; Roháček 1984; Pitkin et al. 1985; Holmes et al. 1992; Roháček and Barták 1999; Stuke and Roháček 2019). First record from southern European Russia (cf. Marshall et al. 2011).

***Spelobia talparum* (Richards, 1927) – TN**

Material. Kubus-smaller, sweep-netting (1), 12.ix.2018, 1♀ (genit. prep.).

Comments. A common microcavernicolous species, widespread in the Palaearctic Region. It is polysaprophagous and inhabits subterranean nests and runs of mammals. There are several records from peat bogs in the Czech Republic (Roháček 1984; Roháček and Barták 1999), in England (Pitkin et al. 1985), and in Wales (Holmes et al. 1992). Roháček (1984) mentioned regular occurrence of this species in runs of *Microtus agrestis* in this habitat. The above record from a montane bog in the Caucasus indicates the presence of voles in this locality.

***Terrilimosina schmitzi* (Duda, 1918) – TN**

Material. Kubus-smaller, sweep-netting, 4.vi.2018, 1♂ (genit. prep.).

Comments. A widespread Holarctic species associated with forest litter in humid montane woodland. It was also ascertained in peat bogs in Wales (Holmes et al. 1992), the Czech Republic (Roháček 1984; Roháček and Barták 1999), and Latvia (Kuznetsova 1987), usually in marginal parts of bogs.

Discussion and conclusions

A total of 38 species of Sphaeroceridae has been found in eight montane and submontane mires of the North Caucasus. Sphaeroceridae appeared to be rather diverse but not abundant in the insect fauna of these mires, as compared to members of many other dipteran families, which were much more common. Extensive sampling with

seven main techniques provided only 119 specimens of Sphaeroceridae. Most Sphaeroceridae species (31) were represented only by 1–3 specimens; most species (32) were found only in one or two mires. Only one species, *Spelobia clunipes*, was relatively common and, at the same time, it was recorded from the highest number of mires (5 of 8). The highest species number (17) was recorded in the habitat-diverse Kurnoyatsu-2, the lowest (2–5), in the most uniform and largest fens of Ushtulu and Chifandzar and in a relatively uniform small mire Kurnoyatsu-3.

Because Sphaeroceridae are usually partly or wholly neglected in studies on insect communities of peat bogs (see Introduction), the above results obtained on the Caucasian mires can only be compared with those from more detailed investigations of this family in the Czech Republic (Roháček 1984; Roháček and Barták 1999) and Wales (Holmes et al. 1992), and (partly, because of limited data) from England (Nelson 1971; Pitkin et al. 1985) and Latvia (Kuznetsova 1987). The fauna of Sphaeroceridae in Central European peat bogs seems to be much more diverse than the Caucasian ones. Roháček (1984) recorded as many as 80 species from nine peat bogs in the Hrubý Jeseník and Králický Sněžník Mts in northern Moravia and Roháček and Barták (1999) recorded 66 species from 14 peat bogs in the Šumava Mts in southern Bohemia (both in the Czech Republic). The peatland survey of Sphaeroceridae in Wales (Holmes et al. 1992) recorded as many as 78 species but this research also included poor and rich fens, not only raised bogs. Thus, the number of species in the Caucasian mires resembles those recorded from mire habitats in England (Nelson 1971: 31 species; Pitkin et al. 1985: 26 species) but is distinctly higher than in two raised bogs in Latvia (Kuznetsova 1987: 17 species). However, it should be stressed that the research of Diptera on peat bogs in the Czech Republic was much more intensive (performed during several years from May/June to September/October by two-weekly to monthly sampling) and the material collected was more numerous. Therefore, the mere comparison of the number of species recorded in the above studies is somewhat misleading and the actual species richness of sphaerocerid flies in bogs under study would be much larger if they were sampled for Diptera during the entire warm season and repeatedly for more years. The qualitative comparison of taxa with distinct affinities to bog habitats is a more important signal to evaluate similarity / dissimilarity of local faunas of Sphaeroceridae in peat bogs.

Tyrphobiont species

In the Caucasian mires under study only one (and new) tyrphobiont species was found, *Pullimosina (P.) turfosa* sp. nov. In Europe, three other species have been formerly placed in this category: two circumpolar (hence Holarctic) Boreo-montane species of Limosininae, *Pullimosina (Dablimosina) dabli* (Duda, 1918) and *Spelobia pappi* Roháček, 1983, and one species of Copromyzinae hitherto only known from raised bogs in the Czech Republic and Austria, *Crumomyia tyrphophila* Roháček, 1999 (see Roháček and Barták 1999). Considering the presence of tyrphobiont species of Sphaeroceridae, the Caucasian mires seems to be dissimilar to those in Central and North Europe which share at least *P. dabli* and *S. pappi*.

Tyrphophilous species

The following ten species have been classified as tyrphophilous by Roháček (1984) and Roháček and Barták (1999) based on studies of peat-bog fauna in the Czech Republic: *Copromyza neglecta* (Malloch, 1913) and *C. stercoraria* (Meigen, 1830) (Copromyzinae), *Ischiolepta nitida* (Duda, 1920) (Sphaerocerinae), *Minilimosina guestphalica* (Duda, 1918) (= *M. v-atrum* auctt.), *Phthitia (Collimosina) spinosa* (Collin, 1930), *Pteremis fenestralis* (Fallén, 1820), *Pullimosina (Pullimosina) pul-lula* (Zetterstedt, 1847), *Spelobia belanica* Roháček, 1983, *S. ibrida* Roháček, 1983, and *S. nana* (Rondani, 1880). Of these only two, viz. *I. nitida* and *S. ibrida*, have been recorded from mires in the North Caucasus but it is suggested above that a third species, *Phthitia (Kimosina) longisetosa* (Dahl, 1909), is also to be included in the tyrphophilous category, despite being hitherto unrecorded from peat bogs in the Czech Republic. However, there are several other tyrphophilous candidates in Sphaeroceridae (Limosininae), particularly *Spelobia bispina* Marshall, 1985, a circumpolar Boreal species known from peatlands in Canada (Marshall 1994) and from Sweden (Florén 1989) and the Baikal area in eastern Siberia (Roháček et al. 2001). *Pseudocollinella abhorrens* (Roháček, 1990) could be a similar case, occurring in the Canadian tundra and some more southern peatlands in Canada and USA (Marshall 1994) and in Sweden (Roháček 1990). *Minilimosina (Minilimosina) tenera* Roháček, 1983, a species described from a single male from the peat bog Skřítek in northern Moravia (Czech Republic) and subsequently recorded from an upland mire in Wales (Holmes et al. 1992), a wet coniferous forest in Sweden (Florén 1989), and near a subarctic forest spring in Finland (Haarto and Kahanpää 2013), could also belong to this category. Thus, up to 14 species can be classified as tyrphophilous in European peat bogs but only three of them have been recorded from montane and submontane mires in the North Caucasus.

Tyrphoneutral species

The vast majority (34 species) of Sphaeroceridae recorded from Caucasian mires belong to this category which is in agreement with the situation in Central and North European bogs. This group is mainly composed of common eurytopic coprophagous or saprophagous species, which are able to survive (and even prosper) in peat bogs if there is enough food supply for their larvae (animal excrement and carrion and decaying vegetation). Five of the eight mires under study can provide favorable conditions to many coprophagous species of Sphaeroceridae as their environs and essentially the bogs are used for grazing horses or cattle (see “Localities under study” for further details). *Borborillus*, *Copromyza*, *Lotophila*, *Norrbomia*, *Chaetopodella*, *Coproica*, *Gonioneura*, and *Opalimosina* species are typical examples of coprophages while *Eulimosina*, *Leptocera*, *Minilimosina*, *Pullimosina*, and most *Spelobia* and *Terrilimosina* species are phytosaprophagous or polysaprophagous. The herein recorded paludicolous *Opacifrons*, *Pseudocollinella*, and *Rachispoda* species

are also eurytopic and can develop in the acidic mud in these mires, perhaps with the exception of *Rachispoda hostica* (Villeneuve, 1917) being obviously an occasional vagrant and hence belonging to the tyrphoxenous category. More interesting is the occurrence of microcavernicolous species living in burrows of small mammals, viz. *Spelobia czizeki* (Duda, 1918) and *S. talparum* (Richards, 1927). The mycophagous *Spelobia parapasio* (Dahl, 1909) is interesting because only males have been found although it is a parthenogenetic species at higher latitudes (Roháček 1983). Apparently, the relatively high altitude of mire localities in the Caucasus is not an obstacle to the occurrence of bisexual populations normally occurring in southern Europe at lower altitudes.

Wing reduction and the loss of or decreased ability to fly has been observed in many different families of Diptera (e.g., Tipulidae, Limoniidae, Chironomidae, Phoridae, Chloropidae, Ephydriidae, Drosophilidae, etc.), primarily in species adapted to cold and open windy habitats, and especially in those living at high latitudes and altitudes (e.g., see Hackman 1964; Byers 1969). Among Sphaeroceridae, wing reduction and/or wing loss occur most commonly among Acalyptratae Diptera also in species living inside wet substrates (e.g., moss, litter, grass tufts, etc.) including peat-bog habitats and in the microcavernicolous species (Roháček 2012). Formerly, several brachypterous (more precisely wing-polymorphic) and even apterous species of Sphaeroceridae have been recorded from peat bogs in Europe. These include two tyrphophilous species, *Phthitia (Collimosina) spinosa* and *Pteremis fenestralis* (both wing-polymorphic), and several tyrphoneutral species, *Terrilimosina corrivalis* (Villeneuve, 1918), *Pullimosina meijerei* (Duda, 1918) (both wing-polymorphic), and the apterous *Aptilotus paradoxus* Mik, 1898 (cf. Roháček 1984). Moreover, some Sphaeroceridae display a tendency to increase wing reduction at higher latitudes and altitudes, e.g., some wing-polymorphic species including *Pteremis fenestralis* (see Roháček 1975, 2012). Hence, the high-montane mire habitat of *P. turfosa* combines several features which can promote wing reduction in Sphaeroceridae.

Acknowledgements

A.A. Przhiboro is grateful to Yu.A. Dunaeva (St. Petersburg, Russia) for her help in fieldwork. Both authors are very grateful to D.A. Philippov (Borok, Yaroslavl Province of Russia) for the identification of monocotyledones and comments on mire typology, to M.A. Boychuk (Petrozavodsk, Russia) for the identification of *Sphagnum* mosses, to P. Chandler (Melksham, England) for comments and English revision of the manuscript, and to the reviewers for helpful criticism. The research of Sphaeroceridae by J. Roháček was supported by the Ministry of Culture of the Czech Republic by institutional financing of long-term conceptual development of research institution (the Silesian Museum, MK000100595). The work of A. Przhiboro was conducted within the framework of State Assignment No. 122031100274-7, Ministry of Science and Higher Education of the Russian Federation.

References

- Anderson R, Mantell A, Nelson B (2017) An invertebrate survey of Scragh Bog, Co Westmeath. Irish Wildlife Manuals, 96. National Parks and Wildlife Service, Department of Arts, Heritage, Regional, Rural and Gaeltacht Affairs, Dublin, 85 pp. <https://www.npws.ie/sites/default/files/publications/pdf/IWM96.pdf>
- Batzer D, Wu H, Wheeler T, Eggert S (2016) Chapter 7. Peatland invertebrates. In: Batzer D, Boix D (Eds) Invertebrates in freshwater wetlands. An international perspective on their ecology. Springer, Cham – Heidelberg – New York – Dordrecht – London, 219–250. https://doi.org/10.1007/978-3-319-24978-0_7
- Botch MS, Masing VV (1979) Mire ecosystems in the USSR. Nauka, Leningrad. 188 pp. [In Russian]
- Botch MS, Masing VV (1983) Mire ecosystems in the U.S.S.R. In: Gore AJP (Ed.) Ecosystems of the World 4B. Mires: swamp, bog, fen and moor. Regional studies. Elsevier, Amsterdam – Oxford – New York, 95–152.
- Boyce DC (2004) A review of the invertebrate assemblage of acid mires. English Nature Research Reports 592, 109 pp.
- Buck M, Marshall SA (2009) Revision of New World *Leptocera* Olivier (Diptera, Sphaeroceridae). Zootaxa 2039(1): 1–139. <https://doi.org/10.11646/zootaxa.2039.1.1>
- Byers GW (1969) Evolution of wing reduction in crane flies (Diptera: Tipulidae). Evolution 23(2): 346–354. <https://doi.org/10.1111/j.1558-5646.1969.tb03517.x>
- Carles-Tolrà M (2001) Two new *Mimilimosina* Roháček species from Andorra (Diptera, Sphaeroceridae). Boletín de la Asociación Española de Entomología 25(3–4): 9–15.
- Coulson JC, Butterfield JEL (1985) The invertebrate communities of peat and upland grasslands in the North of England and some conservation implications. Biological Conservation 34(3): 197–225. [https://doi.org/10.1016/0006-3207\(85\)90093-X](https://doi.org/10.1016/0006-3207(85)90093-X)
- Dahl F (1909) Die Gattung *Limosina* und die biocönotische Forschung. Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin 6: 360–377. https://www.zobodat.at/pdf/Sitzber-Ges-Naturforsch-Freunde-Berlin_1909_0360-0377.pdf
- Doskočil J (1973) Doukřídli (Diptera, Acalyptrata) Pančiské louky v Krkonoších. Die Zweiflügler (Diptera, Acalyptrata) der Pančice-Wiese im Krkonoše Gebirge. Opera Corcontica 10: 211–224. [In Czech, with German summary]
- Drake CM, Godfrey A, Sanderson AC (1989) A survey of the invertebrates of five lowland bogs in Cumbria. England Field Unit 60, Nature Conservancy Council, Peterborough, 113 pp. [+ Appendices 1–3]
- Duda O (1938) 57. Sphaeroceridae (Cypselidae). In: Lindner E (Ed.) Die Fliegen der palaearktischen Region 6, E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, 182 pp.
- Elberg K (1969) On migrations of flies (Diptera Brachycera) on raised bogs. Eesti NSV Teaduste Akadeemia Toimetised, Bioloogia [Izvestiya Akademii nauk Estonskoy SSR] 18(3): 270–275. [In Russian, with Estonian and English summaries] <https://doi.org/10.3176/chem.geol.1969.3.10>
- Elberg KYu (1971) Fauna of Acalyptrata flies (Diptera Brachycera) of mires of Estonia. Abstract of candidate of biological sciences dissertation. University of Tartu, Tartu, 24 pp. [In Russian]

- Evstigneev DA, Glukhova NV (2022) Tephritid flies (Diptera: Tephritidae) of the Caucasus and Transcaucasia: new records and new host plants. *Zoosystematica Rossica* 31(1): 118–129. <https://doi.org/10.31610/zsr/2022.31.1.118>
- Evstigneev DA, Przhiboro AA (2021) New records of flies of the genus *Tephritis* (Diptera: Tephritidae) from the Caucasus and Transcaucasia, with notes on other tephritid species. *Zoosystematica Rossica* 30(1): 13–24. <https://doi.org/10.31610/zsr/2021.30.1.13>
- Florén F (1989) Distribution, phenology and habitats of the lesser dung fly species (Diptera, Sphaeroceridae) of Sweden and Norway, with notes from adjacent countries. *Entomologisk Tidskrift* 110: 1–29. https://www.sef.nu/download/entomologisk_tidskrift/et_1989/ET%201989%201-29w23.pdf
- Haarto A, Kahanpää J (2013) Notes on Finnish Sphaeroceridae (Diptera) with description of the female of *Minilimosina tenera* Rohacek, 1983. *Entomologica Fennica* 24(4): 228–233. <https://doi.org/10.33338/ef.9385>
- Hackman W (1964) On reduction and loss of wings in Diptera. *Notulae Entomologicae* 44: 73–93.
- Harnisch O (1925) Studien über Ökologie und Tiergeographie de Moore. *Zoologische Jahrbücher. Zeitschrift für Systematik. Geographie und Biologie der Tiere, Jena* 51: 1–166.
- Hayashi T (2006) The genus *Pullimosina* Roháček (Diptera, Sphaeroceridae) from Japan. *Japanese Journal of Sanitary Zoology* 57(4): 265–272. <https://doi.org/10.7601/mez.57.265>
- Holmes PR, Valentine J, Boyce DC, Reed DK (1992) Lesser dung flies (Diptera: Sphaeroceridae) in Welsh peatlands. *Dipterists Digest* 8 (1991): 6–13.
- Joosten H, Couwenberg J, Moen A, Tanneberger F (2017) 3. Mire and peatland terms and definitions in Europe In: Joosten H, Tanneberger F, Moen A (Eds) *Mires and peatlands of Europe: Status, distribution and conservation*. Schweizerbart Science Publishers, Stuttgart, 65–96. <https://doi.org/mireseurope/2017/0001-0005>
- Keiper JB, Walton WE, Foote BA (2002) Biology and ecology of higher Diptera from freshwater wetlands. *Annual Review of Entomology* 47(1): 207–232. <https://doi.org/10.1146/annurev.ento.47.091201.145159>
- Krogerus R (1960) Ökologische Studien über nordische Moorarthropoden. *Commentationes Biologicae* 21(3): 1–238.
- Kuznetsova NV (1987) Fauna and ecology of Sphaeroceridae (Diptera) from maritime lowland of Latvia. *Latvijas Entomologs* 30: 60–70. [In Russian, with English summary]
- Marshall SA (1986) A revision of the Nearctic species of the genus *Pullimosina* (Diptera, Sphaeroceridae). *Canadian Journal of Zoology* 64(2): 522–536. <https://doi.org/10.1139/z86-077>
- Marshall SA (1994) Peatland Sphaeroceridae (Diptera) of Canada. *Memoirs of the Entomological Society of Canada* 169(S169): 173–179. <https://doi.org/10.4039/entm126169173-1>
- Marshall SA (1997) Sphaerocerid flies (Diptera: Sphaeroceridae) of the Yukon. In: Danks HV, Downes JA (Eds) *Insects of the Yukon*. Biological Survey of Canada (Terrestrial Arthropods), Ottawa, 663–685.
- Marshall SA, Finnamore AT, Blades DCA (1999) 17. Canadian peatlands: Diversity and habitat specialization of the arthropod fauna. In: Batzer DP, Rader RB, Wissinger SA (Eds) *Invertebrates in freshwater wetlands of North America. Ecology and management*. John

- Wiley & Sons, Inc., New York – Chichester – Weinheim – Brisbane – Singapore – Toronto, 383–400.
- Marshall SA, Roháček J, Dong H, Buck M (2011) The state of Sphaeroceridae (Diptera: Acalyptratae): a world catalog update covering the years 2000–2010, with new generic synonymy, new combinations, and new distributions. *Acta Entomologica Musei Nationalis Pragae* 51(1): 217–298. https://www.aemnp.eu/data/article-1323/1304-51_1_217.pdf
- Nelson JM (1971) The invertebrates of an area of Pennine Moorland within the Moor House Nature Reserve in northern England. *Transactions of the Society for British Entomology* 19(2): 173–235.
- Nelson JM (1981) Some invertebrates from Blawhorn Moss National Nature Reserve, West Lothian. *Forth Naturalist and Historian* 6: 53–61.
- Nelson JM (1982) Some invertebrates from Murder Moss (a fen near Selkirk). *History of the Berwickshire Naturalist's Club* 42: 96–102.
- Nelson JM, Theaker JH (1982) Invertebrates on a bog within the Silver Flowe National Reserve, Galloway. *Transactions of the Dumfriesshire and Galloway Natural History and Antiquarian Society*, ser. 3 57: 23–28.
- Pape T, Beuk P, Pont A, Shatalkin A, Ozerov A, Woźnica A, Merz B, Bystrowski C, Raper C, Bergström C, Kehlmaier C, Clements D, Greathead D, Kameneva E, Nartshuk E, Petersen F, Weber G, Bächli G, Geller-Grimm F, Van de Weyer G, Tschorsnig H, de Jong H, van Zuijlen J, Vaňhara J, Roháček J, Ziegler J, Majer J, Hürka K, Holston K, Rognes K, Greve-Jensen L, Munari L, de Meyer M, Pollet M, Speight M, Ebejer M, Martinez M, Carles-Tolrá M, Földvári M, Chvála M, Barták M, Evenhuis N, Chandler P, Cerretti P, Meier R, Rozkosny R, Prescher S, Gaimari S, Zatwarnicki T, Zeegers T, Dikow T, Korneyev V, Richter V, Michelsen V, Tanasijtshuk V, Mathis W, Hubenov Z, de Jong Y (2015) Fauna Europaea: Diptera – Brachycera. *Biodiversity Data Journal* 3: e4187. [31 pp.] <https://doi.org/10.3897/BDJ.3.e4187>
- Papp L (1973) Sphaeroceridae (Diptera) from Mongolia. *Acta Zoologica Academiae Scientiarum Hungaricae* 19: 369–425.
- Papp L (1974) New species and records of Sphaeroceridae from Central Asia (Diptera). *Annales Historico-Naturales Musei Nationalis Hungarici* 66: 251–268.
- Papp L (1979) New species and records of Sphaeroceridae (Diptera) from the USSR. *Annales Historico-Naturales Musei Nationalis Hungarici* 71: 219–230.
- Papp L, Roháček J (2021) 99 Sphaeroceridae (Lesser Dung Flies). In: Kirk-Spriggs AH, Sinclair BJ (Eds) *Manual of Afrotropical Diptera*, 3. Brachycera-Cyclorrhapha, excluding Calyptratae. Suricata 8. South African National Biodiversity Institute, Pretoria, 2145–2192.
- Pax F (1937) Die Moorfauna des Glatzer Schneeberges. 2. Allgemeine Charakteristik der Hochmoore. *Beiträge zur Biologie des Glatzer Schneeberges*. Breslau 3: 237–266.
- Peus F (1928) Beiträge zur Kenntnis der Tierwelt nordwestdeutscher Hochmoore. *Zeitschrift für Morphologie und Ökologie der Tiere* 12: 533–683. <https://doi.org/10.1007/BF00403122>
- Peus F (1932) Die Tierwelt der Moore. *Handbuch der Moorkunde III*. Borntraeger Verlag, Berlin, 127 pp.
- Pitkin BR, Coulson JC, Butterfield J (1985) The distribution and biology of Sphaeroceridae (Diptera) in upland regions of northern England. *Naturalist* 110: 81–90.

- Prokin AA, Sazhnev AS, Philippov DA (2019) Water beetles (Insecta: Coleoptera) of some peatlands of the North Caucasus. *Nature Conservation Research* 4(2): 57–66. <https://doi.org/10.24189/ncr.2019.016>
- Prokina KI, Philippov DA (2019) Centroheliid heliozoans (Haptista: Centroplasthelida) from mires in the North Caucasus, Russia. *Mires and Peat* 24, article 36: 1–20. <https://doi.org/10.19189/MaP.2019.OMB.StA.1806>
- Przhiboro AA (2012) Aquatic and shore macroinvertebrates and assessment of their abundance. In: Iovchenko NP (Ed.) *Ekosistemy zakaznika “Rakovye ozera”: istoriya i sovremennoe sostoyanie* [Ecosystems of the nature reserve “Lakes Rakovye”: History and present state]. *Trudy S.-Peterburgskogo obshchestva estestvoispytatelei* [Proceedings of St. Petersburg Society of Naturalists], ser. 6, 6: 53–65, 208, 252–272 (Annexes 3 and 4) + 4 pages of photographs. St. Petersburg University Press. [In Russian with English summary]
- Przhiboro A, Paasivirta L (2012) Chironomidae of semiaquatic lake shore habitats in the Karelian Isthmus (northwestern Russia). *Fauna Norvegica* 31: 87–94. <https://doi.org/10.5324/fn.v31i0.1410>
- Rabeler W (1931) Die Fauna der Göldenitzer Hochmoores in Mecklenburg. *Zeitschrift für Morphologie und Ökologie der Tiere* 21(1–2): 173–315. <https://doi.org/10.1007/BF00406497>
- Richards OW (1930) The British species of Sphaeroceridae (Borboridae, Diptera). *Proceedings of the Zoological Society of London* 1930(2): 261–345. <https://doi.org/10.1111/j.1096-3642.1930.tb00979.x>
- Rief S (1996) Einfluß der Bewirtschaftung auf ausgewählte Diptera (Nematocera: Limoniidae; Tipulidae; Trichoceridae; Brachycera: Empididae; Hybotidae; Dolichopodidae) verschiedener Ökosysteme auf Niedermoortorfen. *Faunistisch-Ökologische Mitteilungen* (Supplement 20): 47–76.
- Roháček J (1975) Die Flügelpolymorphie bei den europäischen Sphaeroceridenarten und Taxonomie der *Limosina heteroneura*-Gruppe (Diptera). *Acta Entomologica Bohemoslovaca* 72: 196–207.
- Roháček J (1982a) Revision of the subgenus *Leptocera* (s. str.) of Europe (Diptera, Sphaeroceridae). *Entomologische Abhandlungen. Staatliches Museum für Tierkunde in Dresden* 46(1): 1–44.
- Roháček J (1982b) A monograph and re-classification of the previous genus *Limosina* Macquart (Diptera, Sphaeroceridae) of Europe. Part I. *Beiträge zur Entomologie*, Berlin 32: 195–282. <https://www.contributions-to-entomology.org/article/view/1178/1177>
- Roháček J (1983) A monograph and re-classification of the previous genus *Limosina* Macquart (Diptera, Sphaeroceridae) of Europe. Part II. *Beiträge zur Entomologie*, Berlin 33: 3–195. <https://www.contributions-to-entomology.org/article/view/1184/1183>
- Roháček J (1984) Acalypterate Diptera of peat bogs in North Moravia (Czechoslovakia). Part 6. Sphaeroceridae. *Časopis Slezského Muzea, Opava (A)* 33: 97–131.
- Roháček J (1985) A monograph and re-classification of the previous genus *Limosina* Macquart (Diptera, Sphaeroceridae) of Europe. Part IV. *Beiträge zur Entomologie*, Berlin 35: 101–179. <https://www.contributions-to-entomology.org/article/view/1209/1208>
- Roháček J (1990) New species of Limosiniinae (Diptera, Sphaeroceridae) from northern Europe. *Acta Entomologica Bohemoslovaca* 87: 221–231.

- Roháček J (1991) A monograph of *Leptocera* (*Rachispoda* Lioy) of the West Palaearctic area (Diptera, Sphaeroceridae). Časopis Slezského zemského Muzea, Opava (A) 40: 97–288.
- Roháček J (1998) 3.43. Family Sphaeroceridae. In: Papp L, Darvas B (Eds) Contributions to a Manual of Palaearctic Diptera, 3. Higher Brachycera. Science Herald, Budapest, 463–496.
- Roháček J (2001) The type material of Sphaeroceridae described by J. Villeneuve with lectotype designations and nomenclatural and taxonomic notes (Diptera). Bulletin de la Société entomologique de France 105(5) (2000): 467–478. <https://doi.org/10.3406/bsef.2000.16706>
- Roháček J (2010) West Palaearctic *Minilimosina* (*Svarciella*): a new species, new records, key and taxonomical notes (Diptera: Sphaeroceridae). Časopis Slezského Zemského Muzea Opava (A), 58(2009): 97–114.
- Roháček J (2012) Wing polymorphism in European species of Sphaeroceridae (Diptera). Acta Entomologica Musei Nationalis Pragae 52(2): 535–558. https://www.aemnp.eu/data/article-1389/1370-52_2_535.pdf
- Roháček J (2019) First Sphaeroceridae (Diptera) endemic to Madeira – three new terricolous species of *Spelobia* and *Pullimosina*. Acta Entomologica Musei Nationalis Pragae 59(1): 107–124. <https://doi.org/10.2478/aemnp-2019-0009>
- Roháček J, Barták M (1999) Sphaeroceridae (Diptera) of peat-bogs in the Šumava Mts. (SW Bohemia, Czech Republic). Časopis Slezského zemského muzea Opava (A) 48: 9–32.
- Roháček J, Máca J (1982) Acalypterate Diptera of peat-bogs in North Moravia (Czechoslovakia). Part 2. Ecological classification, Opomyzidae, Anthomyzidae, Asteiidae, Diastatidae, Drosophilidae. Časopis Slezského Muzea, Opava (A) 31: 193–213.
- Roháček J, Marshall SA (1988) A review of *Minilimosina* (*Svarciella*) Roháček, with descriptions of fourteen new species (Diptera: Sphaeroceridae). Insecta Mundi 2: 241–282.
- Roháček J, Przhiboro AA (2022) Anthomyzidae (Diptera) in peat bogs of the North Caucasus (Russia). Entomological Review 101(8)(2021): 1188–1194. <https://doi.org/10.1134/S0013873821080157>
- Roháček J, Marshall SA, Norrbom AL, Buck M, Quiros DI, Smith I (2001) World catalog of Sphaeroceridae (Diptera). Slezské zemské muzeum, Opava, 414 pp.
- Roháček J, Kubík Š, Barták M (2005) Sphaeroceridae. In: Barták M, Kubík Š (Eds) Diptera of Podyjí National Park and its environs. Česká zemědělská univerzita v Praze, Praha, 335–348.
- Salmela J (2004) Semiaquatic flies (Diptera, Nematocera) of three mires in the southern boreal zone, Finland. Memoranda Societatis Pro Fauna et Flora Fennica 80: 1–10.
- Spitzer K, Danks HV (2006) Insect biodiversity of Boreal peat bogs. Annual Review of Entomology 51(1): 137–161. <https://doi.org/10.1146/annurev.ento.51.110104.151036>
- Spungis V (2008) Fauna and ecology of terrestrial invertebrates in raised bogs in Latvia. Latvijas Entomologs (Supplementum 6): 1–84.
- Stuke J-H, Roháček J (2019) Die Kleinen Dungfliegen Niedersachsens und Bremens (Diptera: Sphaeroceridae). Entomologische Zeitschrift Schwanfeld 129(1): 19–47.
- Su L (2011) Lesser Dung Flies. Liaoning University Press, Shenyang, Liaoning, China, 229 pp. [In Chinese]

- Su L-X, Liu G-C, Xu J (2013) Genus *Pullimosina* (Diptera: Sphaeroceridae) in China with description of a new species. *Entomologica Fennica* 24(1): 1–8. <https://doi.org/10.33338/ef.84594>
- Sushko G (2012) The insect fauna of «Yelnia» peat bog, north-west Belarus. LAP Lambert Academic Publishing, Saarbrücken, 104 pp.
- Taillefer AG, Wheeler TA (2010) Effect of drainage ditches on Brachycera (Diptera) diversity in a Southern Quebec peatland. *Canadian Entomologist* 142(2): 160–172. <https://doi.org/10.4039/n09-062>
- Taillefer AG, Wheeler TA (2011) Community assembly of Diptera following restoration of mined boreal bogs: Taxonomic and functional diversity. *Journal of Insect Conservation* 16(2): 165–176. <https://doi.org/10.1007/s10841-011-9403-x>
- Vitt DH (1994) An overview of factors that influence the development of Canadian peatlands. *Memoirs of the Entomological Society of Canada* 169(S169): 7–20. <https://doi.org/10.4039/entm126169007-1>
- Zatwarnicki T (1996) A new reconstruction of the origin of eremoneuran hypopygium and its implications for classification (Insecta: Diptera). *Genus* 7: 103–175.

Revision of *Sphenoraia* Clark, 1865 (Coleoptera, Chrysomelidae, Galerucinae) from China, with descriptions of two new species

Chuan Feng^{1,2,4,5}, Xing-Ke Yang^{3,4,5}, Zhi-Qiang Li^{4,5}, Yang Liu^{1,2}

1 Key Laboratory of Resource Biology and Biotechnology in Western China, Northwest University, Taibai North Road 229, Xi'an 710069, China **2** Shaanxi Key Laboratory for Animal Conservation, College of Life Science, Northwest University, Taibai North Road 229, Xi'an 710069, China **3** Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China **4** Guangdong Public Laboratory of Wild Animal Conservation and Utilization, Institute of Zoology, Guangdong Academy of Sciences Guangzhou, Guangdong 510260, China **5** Guangdong Key Laboratory of Animal Conservation and Resource Utilization, Institute of Zoology, Guangdong Academy of Sciences, Guangzhou, Guangdong 510260, China

Corresponding authors: Zhi-Qiang Li (lizq@giz.gd.cn), Yang Liu (liuyangent@nwu.edu.cn)

Academic editor: Michael Schmitt | Received 3 July 2022 | Accepted 7 November 2022 | Published 25 November 2022

<https://zoobank.org/2F80EC30-E025-4CE4-95F2-E9F99C8BD6B7>

Citation: Feng C, Yang X-K, Li Z-Q, Liu Y (2022) Revision of *Sphenoraia* Clark, 1865 (Coleoptera, Chrysomelidae, Galerucinae) from China, with descriptions of two new species. ZooKeys 1132: 51–83. <https://doi.org/10.3897/zookeys.1132.89858>

Abstract

In this study, ten species of *Sphenoraia* Clack, 1865 are recognized and re-described: *Sphenoraia* (*Sphenoraioides*) *anjiensis* Yang & Li, 1998, *Sphenoraia* (*Sphenoraioides*) *berberii* Jiang, 1992, *Sphenoraia* (*Sphenoraioides*) *duvivieri* (Laboissière, 1925), *Sphenoraia* (*Sphenoraioides*) *haizhuensis* Yang, 2021, *Sphenoraia* (*Sphenoraioides*) *micans* (Fairmaire, 1888), *Sphenoraia* (*Sphenoraioides*) *nebulosa* (Gyllenhal, 1808), *Sphenoraia* (*Sphenoraioides*) *nigromaculata* Jiang, 1992, *Sphenoraia* (*Sphenoraioides*) *punctipennis* Jiang, 1992, *Sphenoraia* (*Sphenoraioides*) *rutilans* (Hope, 1831), and *Sphenoraia* (*Sphenoraioides*) *yajiangensis* Jiang, 1992. Two new species, *Sphenoraia* (*Sphenoraia*) *decemmaculata* Feng, Yang & Li, **sp. nov.** and *Sphenoraia* (*Sphenoraioides*) *flavomarginata* Feng, Yang & Li, **sp. nov.**, are described. Additionally, *Sphenoraia* (*Sphenoraia*) *cupreata* Jacoby, 1890 and *Sphenoraia* (*Sphenoraia*) *nigra* Wang, Li & Yang, 2000 are transferred from *Sphenoraia* to *Gallerucida*. A key to the 12 Chinese species of *Sphenoraia* is given.

Keywords

Leaf beetles, new combination, new species, *Sphenoraia*, taxonomy

Introduction

Sphenoraia was established by Clark (1865), with *Galleruca bicolor* (Hope, 1831) as the type species. *Sphenoraia* is the senior synonym of the subgenus *Neosermylassa* Chûjô, 1956 synonymized by Kimoto (1986). All known species are distributed in the Palearctic and Oriental regions. Currently, there are 25 known species of *Sphenoraia* worldwide, among which 12 species occur in China (Yang et al. 1998; Wang et al. 2000; Nie et al. 2017). In this paper we describe the main generic characters of *Sphenoraia* according to those defined by Wang et al. (2000) based on examination of type material for most species. The species of this genus can be distinguished by the following characters: head small, frontal tubercle distinct, antennae slender and extend to the middle of each elytron, antennomere 2 shortest, antennomere 3 nearly equal in length and shape to antennomere 2 or slightly longer than 2, antennomere 4 longest and longer than antennomeres 2 and 3 combined. The pronotum is wider than the head, being nearly twice as broad as it is long, basal and with the apical border not margined, the lateral border margined; the disc of pronotum is without deep depression. Scutellum triangular, smooth, normally impunctate. The elytra are broader at the base than where they join the pronotum, the humeri are strongly convex, the disc is strongly raised and has punctures. The elytral epipleuron is broad at the base, and gradually narrows from its center, extending to the apex of the elytron. The procoxal cavity is closed behind, and the procoxa is globose. Claws are appendiculate, with a sclerotized appendage underneath. Male with apex of last visible sternite trilobed; female with the last visible sternite complete (Jiang 1992; Wang et al. 2000). This genus can be divided into two subgenera, *Sphenoraiaoides* and *Sphenoraia*, according to the shape of the body and antenna type (Yang et al. 2015).

Materials and methods

The morphological characters were examined with an Olympus SZ61 microscope. The genitalia of males from each species were dissected using the following procedure: for dried or ethanol preserved specimens, the abdomen was removed from each specimen, bathed in boiling water for 5–10 minutes, then transferred to a vial containing 10% KOH solution. The abdomen with the aedeagus was washed in distilled water several times, transferred onto a cavity slide using fine forceps and the aedeagus was separated from the abdomen using a hooked, fine dissecting needle.

Habitus images were taken using a Canon 5DSR/Nikon SMZ25 digital camera. Aedeagus images were taken using a Nikon D610 digital camera, attached to a Zeiss V/A1 microscope (with 5× objective lens). A cable shutter release was used to prevent the camera from shaking. To obtain the full depth of focus, all images were stacked using HELICON FOCUS 7 and the resulting output was edited with Adobe Photoshop CC.

The material in this study is deposited in the following institutions: **GDAS** Institute of Zoology, Guangdong Academy of Sciences, Guangzhou, CHINA and **IZAS** Institute of Zoology, Chinese Academy of Sciences, Beijing, CHINA

Results

Sphenoraia is similar to several genera, and a short key to the more closely related genera of *Sphenoraia* in the large subfamily Galerucinae is provided below.

Key to the similar genera of Hylaspini

- 1 Anterior metasternal process not extending beyond the front edge of the meso-coxal cavities, basal border of pronotum not margined..... **2**
- Anterior metasternal process extending beyond the front edge of the meso-coxal cavities, pronotum borders margined, pronotum with a pair of transverse depressions or without depressions..... **Gallerucida Motschulsky, 1860**
- 2 Anterior and lateral border of pronotum margined, posterior corner of pronotum acute, disc with deep transverse depressions.....
- **Aplosonyx Chevrolat, 1837**
- Lateral border of pronotum margined, posterior corner of pronotum rounded, disc without deep transverse depressions **Sphenoraia Clark, 1865**

Sphenoraia Clark, 1865

Sphenoraia Clark, 1865: 257, 262. Type species: *Galleruca bicolor* Hope, 1831, designated by Gressitt and Kimoto 1963.

Sermylassa subgenus *Neosermylassa* Chujo, 1956: 14. Type species: *Sermylassa* (*Neosermylassa*) *japonica* Chûjô, 1956, by monotypy and original designation. Synonymized by Kimoto 1986: 312.

Key to the Chinese species of *Sphenoraia*

- 1 Body shape elliptical; antennae short, antennomere 3 almost as long as antennomere 2 in male, from antennomere 4 they become gradually broader [*Sphenoraia* (*Sphenoraioides*)] **2**
- Body shape nearly parallel; antennae filiform, antennomere 2 shorter than 3 in male, several antennomeres of apex slightly thick [*Sphenoraia* (*Sphenoraia*)]. Head and pronotum yellowish brown, pronotum without any black spots, antennae and legs black.....
- ***Sphenoraia* (*Sphenoraia*) *decemmaculata* sp. nov.**
- 2 Head and pronotum yellow or yellowish brown, pronotum usually with one pair of black spots, elytron with seven black spots **3**
- Head and pronotum dark green or bluish black **4**
- 3 Scutellum without distinct punctures.....
- ***Sphenoraia* (*Sphenoraioides*) *nebulosa* (Gyllenhal, 1808)**
- Head and scutellum with distinct punctures
 ***Sphenoraia* (*Sphenoraioides*) *haizhuensis* Yang, 2021**

4	Elytra without any spots or stripes	5
–	Elytra with black spots or yellow stripes	7
5	Elytra reddish brown.....	
 <i>Sphenoraia (Sphenoraoides) duvivievi</i> (Laboissière, 1925)	
–	Elytra not reddish brown	6
6	Elytra bluish green or red.....	
 <i>Sphenoraia (Sphenoraoides) micans</i> (Fairmaire, 1888)	
–	Elytra bluish black; pronotum with a pair of shallow depressions laterally.....	
 <i>Sphenoraia (Sphenoraoides) rutilans</i> (Hope, 1831)	
7	Elytra yellow, each elytron with five black spots	
 <i>Sphenoraia (Sphenoraoides) anjiensis</i> Yang & Li, 1998	
–	Elytra blackish green, with yellow stripes	8
8	Epipleuron yellow, elytra surface without any spots or stripes.....	
 <i>Sphenoraia (Sphenoraoides) yajiangensis</i> Jiang, 1992	
–	Epipleuron yellow, elytra surface with stripes	9
9	Elytra surface with one transverse yellow stripe at subapex	
 <i>Sphenoraia (Sphenoraoides) flavomarginata</i> sp. nov.	
–	Elytra with yellow stripes at base and apex	10
10	Stripes at base and apex not joined at the middle suture.....	
 <i>Sphenoraia (Sphenoraoides) berberii</i> Jiang, 1992	
–	Stripes at base and apex joined in middle suture	11
11	Elytra divided into four parts by stripes.....	
 <i>Sphenoraia (Sphenoraoides) punctipennis</i> Jiang, 1992	
–	Elytra divided into seven parts by stripes.....	
 <i>Sphenoraia (Sphenoraoides) nigromaculata</i> Jiang, 1992	

***Sphenoraia (Sphenoraoides) anjiensis* Yang & Li, 1998**

Fig. 1A–F

Sphenoraia (Sphenoraoides) anjiensis Yang & Li, 1998: 132.

Type specimens examined. *Holotype*: ♀, CHINA, Zhejiang Province, Anji, Longwang Mountain; 1500 m; 13 May 1996; Hong Wu leg.; IZAS. *Paratype*: 1♂ CHINA, Zhejiang Province, Anji, Longwang Mountain; 26 Jul. 1996; Hong Wu leg.; IZAS.

Additional specimen examined. 1♀, CHINA, T'ienml Shan (Tianmu Mountain), Musée Heude; 21 Jul. 1936; D. Piel. leg.; IZAS.

Description. Male. Length 7.2 mm, width 4.6 mm.

Head, antennae, pronotum, ventral surface of thorax, scutellum, and legs black, elytra and abdomen yellow; each elytron with five black spots, base with one pair of spots and apex with one spot, median with a large transverse band and subapex with a large spot; abdomen with four pair of round black spots at side on the first, second, third, fourth visible sternites.

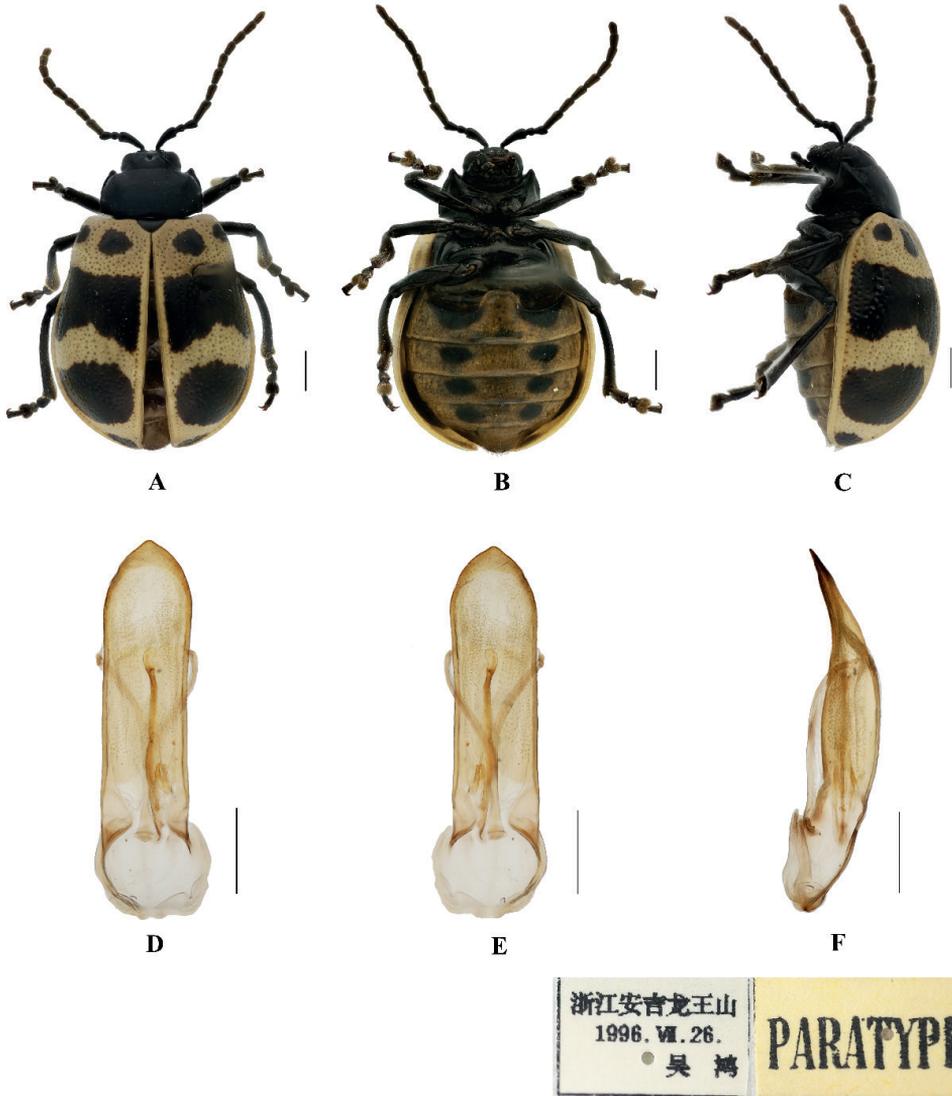


Figure 1. *Sphenoraia* (*Sphenoraiaoides*) *anjiensis* **A–C** habitus **D–F** aedeagus **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars: 1 mm (**A–C**); 0.5 mm (**D–F**).

Vertex covered with punctures finely and sparsely; frontal tubercle distinctly raised, each separated by a deep furrow; antennae slender, extended to the middle of the elytra; antennomeres 1–3 thin, shiny; antennomeres 4–11 wide and flat, with short hairs, antennomere 4 approximately twice as long as it is wide; antennomeres 5–10 each approximately $1.6 \times$ as long as they are wide; antennomere 2 shortest, antennomere 3 slightly longer than 2, $1.5 \times$ as long as antennomere 2; antennomere 4 longest, $1.2 \times$ as long as antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than 4; antennomere 11 slightly longer than 10, pointed.

Pronotum approximately $1.9 \times$ as wide as it is long, with lateral margins straight and parallel slightly, anterior angle thickened, produced forward, disc slightly convex, sparsely covered with small punctures.

Scutellum triangular, with rounded apex, smooth, impunctate.

Bases of both elytra combined wider than the pronotum, gradually widen posteriorly and rounded at the apexes; dorsal surface slightly convex and covered with large and deep regular punctures, partly arranged in ten rows on each elytron, the interstices of the punctures equal to the diameter of the punctures.

Metasternum twice as long as the mesosternum; prothoracic legs shortest, mesothoracic legs slightly longer, metathoracic legs longest.

Ventral surface of the abdomen with five segments, segment 1 longest, segments 2–4 gradually shortened, apical segment slightly longer than segment 4, with three lobes.

Aedeagus slender, parallel-sided, basally widened with triangular apex, distinctly pointed. In lateral view moderately bent.

Female. Length 7.0–7.2 mm, width 4.8–5.0 mm.

Antennae slender, antennomere 2 shortest, antennomere 3 slightly longer than 2, $1.4 \times$ as long as second; antennomere 4 longest, longer than antennomeres 2 and 3 combined slightly; antennomeres 5–10 equal in length, shorter than 4; apical sternite flattened.

Differential diagnosis. This species can be distinguished from other species by its black pronotum and the black spots on the abdomen.

Distribution. China: Zhejiang.

Sphenoraia (Sphenoraoides) berberii Jiang, 1992

Fig. 2A–F

Sphenoraia berberii Jiang, 1992: 665.

Sphenoraia (Sphenoraoides) berberii: Wang et al. 2000: 118.

Type specimens examined. Holotype: ♂, CHINA, Yunnan Province, Deqin, Baimang snowy mountain; 3300 m; 28 Aug. 1987; Shuyong Wang leg.; IZAS. **Paratypes:** 10♂♂6♀♀, same information as holotype. **Allotype:** 1♀, same information as holotype.

Additional specimen examined. 1♀, CHINA, Yunnan Province, Lijiang, Yulong Mountain; 3200 m; 17 Jul. 1984; Jianguo Fan leg. IZAS.

Description. Male. Length 5.9–6.4 mm, width 3.4–3.6 mm.

Head, pronotum, and scutellum blackish green, antennae, elytra, legs, and ventral surface of the body brown; apex of each abdominal segment yellow, elytral epipleuron from base to subapex yellow, connecting with yellow stripes on the base and apex of the elytra.

Vertex covered with punctures finely and sparsely; frontal tubercle distinctly raised, separated from each other by a deep furrow; antennae short, robust, extended to the middle of the elytra; antennomeres 1–3 thin, shiny; antennomeres 4–11 wide and flat,

with short hairs, antennomeres 2 and 3 shortest, antennomere 3 nearly equal in length and shape to antennomere 2, antennomere 4 longest, $1.5 \times$ as long as antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than 4; antennomere 11 slightly longer than 10, pointed.

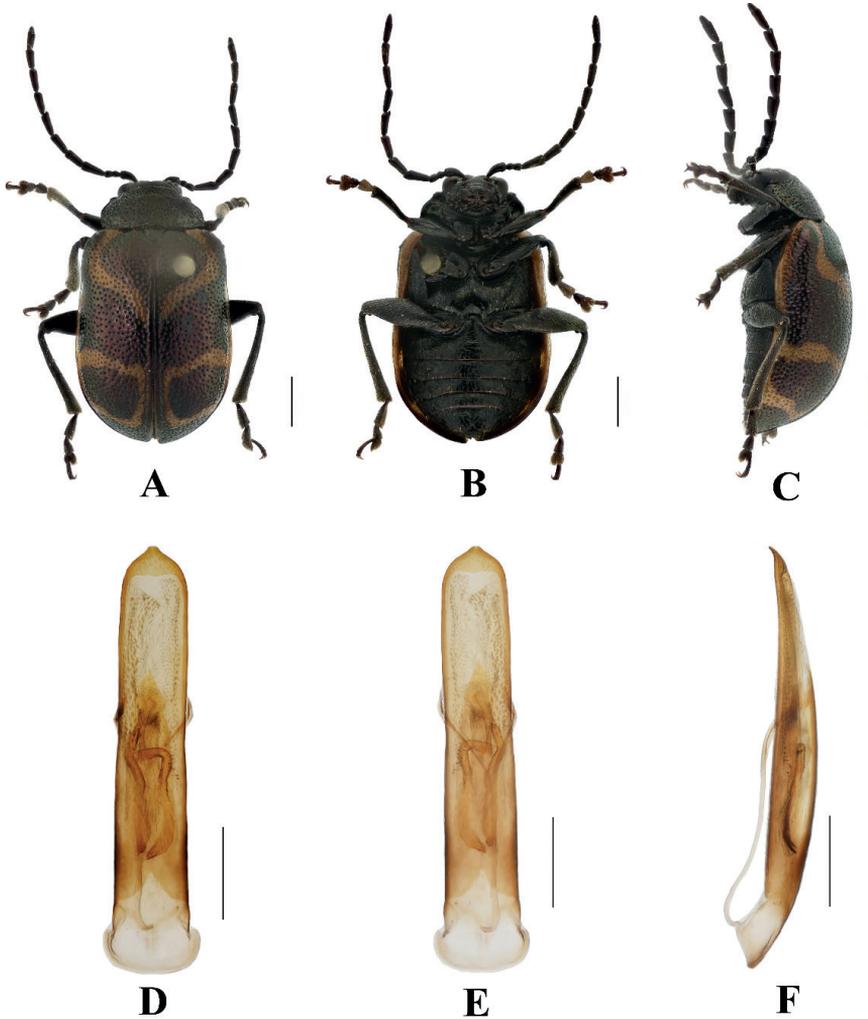


Figure 2. *Sphenoraia* (*Sphenoraiaoides*) *berberii* **A–C** habitus **D–F** aedeagus **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars 1 mm (**A**); 0.5 mm (**D–F**).

Pronotum approximately $1.8 \times$ as wide as long, with lateral margins rounded, disc slightly convex, sparsely covered with punctures in the center, base, and apex of pronotum covered with punctures closely. The interstices between punctures equal to the diameter of each puncture.

Scutellum triangular, only on the base and apex, sparsely covered with punctures.

Bases of both elytra wider than pronotum, gradually widen posteriorly and rounded at apex; dorsal surface slightly convex, irregularly covered with punctures, the interstices between punctures equal to the diameter of individual punctures.

Metasternum twice as long as mesosternum; prothoracic legs shortest, mesothoracic legs slightly longer, metathoracic legs longest.

Ventral surface of abdomen with five segments, segment 1 longest, segments 2–4 gradually shortened, apical segment slightly longer than segment 4, with three lobes.

Aedeagus slender, rounded laterally, basally widened, with triangular apex, distinctly pointed. In lateral view moderately bent.

Female. Length 5.8–6.2 mm, width 3.5–3.8 mm

Antennae slender, antennomere 2 shortest, antennomere 3 slightly longer than 2, $1.2 \times$ as long as second; antennomere 4 longest, twice as long as antennomeres 2 and 3 combined; apical sternite flattened.

Differential diagnosis. This species can be distinguished from other species by its blackish green pronotum and the yellow stripes on the elytra.

Distribution. China: Yunnan.

Host plant. *Berberis* sp.

Sphenoraia (*Sphenoraioides*) *duvivieri* (Laboissière, 1925)

Fig. 3A–F

Sphenoraia indica Duvivier, 1887: 48 (nec. Harold 1880).

Galerucida duvivier Laboissière, 1925: 53 (replacement name for *Sphenoraia indica* Duvivier, 1887).

Sphenoraia (*Sphenoraioides*) *duvivieri*: Laboissière 1934: 134.

Gallerucida amala Maulik, 1936: 549. Synonymized by Laboissière 1940: 30.

Additional specimens examined. 2♂♂, CHINA, Guangdong Province, Enping, Qixingkeng; 100 m; 21 Jun. 2022; Chuan Feng leg.; GDAS. 1♀, CHINA, Guangxi Province, Napo, Beidou; 550 m; 11 Apr. 1998; Tianshan Li leg.; IZAS. 1♂, CHINA, Guangxi Province, Longsheng, Baiyan; 1150 m; 21 Jun. 1963; Yongshan Shi leg.; IZAS. 1♀, CHINA, Guangxi Province, Longzhou; 360 m; 20 Jun. 1963; Yongshan Shi leg.; IZAS. 1♂, CHINA, Guangxi Province, Diding; 1000–1700 m; 23 Jun. 2000; Jian Yao leg.; IZAS. 1♂, CHINA, Guangxi Province, Jinxiu, Shengtang Mountain; 900 m; 17 May 1999; Xuezhong Zhang leg.; IZAS. 1♂, CHINA, Sichuan Province, Youyang; 9 Jul. 1989; Dazhi Dong leg.; IZAS. 1♂, CHINA, Sichuan Province, Youyang; 9 Jul.

1989; Su Lin leg.; IZAS. 1♂, CHINA, Guizhou Province, Guiyang; May–Jul. 1981; IZAS. 1♀, CHINA, Guizhou Province, Maolan; 30 May 1998; Qiongzhang Song leg.; IZAS. 1♀, CHINA, Yunnan Province, Funing; 250 m; 17 Apr. 1998; Chunsheng Wu leg.; IZAS. 2♂♂1♀, Yunnan Province, Xishuangbanna, Yunjinghong; 900 m; 27 Apr. 1958; Yiran Zhang leg.; IZAS. 1♀, CHINA, Yunnan Province, Changning; 1700 m; 16 Jun. 1979; IZAS. 1♀, Yunnan Province, Xishuangbanna, Menglun; 600 m; 11 Sep. 1993; Huanli Xu leg.; IZAS.

Description. Male. Length 6.8–7.8 mm, width 4.8–5.6 mm.

Head, antennae, pronotum, scutellum, legs, and ventral surface of thorax dark blue, elytra and abdomen brown.

Vertex finely and sparsely covered with punctures; frontal tubercle distinctly raised, separated from each other by a deep furrow; antennae short, robust, extended to the middle of elytra; antennomeres 1–3 thin, shiny; antennomeres 4–11 wide and flat, with short hairs, antennomere 4 approximately $2.2 \times$ as long as wide; antennomere 5 approximately $1.8 \times$ as long as wide; antennomeres 6 and 7 each approximately $1.5 \times$ as long as wide; antennomeres 8–10, each approximately $1.2 \times$ as long as wide; antennomere 11 approximately $1.5 \times$ as long as wide; antennomere 2 shortest, antennomere 3 longer than 2 slightly, $1.2 \times$ as long as second; antennomere 4 longest, $1.2 \times$ as long as antennomeres 2 and 3 combined; antennomeres 5–10 differ in length, shorter than 4; antennomere 11 slightly longer than 10, pointed.

Pronotum approximately $2.7 \times$ as wide as long, with rounded lateral margins; disc sparsely covered with punctures, with a lateral pair of shallow impressions.

Scutellum triangular, sparsely covered with punctures.

Bases of both elytra wider than pronotum, gradually widen posteriorly and rounded at apex; dorsal surface slightly convex, irregularly covered with punctures, the interstices between punctures wider than diameter of individual punctures, $1.5 \times$ as wide as the diameter of punctures.

Metasternum twice as long as mesosternum; prothoracic legs shortest, mesothoracic legs slightly longer, metathoracic legs longest.

Ventral surface of abdomen with 5 segments, segment 1 longest, segments 2–4 gradually shortened, apical segment equal in length to segment 1, with three lobes.

Aedeagus slender, parallel-sided, basally widened, with rounded apex. In lateral view, strongly bent.

Female. Length 6.8–7.8 mm, width 4.8–5.6 mm.

Antennae antennomeres 1–5 thin, antennomeres 6–11 wide and flat, each approximately $1.4 \times$ as long as wide; antennomere 2 shortest, antennomere 3 longer than 2 slightly, $1.5 \times$ as long as second; antennomere 4 longest, slightly longer than antennomeres 2 and 3 combined; apical sternite flattened.

Differential diagnosis. This species can be distinguished from other species in the genus by the mottled brown color of the body and shallow impressions of pronotum.

Distribution. China: Hunan, Hong Kong, Guangdong, Guangxi, Guizhou, Sichuan Yunnan; Vietnam, Laos, Thailand, India, and Myanmar.

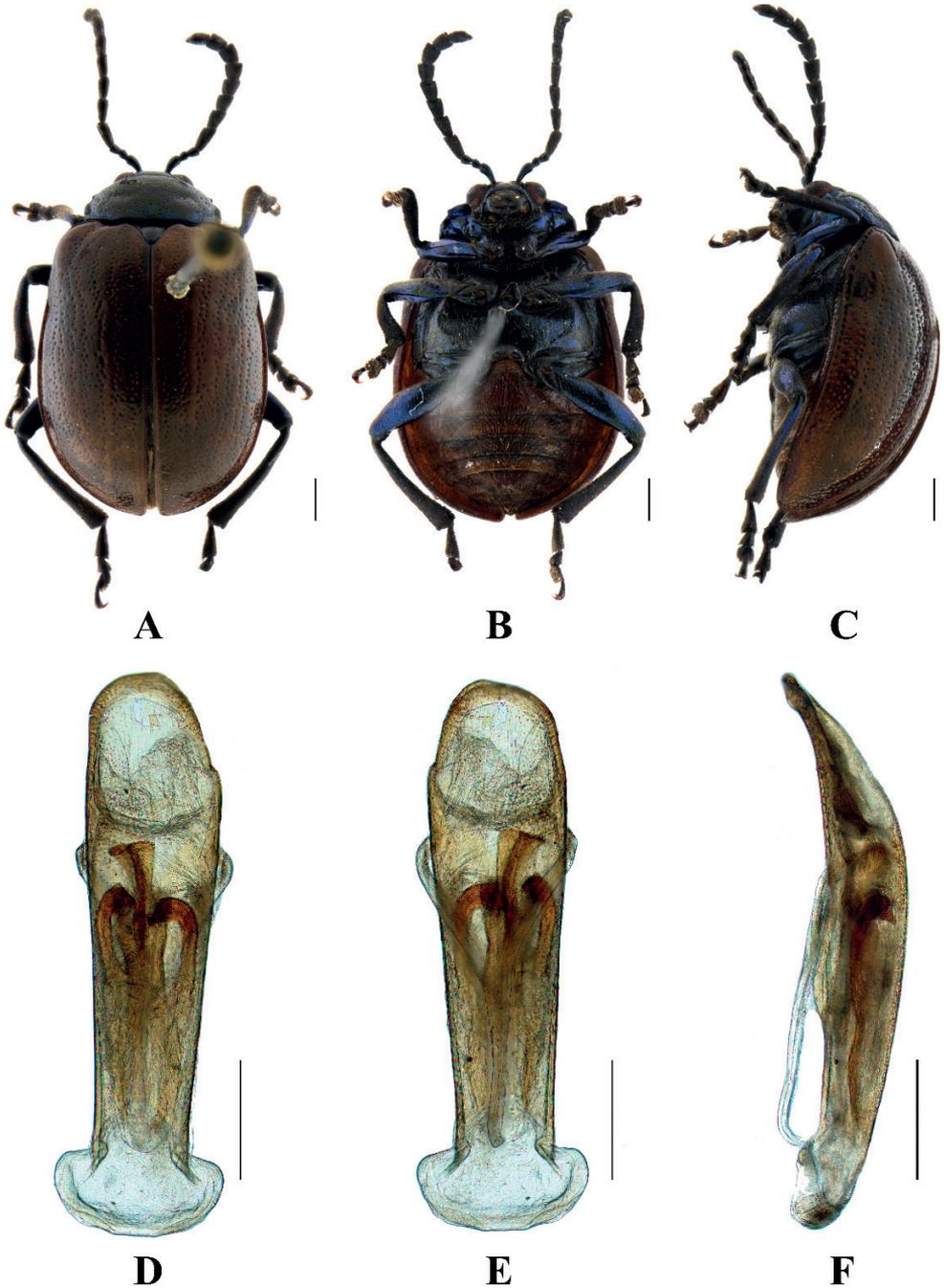


Figure 3. *Sphenoraia (Sphenoraoides) duvivieri* **A–C** habitus **D–F** aedeagus **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars: 1 mm (**A–C**); 0.5 mm (**D–F**).

***Sphenoraia (Sphenoraioides) haizhuensis* Yang, 2021**

Fig. 4A–E

Sphenoraia (Sphenoraioides) haizhuensis Yang, 2021: 245.

Type specimens examined. Holotype: ♂, Guangdong Province, Guangzhou, Haizhu wetland; 113°18'24"E, 23°4'32"N; 20–23 May 2021; FIT-1; GDAS. **Paratype:** 1♂, Guangdong Province, Guangzhou, Haizhu wetland; 113°21'29"E, 23°2'58"N; 2020.9.21–10.19; MT-9; GDAS.

Description. Male. Length. 6.2–6.4 mm, width 4.0–4.2 mm.

Head, pronotum, elytra, and legs yellow, antennae and ventral surface of body yellowish brown, scutellum brown; pronotum with a black spot on each side; each elytron with seven black spots, basal, middle and subapex with one pair of spots and apex with one spot.

Vertex finely and sparsely covered with punctures; frontal tubercles distinctly raised and separated from each other by a deep furrow; antennae short, robust, extended to the middle of elytra; antennomeres 1–3 thin, shiny; antennomeres 4–11 wide and flat, with short hairs, segment 4 approximately twice as long as wide; antennomeres 5–10, each approximately 1.6 × as long as wide; antennomeres 2 and 3 shortest, antennomere 3 nearly equal in length and shape to antennomere 2, antennomere 4 longest, twice as long as antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than 4; antennomere 11 slightly longer than 10, pointed.

Pronotum approximately 2.5 × as wide as long, with rounded lateral margins; disc slightly depressed on each side, sparsely covered with small punctures, with the punctures on pronotum larger than those on the head.

Scutellum triangular, sparsely covered with small punctures.

Base of both elytra wider than pronotum, gradually widen posteriorly and rounded at apex; dorsal surface slightly convex, irregularly covered with large and deep punctures, the interstices between punctures slightly wider than diameter of individual punctures.

Metasternum 2.5 × as long as mesosternum; prothoracic legs shortest, mesothoracic legs slightly longer, metathoracic legs longest.

Ventral surface of abdomen with five segments, segment 1 longest, segments 2–4 gradually shortened, apical segment slightly longer than segment 4, three lobes.

Aedeagus slender, parallel-sided, basally widened, apex rounded. In lateral view strongly bent.

Differential diagnosis. This species can be distinguished from other species by black spots on the elytra. This species closely resembles *Sphenoraia (Sphenoraioides) nebulosa*, but the latter is without punctures in the scutellum.

Distribution. China: Guangdong.

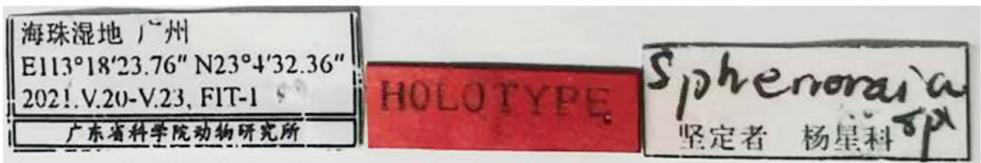
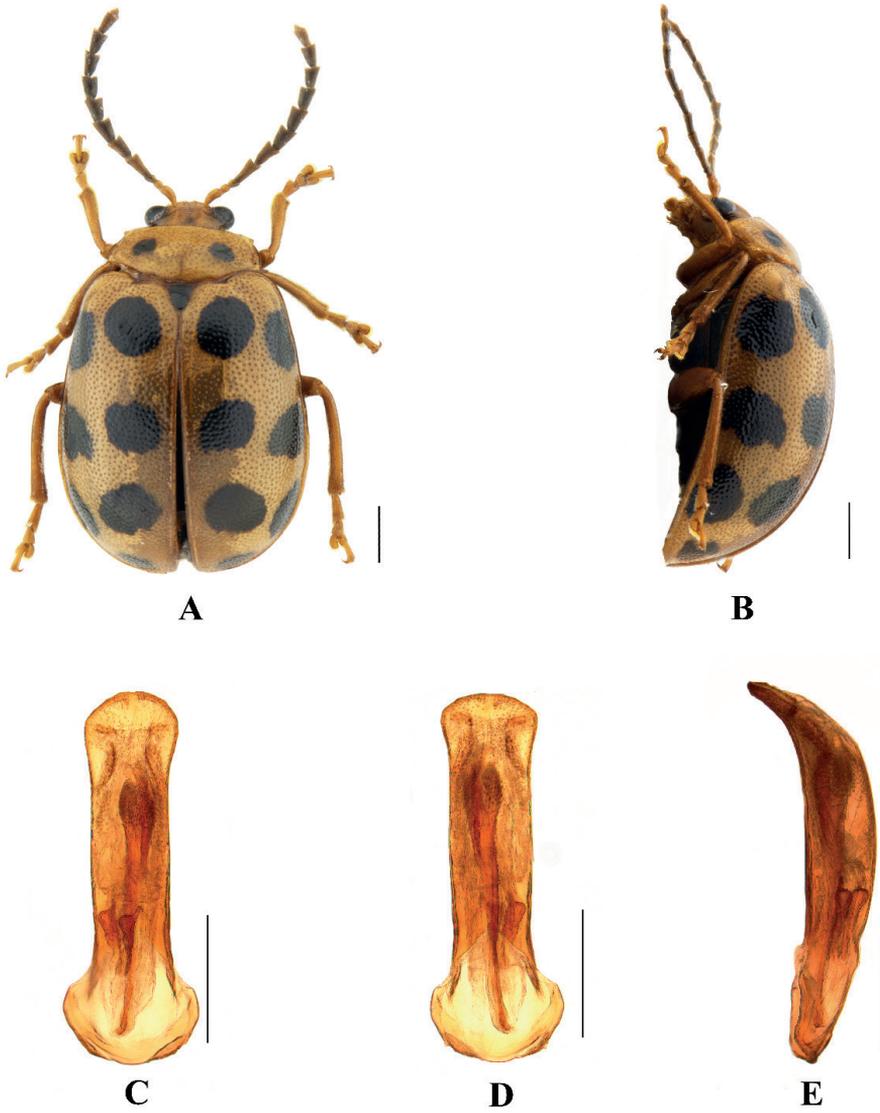


Figure 4. *Sphenoraia (Sphenoraoides) haizhuensis* **A, B** habitus **C–E** aedeagus **A, C** dorsal views **D** ventral views **B, E** lateral views. Scale bars: 1 mm (**A, B**); 0.5 mm (**C–E**).

***Sphenoraia (Sphenoraioides) micans* (Fairmaire, 1888)**

Fig. 5A–F

Eustetha micans Fairmaire, 1888: 42.*Galerucida fulgida* var. *coerulescens* Weise, 1922: 91. Synonymized by Wilcox 1971: 198.*Sphenoraia (Sphenoraioides) micans*: Laboissière 1934: 131.*Sphenoraia (Sphenoraioides) micans* var. *cyanella* Laboissière, 1934: 132. Synonymized by Wilcox 1971: 198.

Other specimens examined. 1♀, CHINA, Henan Province, Luanshan; 1000 m; 10 Jul. 1996; Wanzhi Cai leg.; IZAS. 1♂, CHINA, Henan Province, Luanshan; 1000 m; 10 Jul. 1996; Jikun Yang leg.; IZAS. 1♂1♀, CHINA, Zhejiang Province, Anji, Longwang Mountain; 500 m; 12 Jun. 1996; Xingke Yang leg.; IZAS. 1♂, CHINA, Zhejiang Province, Anji, Longwang Mountain; 14 Jun. 1996; 1400 m; Hong Wu leg.; IZAS. 1♀, CHINA, Zhejiang Province, Tianmu Mountain; Jul. 2000; IZAS. 1♂ CHINA, Zhejiang Province, Tianmu Mountain; Jul. 1999; IZAS. 1♂, CHINA, Zhejiang Province, Tianmu Mountain; 600–800 m; 7 Jun. 1998; Mingyuan Gao leg.; IZAS. 1♀, CHINA, Jiangxi Province, Jinggangshan, xiangzhou; 26 Apr. 2011; Yan Mei leg.; GDAS. 1♀, CHINA, Hunan Province, Sangzhi, Tianpingshan; 700–1450 m; 14 Aug. 1988; Shuyong Wang leg. IZAS. 1♂, CHINA, Wuyi Mountain; 22 Apr. 1997; Yanyu Wu leg.; IZAS. 1♀, CHINA, Fujian Province, Guadangling; 29 Aug. 1983; Jiang Wang leg.; IZAS. 1♂, CHINA, Guangxi Province, Longsheng, Hongtan; 900 m; 14 Jun. 1963; Shuyong Wang leg.; IZAS. 1♀, CHINA, Guizhou Province, Chiqian; 670 m; 24 Jul. 1988; Shuyong Wang leg.; IZAS. 1♀, CHINA, Guizhou Province, Fanjing Mountain; 2 Aug. 1988; Yongkun Li leg.; IZAS.

Description. Male. Length 7.7–8.4 mm, width 5.2–5.8 mm.

Head, pronotum and elytra green, antennae, scutellum, legs, and ventral surface of thorax dark blue, abdomen yellowish brown. Some individuals with blue or red head, pronotum, and elytra.

Vertex finely and sparsely covered with punctures; frontal tubercle distinctly raised, separated from each other by a deep furrow; antennae short, robust, extended to the middle of elytra; antennomeres 1–3 thin, shiny; antennomeres 4–11 wide and flat, with short hairs, antennomere 4 approximately twice as long as wide; antennomeres 5–11, each approximately 1.5 × as long as wide; antennomere 2 shortest, antennomere 3 slightly longer than 2, 1.2 × as long as second; antennomere 4 longest, 1.2 × as long as antennomeres 2 and 3 combined; antennomeres 5–10 unequal in length, shorter than 4; antennomere 11 slightly longer than 10, pointed.

Pronotum approximately 2 × as wide as long, with rounded lateral margins; disc slightly convex, sparsely covered with punctures.

Scutellum triangular, with rounded apex, smooth, impunctate.

Bases of both elytra wider than pronotum, gradually widen posteriorly and rounded at apex; dorsal surface slightly convex, irregularly covered with punctures, densely

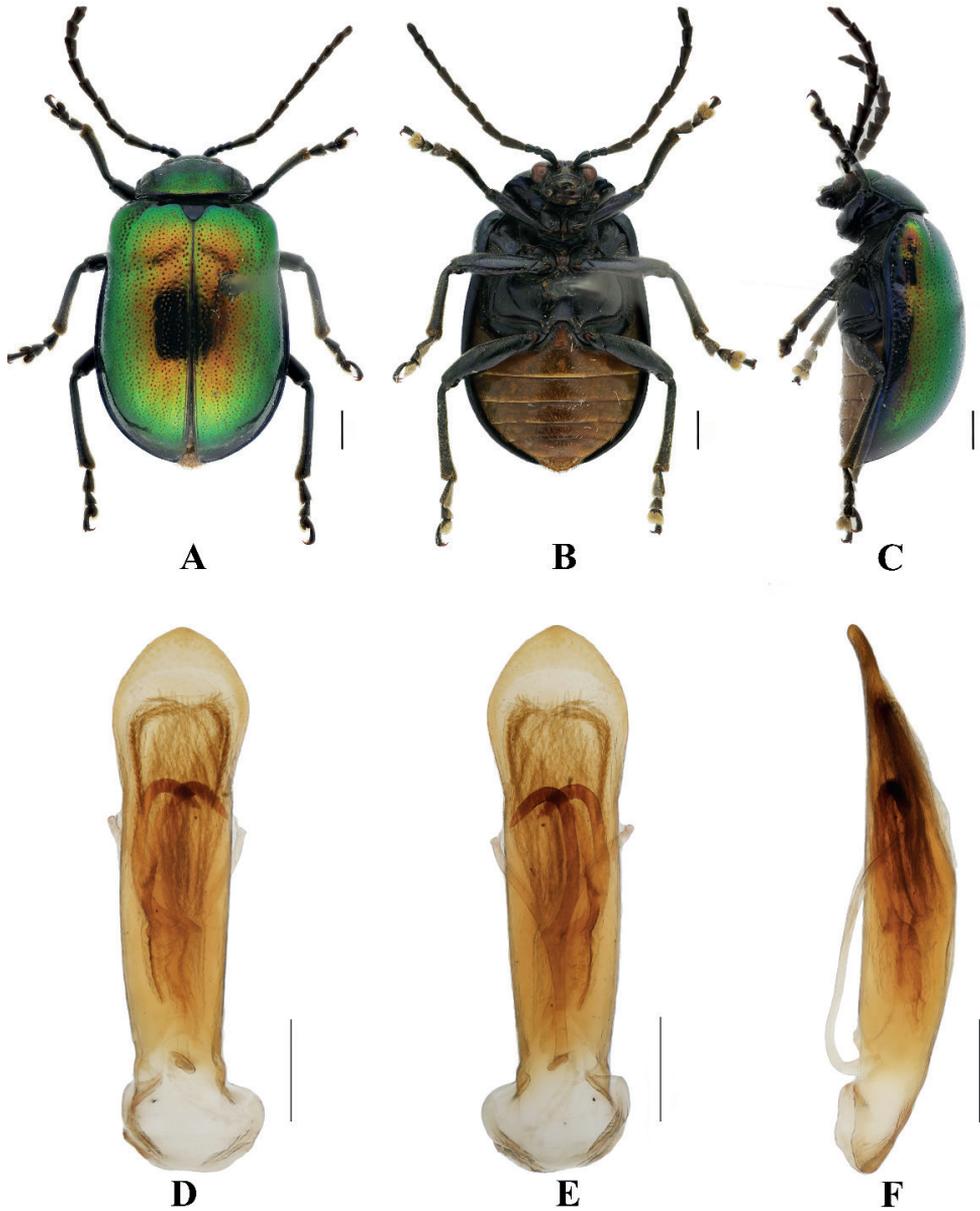


Figure 5. *Sphenoraia (Sphenoraoides) micans* **A–C** habitus **D–F** aedeagus **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars: 1 mm (**A–C**); 0.5 mm (**D–F**).

covered with large punctures on humeral angle and sparsely covered in small punctures on other parts. The interstices between punctures wider than diameter of individual punctures on apex of the elytra, $2 \times$ as wide as the diameter of individual punctures.

Metasternum $2.5 \times$ as long as mesosternum; prothoracic legs shortest, mesothoracic legs slightly longer, metathoracic legs longest.

Ventral surface of abdomen with five segments, segment 1 longest, segments 2–4 gradually shortened, apical segment slightly longer than segment 4, with three lobes.

Aedeagus slender, parallel-sided, basally widened, apically rounded, slightly pointed. In lateral view strongly bent.

Female. Length 7.8–8.4 mm, width 5.3–5.8 mm.

Antennae antennomeres 1–3 thin, antennomeres 7–11 wide and flat, with short hairs, antennomere 7, twice as long as wide; antennomeres 8–11 each approximately $1.6 \times$ as long as wide; antennomere 2 shortest, antennomere 3 longer than 2 slightly, $1.5 \times$ as long as second; antennomere 4 longest, slightly longer than antennomeres 2 and 3 combined; apical sternite flattened.

Differential diagnosis. This species can be distinguished from other species by metallic green, red, or blue coloration of the body.

Distribution. China: Henan, Zhejiang, Jiangxi, Hunan, Fujian, Taiwan, Guangdong, Guangxi, Sichuan, Guizhou, Xizang; Indo-China.

Host plant. Rubiaceae.

Sphenoraia (Sphenoraioides) nebulosa (Gyllenhal, 1808)

Fig. 6A–F

Galleruca nebulosa Gyllenhal, 1808: 292.

Sphenoraia (Sphenoraioides) nebulosa: Laboissière 1934: 132.

Other specimens examined. 1♀, CHINA, Hainan Province; 8 Aug. 1934; IZAS. 1♂, CHINA, Hainan; 24 Mar. 1934; IZAS. 1♂, CHINA, Hainan Province, Jianfengling; 13–17 Apr. 1984; IZAS. 1♂, Lingnan University; 10 May 1948; En-119989; SYSU. 1♂, CHINA, Guangxi Province, Yangshuo; 29 Jun. 1938; IZAS. 1♂, CHINA, Guangxi Province, Yangshuo; 6 Apr. 1938; IZAS. 1♀, CHINA, Guangxi Province, Yangshuo; 14 Oct. 1938; IZAS. 1♀, CHINA, Guangxi Province, Fulong, Pinglong Mountain; 650 m; 13 Mar. 1998; Gexia Qiao leg.; IZAS. 1♂, CHINA, Guangxi Province, Longzhou, Nonggang; 330 m; 15 Jun. 2000; Wenzhu Li leg.; IZAS. 1♂, CHINA, Guangxi Province, Guilin; 14 Aug. 1952; IZAS. 2♀, CHINA, Guangxi Province, Guilin; 19 Sep. 1952; IZAS. 2♀, CHINA, Guangxi Province, Guilin; 19 Sep. 1952; IZAS. 5♂5♀, CHINA, Guangxi Province, Guilin; 6 Mar. 1952; IZAS. 1♀, CHINA, Yunnan Province, Yiwubannan, Menglun; 650 m; 25 Jul. 1959; Yiran Zhang leg.; IZAS. 1♂, CHINA, Yunnan Province, Yiwubannan, Menglun; 650 m; 3 Apr. 1964; Baolin Zhang leg.; 1♂, CHINA, Yunnan Province, Xishuangbanna, Mengla; 620–650 m; 27 May 1959; Fuji Pu leg.; IZAS. 1♂, CHINA, Yunnan Province, Xishuangbanna, Damenglong; 650 m; 13 Apr. 1958; Shuyong Wang leg.; IZAS.

Description. Male. Length 6.2–6.8 mm, width 4.6–5.2 mm.

Head, pronotum, elytra and legs yellow, antennae and ventral surface of the body yellowish brown, scutellum brown; pronotum with a black spot on each side; each elytron with seven black spots, basal, middle, and subapical areas each with one pair of spots, apical area with one spot; some specimens have reduced or dark grey spots on the elytra, some have black spots interconnected.

Vertex finely and sparsely covered with punctures; frontal tubercle distinctly raised, separated from each other by a deep furrow; antennae short, robust, extend to the middle of the elytra; antennomeres 1–3 thin, shiny; antennomeres 4–11 wide and flat, with short hairs, antennomere 4 approximately $2.5 \times$ as long as wide; antennomeres 5–10, each approximately $1.6 \times$ as long as wide; antennomeres 2 and 3 shortest, antennomere 3 similar in length and shape to antennomere 2, antennomere 4 longest, $1.5 \times$ as long as antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than 4; antennomere 11 slightly longer than 10, pointed.

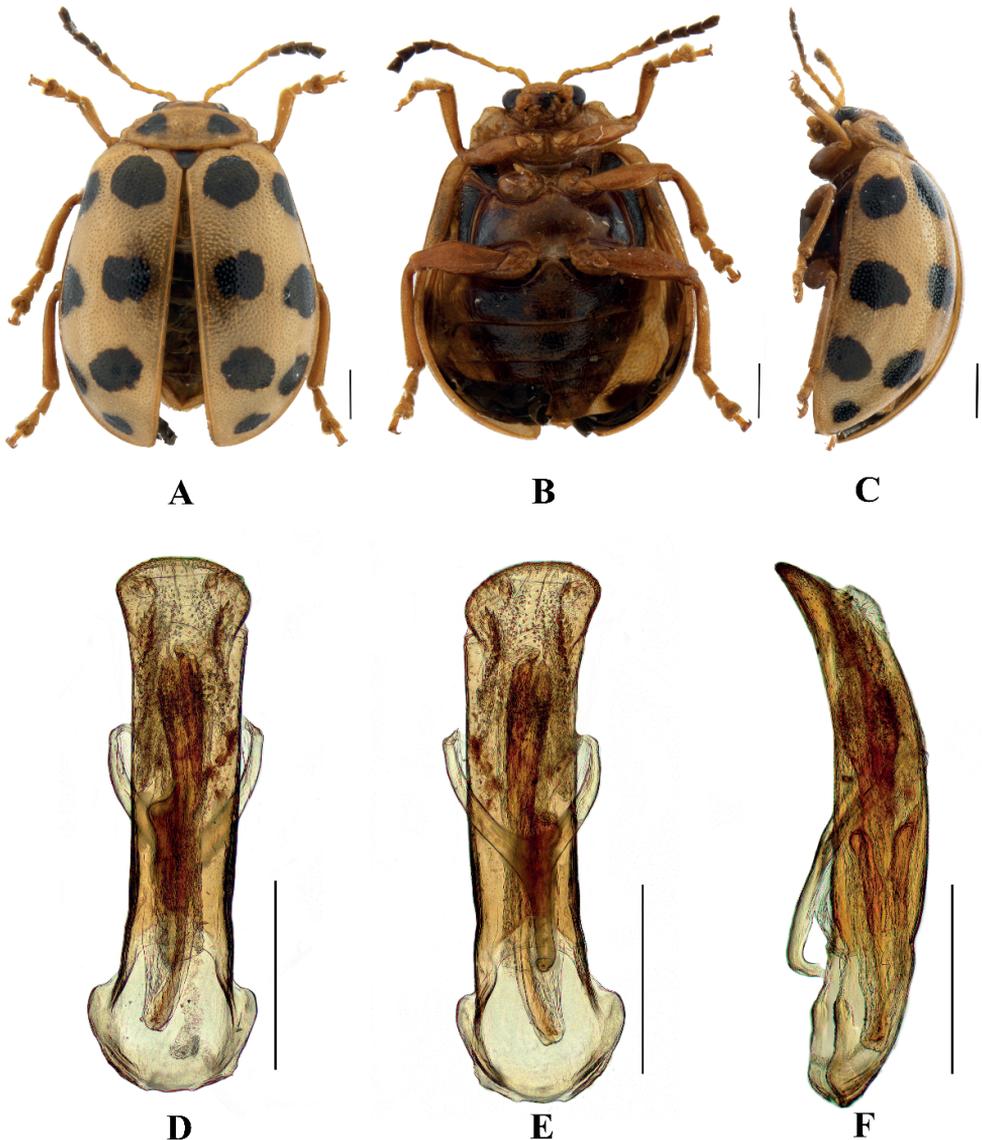


Figure 6. *Sphenoraia (Sphenoraoides) nebulosa* **A–C** habitus **D–F** aedeagus **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars: 1 mm (**A–C**); 0.5 mm (**D–F**).

Pronotum approximately $2.5 \times$ as wide as long, with rounded lateral margins; disc slightly convex, sparsely covered with small punctures, with the punctures on the pronotum larger than those on the head.

Scutellum triangular, smooth, impunctate.

Basal width of both elytra wider than the pronotum, gradually widen posteriorly and rounded at apex; dorsal surface slightly convex, irregularly covered with large and deep punctures, the interstices between punctures slightly wider than diameter of individual punctures.

Metasternum $2.5 \times$ as long as mesosternum; prothoracic legs shortest, mesothoracic legs slightly longer, metathoracic legs longest.

Ventral surface of abdomen with five segments, segment 1 longest, segments 2–4 gradually shortened, apical segment slightly longer than segment 4, with three lobes.

Aedeagus slender, parallel-sided, basally widened, apex rounded. In lateral view moderately bent.

Female. Length 6.2–6.6 mm, width 4.5–5.0 mm.

Antennae yellow, antennomeres 6–11 brown; antennomeres 1–5 thin, antennomeres 6–11 wide and flat, each approximately $1.5 \times$ as long as wide; antennomere 2 shortest, antennomere 3 slightly longer than 2, $1.2 \times$ as long as second; antennomere 4 longest, slightly longer than antennomeres 2 and 3 combined; apical sternite flattened.

Differential diagnosis. This species can be distinguished from the other species by black spots of the pronotum and elytra. However, it especially resembles *Sphenoraia* (*Sphenoraoides*) *haizhuensis*, the former differs in having a scutellum without punctures, and the aedeagus in lateral view being moderately bent.

Distribution: China: Guangdong, Hainan, Guangxi, Yunnan; Vietnam, Laos, Cambodia, Thailand, Myanmar, India, Sikkim.

Sphenoraia (*Sphenoraoides*) *nigromaculata* Jiang, 1992

Fig. 7A–F

Sphenoraia nigromaculata Jiang, 1992: 665.

Sphenoraia (*Sphenoraoides*) *nigromaculata*: Wang et al. 2000: 118.

Type specimen examined. Holotype: ♂, CHINA, Sichuan Province, Maerkang; 2500 m; 17 Aug. 1983; Shuyong Wang leg.; IZAS.

Additional specimen examined. 1♀, CHINA, Sichuan Province, Xiaojin, Fubian; 2900 m; 19 Aug. 1963; Leyi Zheng leg.; IZAS.

Description. Male. Length 6.0 mm, width 3.4 mm.

Head, pronotum and scutellum blackish green, antennae, legs, and ventral surface of body brown, elytra and apex of each abdominal segment yellow; each elytron with seven black spots of different sizes, basal, middle and subapex each with one pair of spots, apex with one spot.

Vertex densely covered with punctures; frontal tubercles distinctly raised, each separated from each other by a deep furrow; antennae short, robust, extending to the

middle of the elytra; antennomere 2 shortest, antennomere 3 slightly longer than 2, $1.2 \times$ as long as second; antennomere 4 longest, twice as long as antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than 4; antennomere 11 slightly longer than 10, pointed.

Pronotum approximately $1.9 \times$ as wide as long, with rounded lateral margins; disc slightly convex, sparsely covered in middle with small punctures with large punctures on other parts. The interstices between punctures slightly narrower than diameter of individual punctures and lightly covered with small punctures in interstices.

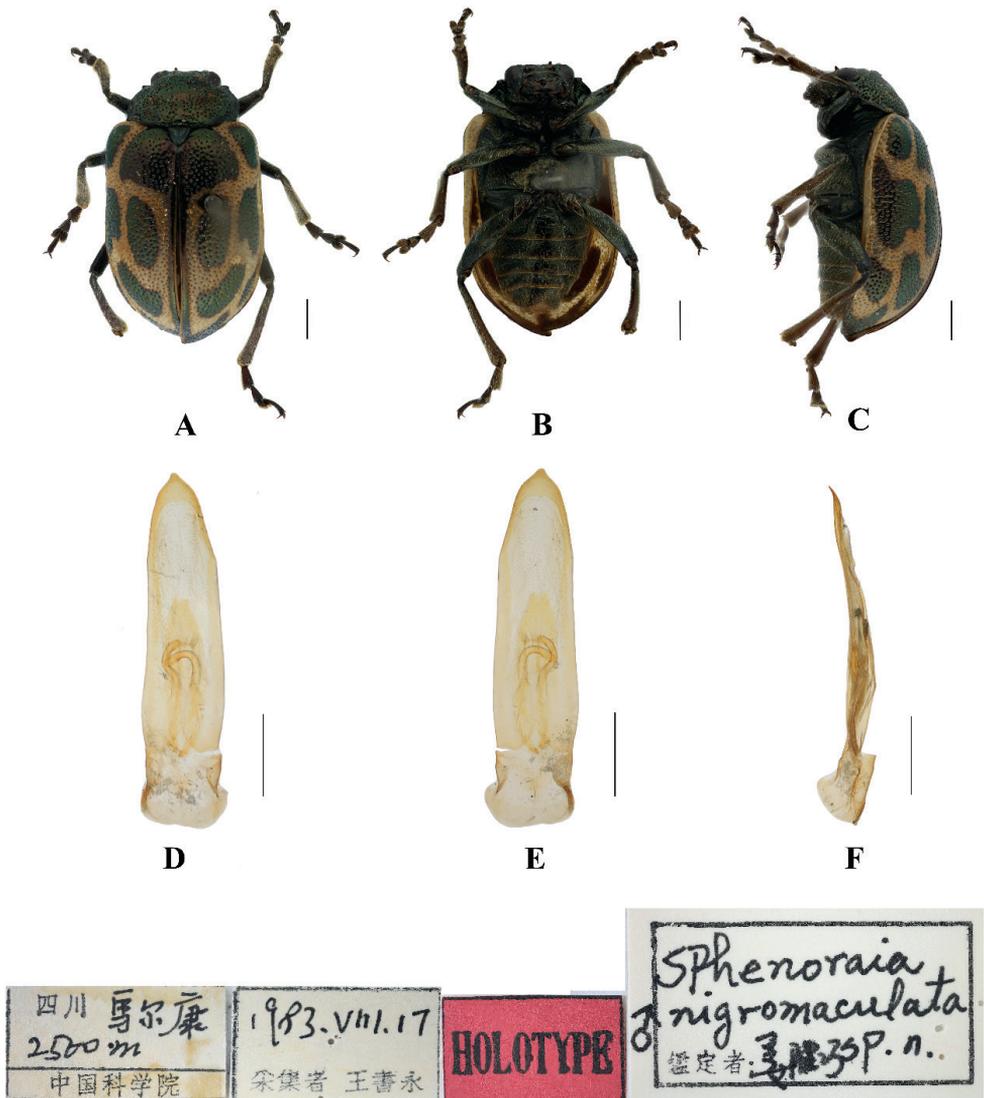


Figure 7. *Sphenoraia (Sphenoraoides) nigromaculata* A–C habitus D–F aedeagus A, D dorsal views B, E ventral views C, F lateral views. Scale bars: 1 mm (A–C); 0.5 mm (D–F).

Scutellum triangular, densely covered with punctures.

Bases of both elytra wider than the pronotum, gradually widen posteriorly and rounded at apex; dorsal surface slightly convex, irregularly covered with large and deep punctures, the interstices between punctures slightly narrower than diameter of individual punctures and lightly covered with small punctures in interstices.

Metasternum twice as long as mesosternum; prothoracic legs shortest, mesothoracic legs slightly longer, metathoracic legs longest.

Ventral surface of abdomen with five segments, segment 1 longest, segments 2–4 gradually shortened, apical segment slightly longer than segment 3, three lobes.

Aedeagus slender, rounded laterally, basally widened, with triangular apex, slightly pointed. In lateral view moderately bent.

Female. Length 5.8 mm, width 3.3 mm.

Antennal antennomere 2 shortest, antennomere 3 slightly longer than 2, $1.4 \times$ as long as second; apical sternite flatted.

Differential diagnosis. This species can be distinguished from other species by the blackish green pronotum and blackish green spots of the elytra.

Distribution. China: Sichuan.

Sphenoraia (Sphenoraioides) punctipennis Jiang, 1992

Fig. 8A–F

Sphenoraia punctipennis Jiang, 1992: 665.

Sphenoraia (Sphenoraioides) punctipennis: Wang et al. 2000: 118.

Type specimen examined. Holotype: ♂, CHINA, Xizang, Mangkang, Haitong; 3250 m; Aug. 1982; Shuyong Wang leg.; IZAS.

Description. Male. Length 6.0 mm, width 3.4 mm.

Head, pronotum and scutellum blackish green, antennae, elytra, legs, and ventral surface of body brown; elytral epipleuron from base to subapex yellow, with middle of suture yellow, connected by yellow stripes from the base to the apex of each elytron.

Vertex finely and sparsely covered with punctures; frontal tubercles distinctly raised, each separated by a deep furrow; antennae short, robust, extended to the middle of the elytra; antennomeres 1–3 thin, shiny; antennomeres 4–11 wide and flat, with short hairs, antennomeres 2 and 3 shortest, antennomere 3 similar in length and shape to antennomere 2, antennomere 4 longest, $1.5 \times$ as long as antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than 4; antennomere 11 slightly longer than 10, pointed.

Pronotum approximately $1.8 \times$ as wide as long, with rounded lateral margins; disc slightly convex, sparsely covered with small punctures in the middle with large punctures on other parts. The interstices between punctures equal to the diameter of individual punctures and lightly covered with small punctures in interstices.

Scutellum triangular, sparsely covered with punctures at base.

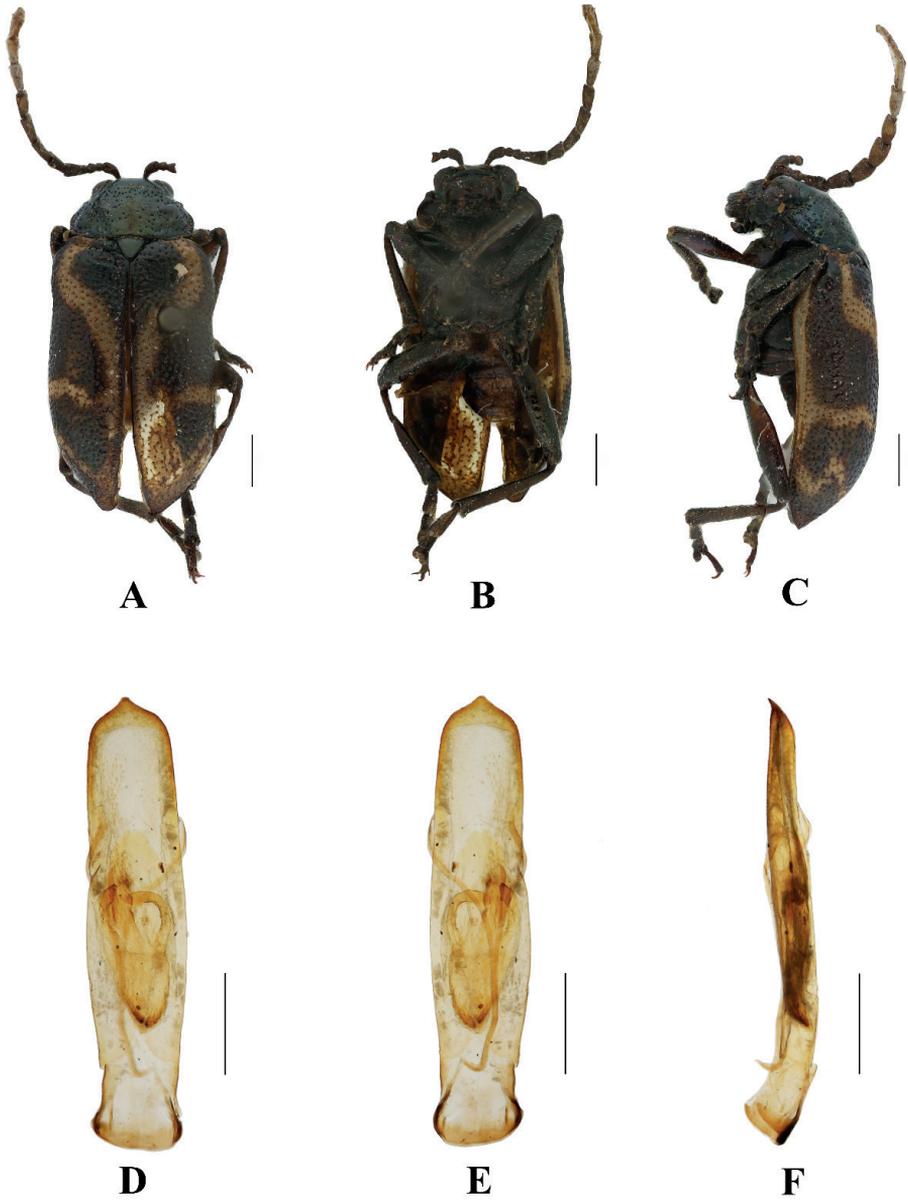


Figure 8. *Sphenoraia* (*Sphenoraoides*) *punctipennis* **A–C** habitus **D–F** aedeagus **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars: 1 mm (**A–C**); 0.5 mm (**D–F**).

Bases of both elytra wider than the pronotum, gradually widen posteriorly, and rounded at apex; dorsal surface slightly convex, irregularly covered with large and deep punctures, the interstices between punctures narrower than the diameter of individual punctures and lightly covered with small punctures in interstices, with their interstices somewhat wrinkled.

Metasternum twice as long as mesosternum; prothoracic legs shortest, mesothoracic legs slightly longer, metathoracic legs longest.

Ventral surface of abdomen with five segments, segment 1 longest, segments 2–4 gradually shortened, apical segment slightly longer than segment 4, three lobes.

Aedeagus slender, rounded laterally, basally widened, with triangular apex, distinctly pointed. In lateral view moderately bent.

Differential diagnosis. This species can be distinguished from other species by blackish green pronotum, yellow stripes of elytra and large punctures on elytra.

Distribution. China: Xizang.

Host plant. *Rheum* sp.

Sphenoraia (*Sphenoraia*) *rutilans* (Hope, 1831)

Fig. 9A–F

Eumolpus rutilans Hope, 1831: 30.

Chrysomela mutabilis Hope, 1831: 30. Synonymized by Maulik 1936: 547.

Galleruca fulgida Kollar & Redtenbacher, 1844: 554. Synonymized by Maulik 1936: 547.

Sphenoraia cyanea Allard, 1890: 92. Synonymized by Laboissière 1940: 30.

Sphenoraia (*Sphenoraia*) *rutilans*: Gressitt and Kimoto 1963: 657.

Other specimens examined. 1♂, CHINA, Yunnan Province, Xishuangbanna, Menglun; 600 m; 22 Apr. 1994; Longlong Yang leg.; IZAS. 1♂, CHINA, Yunnan Province, Xishuangbanna, Mengla; 620–650 m; 2 May 1959; Facai Zhang leg.; IZAS. 1♂, CHINA, Yunnan Province, Xishuangbanna, Mengla; 620–650 m; 3 May 1959; Facai Zhang leg.; IZAS. 1♂, CHINA, Yunnan Province, Xishuangbanna, Mengla; 620–650 m; 3 May 1959; Facai Zhang leg.; IZAS. 1♀, CHINA, Yunnan Province, Xishuangbanna, Mengla; 800 m; 1 Jun. 1958; Shuyong Wang leg.; IZAS. 2♂♂1♀, CHINA, Yunnan Province, Xishuangbanna, Menghuan; 1200–1400 m; 3 Jun. 1958; Shuyong Wang leg.; IZAS. 1♂, CHINA, Yunnan Province, Yiwubannan, Menglun; 650 m; 3 Aug. 1959; Yiran Zhang leg.; IZAS. 1♀, Yunnan Province, Xishuangbanna, Damenglong; 650 m; 5 Oct. 1958; Zhizi Chen leg.; IZAS. 1♀, Yunnan Province, Xishuangbanna, Damenglong; 650 m; 7 Oct. 1958; Zhizi Chen leg.; IZAS.

Description. Male. Length 7.8–8.2 mm, width 4.9–5.2 mm.

Body dark blue, antennae brown.

Vertex finely and sparsely covered with punctures; frontal tubercles distinctly raised, each separated from each other by a deep furrow; antennae short, robust,

extended to the middle of the elytra; antennomeres 1–3 thin, shiny; antennomeres 4–11 wide and flat, with short hairs, antennomere 4 approximately $1.5 \times$ as long as wide; antennomeres 5–6, each approximately $1.2 \times$ as long as wide; the length of each of antennomeres 7–9 equals its width; antennomere 10 approximately $1.2 \times$ as wide as long; antennomere 11 approximately $1.2 \times$ as long as wide; antennomeres 2 and 3 shortest, antennomere 3 similar in length and shape to antennomere 2, antennomere 4

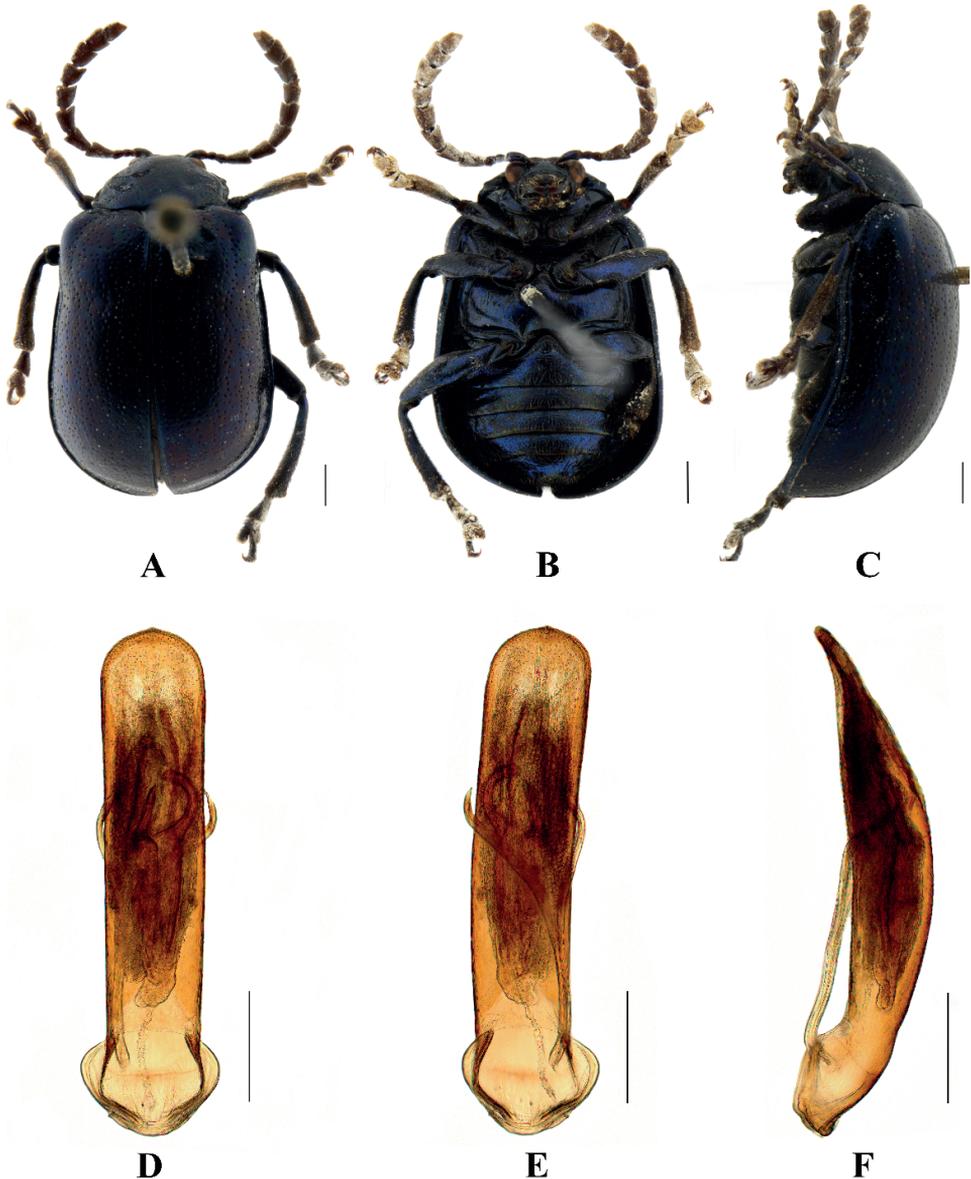


Figure 9. *Sphenoraia* (*Sphenoraoides*) *rutilans* **A–C** habitus **D–F** aedeagus **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars: 1 mm (**A–C**); 0.5 mm (**D–F**).

longest, $1.2 \times$ as long as antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than 4; antennomere 11 slightly longer than 10, pointed.

Pronotum approximately twice as wide as long, with rounded lateral margins; disc sparsely covered with punctures, with a lateral pair of shallow impressions.

Scutellum triangular, with rounded apex, smooth, impunctate.

Bases of both elytra wider than the pronotum, gradually widen posteriorly and rounded at apex; dorsal surface slightly convex, irregularly covered with punctures, the interstices between punctures equal to diameter of individual punctures.

Metasternum twice as long as mesosternum; prothoracic legs shortest, mesothoracic legs slightly longer, metathoracic legs longest.

Ventral surface of abdomen with 5 segments, segment 1 longest, segments 2–4 gradually shortened, apical segment slightly longer than segment 3, three lobes.

Aedeagus slender, parallel-sided, basally widened, apex rounded. In lateral view strongly bent.

Female. Length 8.0–8.2 mm, width 5.0–5.4 mm.

Antennae antennomeres 1–3 thin, shiny; antennomeres 4–11 with short hairs, antennomeres 7–11 wide and flat, each approximately $1.2 \times$ as wide as long; apical sternite flattened.

Differential diagnosis. This species can be distinguished from other species by wide and flat antennae and the shallow impressions of the pronotum.

Distribution. China: Yunnan; Kashmir, Myanmar, India, Nepal, Bhutan, Bangladesh, Pakistan.

Sphenoraia (*Sphenoraioides*) *yajiangensis* Jiang, 1992

Fig. 10A–F

Sphenoraia yajiangensis Jiang, 1992: 667.

Sphenoraia (*Sphenoraioides*) *yajiangensis*: Wang et al. 2000: 118.

Type specimens examined. **Holotype:** ♂, CHINA, SiChuan Province, YaJiang; 3600 m; 26 Aug. 1982; Shuyong Wang leg.; IZAS. **Paratypes:** 3♂♂1♀, same information as holotype. **Allotype:** 1♀, same information as holotype.

Description. Male. Length 5.8–6.2 mm, width 3.6–4.0 mm.

Head, antennae, and legs brown, pronotum, scutellum and elytra blackish green, ventral surface of body black, elytral epipleuron from base to apical $1/3$ and apex of each abdominal segment yellow.

Vertex finely and sparsely covered with punctures; frontal tubercles distinctly raised, separated from each other by a deep furrow; antennae short, robust, extended to the middle of elytra; antennomeres 1–3 thin, shiny; antennomeres 4–11 wide and flat, with short hairs, antennomere 4 approximately twice as long as wide; antennomeres 5–10, each approximately $1.5 \times$ as long as wide; antennomere 2 shortest, antennomere 3 slightly longer than 2, $1.2 \times$ as long as second; antenno-

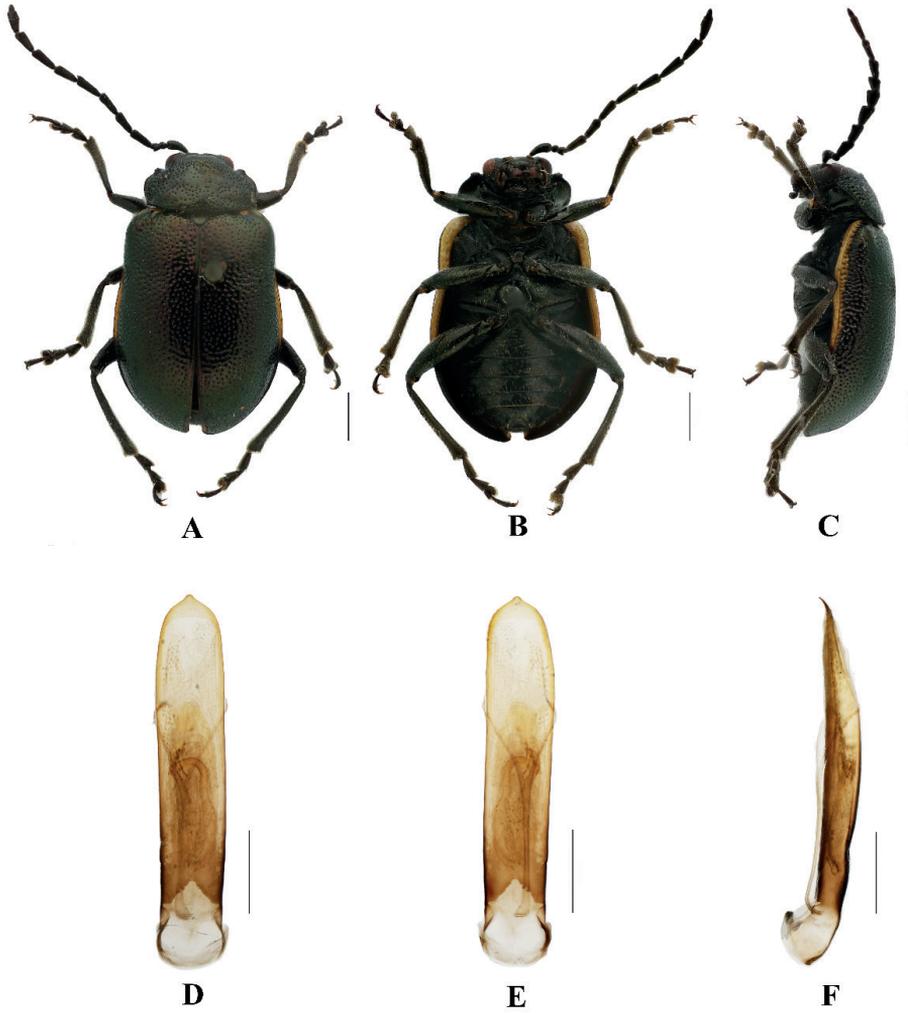


Figure 10. *Sphenoraia* (*Sphenoraoides*) *yajiangensis* A–C habitus D–F aedeagus A, D dorsal views B, E ventral views C, F lateral views. Scale bars: 1 mm (A–C); 0.5 mm (D–F).

mere 4 longest, 1.7 × as long as antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than 4; antennomere 11 slightly longer than 10, pointed.

Pronotum approximately twice as wide as long, with rounded lateral margins, disc slightly convex, sparsely covered in middle with small punctures with large punctures on other parts. The interstices between punctures equal to the diameter of individual punctures and lightly covered with small punctures in interstices.

Scutellum triangular, with rounded apex, covered with small punctures at base.

Bases of both elytra wider than pronotum, gradually widen posteriorly and rounded at apex; dorsal surface slightly convex, irregularly covered with large and deep punctures, the interstices between punctures equal to the diameter of individual punctures and lightly covered with small punctures in interstices.

Metasternum twice as long as mesosternum; prothoracic legs shortest, mesothoracic legs slightly longer, metathoracic legs longest.

Ventral surface of abdomen with five segments, segment 1 longest, segments 2–4 gradually shortened, apical segment slightly longer than segment 4, three lobes.

Aedeagus slender, parallel-sided, basally widened, apex narrowly pointed; in lateral view moderately bent.

Female. Length 5.8–6.3 mm, width 3.5–3.9 mm.

Antennal antennomeres 4–11 thin, antennomere 2 shortest, antennomere 3 slightly longer than 2, $1.5 \times$ as long as second; antennomere 4 longest, $1.2 \times$ as long as antennomeres 2 and 3 combined; apical sternite flattened.

Differential diagnosis. This species can be distinguished from other species by blackish green pronotum and elytra.

Distribution. China: Sichuan.

Host plant. Berberidaceae.

***Sphenoraia* (*Sphenoraia*) *decemmaculata* sp. nov.**

<https://zoobank.org/9C8B84E5-C6E1-4FE1-91EF-A1D4304CAEA3>

Fig. 11A–F

Type specimens examined. *Holotype*: ♂, CHINA, Yunnan Province, E'shan; Aug. 1980; IZAS. *Paratype*: 1♀, CHINA, Sichuan Province, Guichang, liusuo; 10 Jun. 1961; Dingxi Lao leg.; IZAS.

Description. Male. Length 6.2 mm, width 4.5 mm.

Head and pronotum yellowish brown, antennae, scutellum, ventral surface of body and legs black, elytra yellow, each with five black spots, basal and middle areas of each elytron with one pair of spots, subapical area with one spot.

Vertex finely and sparsely covered with punctures; frontal tubercles distinctly raised, separated from each other by a deep furrow; antennae slender, extended to the middle of the elytra; antennomeres 1–3 thin, shiny; antennomeres 4–11 with short hair, antennomere 4 approximately twice as long as wide; antennomeres 5–10, each approximately $1.6 \times$ as long as wide; antennomere 2 shortest, antennomere 3 slightly longer than 2, $1.5 \times$ as long as second; antennomere 4 longest, $1.2 \times$ as long as

antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than 4; antennomere 11 slightly longer than 10, pointed.

Pronotum approximately twice as wide as long, with lateral margins straight and parallel, anterior angle thickened, protruding forwards, disc slightly convex and sparsely covered with small punctures.

Scutellum triangular, sparsely covered with small punctures.

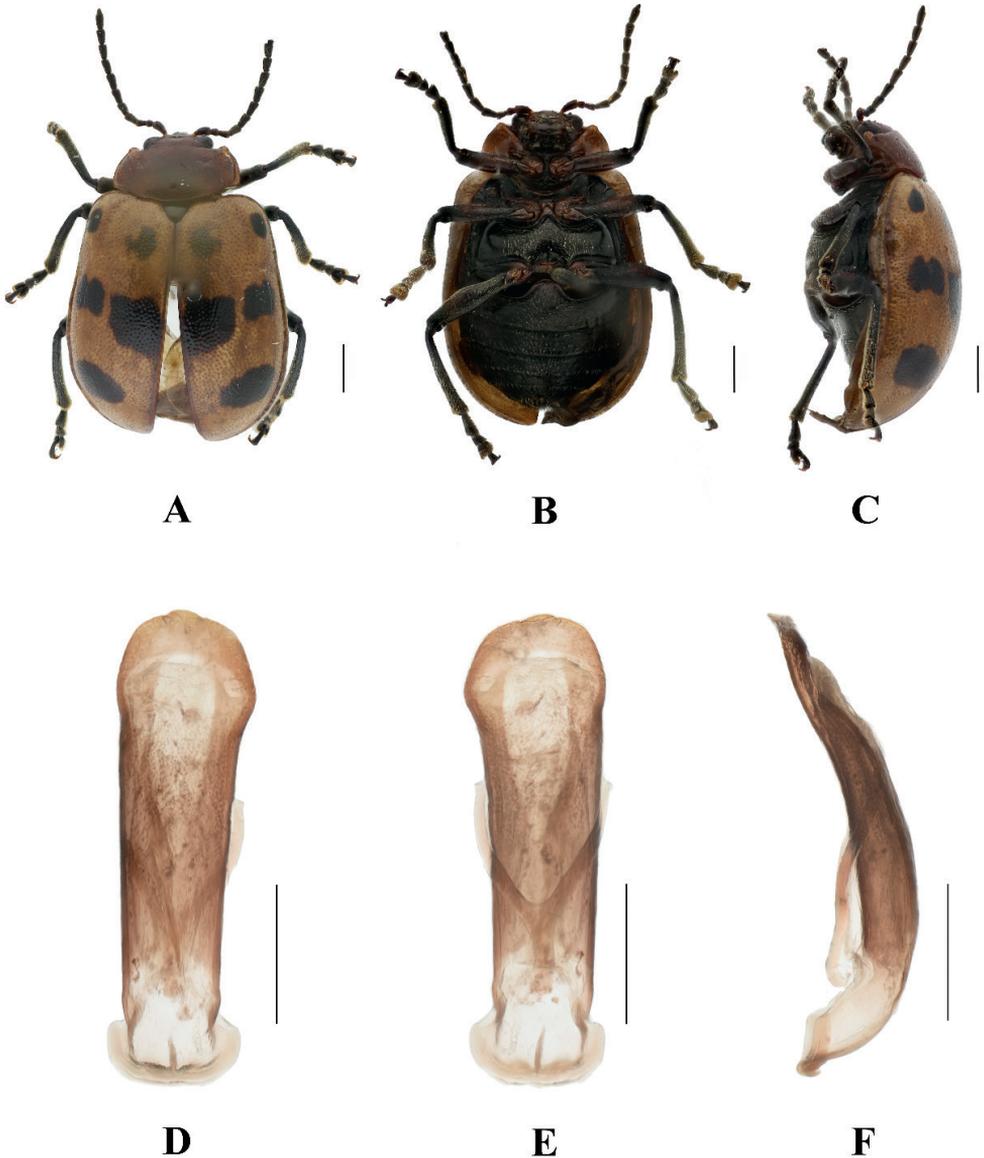


Figure 11. *Sphenoraia* (*Sphenoraia*) *decemmaculata* sp. nov. **A–C** habitus **D–F** aedeagus **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars: 1 mm (**A–C**); 0.5 mm (**D–F**).

Bases of both elytra wider than pronotum, gradually widen posteriorly and rounded at apex; dorsal surface slightly convex and irregularly covered with large, deep punctures, the interstices between punctures slightly wider than the diameter of individual punctures.

Metasternum $2.5 \times$ as long as mesosternum; prothoracic legs shortest, mesothoracic legs slightly longer, metathoracic legs longest.

Ventral surface of abdomen with 5 segments, segment 1 longest, segments 2–4 gradually shortened, apical segment slightly longer than segment 4, three lobes.

Aedeagus short and wide, parallel-sided, gradually widened apically and rounded at apex, basally widened; in lateral view strongly bent.

Female. Length 6.3 mm, width 4.4 mm.

Antennae slender, antennomeres 4–11 thin, with short hairs, antennomere 2 shortest, antennomere 3 slightly longer than 2, $1.2 \times$ as long as second; apical sternite flattened.

Differential diagnosis. The new species closely resembles *Sphenoraia* (*Sphenoraioides*) *anjiensis* but differs due to the black pronotum and yellow abdomen. In the new species the head and pronotum are brown, and each elytron has five black spots: the base and middle of each elytron with a pair of spots, the subapex with one spot. The aedeagus is short and wide, gradually widening apically and is rounded at the apex.

Etymology. Latin: *deca* = ten; *macula* = spot; referring to the ten black spots on the elytra.

Distribution. China: Sichuan, Yunnan.

Sphenoraia (*Sphenoraioides*) *flavomarginata* sp. nov.

<https://zoobank.org/C0361BA0-9E50-42DB-8005-50EA1087710A>

Fig. 12A–F

Type specimens examined. *Holotype*: ♂, CHINA, Sichuan Province, Kangding, liuba; 3700 m; Sep. 1982; S.Y. Wang leg.; IZAS. *Paratype*: 3 ♀♀, same data as holotype.

Description. Male. Length: 5.5–6.0 mm, width: 2.8–3.5 mm.

Antennae, ventral surface of the body, and legs brown. Head, pronotum, scutellum, and elytra blackish green, apical area of each segment of the abdomen yellow, elytra with yellow stripes along the basal margin, extending along the elytral epipleuron from the base to the apical $1/3$, with one transverse yellow stripe at subapex.

Vertex finely and sparsely covered with punctures; frontal tubercles distinctly raised, separated from each other by a deep furrow; antennae short, robust, extend to the middle of the elytra; antennomeres 1–3 thin, shiny; antennomeres 4–11 wide and flat, with short hairs, antennomere 4 approximately $3 \times$ as long as wide; antennomeres 5–10, each approximately $2 \times$ as long as wide; antennomere 2 shortest, antennomere 3 slightly longer than 2, $1.2 \times$ as long as second; antennomere 4 longest, $1.5 \times$ as long as antennomeres 2 and 3 combined; antennomeres 5–10 gradually shortened, shorter than 4; antennomere 11 slightly longer than 10, pointed.

Pronotum approximately twice as wide as long, with rounded lateral margins; disc slightly convex, sparsely covered with small punctures in the middle with large

punctures on other parts of pronotum. The interstices of punctures equal to diameter of punctures slightly, covered with small punctures.

Scutellum triangular, with rounded apex, covered with small punctures and short hairs.

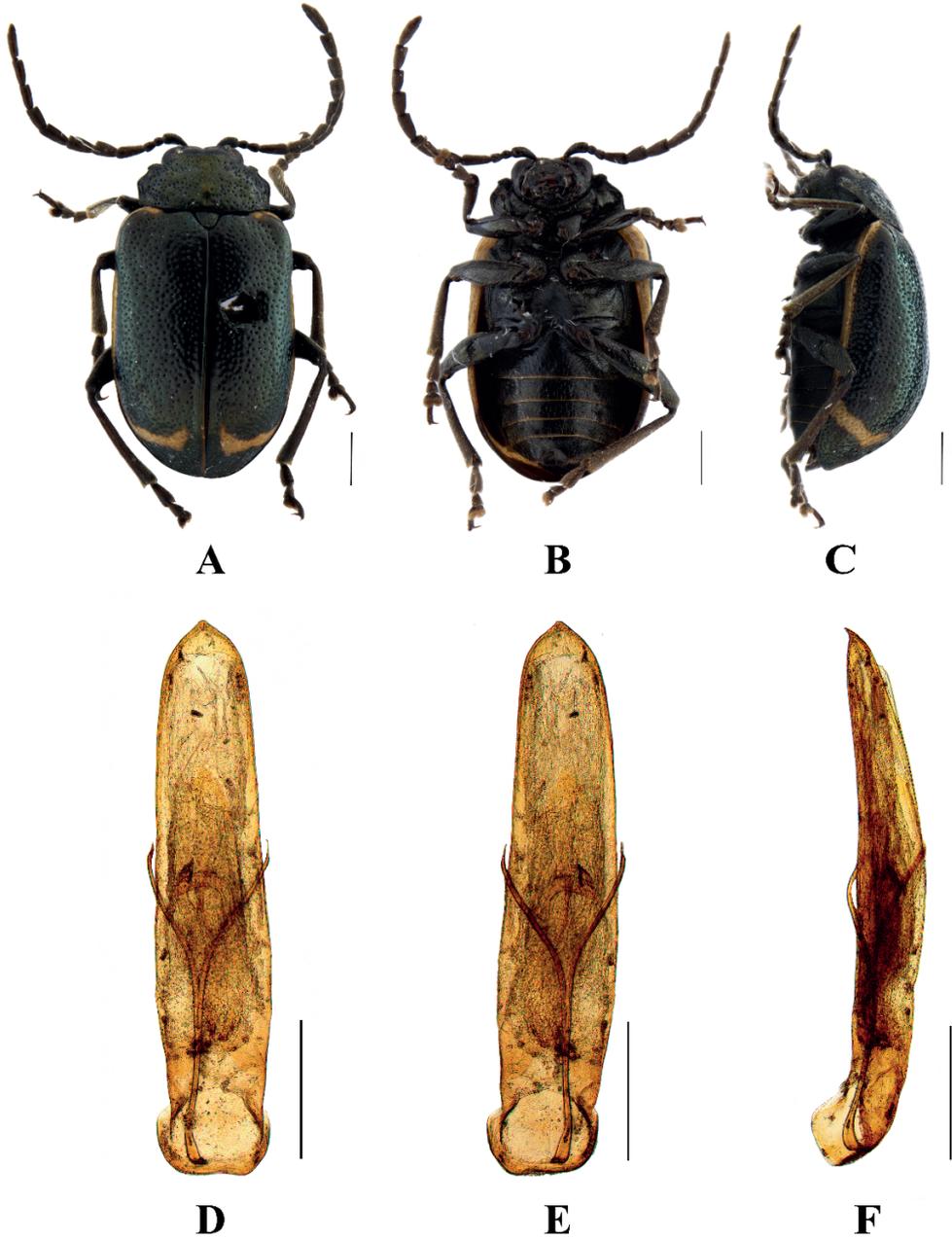


Figure 12. *Sphenoraia (Sphenoraioides) flavomarginata* sp. nov. **A–C** habitus **D–F** aedeagus **A, D** dorsal views **B, E** ventral views **C, F** lateral views. Scale bars: 1 mm (**A–C**); 0.5 mm (**D–F**).

Bases of both elytra wider than pronotum, gradually widen posteriorly and rounded at apex; dorsal surface slightly convex, irregularly covered with large and deep punctures, the interstices between punctures equal to the diameter of individual punctures and lightly covered with small punctures in interstices.

Metasternum twice as long as mesosternum; prothoracic legs shortest, mesothoracic legs slightly longer, metathoracic legs longest.

Ventral surface of abdomen with 5 segments, segment 1 longest, segments 2–4 gradually shortened, apical segment slightly longer than segment 4, three lobes.

Aedeagus slender, parallel-sided, basally widened, apex narrowly pointed; in lateral view moderately bent.

Female. Length: 5.4–6.0 mm, width: 2.9–3.6 mm.

Antennae slender, antennomeres 4–11 thin, antennomere 2 shortest, antennomere 3 slightly longer than 2, $1.2 \times$ as long as second; apical sternite flattened.

Differential diagnosis. The new species closely resembles *Sphenoraia* (*Sphenoraiaoides*) *yajiangensis*. However, the new species has a different pattern in the arrangement of the yellow stripes, with one transverse yellow stripe present at the sub-apex of the elytra, and the pronotum has sparse punctures. The aedeagus is slender, and its apex narrowly pointed.

Etymology. Latin: *flava* = yellow; *margin* = margin; referring to each elytron with a yellow margin.

Distribution. China: Sichuan.

Gallerucida cupreata (Jacoby, 1890), comb. nov.

Fig. 13 A–C

Sphenoraia cupreata Jacoby, 1890, 23: 193.

Type specimen examined. Chang Yang, A. E. Pratt Coll., June 1888; 1st Jacoby Coll.; Type 18239; *S. cupreata* Jac.

Description. Male. Length 4.4 mm, width 3.2 mm

Head, pronotum, elytra, and scutellum green, antennae and legs brown, ventral surface of body yellowish brown.

Vertex finely and sparsely covered with punctures; frontal tubercle distinctly raised, separated from each other by a deep furrow; antennae short, robust, extended to the middle of elytra; antennomeres 1–3 thin, shiny; antennomeres 4–11 wide and flat, with short hairs, antennomeres 2 and 3 shortest, antennomere 3 similar in length and shape to antennomere 2, antennomere 4 longest, $1.2 \times$ as long as antennomeres 2 and 3 combined; antennomeres 5–10 differ in length, shorter than 4; antennomere 11 slightly longer than 10, pointed.

Pronotum approximately $2.5 \times$ as wide as long, with rounded lateral margins; disc sparsely covered with punctures, with a lateral pair of shallow impressions.

Scutellum triangular, covered with small punctures.

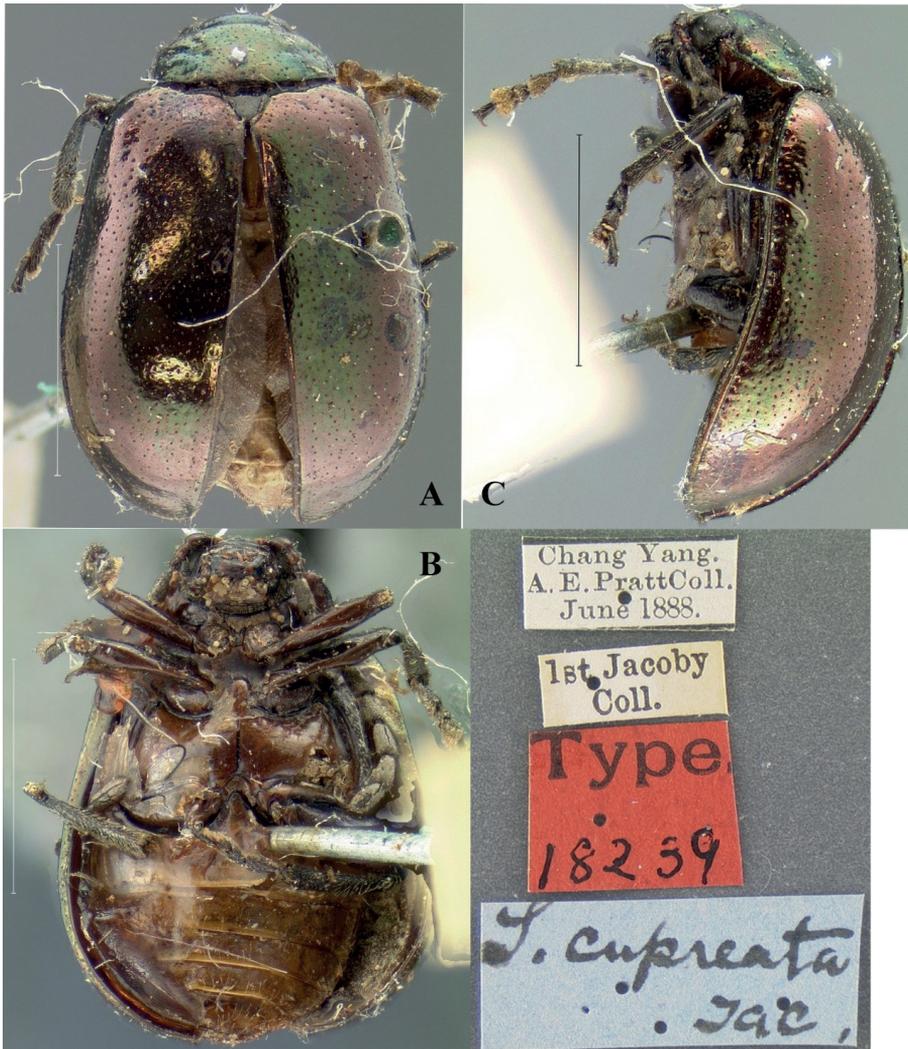


Figure 13. *Gallerucida cupreata*. comb. nov. **A–C** habitus **A** dorsal view **B** ventral view **C** lateral view. Scale bars: 2 mm.

Bases of both elytra wider than pronotum, gradually widen posteriorly and rounded at apex; dorsal surface slightly convex, irregularly covered with large and deep punctures, the interstices between punctures slightly wider than the diameter of individual punctures and covered with small punctures.

Metasternum $2.5 \times$ as long as mesosternum, Anterior metasternal process extending beyond the front edge of the meso-coxal cavities; prothoracic legs shortest, mesothoracic legs slightly longer, metathoracic legs longest.

Ventral surface of abdomen with five segments, segment 1 longest, segments 2–4 gradually shortened, apical segment equal in length to segment 1, with three lobes.

Notes. According to the characteristics of the cylindrical process of the metasternum, *Sphenoraia* (*Sphenoraia*) *cupreata* is transferred from *Sphenoraia* to *Gallerucida*.

Distribution. China: Hubei.

***Gallerucida nigra* (Wang, Li & Yang, 2000), comb. nov.**

Fig. 14A–C

Sphenoraia (*Sphenoraia*) *nigra* Wang, Li & Yang, 2000: 118.

Type specimens examined. *Holotype*: ♀, CHINA, Gansu Province, Dangchang; 1700–2300 m; 9 Jul. 1998; Shuyong Wang leg.; IZAS. *Paratype*: 1♀, CHINA, Gansu Province, Wen Country; 1400 m; 2 Jun. 1992; Hongjian Wang leg.; IZAS. 1♀, CHINA, Gansu Province, Zhouqu; 2350 m; 5 Jul. 1998; Jun Chen; IZAS.

Other specimens examined. 1♀, CHINA, Henan, Baiyun Mountain; 1900 m; 23 Jul. 2002; Lijie Zhang leg.; IZAS.

Description. Female. Length: 6.6–6.8 mm, width: 4.0–4.5 mm.

Head, antennae, pronotum, scutellum, ventral surface of the body, and legs black, elytra brown; each elytron with eight black spots, basal and middle sections with one pair of spots, subapical area with three spots and apical area with one spot.

Vertex finely and sparsely covered with punctures; frontal tubercles distinctly raised, separated from each other by a deep furrow; antennae short, robust, extend to the middle of the elytra; antennomeres 1–3 thin, shiny; antennomeres 4–11 wide and flat, with short hairs, each approximately $2.5 \times$ as long as wide; antennomere 2 shortest, antennomere 3 slightly longer than 2, $1.5 \times$ as long as second; antennomere 4 longest, $1.2 \times$ as long as antennomeres 2 and 3 combined; antennomeres 5–10 unequal in length, shorter than 4; antennomere 11 slightly longer than 10, pointed.

Pronotum approximately $1.8 \times$ as wide as long, with rounded lateral margins; disc slightly convex, sparsely covered in middle with small punctures with large punctures laterally.

Scutellum triangular, smooth, impunctate.

Bases of both elytra wider than pronotum, gradually widen posteriorly and rounded at apex; dorsal surface slightly convex, irregularly covered with large and deep punctures, the interstices between punctures slightly wider than the diameter of individual punctures and covered with small punctures.

Metasternum $2.5 \times$ as long as mesosternum, Anterior metasternal process extending beyond the front edge of the meso-coxal cavities; prothoracic legs shortest, mesothoracic legs slightly longer, metathoracic legs longest.

Notes. According to the anterior metasternal process clearly extending beyond the front edge of the meso-coxal cavities, *Sphenoraia* (*Sphenoraia*) *nigra* is transferred from *Sphenoraia* to *Gallerucida*.

Distribution. China: Henan, Gansu.

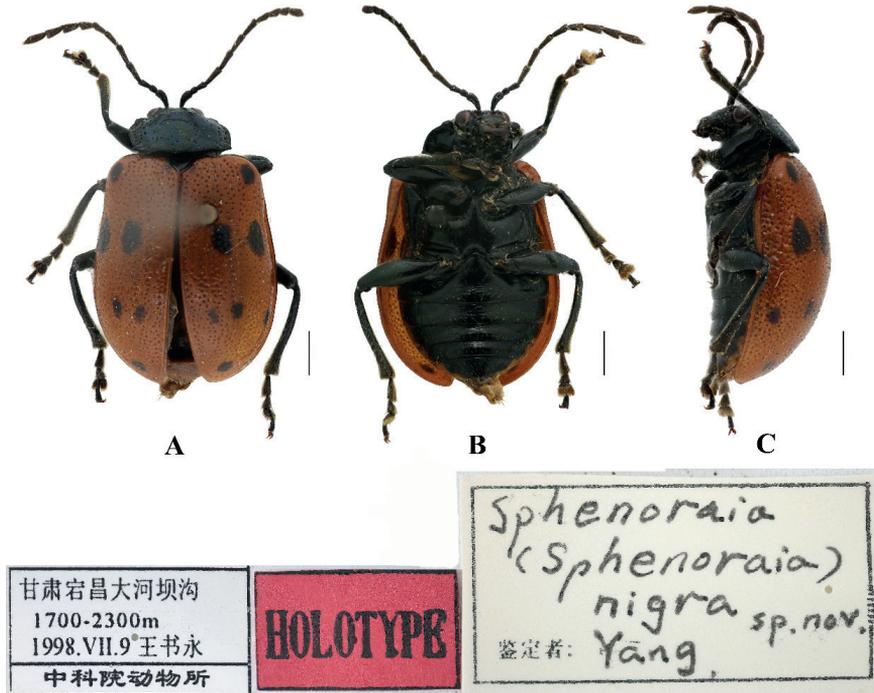


Figure 14. *Gallerucida nigra*, comb. nov. **A–C** habitus **A** dorsal view **B** ventral view **C** lateral view. Scale bars: 1 mm.

Acknowledgements

We extend our heartfelt gratitude to Prof. Derek Dunn for revising this manuscript. This study was supported by the GDAS Special Project of Science and Technology Development (Grant Nos. 2020GDASYL-20200301003, 2020GDASYL-20200102021).

References

- Allard E (1890) Troisième note sur les galérucoïdes. Bulletin ou Comptes-rendus des Séances de la Société Entomologique de Belgique 80–94.
- Chûjô M (1956) A taxonomic study on the Chrysomelidae (Insecta: Coleoptera) from Formosa Part VIII. Subfamily Eumolpinae. Philippine Journal of Science 85: 1–180.
- Clark H (1865) An examination of the Dejeanian genus *Caelomera* (Coleoptera Phytophaga) and its affinities. Annals & Magazine of Natural History 15(3): 256–268. <https://doi.org/10.1080/00222936508679421>
- Duvivier A (1887) Description de trois Galerucindes nouvelles. Bulletin ou Comptes-Rendus des Séances de la Société Entomologique de Belgique 1887: 47–50.
- Fairmaire L (1888) Coléoptères de l'intérieur de la Chine (Suite.). Annales de la Société Entomologique de Belgique 32: 7–46.

- Gressitt JL, Kimoto S (1963) The Chrysomelidae (Coleopt.) of China and Korea. Part II. Pacific Insects Monograph 1B: 301–1026.
- Gyllenhal L (1808) Insecta Suecica Descripta. Classis I. Coleoptera sive Eleutherata. Tome I. Scaris: Leverenta, [viii+ [4] +]572 pp. <https://doi.org/10.5962/bhl.title.8767>
- Harold E von (1880) Über ostindische Galeruciden. Stettiner Entomologische Zeitung (41): 142–157.
- Hope FW (1831) Synopsis of the new species of Nepaul insects in the collection of Major General Hardwicke. In: Gray JE (Ed.) Zoological Miscellany. Vol. 1, London, 21–32. [40 pp]
- Jacoby M (1890) Descriptions of new species of phytophagous Coleoptera received by Mr. J. H. Leech, from Chang-Yang, China. The Entomologist 23, 84–89, 114–118, 161–167, 193–197, 214–217, 253–254, 2 pls.
- Jiang S-Q (1992) Coleoptera: Chrysomelidae: Galerucinae. Science Press, 646–674.
- Kimoto S (1986) New or little known Chrysomelidae (Coleoptera) from Japan and its adjacent regions, 4. Coleopterists' Association of Japan, Tokyo, 309–313.
- Kollar V, Redtenbacher L (1844) Aufzählung und Beschreibung der von Freiherrn Carl v. Hügel auf seiner Reise durch Kaschmir und das Himalayagebirge gesammelten Insecten. [393–564] In: Hügel KF von (Ed.) Kaschmir und das Reich der Siek. Vierter Band, Zweite Abtheilung. Hallbergerischer Verlag, Stuttgart, 244–586.
- Laboissière V (1925) Supplément au Catalogus Coleopterorum, pars 78 (Galerucinae) de J. Weise, précédé de remarques sur la classification des Galerucini. Encyclopédie Entomologique (B) 1: 38–62.
- Laboissière V (1934) Coléoptères galéricines nouveaux ou peu connus de la faune indo-malaise. Annales de l'Association des Naturalistes de Levallois-Perret 21(1932–1934): 109–137.
- Laboissière V (1940) Observations sur les Galeruinae des collections du Musée royal d'Histoire naturelle de Belgique et descriptions de nouveaux genres et espèces. Bulletin du Musée d'Histoire Naturelle de Belgique 16(37): 1–41.
- Maulik S (1936) The Fauna of British India, including Ceylon and Burma. Coleoptera. Chrysomelidae (Galerucinae). Taylor & Francis, London, [xiv +] 648 pp. [1 pl.] <https://doi.org/10.5962/bhl.title.48423>
- Nie R-E, Bezdek J, Yang X-K (2017) How many genera and species of Galerucinae s. str. do we know? Updated statistics (Coleoptera, Chrysomelidae). ZooKeys 720: 91–102. <https://doi.org/10.3897/zookeys.720.13517>
- Wang H-J, Li W-Z, Yang X-K (2000) Study on the genus *Sphenoraia* Clark (Coleoptera: Chrysomelidae: Galerucinae) from China. China Agriculture Press, Beijing, 117–121.
- Weise J (1922) Chrysomeliden der Indo-Malayischen Region. Tijdschrift voor Entomologie 65: 39–130.
- Wilcox JA (1971) Chrysomelidae: Galerucinae. (Oidini, Galerucini, Metacyclini, Sermlylini). In: Wilcox JA (Ed.) Coleopterorum Catalogus Supplementa. Pars 78(1), 2nd edn. W. Junk, s-Gravenhage, 220 pp.
- Yang X-K, Li W-Z, Wu H (1998) Coleoptera: Chrysomelidae: Galerucinae. China Forestry Publishing House, Beijing, 128–135.
- Yang X-K, Ge S-Q, Nie R-E, Ruan Y-Y, Li W-Z (2015) Chinese Leaf Beetles. Science Press, Beijing, 507 pp.

A further step towards the characterisation of *Terebellides* (Annelida, Trichobranchidae) diversity in the Northeast Atlantic, with the description of a new species

María Barroso¹, Juan Moreira², María Capa³, Arne Nygren^{4,5}, Julio Parapar¹

1 Departamento de Biología, Universidade da Coruña, A Coruña, Spain **2** Departamento de Biología (Zoología) & Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM), Facultad de Ciencias, Universidad Autónoma de Madrid, Madrid, Spain **3** Departament de Biologia, Universitat de les Illes Balears, Mallorca, Spain **4** Sjöfartsmuseet Akvariet, Göteborg, Sweden **5** Institutionen för marina vetenskaper, Göteborgs Universitet, Göteborg, Sweden

Corresponding author: María Barroso (maria.p.barroso@udc.es)

Academic editor: Greg Rouse | Received 4 August 2022 | Accepted 23 October 2022 | Published 28 November 2022

<https://zoobank.org/4168C32E-37A7-4912-A909-4912E69030AA>

Citation: Barroso M, Moreira J, Capa M, Nygren A, Parapar J (2022) A further step towards the characterisation of *Terebellides* (Annelida, Trichobranchidae) diversity in the Northeast Atlantic, with the description of a new species. ZooKeys 1132: 85–126. <https://doi.org/10.3897/zookeys.1132.91244>

Abstract

Several new species of genus *Terebellides* Sars, 1835 (Annelida, Trichobranchidae) have been recently described from the Northeast Atlantic Ocean after the detection of a large complex of species based on DNA sequence data from previous research. Some of those species (belonging to the so-called Group A) have already been described elsewhere. In this paper, we revise several *Terebellides* clades belonging to Groups B, C and D resulting in the identification of five nominal species: *Terebellides gracilis* Malm, 1874, *Terebellides atlantis* Williams, 1984, *Terebellides williamsae* Jirkov, 1989, *Terebellides irinae* Gagaev, 2009, and *Terebellides shetlandica* Parapar, Moreira & O'Reilly, 2016, plus one new species described here as *Terebellides lavesquei* **sp. nov.** All these species are characterised by a combination of morphological features complemented with a nucleotide diagnostic approach (specific COI nucleotides in the alignment position). Morphological characters used to discriminate between taxa refer to the branchial shape, presence/absence of ciliated papillae dorsal to thoracic notopodia and the morphology of thoracic and abdominal uncinial teeth. An updated identification key to all described species of this genus in NE Atlantic waters is also included.

Keywords

DNA barcoding, DNA species delineation, identification key, integrative taxonomy, Northeast Atlantic, polychaetes, SEM, systematics

Introduction

The genus *Terebellides* Sars, 1835 (Annelida) is distinguishable from other members of Trichobranchidae by the unique mid-dorsal stalk bearing the characteristic branchial lobes, provided with packed branchial lamellae. This taxon is morphologically homogenous and boundaries between species are difficult to assess because relevant characters rely on some microscopic details. These include features of branchiae, chaetae and uncini that need examination with Scanning Electron Microscopy (Parapar et al. 2016c, 2020a; Lavesque et al. 2019). In addition, further work is still needed to assess morphological intra- and interspecific variability for some characters.

A recent comprehensive molecular survey and a set of analytical methods (Nygren et al. 2018) revealed that the actual diversity of *Terebellides* is much higher than expected increasing from 5 to 25 the total number of species present in the NE Atlantic. Furthermore, molecular-based phylogenetic analyses by Nygren et al. (2018) facilitated the search of diagnostic characters. Thus, three nominal species have been identified, including the type species, *Terebellides stroemii* Sars, 1835, and six have been described new to science (Parapar et al. 2020a). All these belonged to the so-called Group A (sensu Nygren et al. 2018). In addition, Lavesque et al. (2019) described eight new species from France based in a molecular survey as well. Many of these recently described species had been usually misidentified as *T. stroemii*; this taxon was previously thought as having a cosmopolitan distribution and resulted therefore in many species being overlooked worldwide.

Nygren et al. (2018) established four main groups of species: A, B, C, and D, which differ from each other by several morphological characters. Parapar et al. (2020b) studied group A species that are characterised by greater overall body length (10.0–50.0 mm), branchial lobes almost completely fused with ventral lobes that were partially or totally obscured, and the presence of papillae on margins of branchial lamellae in some species.

The aim of the present study is the morphological and molecular characterisation of members of Groups B, C, and D after Nygren et al. (2018). A total of five nominal species was identified and a new species is here described as *Terebellides lavesquei* sp. nov.

Materials and methods

This paper is based on the study of 215 *Terebellides* specimens belonging to Groups B, C, and D as defined in Nygren et al. (2018) (Table 1); five correspond to previously described species and one is new to science. This material is deposited in the Zoological Museum Bergen (ZMBN, Bergen, Norway), Goteborg Natural History Museum (GNM, Goteborg, Sweden), and the Norwegian University of Science and Technology, Science Museum (NTNU-VM, Trondheim, Norway; Bakken et al. 2020).

These specimens are part of a large collection of *Terebellides* specimens (table S1 in Nygren et al. 2018) mostly collected in the Norwegian and Swedish continental shelf

but also from the Irish and Celtic seas, North Sea, Barents Sea, Greenland Sea, South Icelandic coast, and the Arctic Ocean.

Light microscope photographs were done using an Olympus SZX12 stereomicroscope equipped with an Olympus C-5050 digital camera. Line drawings were made with a Wacom CTL-4100K-S pen tablet based on photographs and observations made with an Olympus BX40 stereomicroscope. Specimens for Scanning Electron Microscopy (SEM) were prepared by critical point drying, covered with gold and examined and photographed under a JEOL JSM-6400 electron microscope at the Servizos de Apoió á Investigación (SAI, Universidade da Coruña, Spain).

For staining procedures, 10 mg of Methyl Green (MG) colourant were dissolved in 5 ml of 20% ethanol and specimens were held in there for 30 s. MG staining patterns and thoracic uncini morphology were characterised based on the classifications proposed by Schüller and Hutchings (2010, 2013) and Parapar et al. (2020b), respectively; only specimens of similar/comparable size were considered.

For each species, the list of the museum registration numbers and collection details (geographic area, locality, coordinates, depth, collecting date and habitat) is provided in Suppl. material 1. Unless specified, each registration number holds a single specimen; associated GenBank DNA sequence accession numbers are provided in Suppl. material 2.

The correspondence between species numerals (Nygren et al. 2018) and names is as follows: species 1 – *Terebellides shetlandica* Parapar, Moreira & O'Reilly, 2016; species 5 – *Terebellides lavesquei* sp. nov.; species 16 – *Terebellides atlantis* Williams, 1984; species 24 – *Terebellides irinae* Gagaev, 2009; species 2 – *Terebellides williamsae* Jirkov, 1989; species 3 – *Terebellides gracilis* Malm, 1874.

The present study deals with the main *Terebellides* groups B, C, and D, proposed by Nygren et al. (2018) after phylogenetic analyses of nuclear (28S rDNA and internal transcriber spacer 2, ITS2) and mitochondrial (cytochrome C oxidase I and 16S rDNA) markers from specimens of Northeast Atlantic (NEA) *Terebellides*, representing a follow-up to Parapar et al. (2020a) who characterised the species within Group A. In this way, additional analyses with only the COI dataset have been performed in order to assess diagnostic nucleotides for each of the species and the genetic distances between them. Phylogenetic analyses of COI *Terebellides* sequences in GenBank generated by Nygren et al. (2018) and Lavesque et al. (2019) were performed, using *Trichobranthus roseus* (Malm, 1874), *Polycirrus* sp., and *Pista* cf. *crystata* (Müller, 1776) as outgroups (Nygren et al. 2018). Methodology followed that described by Parapar et al. (2020a) and included alignment of 471 sequences with MAFFT version 7.017 (Katoh et al. 2002), calculation of the best substitution model (TVM+F+I+G4), according to Bayesian information criterion – BIC with IQTREE version 1.6.11 (Nguyen et al. 2015). Maximum likelihood phylogenetic analyses were run in IQTREE version 1.6.11 (Nguyen et al. 2015), with ultrafast bootstrap (Hoang et al. 2018). Unequivocal nucleotide diagnostic characters are provided as the positions in the alignment, shown in Suppl. material 2.

The most distinctive taxonomic morphological characters for *Terebellides* include morphology of branchiae (sensu Parapar et al. 2016a), type of thoracic uncini (sensu Parapar et al. 2020b) and abdominal uncini (sensu Parapar et al. 2020a); Methyl Green (MG) staining pattern (sensu Schüller and Hutchings 2010, 2013) and geographic and bathymetric distribution data are also useful to discern species. Regarding branchiae, Parapar et al. (2016a) proposed four types: type 1, with large lobes almost completely fused; type 2, with lobes fused ~ 50% of their length; type 3, with lobes only fused at base; and type 4, with small lobes not fused and reduced dorsal lobes. Parapar et al. (2020a, b) also defined four types of thoracic uncini and three types of abdominal uncini based on the rostrum vs. capitium length ratio (RvC), and the relative size of the capitium teeth. In the species studied here, three types of thoracic uncini have been identified: type 1 – RvC = 2(3)/1, capitium with two or three large teeth and subsequent ones much smaller; type 3 – RvC = 1/1, capitium with four or five mid-sized teeth followed by slightly smaller teeth; type 4 – RvC = 1/ 1, capitium with 5–7 small teeth and remaining ones similar in size at least in two rows. Two types of abdominal uncini were also identified: type 1A – RvC = 1/0.7, capitium with 3–5 large teeth in first row and one or two in a second row; type 2 – RvC = 1/0.9, capitium with four or five teeth and remaining ones smaller.

Schüller and Hutchings (2010, 2013) defined several types of Methyl Green staining patterns. The patterns observed in the species studied here are similar to the following patterns: pattern 1, segments (SG) 1–6 solid and SG 7–14 striped; pattern 2, SG 1–5 solid, SG 6 white and SG 7–14 striped; and pattern 9, SG 1–5 solid, SG 3 with J-shape glandular region, SG 6 dark solid and SG 7–18 striped.

Abbreviations used in text, table, and figures:

abl	anterior branchial lobe (lobe #5);
bdl	branchial dorsal lobes;
bdltp	branchial dorsal lobe terminal papilla;
bf	branchial filament;
bvl	branchial ventral lobes;
cap	capitium;
cop	copepod;
cr	ciliary row;
ct	ciliary tuft;
dpn	dorsal projection of notopodium;
gc	geniculate chaetae;
MG	Methyl Green;
NEA	Northeast Atlantic;
nc	notochaetae;
ooc	oocytes;
RvC	rostrum vs. capitium length ratio;
SEM	Scanning Electron Microscope;

SG	segment;
STM	stereomicroscope;
TC	thoracic chaetiger;
tdp	thoracic dorsal papilla;
tl	thoracic lateral lappets;
tm	tentacular membrane;
TU	thoracic unciniger;
wTC	white thoracic chaetiger.

Systematic account

Five lineages of the *Terebellides* Groups B, C, and D (sensu Nygren et al. 2018) were identified as nominal species already reported in the Northeast Atlantic: *Terebellides gracilis* Malm, 1874, *T. atlantis* Williams, 1984, *T. williamsae* Jirkov, 1989, *T. irinae* Gagaev, 2009, and *T. shetlandica* Parapar, Moreira & O'Reilly, 2016. In addition, one of the lineages did not match any of the previously known *Terebellides* species and is herein describes as new: *Terebellides lavesquei* sp. nov. (Fig. 1).

Following Nygren et al. (2018) nomenclature and grouping, species have been here grouped as follows: Group B – species 1, 5, and 16, Group C – species 24, and Group D – species 2 and 3; description of each taxon will follow this order. Species 17, 27 (Group B), and 22 (Group C) are represented by 1–4 specimens each (see appendix S36 in Nygren et al. 2018) and are pending formal description until more material is available. Species 4, 14, and 26 (Group B), 25 (Group C), and 15 (Group D) will be described by D. Gaeva and I. Jirkov (Shirshov Institute of Oceanology, Russia). For correspondence between species names and numerals see below.

Family Trichobranchidae Malmgren, 1866

Genus *Terebellides* Sars, 1835 emended by Schüller & Hutchings, 2013

Type species. *Terebellides stroemii* Sars, 1835, redescribed by Parapar and Hutchings (2014) and neotype deposited.

Terebellides Group B (sensu Nygren et al. 2018)

Figs 2–12

Description. The morphological features shared by all examined species in Group B in this paper (clades 1, 5, and 16) are itemised below. Some of these are also shared by Groups A, C, and D as defined in Nygren et al. (2018) (see Remarks below). Clades 4, 14, and 26 will be studied elsewhere; formal descriptions of clades 17 and 27 will wait until more material is available.

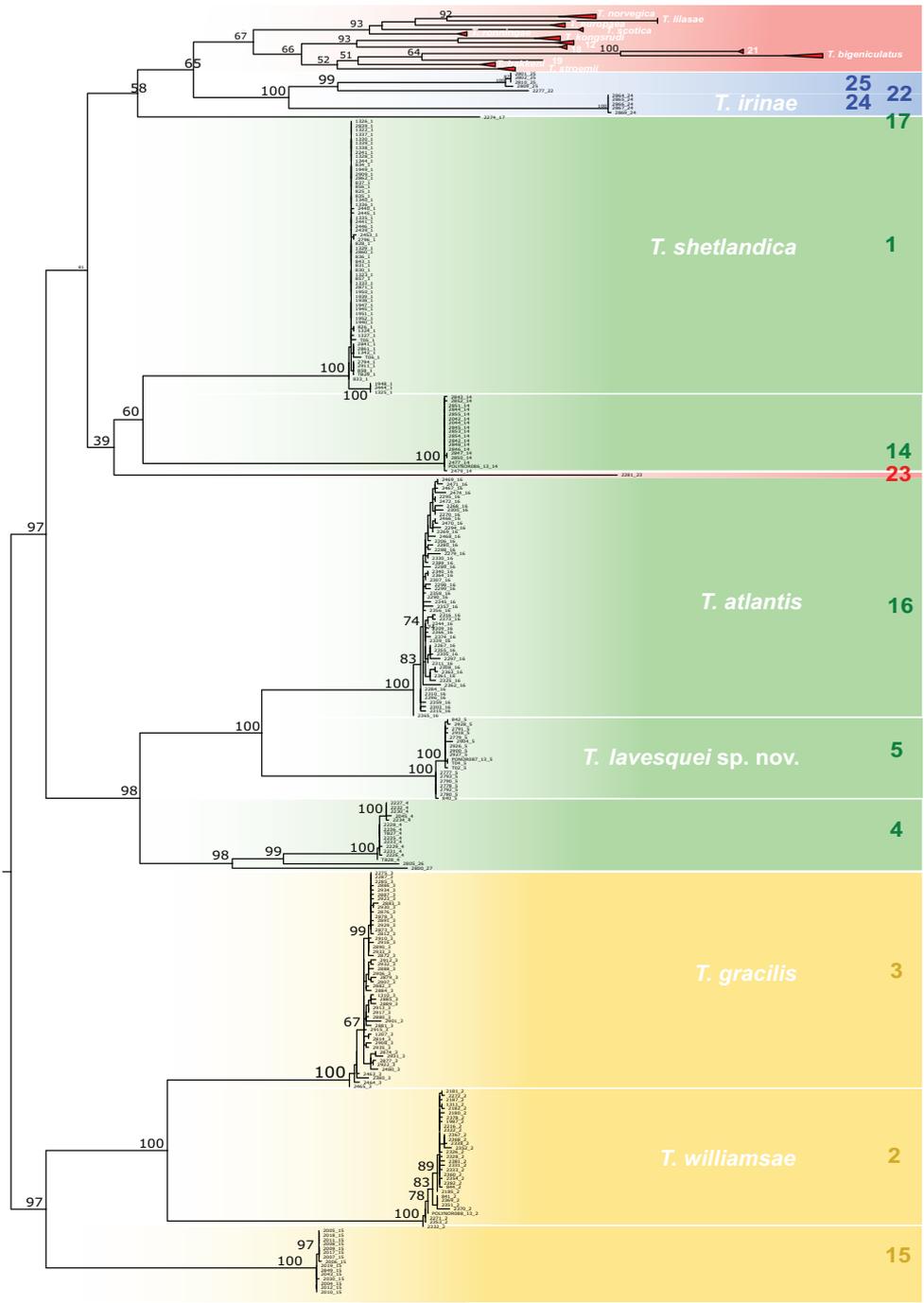


Figure 1. Phylogenetic tree after Maximum Likelihood analyses on a dataset of all COI sequences in Nygren et al. (2018) and Lavesque et al. (2019). Bootstrap support values above nodes. Species other than members of Groups B, C, and D are collapsed.

Body appearance. Complete individuals ranging from 5.0–35.0 mm in length. Body tapering posteriorly with segments increasingly shorter and crowded towards pygidium. Prostomium compact; large tentacular membrane surrounding mouth (Figs 2B, 3B, C), with typical buccal tentacles with expanded tips (Figs 2A, B, 3A, B). SG 1 as an expanded structure below tentacular membrane in a lower lip.

Branchiae. Branchiae arising as single structure from SG 3, with a single stalked mid-dorsal stem (Figs 2A, B, 3B, C, 4B), lobes not fused or partially fused, ventral ones obscured or not by dorsal ones (Figs 2A, B, 3A–C, 4A, B). Dorsal lobes ending posteriorly in short terminal papilla and ventral lobes ending in long filaments (Figs 2B, 3A, B). Anterior projection of dorsal lobes (fifth lobe) normally absent but present only in clade 5 (Fig. 3B). Posterior end of dorsal lobes reaching TC 4 (Figs 2A, B, 3A, B). Branchial lamellae provided with several parallel rows of cilia in inner face (Fig. 6C) and ciliary tufts not observed. Ciliary papillae absent in branchial lamellae margin.

Thorax. Eighteen pairs of notopodia (SG 3–20), those of TC 1 ca. as long as subsequent ones or slightly shorter (Figs 2A, 3A–C). Lateral lappets and dorsal projections of notopodia in anterior thoracic chaetigers with different degree of development depending on size and preservation conditions, but both more conspicuous on TC 1–4 (Fig. 3A–C). All notochoetae as simple capillaries (Fig. 5B). Size of notochoetae of TC 1 similar to subsequent ones. Neuropodia as sessile pinnules from TC 6 to body end, with uncini in single or double rows, from TC 7 throughout. Neuropodia on TC 6, provided with several sharply bent, acute-tipped, geniculate chaetae with minute teeth forming a capitium only visible with SEM (Figs 5C, 7A, 8C). From TC 7, neuropodia with one or several rows of uncini per torus (Figs 5D, 7B, C, 8D), with long shafted denticulate hooks, with large main fang (rostrum) longer than upper crest of teeth (capitium), rostrum/capitium length ratio of ~ 2:1, capitium composed by several teeth above main fang of decreasing length (Figs 5D, 7B, 8D).

Abdomen and pygidium. Approximately half as long as thorax and progressively thinner (Fig. 2A–C). Neuropodia ranging from 18–34 chaetigers and forming erect pinnules (Figs 5E, 8E) with several uncini per torus, number depending on specimen size. Uncini provided with several teeth above rostrum surmounted by a capitium composed of several teeth of decreasing length (Figs 5F, 7D, 8F). Pygidium blunt, as funnel-like depression.

Colour pattern. Colour in preserved specimens whitish or pale brown (Fig. 3A–C). MG staining pattern characterised by 1) compact green colourant in SG 1–6, then turning into striped pattern in SG 7–14 and fading in following segments or 2) by compact green colourant in SG 1–6, J-shaped glandular region in SG 3–5, and striped pattern in SG 7–14 (Fig. 12).

Remarks. Among the aforementioned characters, branchial features might serve to distinguish most of Group B species from those of Groups A, C, and D. Those include size of branchial lobes, lobes not fused, presence of long filaments on ventral ones, and presence of ciliary rows on branchial lamellae. Other taxa described or reported worldwide bear the same type of branchiae (type 3), including *Terebellides ehlersi* McIntosh, 1885, *T. intoshi* Caullery, 1915, *T. lobatus* Hartman & Fauchald, 1971, *T. mundora* Hutchings & Peart, 2000 and *T. sepultura* Garraffoni & Lana, 2003 (Parapar et al. 2016a, b).

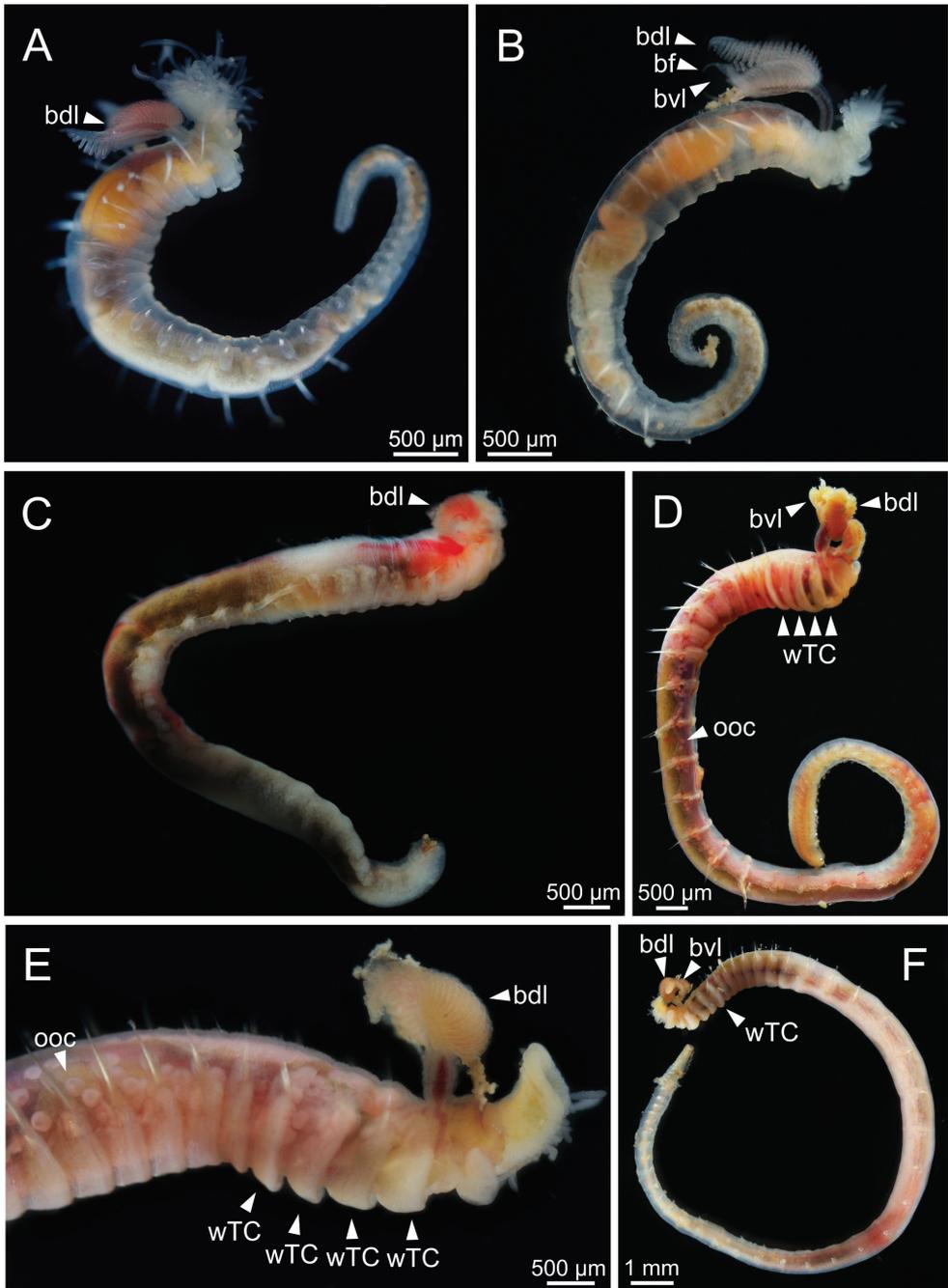


Figure 2. STM photographs of live specimens of several *Terebellides* species (non-type specimens) **A,B** *Terebellides shetlandica* Parapar, Moreira & O'Reilly, 2016 (species 1; **A** ZMBN116171 **B** ZMBN116181) **C** *Terebellides lavesquei* sp. nov. (species 5; GNM15112) **D,E** *Terebellides williamsae* Jirkov, 1989 (species 2; **D** GNM15108 **E** GNM15109) **F** *Terebellides gracilis* Malm, 1874 (species 3; GNM15111). Abbreviations: bdl – branchial dorsal lobe; bf – branchial filament; bvl – branchial ventral lobe; ooc – oocytes; wTC – white thoracic chaetiger.

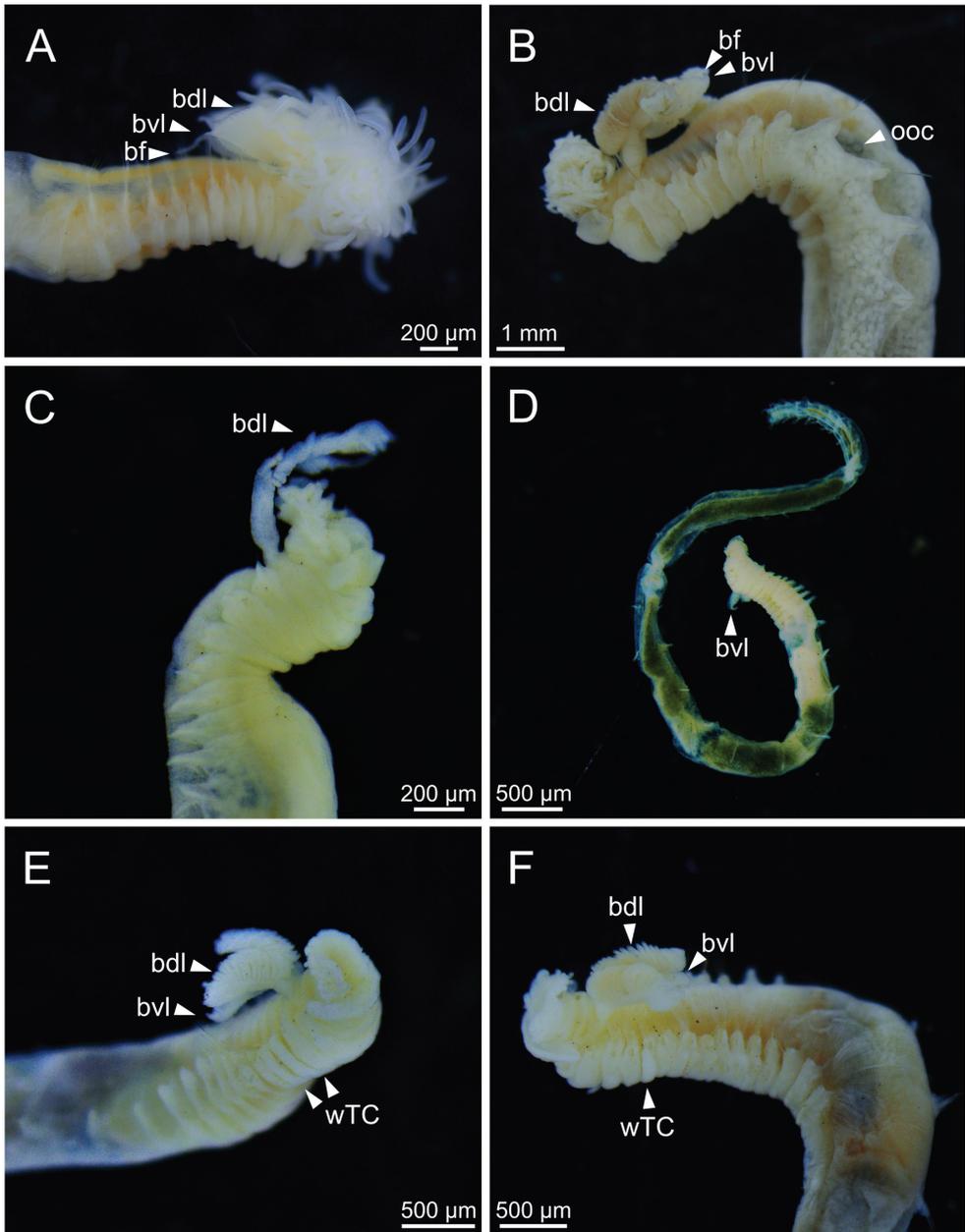


Figure 3. STM photographs of several *Terebellides* species (**A, C–F** non-type specimens) **A** *Terebellides shetlandica* Parapar, Moreira & O’Reilly, 2016 (species 1; ZMBN116186) **B** *Terebellides lavesquei* sp. nov. (species 5; holotype, ZMBN116322) **C** *Terebellides atlantis* Williams, 1984 (species 16; ZMBN116472) **D** *Terebellides irinae* Gagaev, 2009 (species 24; ZMBN116498) **E** *Terebellides williamsae* Jirkov, 1989 (species 2; ZMBN116269) **F** *Terebellides gracilis* Malm, 1874 (species 3; ZMBN116283). Abbreviations: bdl – branchial dorsal lobe; bf – branchial filament; bvl – branchial ventral lobe; ooc – oocytes; wTC – white thoracic chaetiger.

***Terebellides shetlandica* Parapar, Moreira & O'Reilly, 2016**

Figs 2A, B, 3A, 4A, 5, 9, 10A, 11, 12, Table 1, Suppl. materials 1, 2

Terebellides shetlandica Parapar, Moreira & O'Reilly, 2016a: 211–225, figs 1–9, 11.
Species 1 – Nygren et al. 2018: 18–22, figs 6, 10.

Material examined. 30 specimens (Suppl. material 1), Skagerrak (GNM14640); Swedish coast (ZMBN116171, ZMBN116181, ZMBN116185, ZMBN116186, ZMBN116187, ZMBN116188, ZMBN116191, ZMBN116192, ZMBN116193, ZMBN116196, ZMBN116198, ZMBN116200, ZMBN116201, ZMBN116202, ZMBN116203, ZMBN116204, ZMBN116206); Norwegian coast (ZMBN116207, ZMBN116208, ZMBN116214, ZMBN116216, ZMBN116219, ZMBN116220, ZMBN116221, ZMBN116226, ZMBN116227, ZMBN116228, ZMBN116235, ZMBN116242).

GenBank accession numbers of material examined (COI). MG024894, MG024895, MG024896, MG024897, MG024898, MG024899, MG024900, MG024901, MG024902, MG024903, MG024904, MG024905, MG024906, MG024907, MG024908, MG024909, MG024910, MG024911, MG024912, MG024913, MG024914, MG024915, MG024916, MG024917, MG024918, MG024919, MG024920, MG024921, MG024922, MG024923, MG024924, MG024925, MG024926, MG024927, MG024928, MG024929, MG024930, MG024931, MG024932, MG024933, MG024934, MG024935, MG024936, MG024937, MG024938, MG024939, MG024940, MG024941, MG024942, MG024943, MG024944, MG024945, MG024946, MG024947, MG024948, MG024949, MG024950, MG024951, MG024952, MG024953, MG024954, MG024955, MG024956.

Diagnostic features of studied material. Complete individuals ranging from 5.0–16.0 mm in length (Fig. 9). Branchial dorsal lobes lamellae provided with well-developed papillary projections and branchial ventral lobes provided with long filaments, ranging from 175.0–225.0 μm in length (Figs 2A, B, 4A, 5A, B). Between 22–26 lamellae on dorsal lobes (Fig. 5A, B). Lateral lappets present on TC 1–4; dorsal projections of thoracic notopodia on TC 2 and TC 3 (Fig. 5B). Geniculate chaetae in TC 5, acutely bent, with poorly marked capitium (Fig. 5C). Ciliated papilla dorsal to thoracic notopodia not observed. From TC 7, neuropodia with one row of type 4 thoracic uncini per torus, with rostrum/capitium length ratio of ~ 2:1 and capitium with a first row of small teeth, followed by several smaller teeth (Fig. 5D). Abdomen with 25–34 pairs of neuropodia with type 2 uncini (Fig. 5E, F). Copepods attached to body surface in three specimens (Fig. 5B).

Colour pattern. MG staining pattern characterised by compact green colourant in SG 1–6, then turning into striped pattern in SG 7–14 and fading in following segments (Fig. 12). Similar to pattern 1.

Nucleotide diagnostic features. All sequences of *Terebellides shetlandica* share and are distinguished from other available *Terebellides* sequences in unique combinations

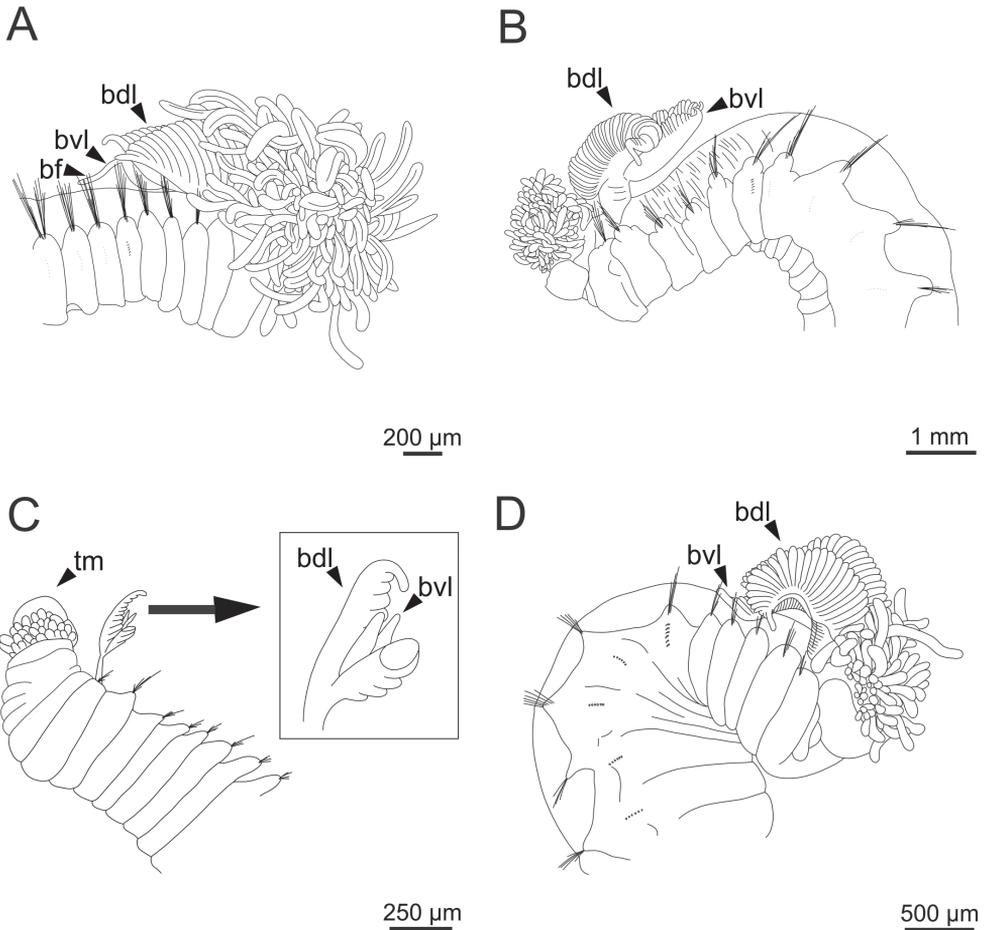


Figure 4. Line drawings of several *Terebellides* species (**A, C, D** non-type specimens) **A** *Terebellides shetlandica* Parapar, Moreira & O'Reilly, 2016 (species 1; ZMBN116186), anterior end, right lateral view **B** *Terebellides lavesquei* sp. nov. (holotype; ZMBN116322), anterior end, left lateral view **C** *Terebellides irinae* Gagev, 2009 (species 24; ZMBN116498), anterior end, ventral view **D** *Terebellides gracilis* Malm, 1874 (species 3; ZMBN116283), anterior end, right lateral view. Abbreviations: bdl – branchial dorsal lobe; bf – branchial filament; bvl – branchial ventral lobe; tm – tentacular membrane.

of nucleotides (underlined) at the given position of our alignment: 78–98: CCAAC-
CCGGAGCCTATTTAGGT, 186–192: CGGAAAC, 210–219: GCTAGGCGCC,
228–234: GGCATTC, 264–276: TCTCCCGCCTGCC, 288–292: CGTT, 306: C,
333–342: CGTCTACCCT, 351–369: AGACAATATGGCACACGCC, 381–402:
AGATCTGGCTATTTTCTCCCTA, 453–459: AGTAATA, 511–522: TCAGC-
TATAATC, 535–558: TTA^uCTTCTTTCTCTG^uCCAGTTCTG.

Type locality. NW Hutton Oilfield, between Shetland Islands and Norway, 61°10'N, 01°12'E (Parapar et al. 2016a).

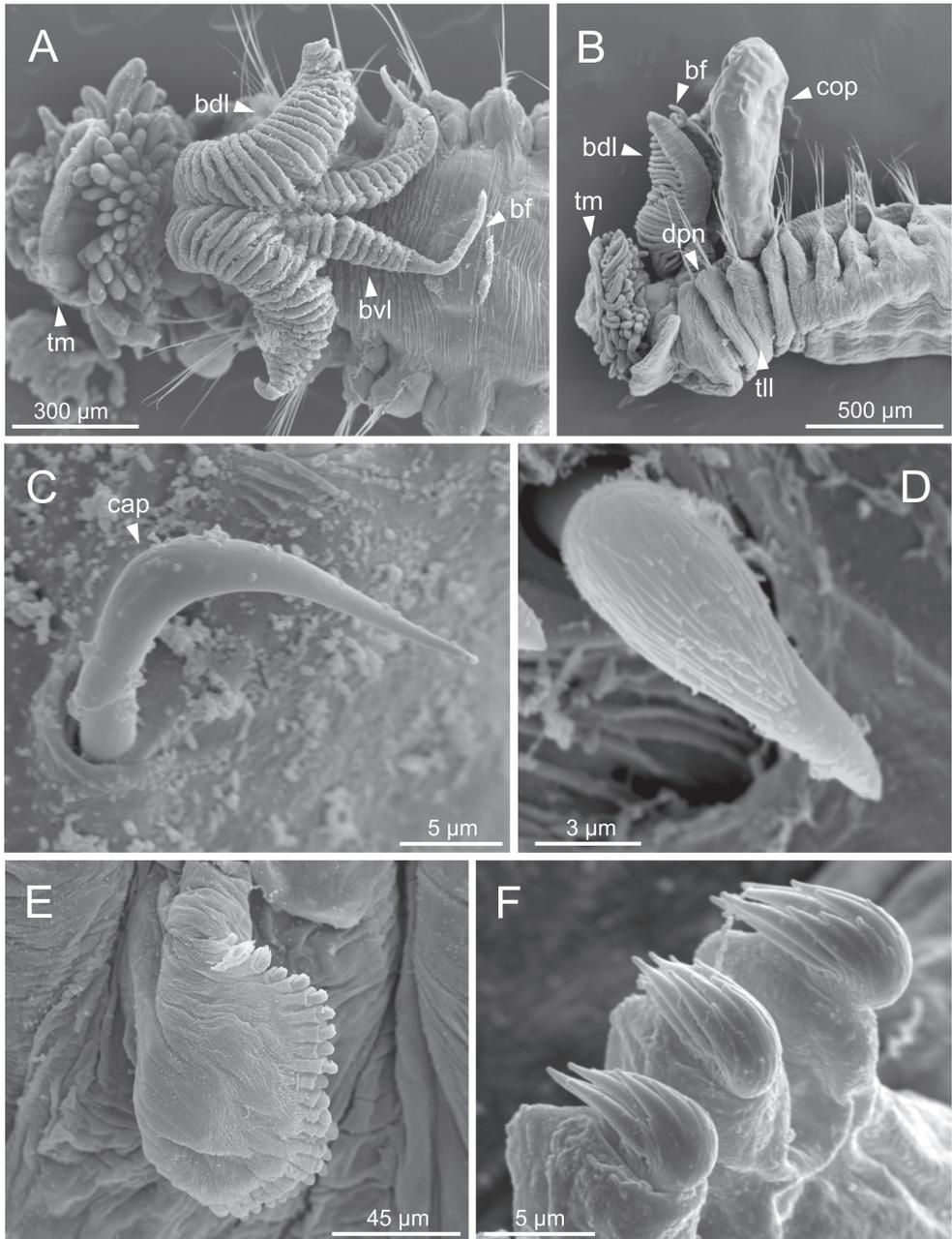


Figure 5. *Terebellides sbetlandica* Parapar, Moreira & O'Reilly, 2016 (species 1; non-type specimens, ZMBN116181, ZMBN116204 and ZMBN116219), SEM micrographs **A** anterior end, dorsal view **B** anterior end, left lateral view **C** TC 6 (TU1), geniculate chaeta **D** thoracic uncinus **E** abdominal neuropodium **F** abdominal uncini. Abbreviations: bdl – branchial dorsal lobe; bf – branchial filament; bvl – branchial ventral lobe; cap – capitium; cop – copepod; dpn – dorsal projection of notopodium; TC – thoracic chaetiger; tll – thoracic lateral lobes; tm – tentacular membrane; TU – thoracic unciniger.

Distribution and bathymetry. Norwegian coast and shelf, North Sea, Skagerrak, Kattgat; 25–375 m deep; 92.7% of specimens present at depths below 200 m (Figs 10A, 11, Suppl. material 1).

Remarks. *Terebellides shetlandica* is a small species, reaching up to 16 mm length and is characterised by having branchiae of type 3 and long filaments in ventral branchial lobes, thoracic uncini of type 4, abdominal uncini of type 2 and lacking papillae on margins of branchial lamellae (Table 1). Parapar et al. (2016a) pointed out that *T. atlantis* is the most similar species to *T. shetlandica*; this is confirmed here according to molecular analyses and morphological examination. Both species are small sized (length: *T. shetlandica*, 5–16 mm; *T. atlantis*, 10–16 mm) and have branchiae of type 3, with free branchial lobes. However, the branchiae of *T. shetlandica* have a high number (22–26) of tightly packed branchial lamellae, all lobes are similar in shape and length and ventral ones bear long filaments whereas *T. atlantis* has a fewer number of branchiae (10–11), lamellae are not packed, lobes differ in shape and size and ventral lobes bear shorter filaments. Furthermore, the range of abdominal chaetigers number is higher in *T. shetlandica* than in *T. atlantis* (25–34 vs. 23–28 respectively).

***Terebellides lavesquei* sp. nov.**

<https://zoobank.org/2D993190-50A3-42C0-B11E-508EA59276B6>

Figs 2C, 3B, 4B, 6, 7, 9, 10B, 11, 12, Table 1, Suppl. materials 1, 2

Species 5 – Nygren et al. 2018: 18–22, figs 6, 10.

Material examined. Type material. **Holotype:** ZMBN116322. **Paratypes** (16 specimens): Skagerrak (GNM15112); Norwegian coast (NTNU-VM61386, NTNU-VM61387, NTNU-VM68252, ZMBN116319, ZMBN116320, ZMBN116321, ZMBN116323, ZMBN116324, ZMBN116325, ZMBN116326, ZMBN116327, ZMBN116328, ZMBN116329, ZMBN116330, ZMBN116331, ZMBN116332).

Holotype. Complete specimen, 34.0 mm long and 2.0 mm wide (Fig. 4B); female with oocytes in body cavity.

GenBank accession numbers of material examined (COI). MG025054, MG025055, MG025056, MG025057, MG025058, MG025059, MG025060, MG025061, MG025062, MG025063, MG025064, MG025065, MG025066, MG025067, MG025068, MG025069, MG025070.

Diagnostic features of type material. Complete individuals ranging from 5.0–35.0 mm in length (Fig. 9). Branchial dorsal lobes lamellae provided with well-developed papillary projections and branchial ventral lobes provided with long filaments, ranging from 125.0–250.0 µm in length (Fig. 6A). Between 17–42 lamellae on dorsal lobes (Fig. 6A, B). Ciliary rows present on lamellae inner face (Fig. 6B, C). Ventral branchial lobes hidden in between dorsal ones but sometimes discernible below (Fig. 3B). Lateral lappets present on T C1–4; dorsal projection of thoracic notopodia on TC 2–4 (Fig. 3B). Geniculate chaetae in TC 5, acutely bent, with well-defined capitium (Fig. 7A). Ciliated papilla dorsal to

thoracic notopodia not observed. From TC 7, neuropodia with one or two rows of type 3 thoracic uncini per torus, with rostrum/capitium length ratio of ~ 2:1 and capitium with a first row of four or five medium-sized teeth, followed by several smaller teeth (Fig. 7B, C). Abdomen with 30–31 pairs of neuropodia with type 2 uncini (Fig. 7D). Copepods observed attached to body dorsal surface in one specimen (Fig. 6D, E).

Colour pattern. MG staining pattern characterised by compact green colourant in SG 1–6, J-shaped glandular region in SG 3–5 and striped pattern in SG 7–14 (Fig. 12). Similar to pattern 9.

Nucleotide diagnostic features. All sequences of *Terebellides lavesquei* sp. nov. share and are distinguished from other available *Terebellides* sequences in unique combinations of nucleotides (underlined) at the given position of our alignment: 78–99: TCAACCCGGTGCTTACCTCGGT, 156–174: TTTAGTTATGC-CAGTCTTC, 261–264: GTTA, 270–279: TCCAGCACTT, 315–336: AGTTGG-GACCGGTTGAACCGTT, 351–369: AGACAATATAGCTCATGCG, 405–411: CTTGGCT, 426–447: CCTAGGATCAATTAACCTTTATC, 459–483: CAACAT-ACGCTGAAAAGGTTTACGA, 510–525: GTCCGCGGTTATCACA, 534–558: ACTTCTTTTATCCCTTCCAGTCTTG, 573–580: CATGCTTC, 606–627: CTTTTTCGACCCAGCTGGTGGG.

Type locality. Hordaland, Lysefjord (Norway), 60°07'N, 05°04'E; 119 m deep.

Distribution and bathymetry. Norwegian coast and shelf, Skagerrak; 115–534 m deep; ~ 50% of specimens collected at depths above 200 m (Figs 10B, 11, Suppl. material 1).

Etymology. This species is dedicated to Nicolas Lavesque, Station Marine d’Arcachon, CNRS (France) for his remarkable recent contributions to the diversity of Terebellidae and Trichobranchidae in Atlantic waters.

Table 1. Comparison of discriminating taxonomic characters of the species studied in this work. Cells in italics show discriminatory characters of each subgroup. ⁽¹⁾ sensu Parapar et al. (2016a); ⁽²⁾ sensu Parapar et al. (2020b); ⁽³⁾ sensu Parapar et al. (2020a); ⁽⁴⁾ dominant trend in bold; ⁽⁵⁾ Skagerrak.

Groups		B		C		D	
Putative species sensu Nygren et al. (2018)		1	5	16	24	2	3
Species (as reported/described herein)							
		<i>T. shetlandica</i> Parapar, Moreira & O’Reilly, 2016	<i>T. lavesquei</i> sp. nov.	<i>T. atlantis</i> Williams, 1984	<i>T. irinae</i> Gagaev, 2009	<i>T. williamsae</i> Jirkov, 1989	<i>T. gracilis</i> Malm, 1874
Branchiae	type ⁽¹⁾	3	2	3	4	2	2
	papillae on lamellae edge	no	no	no	no	no	no
Thorax	ciliated papilla dorsal to notopodium	no (?)	no (?)	no (?)	no (?)	yes	yes
	chaetiger with geniculate chaetae	TC 6	TC 6	TC 6	TC 6	TC 6	TC 6
	uncini type ⁽²⁾	4	3	3	3	1	1
Abdomen	uncini type ⁽³⁾	2	2	2	2	1A	1A
Bathymetry – Above (A) / Below (B) 200 m depth ⁽⁴⁾		A/B	A/B	B	B	B	B
Distribution – North (N) /South (S) of 60°N ⁽⁴⁾		N/S ⁽⁵⁾	N/S	N	N	N/S ⁽⁵⁾	N/S ⁽⁵⁾

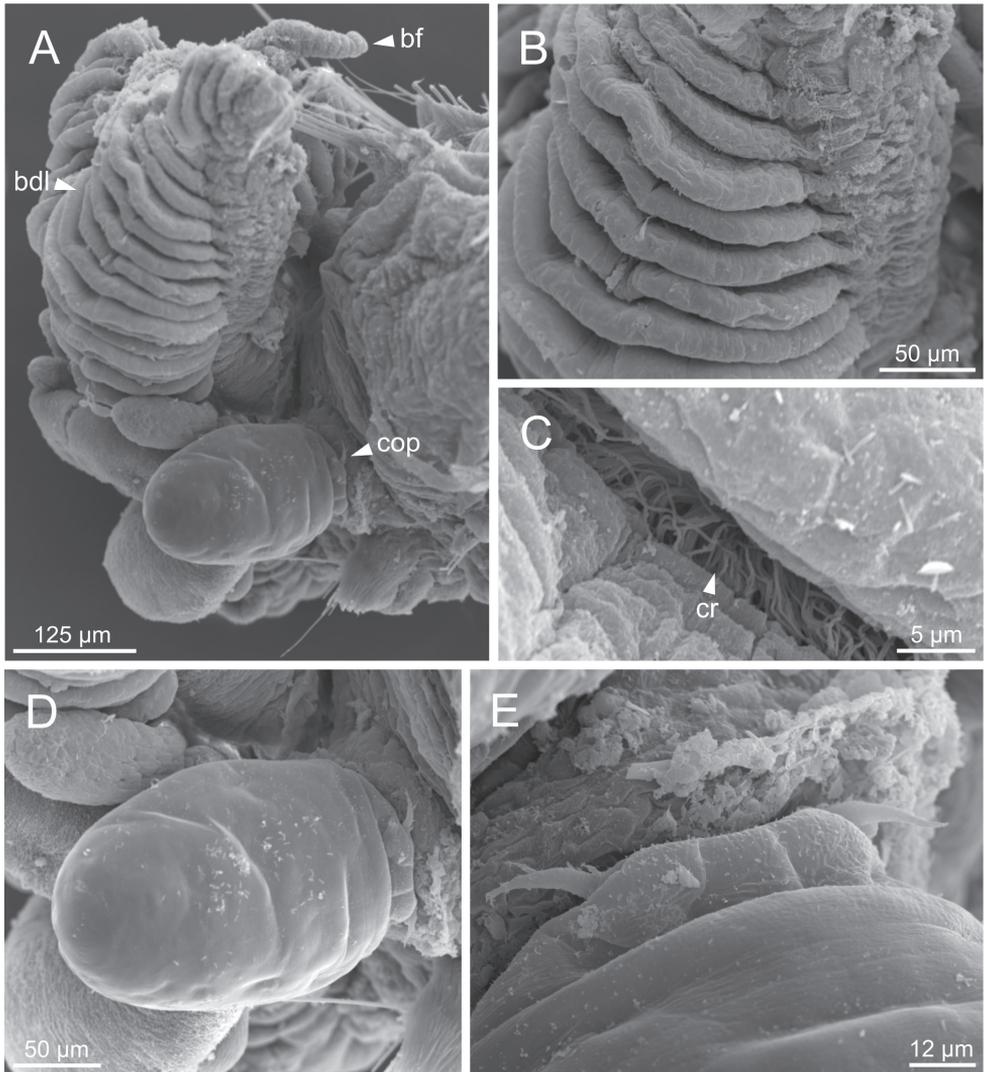


Figure 6. *Terebellides lavesquei* sp. nov. (non-type specimen, ZMBN116332), SEM micrographs **A** anterior end, left lateral view **B** branchial lamellae, detail **C** ciliary row, detail **D** copepod **E** copepod, anterior end. Abbreviations: bdl – branchial dorsal lobe; bf – branchial filament; cop – copepod; cr – ciliary row.

Remarks. *Terebellides lavesquei* sp. nov. is a medium-sized species, reaching up to 35 mm in length. It is characterised by the lack of papillae on margins of branchial lamellae and by having branchiae of type 2, filaments on ventral branchial lobes, thoracic uncini of type 3 and abdominal uncini of type 2 (Table 1). *Terebellides lavesquei* sp. nov. is genetically close to *T. shetlandica* and *T. atlantis* but mostly differs from them regarding branchiae features (Table 1). Lobes are partially fused and have many

tightly packed lamellae (17–42) in comparison with these species. *Terebellides lavesquei* sp. nov. is also similar to *Terebellides parapari* Lavesque, Hutchings, Daffe, Nygren & Londoño-Mesa, 2019 in having filaments in ventral branchial lobes and the presence of glandular regions, but they differ in the branchial morphology, with lobes fused ca. half of their length in *T. lavesquei* sp. nov. and fused only at the base in *T. parapari*. They also differ in TC 1 notochaetae length, being all similar in *T. lavesquei* sp. nov. but longer than those in following chaetigers in *T. parapari*.

Branchial shape of *T. lavesquei* sp. nov. is similar to that of *Terebellides narribri* Hutchings & Peart, 2000, because both lobes are fused to each other for ca. half their length and have a high number of tightly packed lamellae. However, *T. narribri* have thoracic uncini of type 1 whereas *T. lavesquei* sp. nov. have thoracic uncini of type 3. Furthermore, *T. lavesquei* sp. nov. and *T. shetlandica* seem to have a more restricted bathymetric distribution in shallow waters (down to 534 and 375 m, respectively) whereas *T. atlantis* reaches depths of 2750 m (see below).

***Terebellides atlantis* Williams, 1984**

Figs 3C, 8, 9, 10C, 11, 12, Table 1, Suppl. materials 1, 2

Terebellides atlantis Williams, 1984: 121–123, fig. 4, table 1.

Species 16 – Nygren et al. 2018: 18–22, figs 6, 10.

Material examined. 15 specimens (Suppl. material 1), Barents Sea (ZMBN116454, ZMBN116455, ZMBN116458, ZMBN116459, ZMBN116460, ZMBN116462, ZMBN116463, ZMBN116465, ZMBN116467, ZMBN116468, ZMBN116470, ZMBN116471, ZMBN116472, ZMBN116474); Norwegian coast (ZMBN116476).

GenBank accession numbers of material examined (COI). MG025258, MG025259, MG025260, MG025261, MG025262, MG025263, MG025264, MG025265, MG025266, MG025267, MG025268, MG025269, MG025270, MG025271, MG025272, MG025273, MG025274, MG025275, MG025276, MG025277, MG025278, MG025279, MG025280, MG025281, MG025282, MG025283, MG025284, MG025285, MG025286, MG025287, MG025288, MG025289, MG025290, MG025291, MG025292, MG025293, MG025294, MG025295, MG025296, MG025297, MG025298, MG025299, MG025300, MG025301, MG025302, MG025303, MG025304, MG025305, MG025306, MG025307, MG025308, MG025309, MG025310, MG025311, MG025312.

Diagnostic features of studied material. Complete individuals ranging from 10.0–16.0 mm in length (Fig. 9). Branchial dorsal lobes lamellae provided with well-developed papillary projections and branchial ventral lobes (Fig. 8A, B) provided with long filaments (sometimes broken), 175.0 µm in length. Between 10–11 lamellae on dorsal lobes. Lateral lappets present on TC 1–4; dorsal projection of thoracic notopodia on TC 2–4 (Fig. 8A). Genuiculate chaetae in TC 5, acutely bent, with well-defined capitium (Fig. 8C). Ciliated papilla dorsal to thoracic notopodia not observed. From

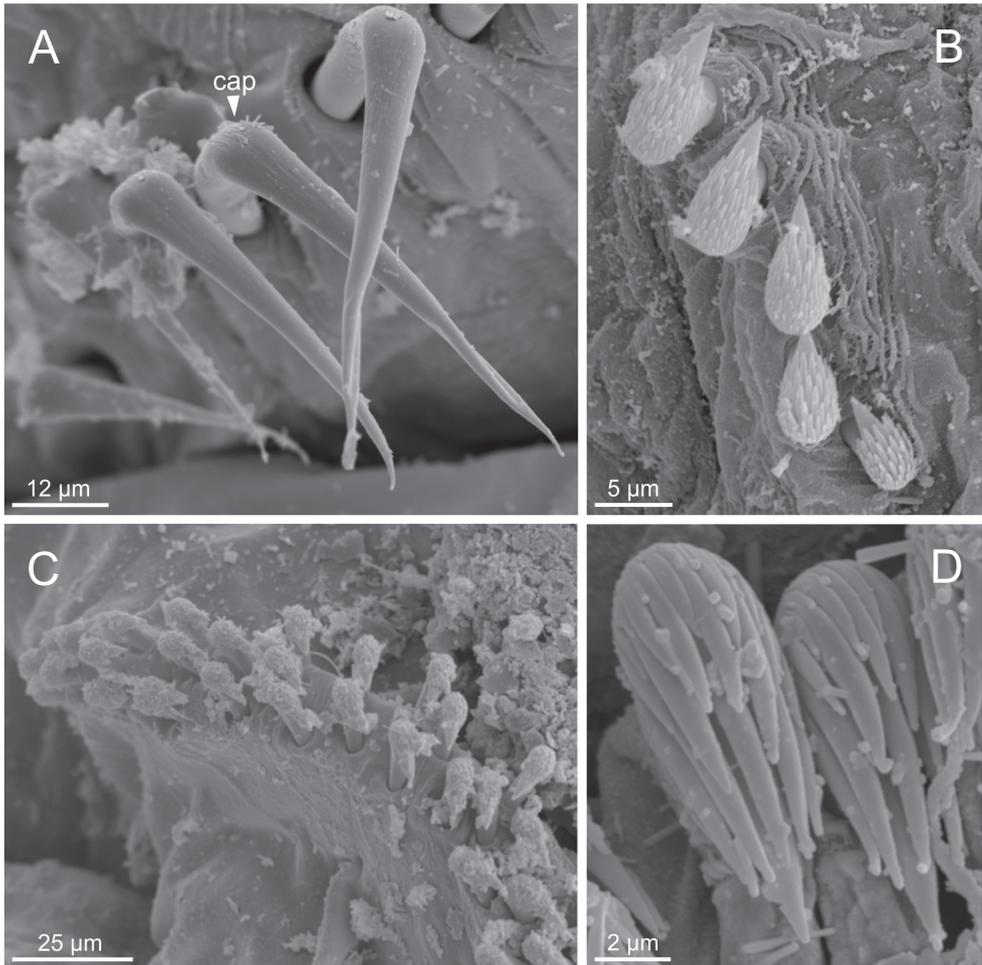


Figure 7. *Terebellides lavesquei* sp. nov. (non-type specimens, NTNU–VM61387 and ZMBN116332), SEM micrographs **A** TC 6 (TU1), geniculate chaetae **B** thoracic uncini **C** double row of thoracic uncini **D** abdominal uncini. Abbreviations: cap – capitium; TC – thoracic chaetiger; TU – thoracic unciniger.

TC 7, neuropodia with one row of type 3 thoracic uncini per torus, with rostrum/capitium length ratio of $\sim 2:1$ and capitium with a first row of three or four medium-sized teeth, followed by several smaller teeth (Fig. 8D). Abdomen with 23–28 pairs of neuropodia with type 2 uncini (Fig. 8E, F).

Colour pattern. MG staining pattern characterised by compact green colourant in SG 1–6, J-shaped glandular region in SG 3–5 and striped pattern in SG 7–14 (Fig. 12). Similar to pattern 9.

Nucleotide diagnostic features. All sequences of *Terebellides atlantis* share and are distinguished from other available *Terebellides* sequences in unique combinations of nucleotides (underlined) at the given position of our alignment:

60–84: TATTCGTATTGAGCTAGGGCAACCT, 132–150: ACATGCATTTT-TAATAATC, 171–189: TTTTATTGGTGGATTGGT, 213–231: GGGAGCTC-CTGATATAGCC, 264–294: ACTACCACCAGCCTTAATCTTATTAGTAAGC, 345–363: ATTATCTGATAATATGGCT, 384–399: CCTTGCTATTTTTTCA, 477–484: GCTACGAC, 549–573: TCCAGTCTTAGCTGGTGCAATCACT, 558–591: CCGT, 615–630: TCCAGCTGGTGGTGGT.

Type locality. Atlantic Ocean, off New England, 39°56.5'N, 70°39.9'W (Williams 1984).

Distribution and bathymetry. Barents Sea, Greenland Sea, South Iceland, Norwegian coast and shelf; 219–2750 m deep (Figs 10C, 11, Suppl. material 1).

Remarks. *Terebellides atlantis* is a small species, reaching up to 16 mm in length. It is characterised by the lack of papillae on margins of branchial lamellae, and by having branchiae of type 3 and filaments in ventral branchial lobes, thoracic uncini of type 3 and abdominal uncini of type 2 (Table 1). The most similar species to *T. atlantis* are *T. shetlandica* and *T. lavesquei* sp. nov. but *T. atlantis* differs from the latter in the size and type of branchiae (see remarks for *T. lavesquei* sp. nov. above). Branchial lobes are often missing as previously highlighted by Parapar et al. (2011). Finally, *T. atlantis* has the widest geographical distribution and depth range (219 to 2750 m) among Group B species.

***Terebellides* Group C (sensu Nygren et al. 2018)**

Figs 3, 4, 9–13

Description. The morphological features of the examined species in Group C in this paper (clade 24) are itemised below. Some of these are also shared by Groups A, B, and D as defined in Nygren et al. (2018) (see Remarks below). Clade 25 will be studied elsewhere; formal description of clade 22 will wait until more material is available.

Body appearance. Incomplete individuals ranging from 10.0–17.0 mm in length. Body tapering posteriorly with segments increasingly shorter and crowded towards pygidium. Prostomium compact; large tentacular membrane surrounding mouth (Fig. 3D), with typical buccal tentacles with expanded tips (Fig. 3D). SG 1 as an expanded structure below tentacular membrane in a lower lip (Fig. 3D).

Branchiae. Branchiae arising as single structure from SG 3, with a single stalked mid-dorsal stem, lobes not fused (Fig. 4C). Dorsal lobes ending posteriorly in short terminal papilla (Fig. 3D) and ventral lobes ones ending in long filaments. Anterior projection of dorsal lobes (fifth lobe) present. Posterior end of dorsal lobes reaching TC 4. Ciliary rows of cilia and ciliary tufts in inner face of branchial lamellae not observed. Ciliary papillae absent in branchial lamellae margin.

Thorax. Eighteen pairs of notopodia (SG 3–20) (Fig. 3D), those of TC 1 approximately as long as subsequent ones (Fig. 4C). Lateral lappets and dorsal projections of notopodia in anterior thoracic chaetigers with different degree of development depending on size and preservation conditions, but both more conspicuous on

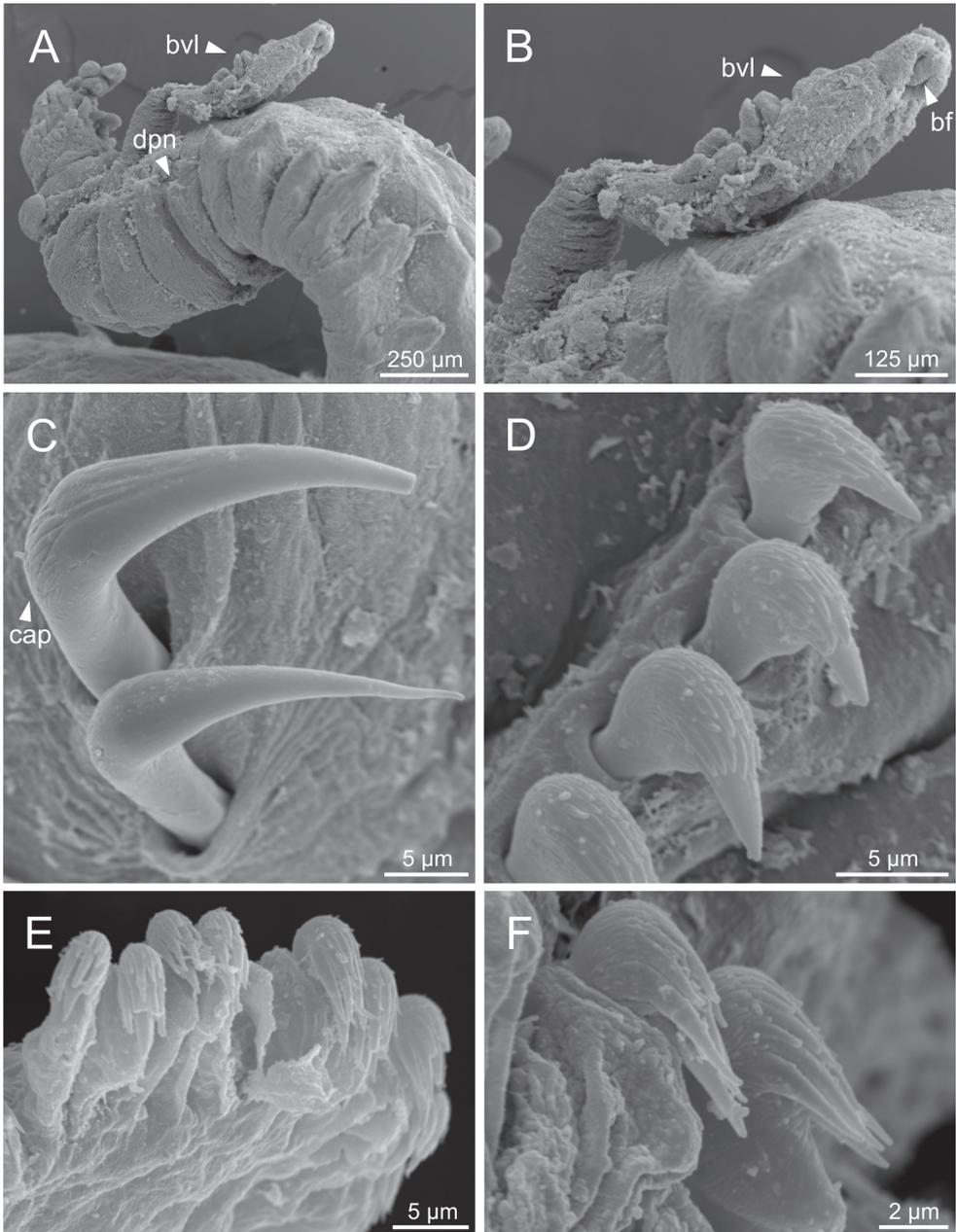


Figure 8. *Terebellides atlantis* Williams, 1984 (species 16; non-type specimens, ZMBN116454 and ZMBN116459), SEM micrographs **A** anterior end, left lateral view **B** branchiae, detail **C** TC 6 (TU1), geniculate chaetae **D** thoracic uncini **E** abdominal neuropodium **F** abdominal uncini. Abbreviations: bf – branchial filament; bvl – branchial ventral lobe; cap – capitium; dpn – dorsal projection of notopodium; TC – thoracic chaetiger; TU – thoracic unciniger.

TC 1–5. All notochaetae as simple capillaries. Size of notochaetae of TC 1 similar to subsequent ones. Neuropodia as sessile pinnules from TC 6 to body end, with uncini in single rows, from TC 7 throughout. Neuropodia on TC 6, provided with several sharply bent, acute-tipped, geniculate chaetae (Fig. 13B) with minute teeth forming a capitium only visible with SEM (Fig. 13B). From TC 7, neuropodia with one row of uncini per torus (Fig. 13C), with long shafted denticulate hooks, with large main fang (rostrum) longer than upper crest of teeth (capitium), rostrum/capitium length ratio of ~ 2:1, capitium composed by several teeth above main fang of decreasing length (Fig. 13D).

Abdomen and pygidium. Approximately half as long as thorax and progressively thinner (Fig. 3D). Neuropodia ranging from 18–20 chaetigers and forming erect pinnules with several uncini per torus, number depending on specimen size. Uncini provided with several teeth above rostrum surmounted by a capitium composed of several teeth of decreasing length (Fig. 13E, F). Pygidium blunt, as funnel-like depression.

Colour pattern. Colour in preserved specimens whitish (Fig. 3D). MG staining pattern characterised by compact green colourant in SG 1–4, then turning into striped pattern in SG 5–14 and fading in following segments (Fig. 12).

Remarks. Among the above-mentioned characters, branchial features might serve to distinguish most of Group C species from those of Groups A, B and D. Those include branchial lobes size, presence of filaments in ventral ones and lobes which are not fused. Other taxa such as *Terebellides mira* Schüller & Hutchings, 2013 and *T. rigel* Schüller & Hutchings, 2013 also bear branchiae with similar shape (Parapar et al. 2016a).

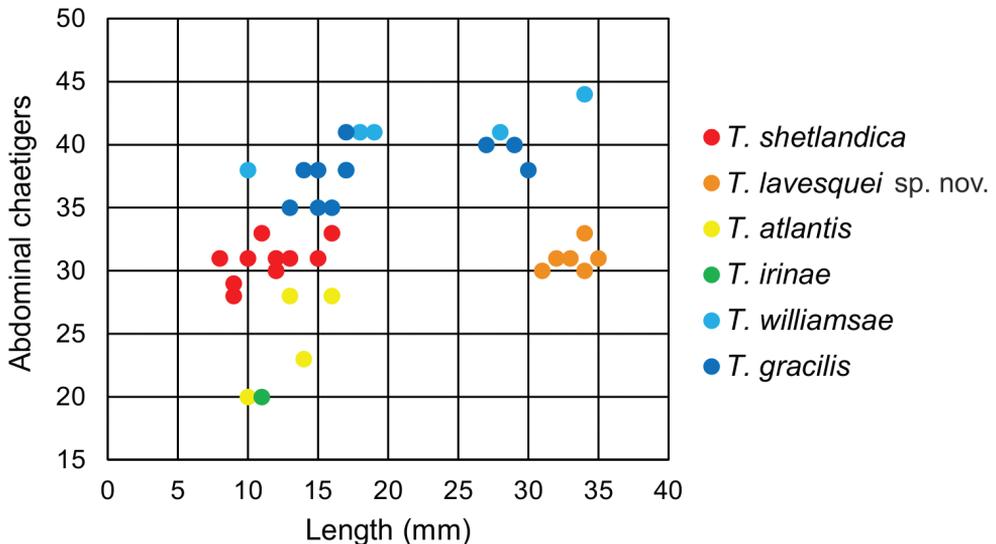


Figure 9. Relationship between number of abdominal chaetigers and body length (complete specimens considered except for *T. irinae*).

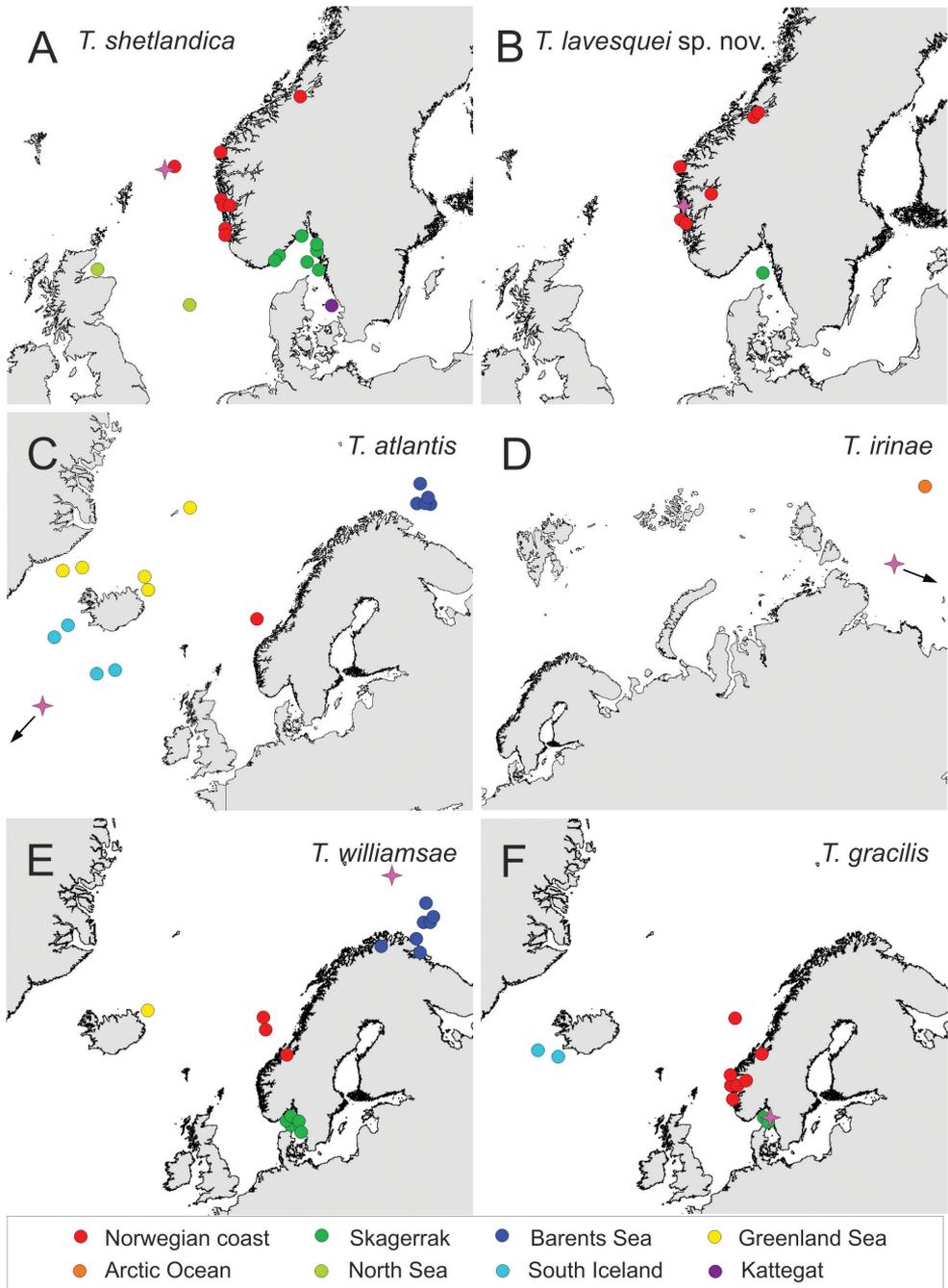


Figure 10. Geographic distribution of species of *Terebellides* in Northeast Atlantic Ocean **A** *Terebellides shetlandica* Parapar, Moreira & O'Reilly, 2016 **B** *Terebellides lavesquei* sp. nov. **C** *Terebellides atlantis* Williams, 1984 **D** *Terebellides irinae* Gagaev, 2009 **E** *Terebellides williamsae* Jirkov, 1989 **F** *Terebellides gracilis* Malm, 1874. Pink star denotes the type locality of each taxon.

***Terebellides irinae* Gagaev, 2009**

Figs 3D, 4C, 9, 10D, 11–13, Table 1, Suppl. materials 1, 2

Terebellides irinae Gagaev, 2009: 474–478.

Species 24 – Nygren et al. 2018: 18–22, figs 6, 10.

Material examined. 6 specimens (Suppl. material 1), Arctic Ocean (ZMBN116496, ZMBN116497, ZMBN116498, ZMBN116499, ZMBN116500, ZMBN116501).

GenBank accession numbers of material examined (COI). MG025340, MG025341, MG025342, MG025343, MG025344.

Diagnostic features of studied material. Incomplete individuals ranging from 10.0–17.0 mm in length (Fig. 9). Branchial dorsal lobes provided with filaments, 75.0 µm in length (Fig. 3D) and branchial ventral lobes reduced, distinctly smaller than dorsal ones (Fig. 4C). Dorsal lobes provided with seven lamellae (Fig. 4C). Lateral lappets present on TC 1–4; dorsal projection of thoracic notopodia on TC 2–5 (Fig. 3D). Geniculate chaetae in TC 5, acutely bent and provided with hardly distinguishable capitium (Fig. 13B). Ciliated papilla dorsal to thoracic notopodia not observed. From TC 7, neuropodia with one row of type 3 thoracic uncini per torus, with rostrum/capitium length ratio of ~ 2:1 and capitium with a first row of four or five medium-sized teeth, followed by several smaller teeth (Fig. 13C, D). Abdomen with at least 20 pairs of neuropodia with type 2 uncini (Fig. 13E, F).

Colour pattern. MG staining pattern characterised by compact green colourant in SG 1–4, then turning into striped pattern in SG 5–14 and fading in following segments (Fig. 12). Similar to pattern 1.

Nucleotide diagnostic features. All sequences of *Terebellides irinae* share and are distinguished from other available *Terebellides* sequences in unique combinations of nucleotides (underlined) at the given position of our alignment: 177–204: CGGGGGGTTTGGAACTGGTTAATCCCC, 213–225: TGGGGC-CCCAGAC, 249–258: CATAAGGTTC, 273–303: GGCCCTCATCCTAC-TAGTCAGCTCAGCTGCT, 305–321: GGCTGGT, 327–336: ATGAACTGTA, 342–372: ACCACTTTCAGACAACATCGCTCATGCCGGA, 381–399: AG-ATCTAGCAATTTTCTCA, 426: CCTAGGTTCTATTAAC TTCATCACAACA-GTC, 483–499: TCTAGAACGAATCCCAC, 535–573: TTATTACTATCACTAC-CAGTGCTAGCCGGAGCTATTACC, 594–612: CATTAACACATCATTCTTC, 618–636: AGCCGGTGGTGGTGATCCT.

Type locality. Arctic Ocean, 73°04'N, 157°12'W (Gagaev 2009).

Distribution and bathymetry. Arctic Ocean; 4038–4380 m deep (Figs 10D, 11, Suppl. material 1).

Remarks. *Terebellides irinae* is a small species, reaching up to 17 mm in length and is characterised by the lack of papillae on margins of branchial lamellae, and by having branchiae of type 4, filaments in ventral branchial lobes, thoracic uncini of type 3 and abdominal uncini of type 2 (Table 1). Jirkov and Leontovich (2013) proposed

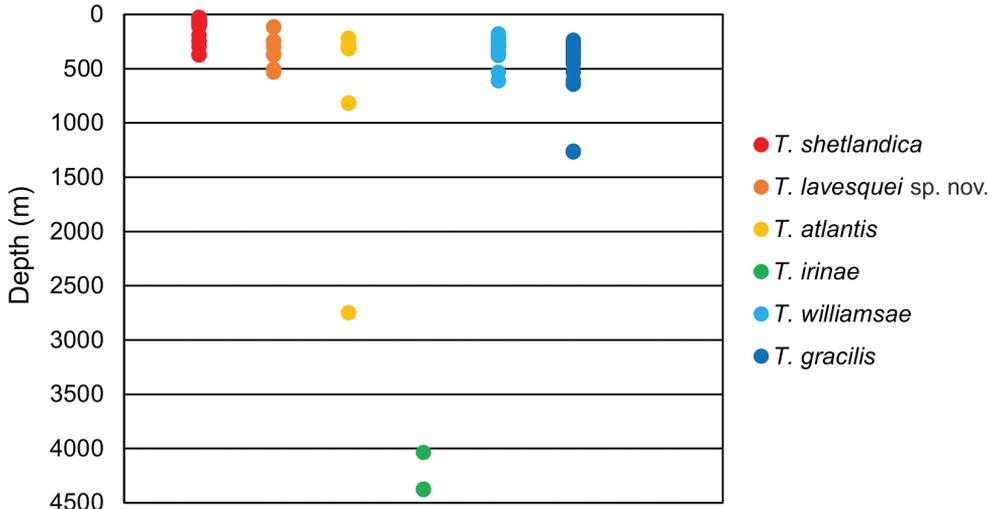


Figure 11. Bathymetric distribution of *Terebellides* species studied in this work.

T. irinae as synonym of *T. stroemii* because it fit within the variability of the latter. However, Parapar and Hutchings (2014) redescribed *T. stroemii* designating a neotype and *T. irinae* not fit in this concept. Later, Nygren et al. (2018) recognised *T. irinae* as different from *T. stroemii* after molecular analyses and pointed out that *T. irinae* is the only species present in the Arctic Ocean at depths below 4000 m (Fig. 11). Furthermore, *T. irinae* is the only species in Northeast Atlantic Ocean bearing branchiae of type 4 and therefore is also considered as a valid species in this work. Other taxa from elsewhere such as *T. mira* and *T. rigel* also bear the same branchial type, these two species have branchial lobes free from each other with few numbers of not packed lamellae and ventral lobes are also distinctly smaller than the dorsal ones.

***Terebellides* Group D (sensu Nygren et al. 2018)**

Figs 2–4, 9–18

Description. The morphological features shared by all examined species in Group D in this paper (clades 2 and 3) are itemized below. Some of these are also shared by Groups A, B, and C as defined in Nygren et al. (2018) (see Remarks below). Clade 15 will be studied elsewhere.

Body appearance. Complete individuals ranging from 5.0–34.0 mm in length. Body tapering posteriorly with segments increasingly shorter and crowded towards pygidium. Prostomium compact; large tentacular membrane surrounding mouth (Figs 2D–F, 3E, F), with typical buccal tentacles with expanded tips (Figs 2E, F, 3E, F). SG 1 as an expanded structure below tentacular membrane in a lower lip (Figs 2D, E, 3E, F).

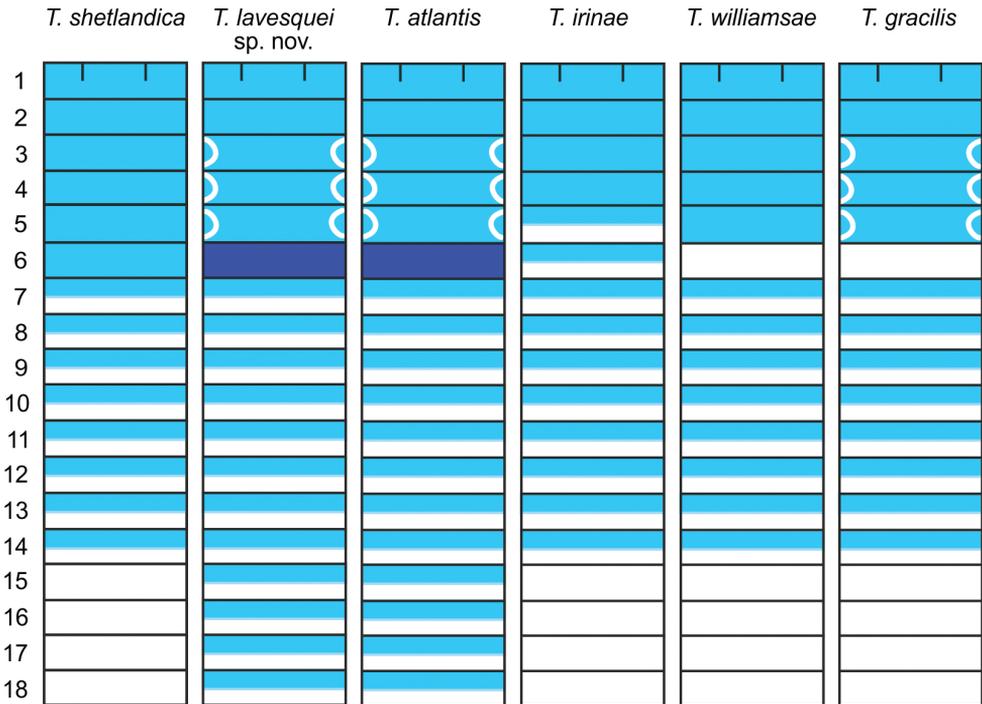


Figure 12. Body MG staining patterns in ventral view of *Terebellides* species. *Terebellides shetlandica* Parapar, Moreira & O'Reilly, 2016, *Terebellides lavesquei* sp. nov., *Terebellides atlantis* Williams, 1984, *Terebellides irinae* Gagaev, 2009, *Terebellides williamsae* Jirkov, 1989 and *Terebellides gracilis* Malm, 1874. Segments indicated in Arabic numbers.

Branchiae. Branchiae arising as single structure from SG 3, with a single stalked mid-dorsal stem (Figs 2D, E, 3E, F), one pair of dorsal (upper) partially fused lobes (Figs 2D, E, 3E, F), and a pair of shorter ventral (lower) lobes (Fig. 3E, F) obscured or not by dorsal ones (Figs 2D–F, 3E, F). Dorsal lobes ending posteriorly in short terminal papilla (Fig. 3E, F) and ventral lobes ending in long filaments. Anterior projection of dorsal lobes (fifth lobe) present (Fig. 2D–F). Posterior end of dorsal lobes reaching TC 4–5 (Figs 2D–F, 3E, F). Branchial lamellae provided with several parallel rows of cilia and ciliary tufts present in inner face (Figs 14B, C, 16B, C, 17B). Ciliary papillae absent on the margin of branchial lamellae.

Thorax. Eighteen pairs of notopodia (SG 3–20) (Fig. 2D, E), those of TC 1 approximately as long as subsequent ones (Fig. 2D, E). Lateral lappets and dorsal projections of notopodia in anterior thoracic chaetigers with different degree of development depending on size and preservation conditions, but both more conspicuous on TC 1–5 (Figs 2D–F, 3E, F). White ventral colouration present on TC 1–4 (Figs 2D, 3E) or only on TC 4 (Figs 2E, F, 3F). All notochaetae as simple capillaries (Fig. 15A). Size of notochaetae of TC 1 similar to subsequent ones. Neuropodia as sessile pinnules from TC 6 to body end, with uncini in single or double rows, from TC 7 throughout. Neuropodia on TC 6, provided with several sharply bent, acute-tipped, geniculate

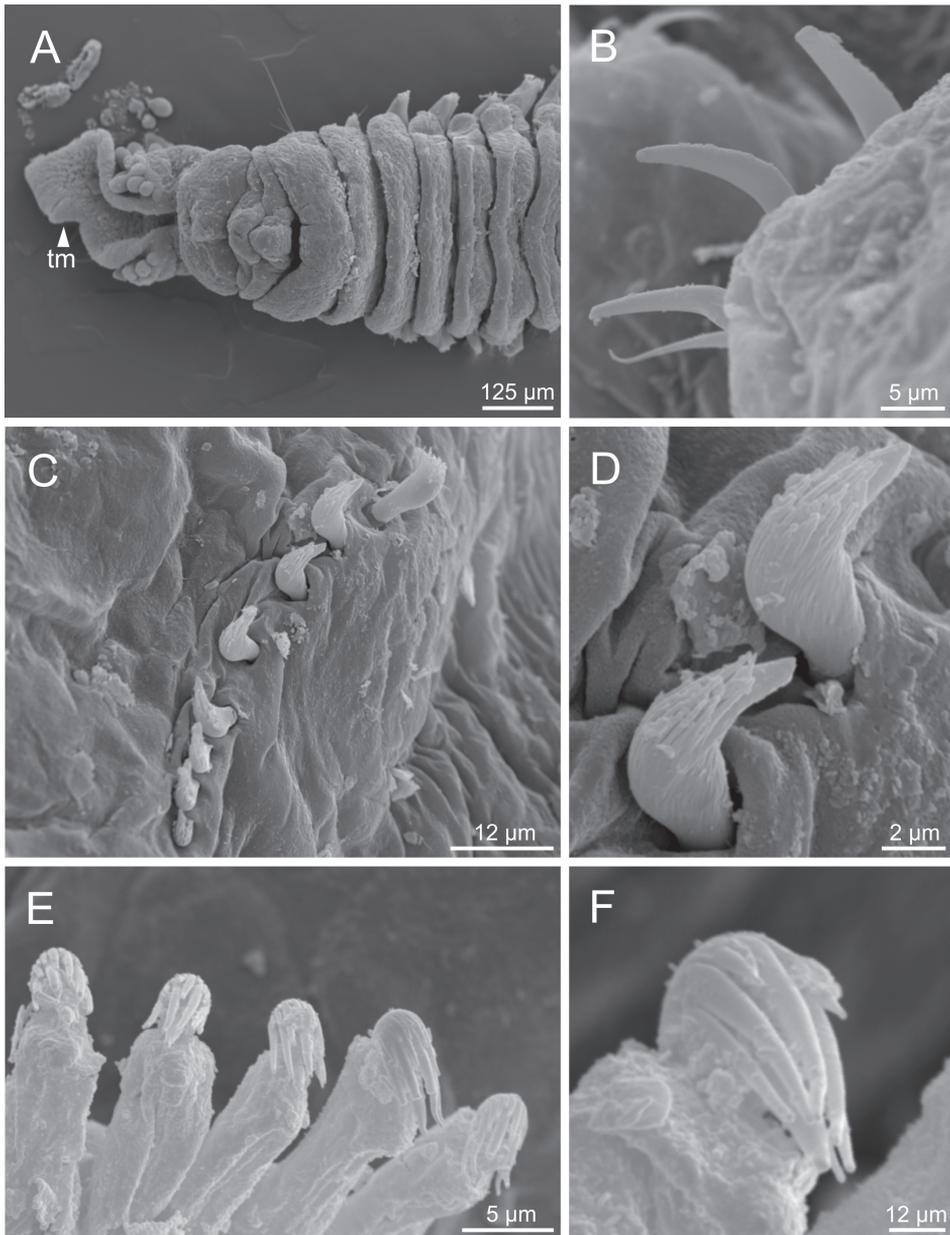


Figure 13. *Terebellides irinae* Gageev, 2009 (species 24; non-type specimen, ZMBN116501), SEM micrographs. **A** anterior end, ventral view **B** TC 6 (TU1), geniculate chaetae **C** row of thoracic uncini **D** thoracic uncini **E** abdominal uncini **F** abdominal uncinus, detail. Abbreviations: tc – thoracic chaetiger; tm – tentacular membrane; tu – thoracic unciniger.

chaetae (Figs 15B, 18A) with minute teeth forming a capitium only visible with SEM (Fig. 18A, B). From TC 7, neuropodia with one row of uncini per torus (Figs 15C, 18C), with long shafted denticulate hooks, with large main fang (rostrum) longer than

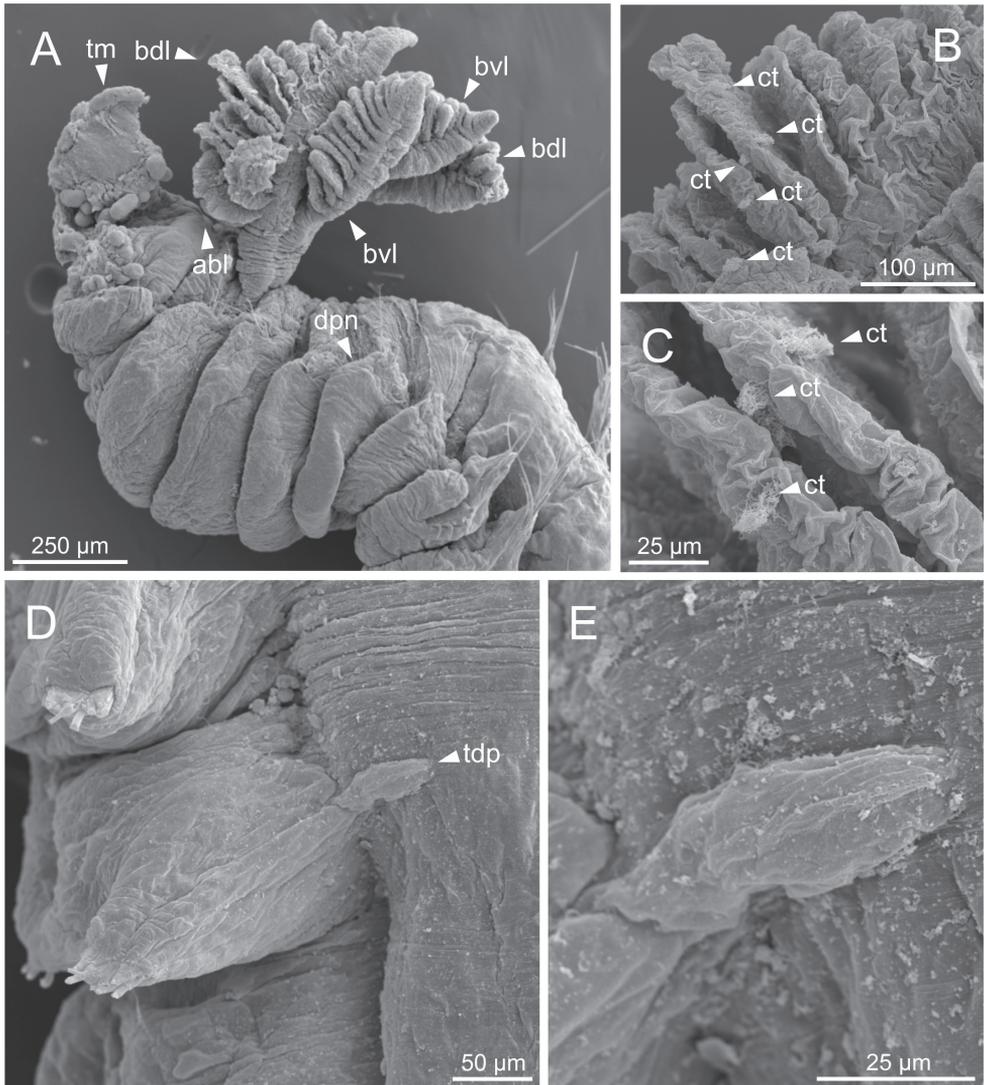


Figure 14. *Terebellides williamsae* Jirkov, 1989 (species 2; non-type specimens, ZMBN116249 and ZMBN116251), SEM micrographs **A** anterior end, left lateral view **B** branchial lamellae, detail **C** ciliary tufts, detail **D** TC and thoracic dorsal papilla **E** thoracic dorsal papilla, detail. Abbreviations: abl – anterior branchial lobe; bdl – branchial dorsal lobe; bvl – branchial ventral lobe; ct – ciliary tuft; dpn – dorsal projection of notopodium; TC – thoracic chaetiger; tdp – thoracic dorsal papilla; tm – tentacular membrane.

upper crest of teeth (capitium), rostrum/capitium length ratio of ~ 2:1, capitium composed by several teeth above main fang of decreasing length (Figs 15D, 18D).

Abdomen and pygidium. Approximately half as long as thorax and progressively thinner (Fig. 2D, E). Neuropodia ranging from 18–44 chaetigers and forming erect pinnules (Figs 15E, 18E) with several uncini per torus, number depending on specimen size. Uncini provided with several teeth above rostrum surmounted by a capitium

composed of several teeth of decreasing length (Figs 15F, 18F). Pygidium blunt, as funnel-like depression.

Colour pattern. Colour in preserved specimens whitish or pale brown (Fig. 3E, F). MG staining pattern characterised by compact green colourant in SG 1–5 and SG 7–13, SG 6 white and SG 14 striped (Fig. 12).

Remarks. Among the aforementioned characters, the white ventral colouration in anterior thoracic chaetigers may be a useful character to distinguish Group D species from those of Groups A–C. Other taxa described or reported worldwide showing this colouration pattern are *Terebellides distincta* Williams, 1984 and *T. ceneresi* Lavesque, Hutchings, Daffe, Nygren & Londoño-Mesa, 2019.

Terebellides williamsae Jirkov, 1989

Figs 2D, 3E, 9, 10E, 11, 12, 14, 15, Table 1, Suppl. materials 1, 2

Terebellides williamsae Jirkov, 1989: 124.

Species 2 – Nygren et al. 2018: 18–22, figs 6, 10.

Material examined. 20 specimens (Suppl. material 1), Skagerrak (GNM14639, GNM15107, GNM15108); Barents Sea (ZMBN116246, ZMBN116247, ZMBN116248, ZMBN116249, ZMBN116251, ZMBN116252, ZMBN116253, ZMBN116254, ZMBN116255, ZMBN116257, ZMBN116260, ZMBN116262, ZMBN116263, ZMBN116266, ZMBN116269, ZMBN116270, ZMBN116271).

GenBank accession numbers of material examined (COI). MG024957, MG024958, MG024959, MG024960, MG024961, MG024962, MG024963, MG024964, MG024965, MG024966, MG024967, MG024968, MG024969, MG024970, MG024971, MG024972, MG024973, MG024974, MG024975, MG024976, MG024977, MG024978, MG024979, MG024980, MG024981, MG024982, MG024983, MG024984, MG024985, MG024986, MG024987, MG024988.

Diagnostic features of studied material. Complete individuals ranging from 9.0–34.0 mm in length (Fig. 9). Branchial dorsal lobes lamellae provided with well-developed papillary projections and branchial ventral lobes provided with short posterior filaments, 50.0 µm in length (Figs 3E, 14A). Between 16–18 lamellae on dorsal lobes (Fig. 14A, B). Ciliary tufts present in inner face of lamellae (Fig. 14B, C). Ventral branchial lobes hidden in between dorsal ones but sometimes discernible below (Fig. 14A). Lateral lappets present on TC 1–4; dorsal projection of thoracic notopodia on TC 2–4 (Fig. 14A). White ventral colouration present on TC 1–4 (Figs 2D, 3E). Geniculate chaetae in TC 5, acutely bent, with well-marked capitium (Fig. 15B). Ciliated papilla dorsal to thoracic notopodia observed in TC 7 (Fig. 14D, E). From TC 7, neuropodia with one row of type 1 thoracic uncini per torus, with rostrum/capitium length ratio of ~ 2:1 and capitium with a first row of two or three large teeth, followed by many smaller teeth (Fig. 15C, D). Abdomen with 38–44 pairs of neuropodia with type 1A uncini (Fig. 15E, F).

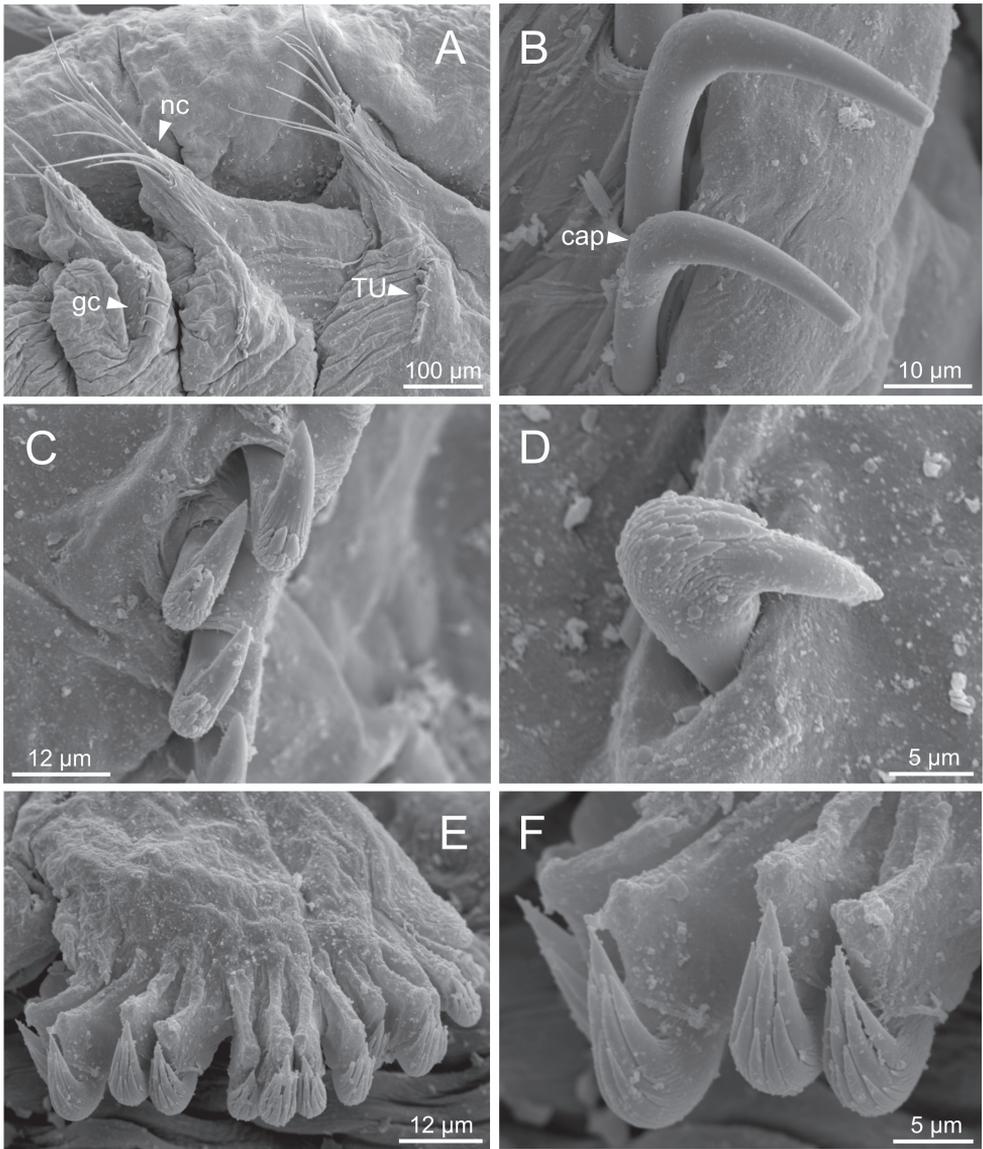


Figure 15. *Terebellides williamsae* Jirkov, 1989 (species 2; non-type specimen, ZMBN116249), SEM micrographs **A** TC 5–7, lateral view **B** TC 6 (TU1), geniculate chaetae **C** row of thoracic uncini **D** thoracic uncinus **E** abdominal neuropodium **F** abdominal uncini. Abbreviations: cap – capitium; gc – geniculate chaetae; nc – notochaetae; TC – thoracic chaetiger; TU – thoracic unciniger.

Colour pattern. MG staining pattern characterised by compact green colourant in SG 1–5 and SG 7–13, SG 6 white and SG 14 striped, J-shaped glandular regions in SG 3–5 (Fig. 12). Similar to pattern 2.

Nucleotide diagnostic features. All sequences of *Terebellides williamsae* share and are distinguished from other available *Terebellides* sequences in unique combinations of nucleotides (underlined) at the given position of our alignment: 59–62: TATC,

75–96: TGGACAACCTGGGGCATTTCCTG, 132–144: TCATGCTTTTTTTA, 153–157: TTTCC, 216–234: TGCTCCTGATATAGCTTTC, 264–277: CCTCCCTCCAGCTT, 315–318: GGTT, 327–342: CTGAACAGTATACCCC, 381–399: AGATTTGGCTATTTTCT, 414–432: TATCTCCTCTATTCTTGGC, 450–454: TACA, 515–529: AAAAATCACTACCA, 543–573: TTCACTTCCTGTATTAGCAGGAGCTATTACA, 600–609: CACTTCCTTT, 630–640: CGACCCAATTT.

Type locality. Barents Sea, Norway, 74°30'N, 28°00'E (Jirkov 1989).

Distribution and bathymetry. Barents Sea, Greenland Sea, Norwegian coast and shelf, Skagerrak; at depths of 178–612 m but most of the specimens (97%) were collected above 200 m (Figs 10E, 11, Suppl. material 1).

Remarks. *Terebellides williamsae* is a medium-sized species, reaching up to 34 mm in length; it is characterised by the lack of papillae on margins of branchial lamellae and by having branchiae of type 2 and posterior filaments in ventral branchial lobes, thoracic uncini of type 1 and abdominal uncini of type 1A (Table 1). All these features are shared with *T. gracilis*; in fact, Parapar et al. (2011) suggested this species as a synonym to *T. gracilis* after examining specimens from Iceland. Nygren et al. (2018) pointed out that there were no morphological differences between both species, but their molecular analyses indicate that specimens from the Barents Sea (“Species 2”) would correspond to *T. williamsae*. Nygren et al. (2018) suggested therefore that *T. williamsae* might be a valid species and different from *T. gracilis* (“Species 3”, see below). Here, examination of specimens of *T. williamsae* show that they differ from *T. gracilis* in the number of chaetigers with white ventral colouration, i.e., in *T. williamsae* white colouration is present in TC 1–4 while in *T. gracilis* it is only present on TC 4.

***Terebellides gracilis* Malm, 1874**

Figs 2E, F, 3F, 4D, 9, 10F, 11, 12, 16–18, Table 1, Suppl. materials 1, 2

Terebellides gracilis Malm, 1874: 67–105, p. 100.

Species 3 – Nygren et al. 2018: 18–22, figs 6, 10.

Material examined. 20 specimens (Suppl. material 1), Skagerrak (GNM15110, GNM15111); Norwegian coast (ZMBN116276, ZMBN116278, ZMBN116282, ZMBN116283, ZMBN116284, ZMBN116285, ZMBN116287, ZMBN116289, ZMBN116293, ZMBN116295, ZMBN116297, ZMBN116298, ZMBN116301, ZMBN116306, ZMBN116307, ZMBN116309, ZMBN116310, 116313).

GenBank accession numbers of material examined (COI). MG024583, MG024584, MG024585, MG024586, MG024587, MG024588, MG024589, MG024590, MG024591, MG024592, MG024593, MG024594, MG024595, MG024596, MG024597, MG024598, MG024599, MG024600, MG024601, MG024602, MG024603, MG024604, MG024605, MG024606, MG024607, MG024608, MG024609, MG024610, MG024611, MG024612, MG024613, MG024614, MG024615, MG024616, MG024617, MG024618, MG024619, MG024620, MG024621, MG024622, MG024623, MG024624, MG024625,

MG024626, MG024627, MG024628, MG024629, MG024630, MG024631, MG024632, MG024633, MG024634, MG024635, MG024636, MG024637.

Diagnostic features of studied material. Complete individuals ranging from 5.0–29.0 mm in length (Fig. 9). Branchial dorsal lobes lamellae provided with well-developed papillary projections and branchial ventral lobes provided with long posterior filaments, ranging from 125.0–175.0 μm in length (Fig. 16D, E). Between 23–32 lamellae on dorsal lobes (Figs 4C, 16A, D, E, 17A). Ciliary rows and ciliary tufts on inner branchial lamellae present (Figs 16B, C, 17B). Ventral branchial lobes hidden in between dorsal ones but sometimes discernible below (Figs 16A, D, 17A). Lateral lappets present on TC 1–4; dorsal projection of thoracic notopodia on TC 1–5 (Fig. 16D). White ventral colouration presents only on TC 4 (Figs 2E, F, 3F). Geniculate chaetae present in TC 5,

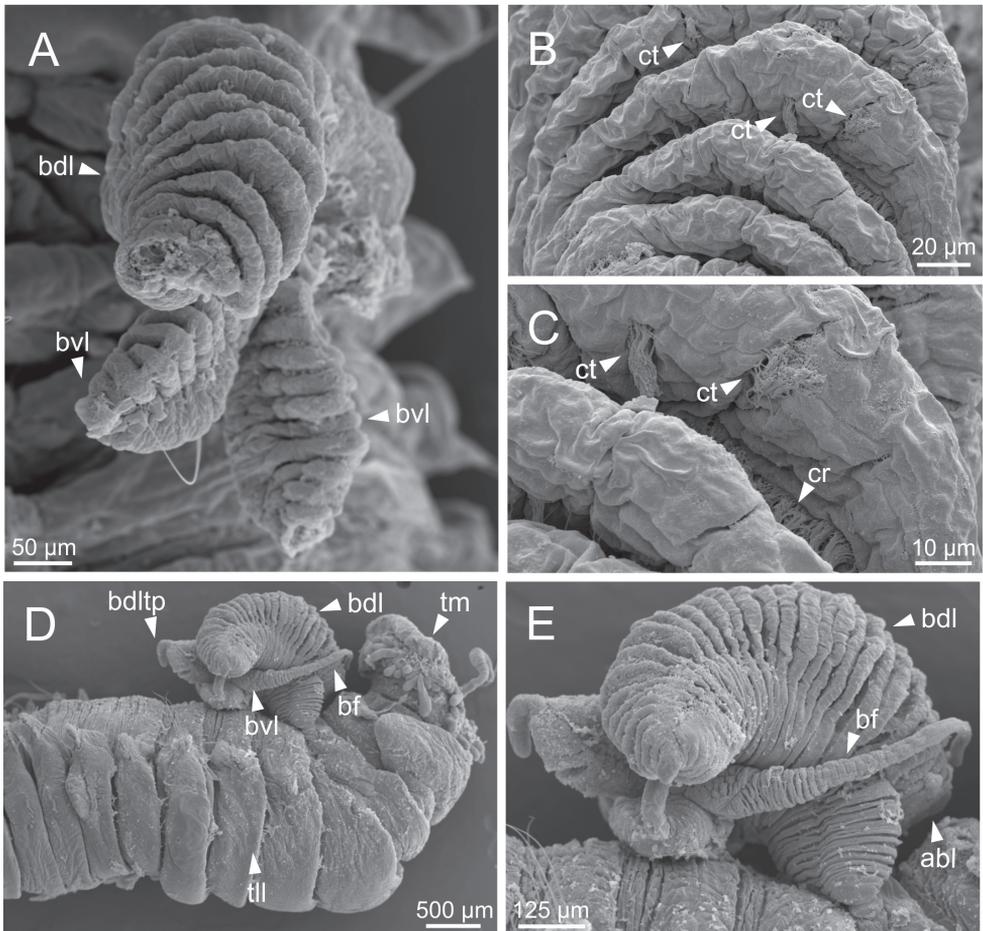


Figure 16. *Terebellides gracilis* Malm, 1874 (species 3; non-type specimens, GNM15110 and ZMBN116313), SEM micrographs **A** branchiae, dorsal view **B** branchial lamellae, detail **C** ciliary tufts, detail **D** anterior end, right lateral view **E** branchiae, lateral view. Abbreviations: abl – anterior branchial lobe; bdl – branchial dorsal lobe; bdltp – branchial dorsal lobe terminal papilla; bf – filament; bvl – branchial ventral lobe; cr – ciliary row; ct – ciliary tuft; tll – thoracic lateral lobes; tm – tentacular membrane.

acutely bent, with marked capitium (Fig. 18A, B). Ciliated papilla dorsal to thoracic notopodia observed in TC 2–4 (Fig. 17A, C, D). From TC 7, neuropodia with one row of type 1 thoracic uncini per torus, with rostrum/capitium length ratio of ~ 2:1 and capitium with a first row of two or three large teeth, followed by many smaller teeth (Fig. 18C, D). Abdomen with 34–41 pairs of neuropodia with type 1A uncini (Fig. 18E, F).

Colour pattern. MG staining characterised by compact green colourant in SG 1–5 and SG 7–13, SG 6 white and SG 14 striped (Fig. 12). Similar to pattern 2.

Nucleotide diagnostic features. All sequences of *Terebellides gracilis* share and are distinguished from other available *Terebellides* sequences in unique combinations of nucleotides (underlined) at the given position of our alignment: 39–63: TG-GTACTTCAATAAGACTTCTTATC, 84–96: TGGGGCATTCTCTG, 111–132: TTATAACACAATTGTTACTGCT, 138–157: TTTTTTAATAATTTTTTTTCC, 216–234: TGCTCCTGATATAGCTTTC, 264–277: CCTCCCTCCAGCTT, 315–327: AGCTGGGACAGGT, 333–351: AGTCTACCCTCCTTTATCT, 381–399: AGATTTGGCTATTTTTTCT, 414–432: TATCTCCTCTATTCTTGGC, 450–545: TACA, 516–529: AAAAATCACTACCA, 543–552: TTCACTTCCT, 600–609: CACTTCCTTT, 630–640: CGACCCAATTT.

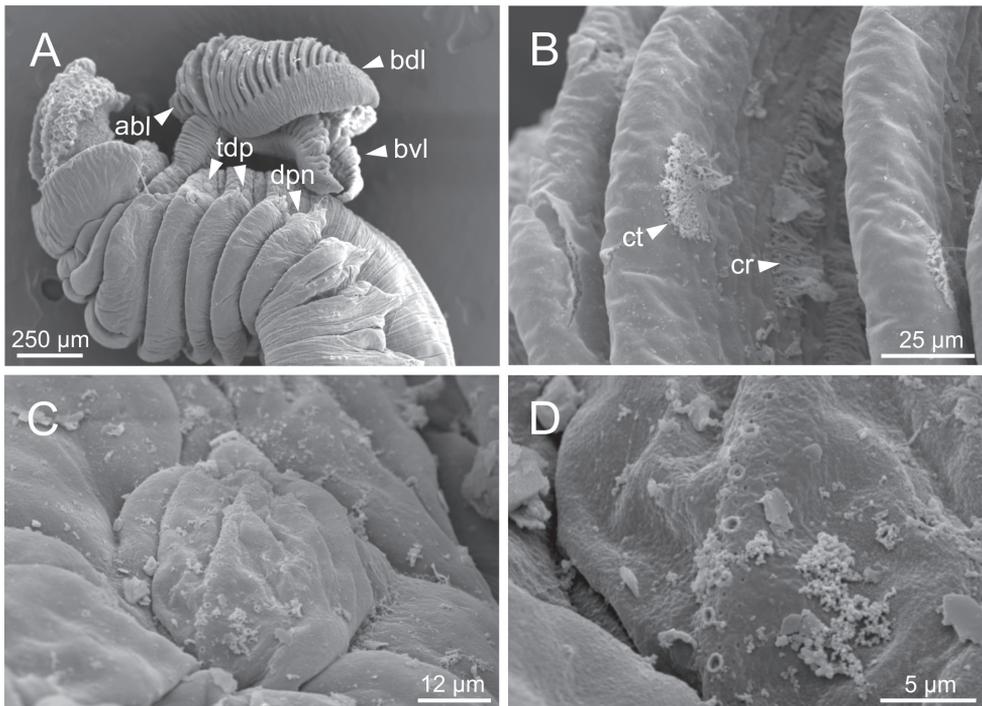


Figure 17. *Terebellides gracilis* Malm, 1874 (species 3; non-type specimen, ZMBN116282), SEM micrographs **A** anterior end, left lateral view **B** ciliary tufts and ciliary row, detail **C** dorsal projection of notopodium **D** pores of dorsal projection of notopodium, detail. Abbreviations: abl – anterior branchial lobe; bdl – branchial dorsal lobe; bvl – branchial ventral lobe; cr – ciliary row; ct – ciliary tuft; dpn – dorsal projection of notopodium; tdp – thoracic dorsal papilla.

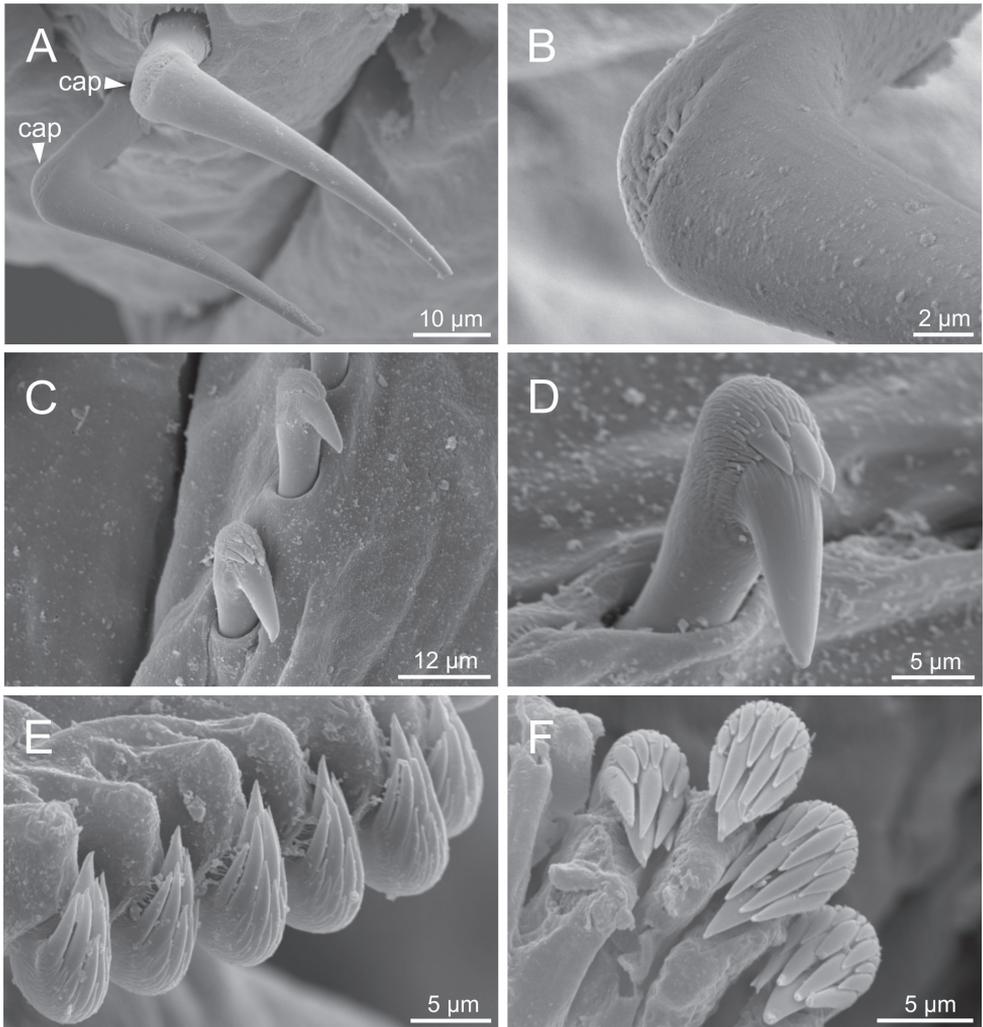


Figure 18. *Terebellides gracilis* Malm, 1874 (species 3; non-type specimens, ZMBN116282 and ZMBN116313), SEM micrographs **A** TC 6 (TU1), geniculate chaetae **B** capitum of geniculate chaeta, detail **C** thoracic uncini **D** thoracic uncinus **E** abdominal neuropodium **F** abdominal uncini. Abbreviations: cap – capitum; TC – thoracic chaetiger; TU – thoracic unciniger.

Type locality. Atlantic Ocean, Norway (Malm 1874).

Distribution and bathymetry. South Iceland, Norwegian coast and shelf, Skagerrak; 237–1268 m deep (Figs 10F, 11, Suppl. material 1).

Remarks. *Terebellides gracilis* is a medium-sized species, reaching up to 29 mm in length and is characterised by the lack of papillae on margins of branchial lamellae, having branchiae of type 2 and filaments in ventral branchial lobes, presence of thoracic uncini of type 1 and abdominal uncini of type 1A (Table 1). As stated above, these features are shared with *T. williamsae* but both species differ in the pattern of white

ventral thoracic colouration. Besides, they show a MG pattern close to type 2 but only *T. gracilis* showed J-shaped glandular regions in SG 3–5 as observed in the specimens studied here. *Terebellides gracilis* has apparently a more restricted geographical distribution than *T. williamsae* but reaching deeper depths (down to 1268 m).

Key to Northeast Atlantic Ocean species of *Terebellides*

The following key of European species of *Terebellides* is based on those by Lavesque et al. (2019) and Parapar et al. (2020a) but has been updated to include the species belonging to Groups B, C and D studied herein. The order of the presentation of the discriminating characters and the taxa has been changed to fit better with the clades recovered in the phylogenetic trees by Nygren et al. (2018) and Lavesque et al. (2019).

The characters considered were the ventral pigmentation of anterior thoracic chaetigers in live and fixed specimens, types of thoracic uncini (sensu Parapar et al. 2020b), morphology of branchiae (sensu Parapar et al. 2016a), morphology of the abdominal uncini (sensu Parapar et al. 2020a), the size of species (small species: < 20 mm in length; medium: 20–40 mm; large: > 40 mm), the presence of geniculate chaetae in TC 5–6 or only in TC 6, the presence or absence of papillae in branchial lamellae margins, the shape of glandular region in TC 3, and the presence or absence of ciliary tufts in branchial lamellae. In those cases where two species are considered as cryptic and only distinguished by molecular characters, geographic and bathymetric distribution has been provided instead.

- 1 White ventral colouration on anterior thoracic chaetigers 2
- No distinct ventral colouration on anterior thoracic chaetigers 4
- 2 Medium/large species (>20 mm in length); 5th branchial lobe present; notochoetae of TC 1 similar to subsequent ones; main fang of thoracic uncini straight; thoracic uncini with capitium composed of 2–3 large teeth and subsequent ones much smaller 3
- Small species (< 20 mm in length); 5th branchial lobe absent; notochoetae of TC 1 absent or shorter than subsequent ones; thoracic uncini with capitium composed of 4 or 5 mid-sized teeth and following of slightly smaller teeth
... *T. ceneresi* Lavesque, Hutchings, Daffe, Nygren & Londoño-Mesa, 2019
- 3 White ventral colouration on TC 1 to TC 4 *T. williamsae* Jirkov, 1989
- White ventral colouration only on TC 4 *T. gracilis* Malm, 1874
- 4 Branchial lobes all small and not fused; reduced dorsal lobes
..... *T. irinae* Gagaev, 2009
- Branchiae otherwise 5
- 5 Lower branchial lobes with posterior projections as filaments; branchiae with lobes fused ~ 50% of their length or with lobes only fused at base; small/medium species (<40 mm in length) 6
- Lower branchial lobes with posterior projections; branchiae with large lobes almost completely fused; large species (> 40 mm in length) 9

- 6 Thoracic uncini with capitium composed of 5–7 small teeth, remaining ones similar in size at least in two rows ***T. shetlandica* Parapar, Moreira & O’Reilly, 2016**
- Thoracic uncini with capitium composed of 4–5 mid-sized teeth and followed by slightly smaller teeth 7
- 7 Branchiae with lobes fused ~ 50% of their length; medium-sized species (> 20 mm in length) ***T. lavesquei* sp. nov.**
- Branchiae with lobes only fused at base; small species (< 20 mm in length) 8
- 8 Glandular region in TC 3 present; notochaetae from TC 1 longer than subsequent ones ***T. parapari* Lavesque, Hutchings, Daffe, Nygren & Londoño-Mesa, 2019**
- Glandular region in TC 3 not observed; all notochaetae of similar size ***T. atlantis* Williams, 1984**
- 9 Genuiculate chaetae in TC 5 and TC 6; abdominal uncini with RvC = 1/0.7, capitium with 4–5 teeth and remaining ones smaller ***T. bigeniculatus* Parapar, Moreira & Helgason, 2011**
- Genuiculate chaetae in TC 6 only 10
- 10 Branchial lamellae margins lacking papillae 11
- Branchial lamellae margins with papillae 13
- 11 Branchiae with lobes fused ~ 50% of their length ***T. gralli* Lavesque, Hutchings, Daffe, Nygren & Londoño-Mesa, 2019**
- Branchiae with large lobes almost completely fused 12
- 12 Abdominal uncini with RvC = 1/0.7, capitium with 4–5 teeth and remaining ones smaller ***T. stroemii* Sars, 1835**
- Abdominal uncini with RvC = 1/0.9, capitium composed of 3–5 large teeth in first row and 1–2 in a second row ***T. kongsrudi* Parapar, Capa, Nygren & Moreira, 2020** and ***T. bakkeni* Parapar, Capa, Nygren & Moreira, 2020**
- 13 Glandular region in TC 3 round or oval 14
- Glandular region in TC 3 otherwise 15
- 14 Glandular region in TC 3 remained white with MG; branchial lamellae with rounded papillae; TC 1–3 without conspicuous dorsal projection ***T. lilasae* Lavesque, Hutchings, Daffe, Nygren & Londoño-Mesa, 2019**
- Glandular region in TC 3 stained blue with MG; branchial lamellae with conical papillae; TC 1–3 with conspicuous dorsal projection ***T. bonifi* Lavesque, Hutchings, Daffe, Nygren & Londoño-Mesa, 2019**
- 15 Branchial ciliary tufts present ***T. gentili* Lavesque, Hutchings, Daffe, Nygren & Londoño-Mesa, 2019**
- Branchial ciliary tufts absent 16
- 16 Most branchial lamellae with marginal papillae; mouth with upper lip elongated ***T. resomari* Lavesque, Hutchings, Daffe, Nygren & Londoño-Mesa, 2019**
- Only anterior branchial lamellae with marginal papillae; upper lip not elongated 17

- 17 Thoracic uncini with capitium composed of 2–3 large teeth and subsequent ones much smaller..... *T. ronningae* Parapar, Capa, Nygren & Moreira, 2020
- Thoracic uncini with capitium composed of 4 or 5 mid-sized teeth and following slightly smaller ones..... 18
- 18 Deep-water species; usually at depths below 200 m
..... *T. norvegica* Parapar, Capa, Nygren & Moreira, 2020
- Shallow-water species; mostly at depths above 100 m
..... *T. europaea* Lavesque, Hutchings, Daffe, Nygren & Londoño-Mesa, 2019 and *T. scotica* Parapar, Capa, Nygren & Moreira, 2020

Discussion

Species groups

According to Nygren et al. (2018), *Terebellides* is divided in four main groups of species: A, B, C and D, which differ from each other by several morphological characters. Species of Group A were studied by Parapar et al. (2020a). Species in Group B are characterised by small-medium body length (5.0–35.0 mm), branchiae of type 2 or 3 with incompletely fused or free lobes (only fused at their base), long posterior filaments in ventral lobes, thoracic uncini of type 3 or 4 and abdominal uncini of type 2. *Terebellides lavesquei* sp. nov. belongs to this group and is also characterised by the lack of papillae on margins of branchial lamellae and by having branchiae of type 2 and thoracic uncini of type 3. Group C is defined by having thoracic uncini of type 3 only and abdominal uncini of type 2. Finally, Group D species are of medium length and bear white ventral colouration in anterior chaetigers, branchiae of type 2 with incompletely fused lobes, ventral branchial lobes with posterior filaments, ciliary tufts in the inner face of branchial lamellae, thoracic uncini of type 1 and abdominal uncini of type 1A.

Integrative taxonomy

The apparently morphological homogeneity of members of *Terebellides* has hidden an unexpected species richness in the Northeast Atlantic. Species delimitation analyses of DNA sequence data have allowed to reveal some of the *Terebellides* species that otherwise would have gone unnoticed (Nygren et al. 2018; Lavesque et al. 2019; Parapar et al. 2020a). Moreover, molecular data have provided further evidence of species hypothesis diagnosed solely based on morphological features (e.g., Gagaev 2009; Parapar et al. 2011, 2016c; Parapar and Hutchings 2014).

An integrative approach, that aims at considering different sources of evidence, has become a common and grounded method for general species delineation (Dayrat 2005; Schlick-Steiner et al. 2010) including marine annelids (Capa et al. 2010, 2013; Capa and Murray 2015; Aguado et al. 2019; Kara et al. 2020; Teixeira et al. 2020). In

addition, the integration of a variety of types of data has been used in formal species descriptions, a crucial step that includes providing a new name and facilitates communication about these entities (Goldstein and DeSalle 2011) and their diagnoses, which allows the correct identification for the species (Pante et al. 2015). In fact, the inclusion of DNA sequence information in formal species descriptions or diagnoses has been revealed as a useful practice to identify taxonomic groups (Renner 2016), especially with a high proportion of cryptic and pseudo-cryptic species such as it happens in annelids (Halt et al. 2009; Nygren and Pleijel 2011; Parapar et al. 2020a; Grosse et al. 2021).

In the present study, following the aims and methods of the similar previous study by Parapar et al. (2020a), who dealt with species belonging to Group A, several of the Northeast Atlantic Ocean *Terebellides* molecular lineages recovered within Groups B, C and D and compatible with a hypothetical species rank (after Nygren et al. 2018) are newly described, including morphological and COI sequence traits allowing to distinguish them from other congeners. In addition, a new species, *Terebellides lavesquei* sp. nov. is also described following the same approach. The difference between the present work and the previous (Parapar et al. 2020a) relies on the recognition of the diagnostic COI nucleotides for the species described. Parapar et al. (2020a) provided a list of unequivocal single nucleotides (autapomorphies) in specific positions of the alignment while in the present study a short sequence of nucleotides is provided to ease the identification along the alignment, and these include a unique combination of single nucleotides together with others that do not show variation within the sequences available.

Group B comprises eight species; one of them was identified herein as *T. atlantis*, matching the diagnostic characters and distribution of *T. atlantis*, originally described by Williams (1984) and from specimens collected in deep Icelandic waters by Parapar et al. (2011). A second species was recognised as *T. shetlandica* according to the description by Parapar et al. (2016a). The remaining six species represent undescribed taxa that will be dealt with elsewhere. Group C was composed by three species; one species was identified as *T. irinae* and the other two represent undescribed taxa that will be dealt with elsewhere. Finally, Group D comprises three species: *T. gracilis*, that matches the diagnostic characters and distribution originally described by Malm (1874), *T. williamsae* following the original description by Jirkov (1989), and one undescribed taxon that will be dealt with elsewhere.

Species distributions

The range of distribution of all nominal species identified here is expanded. Nygren et al. (2018) pointed out that species such as *T. shetlandica* and *T. atlantis* have a wide distribution and were more frequent in samples, while *T. lavesquei* sp. nov. seems restricted to the Norwegian and Swedish coast. Some species were found at shallow depths, reaching the continental shelf border (0–200 m) such as *T. shetlandica*, while *T. atlantis* and *T. lavesquei* sp. nov. were found at depths below 200 m. *Terebellides atlantis* showed the wider bathymetric distribution (219–2750 m deep) among the species of this group. *Terebellides irinae* appeared at depths below 4000 m and its distribution seems to be restricted to the Arctic Ocean. Species of Group D, *T. williamsae* and *T. gracilis*, show a wide geographic and bathymetric distribution.

Comparisons with other NEA species of the genus *Terebellides*

Lavesque et al. (2019) described eight species from the Atlantic and Mediterranean coasts of France (see Key above), six of them belong to Group A sensu Nygren et al. (2018) and two are morphologically similar to those of Groups B and D, namely *T. ceneresi* and *T. parapari*. Lavesque et al. (2019) and Parapar et al. (2020a) considered *T. parapari* as related to Group B and particularly to *T. shetlandica*. *Terebellides parapari* shares with *T. shetlandica* and *T. atlantis* the presence of branchiae of type 3 and branchial lobes that are free from each other; *T. parapari* also shares with *T. shetlandica*, *T. lavesquei* sp. nov. and *T. atlantis* the presence of posterior filaments in lower branchial lobes, thoracic uncini of type 3 and abdominal uncini of type 2. However, branchial filaments in *T. shetlandica*, *T. lavesquei* sp. nov. and *T. atlantis* are longer and all notochaetae are of similar length while in *T. parapari* notochaetae in TC 1 are longer than subsequent ones.

On the other hand, *T. ceneresi* shares many morphological similarities with *T. williamsae* and *T. gracilis* and therefore was related to Group D by Lavesque et al. (2019) and Parapar et al. (2020a). These three species show white ventral colouration in anterior thoracic chaetigers, but in *T. williamsae* it is present in TC 1–4 while in *T. ceneresi* and *T. gracilis* is present only in TC 4. Other shared characters are the presence of ciliary tufts in the inner face of branchial lamellae and abdominal uncini of type 1A. However, *T. ceneresi* lacks the anterior branchial lobe (5th lobe) that is present in *T. gracilis* and *T. williamsae*; the branchial lobes of *T. ceneresi* are not fused while in *T. williamsae* and *T. gracilis* they are partially fused. Finally, *T. ceneresi* bears thoracic uncini of type 3 whereas *T. williamsae* and *T. gracilis* bear type 1.

Among the remaining clades that will be described elsewhere, clades 4, 14 and 26 do not correspond either to *T. atlantis* or *T. shetlandica* because of differences in the branchiae type (i.e., type 2: incompletely fused lobes) and the absence of posterior filaments in branchial ventral lobes; they also differ in geographic distribution, being the aforementioned clades restricted to some areas in NEA. Likewise, clade 25 does not fit within *T. irinae* due to being medium sized and by having branchiae of type 1 (=large lobes almost totally fused). Finally, clade 15 does not match either to *T. williamsae* or *T. gracilis* because of having a ventral colouration extending across more segments (TC 1–10 vs TC 1–4 or TC 4 in *T. gracilis* and *T. williamsae* respectively).

Characters and identification key

In this work, the following characters have been studied in all specimens: morphology of branchiae (sensu Parapar et al. 2016a), types of thoracic uncini (sensu Parapar et al. 2020b), abdominal uncini (sensu Parapar et al. 2020a), MG staining patterns (sensu Schüller and Hutchings 2010, 2013), and geographic and bathymetric distributions.

Among the species studied here, branchiae of *T. lavesquei* sp. nov., *T. williamsae*, and *T. gracilis* correspond to type 2, *T. shetlandica* and *T. atlantis* to type 3, and *T. irinae* to type 4. Regarding thoracic uncini, *T. williamsae* and *T. gracilis* have type 1, *T. lavesquei* sp. nov., *T. atlantis*, and *T. irinae* have type 3 and *T. shetlandica* bears

type 4. Finally, considering abdominal uncini, *T. williamsae* and *T. gracilis* have type 1A and *T. shetlandica*, *T. lavesquei* sp. nov., *T. atlantis*, and *T. irinae* have type 2.

Schüller and Hutchings (2010, 2013) defined several types of MG staining patterns according to the presence or absence of coloured bands in the segments along the body and their solid/striped appearance. The patterns observed in the species studied here are similar to those patterns described by Schüller and Hutchings (2010, 2013): *T. shetlandica* and *T. irinae* agree to pattern 1, *T. williamsae* and *T. gracilis* to pattern 2, and *T. lavesquei* sp. nov. and *T. atlantis* to pattern 9. However, we found that species with types 2 and 9 bear a J-shaped glandular region that is composed of three segments instead of only one as reported by Schüller and Hutchings (2010, 2013). These variations suggest that new staining patterns with taxonomic relevance might be determined when specimens from elsewhere are studied.

The species key is an update to those by Lavesque et al. (2019) and Parapar et al. (2020b) but still does not allow for morphological discrimination between three species (*T. norvegica*, *T. europaea*, and *T. scotica*). At present, these species can be differentiated only genetically and according to their geographical or bathymetric distributions.

Conclusions

A total of five nominal species has been identified as belonging to *Terebellides* Groups B, C, and D (according to Nygren et al. 2018): *Terebellides gracilis* Malm, 1874, *Terebellides atlantis* Williams, 1984, *Terebellides williamsae* Jirkov, 1989, *Terebellides irinae* Gagaev, 2009 and *Terebellides shetlandica* Parapar, Moreira & O'Reilly, 2016, and a new species is here described as *Terebellides lavesquei* sp. nov. Other species outlined by species delimitation analyses within these Groups will be either described elsewhere or would require additional material to be found.

The five species identified herein have been characterised based on morphological and molecular characters. The most relevant morphological features discriminating between species are branchial shape, ventral pigmentation of anterior thoracic chaetigers in live and fixed specimens, and the morphology of thoracic and abdominal uncini. For the molecular recognition of the species described, short sequences of nucleotides among the COI alignment have been provided as diagnostic to ease the identification.

Acknowledgements

We would like to thank all people involved in the paper by Nygren et al. (2018), for providing the specimens studied herein. Thanks also to Ada Castro and Catalina Sueiro (Servizos de Apoio á Investigación, Universidade da Coruña) for SEM assistance, and to María Candás (Estación de Bioloxía Mariña da Graña-Ferrol, Universidade de Santiago de Compostela, Spain) for assistance with the stereomicroscope photographs. This study was partly supported by the FAUNA IBÉRICA research project Polychaeta VII, Palpata, Canalpalpata II (PGC2018–095851–B–C64) funded by the Agencia Estatal

de Investigación, Ministerio de Ciencia e Innovación, and coordinated by JP. Funding was also provided from the Ramón y Cajal program (RYC-2016- 20799) funded by Spanish MINECO, Agencia Estatal de Investigación, Comunidad Autónoma de las Islas Baleares and the European Social Fund to MC. Financial support was also provided by the Norwegian Taxonomy Initiative: Cryptic polychaete species in Norwegian waters, knr 49-13, project no. 70184228 to AN; Polychaetes in the Norwegian Sea, project no. 70184227; Polychaetes in Skagerrak, project no.70184216; and the MAREANO program. We are deeply grateful to the reviewers of the manuscript, Pat Hutchings and Nicolas Lavesque, as well as Greg Rouse, ZooKeys Subject Editor and Nathalie Yonow, ZooKeys Copy Editor, for their constructive suggestions, which greatly improved the quality of the manuscript. We also thank Yordanka Banalieva and Tsvetelina Milenkova for their valuable help in the efficient manuscript editorial and accounting management processes.

References

- Aguado MT, Capa M, Lago-Barcia D, Gil J, Pleijel F, Nygren A (2019) Species delimitation in *Amblyosyllis* (Annelida, Syllidae). PLoS ONE 14(4): e0214211. <https://doi.org/10.1371/journal.pone.0214211>
- Bakken T, Hårsaker K, Daverdin M (2020) Marine invertebrate collection NTNU University Museum. Version 1.535. NTNU University Museum. [Occurrence dataset:] <https://doi.org/10.15468/ddbs14> [accessed on 26 June 2020]
- Capa M, Murray A (2015) Integrative taxonomy of *Parasabella* and *Sabellomma* (Sabellidae: Annelida) from Australia: description of new species, indication of cryptic diversity, and translocation of some species out of their natural distribution range. Zoological Journal of the Linnean Society 175(4): 764–811. <https://doi.org/10.1111/zoj.12308>
- Capa M, Bybee DR, Bybee SM (2010) Establishing species and species boundaries in *Sabellastarte* Krøyer, 1856 (Annelida: Sabellidae): an integrative approach. Organisms, Diversity & Evolution 10(5): 351–371. <https://doi.org/10.1007/s13127-010-0033-z>
- Capa M, Pons J, Hutchings P (2013) Cryptic diversity, intraspecific phenetic plasticity and recent geographical translocations in *Branchiomma* (Sabellidae, Annelida). Zoologica Scripta 42(6): 637–655. <https://doi.org/10.1111/zsc.12028>
- Caulley M (1915) Sur les *Terebellides* Malmgren du Siboga et les *Terébelliens* voisins. Bulletin de la Société Zoologique de France 40: 111–116.
- Dayrat B (2005) Towards integrative taxonomy. Biological Journal of the Linnean Society. Linnean Society of London 85(3): 407–417. <https://doi.org/10.1111/j.1095-8312.2005.00503.x>
- Gagaev SY (2009) *Terebellides irinae* sp. n., a new species of *Terebellides* (Polychaeta: Terebellidae) from the Arctic basin. Russian Journal of Marine Biology 35(6): 474–478. <https://doi.org/10.1134/S1063074009060042>
- Garraffoni ARS, Lana PC (2003) Species of *Terebellides* (Polychaeta, Terebellidae, Trichobranchinae) from the Brazilian coast. Iheringia. Série Zoologia 93(4): 355–363. <https://doi.org/10.1590/S0073-47212003000400002>

- Goldstein PZ, DeSalle R (2011) Integrating DNA barcode data and taxonomic practice: Determination, discovery, and description. *BioEssays* 33(2): 135–147. <https://doi.org/10.1002/bies.201000036>
- Grosse M, Capa M, Bakken T (2021) Describing the hidden species diversity of *Chaetozone* (Annelida, Cirratulidae) in the Norwegian Sea using morphological and molecular diagnostics. *ZooKeys* 1039: 139–176. <https://doi.org/10.3897/zookeys.1039.61098>
- Halt MN, Kupriyanova EK, Cooper SJ, Rouse GW (2009) Naming species with no morphological indicators: species status of *Galeolaria caespitosa* (Annelida: Serpulidae) inferred from nuclear and mitochondrial gene sequences and morphology. *Invertebrate Systematics* 23(3): 205–222. <https://doi.org/10.1071/IS09003>
- Hartman O, Fauchald K (1971) Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic Areas. Part II. Allan Hancock Monographs in Marine Biology 6: 1–327.
- Hoang DT, Chernomor O, Von Haeseler A, Minh BQ, Vinh LS (2018) UFBoot2: Improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution* 35(2): 518–522. <https://doi.org/10.1093/molbev/msx281>
- Hutchings P, Peart R (2000) A revision of the Australian Trichobranchidae (Polychaeta). *Invertebrate Systematics* 14(2): 225–272. <https://doi.org/10.1071/IT98005>
- Jirkov IA (1989) Bottom fauna of the USSR. Polychaeta. Moscow State University Press, Moscow, 141 pp. [English translation from Russian]
- Jirkov IA, Leontovich MK (2013) Identification keys for Terebellomorpha (Polychaeta) of the eastern Atlantic and the North Polar Basin. *Invertebrate Zoology* 10(1): 217–243. <https://doi.org/10.15298/invertzool.10.2.02>
- Kara J, Molina-Acevedo IC, Zanol J, Simon C, Idris I (2020) Morphological and molecular systematic review of *Marphysa* Quatrefages, 1865 (Annelida: Eunicidae) species from South Africa. *PeerJ* 8: e10076. <https://doi.org/10.7717/peerj.10076>
- Katoh K, Misawa K, Kuma KI, Miyata T (2002) MAFFT: A novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* 30(14): 3059–3066. <https://doi.org/10.1093/nar/gkf436>
- Lavesque N, Hutchings P, Daffe G, Nygren A, Londoño-Mesa MH (2019) A revision of the French Trichobranchidae (Polychaeta), with descriptions of nine new species. *Zootaxa* 4664(2): 151–190. <https://doi.org/10.11646/zootaxa.4664.2.1>
- Malm AW (1874) Annulater i hafvet utmed Sverges vestkust och omkring Göteborg. Kongelige Vetenskaps och Viterrhets Samhällets Göteborgs Handlingar 14: 71–105.
- McIntosh WC (1885) Report on the Annelida Polychaeta collected by HMS Challenger during the years 1873–76. Report of the Scientific Results of the Voyage of HMS Challenger 1873–76(12): 1–554.
- Müller OF (1776) Zoologiae Danicae prodromus, seu, Animalium Daniae et Norvegiae indigenarum characteres, nomina, et synonyma imprimis popularium. Impensis auctoris. <https://doi.org/10.5962/bhl.title.63795>
- Nguyen LT, Schmidt HA, Von Haeseler A, Minh BQ (2015) IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* 32(1): 268–274. <https://doi.org/10.1093/molbev/msu300>

- Nygren A, Pleijel F (2011) From one to ten in a single stroke—resolving the European *Eumida sanguinea* (Phyllodoceidae, Annelida) species complex. *Molecular Phylogenetics and Evolution* 58(1): 132–141. <https://doi.org/10.1016/j.ympev.2010.10.010>
- Nygren A, Parapar J, Pons J, Meißner K, Bakken T, Kongsrud JA, Oug E, Gaeva D, Sikorski A, Johansen RA, Hutchings PA, Lavesque N, Capa M (2018) A mega-cryptic species complex hidden among one of the most common annelids in the North-East Atlantic. *PLoS ONE* 13(6): e0198356. <https://doi.org/10.1371/journal.pone.0198356>
- Pante E, Schoelinc C, Puillandre N (2015) From integrative taxonomy to species description: One step beyond. *Systematic Biology* 64(1): 152–160. <https://doi.org/10.1093/sysbio/syu083>
- Parapar J, Hutchings P (2014) Redescription of *Terebellides stroemii* (Polychaeta, Trichobranchidae) and designation of a neotype. *Journal of the Marine Biological Association of the United Kingdom* 95(2): 323–337. <https://doi.org/10.1017/S0025315414000903>
- Parapar J, Moreira J, Helgason GV (2011) Taxonomy and distribution of *Terebellides* (Polychaeta, Trichobranchidae) in Icelandic waters, with the description of a new species. *Zootaxa* 2983(1): 1–20. <https://doi.org/10.11646/zootaxa.2983.1.1>
- Parapar J, Moreira J, O'Reilly M (2016a) A new species of *Terebellides* (Polychaeta: Trichobranchidae) from Scottish waters with an insight into branchial morphology. *Marine Biodiversity* 46(1): 211–225. <https://doi.org/10.1007/s12526-015-0353-5>
- Parapar J, Moreira J, Martin D (2016b) On the diversity of the SE Indo-Pacific species of *Terebellides* (Annelida; Trichobranchidae), with the description of a new species. *PeerJ* 4: e2313. <https://doi.org/10.7717/peerj.2313>
- Parapar J, Moreira J, Gil J, Martin D (2016c) A new species of the genus *Terebellides* (Polychaeta, Trichobranchidae) from the Iranian coast. *Zootaxa* 4117(3): 321–340. <https://doi.org/10.11646/zootaxa.4117.3.2>
- Parapar J, Capa M, Nygren A, Moreira J (2020a) To name but a few: Descriptions of five new species of *Terebellides* (Annelida, Trichobranchidae) from the North-East Atlantic. *ZooKeys* 992: 1–58. <https://doi.org/10.3897/zookeys.992.55977>
- Parapar J, Martin D, Moreira J (2020b) On the diversity of *Terebellides* (Annelida, Trichobranchidae) in West Africa, seven new species and the redescription of *T. africana* Augener, 1918 stat. prom. *Zootaxa* 4771(1): 1–61. <https://doi.org/10.11646/zootaxa.4771.1.1>
- Renner SS (2016) A return to Linnaeus's focus on diagnosis, not description: The use of DNA characters in the formal naming of species. *Systematic Biology* 65(6): 1085–1095. <https://doi.org/10.1093/sysbio/syw032>
- Sars M (1835) Beskrivelser og iagttagelser over nogle mærkelige eller nye i havet ved den bergenske kyst levende dyr af polypernes, acalaphernes, radiaternes, annelidernes, og molluskernes classer: med en kort oversigt over de hidtil af forfatteren sammesteds fundne arter og deres forekommen. Dahl. <https://doi.org/10.5962/bhl.title.13017>
- Schlick-Steiner BC, Steiner FM, Seifert B, Stauffer C, Christian E, Crozier RH (2010) Integrative taxonomy: A multisource approach to exploring biodiversity. *Annual Review of Entomology* 55(1): 421–438. <https://doi.org/10.1146/annurev-ento-112408-085432>
- Schüller M, Hutchings PA (2010) New insights in the taxonomy of Trichobranchidae (Polychaeta) with the description of a new *Terebellides* from Australia. *Zootaxa* 2395(1): 1–16. <https://doi.org/10.11646/zootaxa.2395.1.1>

- Schüller M, Hutchings PA (2013) New species of *Terebellides* (Polychaeta: Trichobranchidae) from the deep Southern Ocean, with a key to all described species. *Zootaxa* 3619(1): 1–45. <https://doi.org/10.11646/zootaxa.3619.1.1>
- Teixeira MA, Vieira PE, Pleijel F, Sampieri BR, Ravara A, Costa FO, Nygren A (2020) Molecular and morphometric analyses identify new lineages within a large *Eumida* (Annelida) species complex. *Zoologica Scripta* 49(2): 222–235. <https://doi.org/10.1111/zsc.12397>
- Williams SJ (1984) The status of *Terebellides stroemi* (Polychaeta; Trichobranchidae) as a cosmopolitan species, based on a worldwide morphological survey, including description of new species. In: Hutchings PA (Ed.) *Proceedings of the First International Polychaete Conference, Sydney, Australia, 1984*. The Linnean Society of New South Wales, 118–142.

Supplementary material 1

Abiotic data and more information of the material used

Authors: María Barroso, Juan Moreira, María Capa, Arne Nygren, Julio Parapar

Data type: Abiotic data

Explanation note: The table shows the abiotic data and more information of the material used: Specimen voucher, Site, Geographic area, Locality, Latitude, Longitude, Depth, Collecting date, Habitat, Remarks and figures.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zookeys.1132.91244.suppl1>

Supplementary material 2

List of COI sequences considered in present study

Authors: María Barroso, Juan Moreira, María Capa, Arne Nygren, Julio Parapar

Data type: Molecular data

Explanation note: List of COI sequences considered in present study (Group B, C and D), museum vouchers and GenBank accession numbers.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zookeys.1132.91244.suppl2>

Japanese species of *Ormosia* Rondani (Diptera, Limoniidae): revision of the subgenera *Oreophila* Lackschewitz and *Parormosia* Alexander

Daichi Kato¹, Kozo Watanabe², Levente-Péter Kolcsár²

1 Echigo-Matsunoyama Museum of Natural Science, 'Kyororo', 1712-2 Matsunoyama-Matsuguchi, Tōkamachi, 942-1411, Japan **2** Center for Marine Environmental Studies (CMES), Ehime University, Matsuyama, Ehime 790-8577, Japan

Corresponding author: Levente-Péter Kolcsár (kolcsar.peter@gmail.com)

Academic editor: Kurt Jordaens | Received 30 April 2022 | Accepted 7 November 2022 | Published 29 November 2022

<https://zoobank.org/46E68453-A2FA-4D22-A0D7-4509DFFB7C1B>

Citation: Kato D, Watanabe K, Kolcsár L-P (2022) Japanese species of *Ormosia* Rondani (Diptera, Limoniidae): revision of the subgenera *Oreophila* Lackschewitz and *Parormosia* Alexander. ZooKeys 1132: 127–162. <https://doi.org/10.3897/zookeys.1132.86022>

Abstract

Japanese species of the subgenera *Oreophila* Lackschewitz and *Parormosia* Alexander of the genus *Ormosia* Rondani (Limoniidae) are revised. Two new species *Ormosia* (*Oreophila*) *komazawai* Kato & Kolcsár, **sp. nov.** and *Ormosia* (*Parormosia*) *phalana* Kato & Kolcsár, **sp. nov.** are described. The identities of all Japanese species of the two subgenera are clarified and redescribed with images of habitus and wings, and drawings of male and female terminalia. The first DNA barcode sequences of the species *Ormosia* (*Parormosia*) *diversipes* Alexander and *Ormosia* (*Parormosia*) *phalana* Kato & Kolcsár, **sp. nov.** are also provided. A key to, and distribution maps of, the Japanese species are provided.

Keywords

Crane flies, new species, subapterous, taxonomy, terminalia, Tipuloidea

Introduction

Ormosia Rondani (1856) is a relatively large genus of the subfamily Chioneinae (family Limoniidae) and includes 224 species worldwide (Oosterbroek 2022). Twelve fossil species of the genus have been described from the Baltic amber (Podénas 1999). The adults are characterized by wing cells covered with hair-like setae and well-developed

meron separating mid and hind coxae. Similar morphological characters occur in genera *Amphineurus* Skuse, *Rhypholophus* Kolenati, *Scleroprocta* Edwards, *Molophilus* (*Trichomolophilus*) Alexander, and *Trichotrimicra* Alexander, but *Ormosia* is distinguished from these by the following combination of characters: wing vein M_3 joining vein M_{1+2} or vein M_4 beyond cord; male terminalia rotated by 90–180 degrees; clasper of gonostylus not dilated or bifid on distal part; aedeagus simple, not bifid at tip. The genus is divided into four subgenera: *Neserioptera* Alexander (2 spp., Afrotropical); *Oreophila* Lackschewitz (17 spp., Nearctic, Palaearctic and Oriental); *Ormosia* (182 spp., Nearctic, Palaearctic and Oriental); *Parormosia* Alexander (23 spp., Eastern Palaearctic, Nearctic and Oriental).

Immature stages of *Ormosia* spp. are known to inhabit wet soil or moist dead woods (Alexander 1920; Brinkmann 1991; Krivosheina and Krivosheina 2011), but our knowledge on the biology of immature stages is still sporadic.

Twenty-two species of *Ormosia* are reported from Japan, represented by two species of each of the subgenera *Oreophila* and *Parormosia* and by 18 species belong to the subgenus *Ormosia* s. s. (Nakamura 2014; Oosterbroek 2022).

As a first step in clarifying the taxonomy of the genus *Ormosia* in Japan, species of the subgenera *Oreophila* and *Parormosia* are revised in this paper. In addition to re-describing the four already known species, viz. *Ormosia* (*Oreophila*) *confluenta* Alexander, 1922, *Ormosia* (*Oreophila*) *sootryeni* (Lackschewitz, 1935), *Ormosia* (*Parormosia*) *diversipes* Alexander, 1919, and *Ormosia* (*Parormosia*) *nippoalpina* Alexander, 1941, two new species are described. Images of the habitus and wings, drawings of the male terminalia, and a key to and distribution maps of the Japanese species are provided. DNA barcode sequences of the species *Ormosia* (*Parormosia*) *diversipes* Alexander and *Ormosia* (*Parormosia*) *phalara* Kato & Kolcsár, sp. nov. are uploaded to The Barcode of Life Data System (BOLD) (Ratnasingham and Hebert 2007).

Materials and methods

Specimens were collected using insect nets, Malaise traps or at light traps and preserved in 70% or 90% ethanol or pinned. Overall descriptions of the species were based on the observations through a Leica S APO and Zeiss Stemi 508 stereomicroscopes. Male terminalia were put in vials filled with a solution of 10% KOH and the vials were heated in hot water for several minutes. Then the terminalia were rinsed in a solution of 70% ethanol with 3% acetic acid for neutralization, transferred to glycerol for examination and drawing, and preserved in genitalia tubes filled with glycerol. The genitalia tubes were pinned below the body remains. Drawings were made using the stereomicroscope equipped with a grid eyepiece micrometer. Terminology followed Cumming and Wood (2017) for general description, de Jong (2017) for wing venation, Ribeiro (2008) for male terminalia, and Starý and Brodo (2009) for female terminalia. General distributions of species were referred to Catalogue of the Craneflies of

the World (Oosterbroek 2022). For the rotated male terminalia in *Ormosia*, directions as “dorsal” and “ventral” are used correspondingly to the tergal and sternal positions.

Specimens from the following depositories were examined:

- BLKU** Biosystematics Laboratory, Kyushu University, Japan;
CKLP Private collection of Levente-Péter Kolcsár;
CMK Komazawa's Private Collection, Asahikawa City, Hokkaido, Japan;
EUMJ Ehime University Museum, Matsuyama, Japan;
USNM National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

Mitochondrial DNA was extracted using DNeasy Blood & Tissue kits (Qiagen GmbH, Hilden, Germany). The 658 bp fragment of COI gene was amplified using LCO-1490 and HCO-2198 primers (Folmer et al. 1994). The PCR products were sequenced by Eurofins Operon (Tokyo, Japan). Forward and reverse reads were assembled using CodonCode Aligner v 3.5 (Codon Code Corporation, Dedham, USA). Consensus barcode sequences were submitted to BoldSystems (<http://www.boldsystems.org>).

Abbreviations

- ea** ejaculatory apodeme;
ad aedeagus;
as aedeagal sheath;
cg clasper of gonostylus;
cr cercus;
dca dorsal arm of clasper of gonostylus;
hv hypogynial valve;
ib interbase;
ga gonocoxal apodeme;
gc gonocoxite;
gf genital fork;
go genital opening;
lag lateral arm of genital fork;
lg lobe of gonostylus;
ml mesal-apical lobe of interbase;
pm paramere;
sd spermathecal duct;
sp sperm pump;
s sternite;
t tergite;
vca ventral arm of clasper of gonostylus.

Results

Taxonomic treatment

Genus *Ormosia* Rondani, 1856

Type species. *Erioptera nodulosa* Macquart, 1826 (Macquart 1826) by original designation.

Subgenus *Oreophila* Lackschewitz, 1935

Type species. *Rypholophus bergrothi* Strobl, 1895 (Strobl 1895) by original designation.

Note. This subgenus includes 17 species worldwide, prior to this article (7 Palaearctic, 7 Nearctic, and 3 Oriental species) (Oosterbroek 2022).

Ormosia (*Oreophila*) *confluenta* Alexander, 1922

Figs 1A, 2–4, 5A

Ormosia confluenta in Alexander 1922: 183: original description (type locality: Japan, Honshu, Ôsaka, Mt. Minomo).

Ormosia (*Ormosia*) *confluenta* in Alexander 1953a: 71: faunistic record.

Ormosia (*Oreophila*) *confluent* in Nakamura 2002: 169: faunistic record; Nakamura 2014: 31: distribution; Oosterbroek 2022: distribution.

Type material examined. *Paratype.* JAPAN • ♀; Honshu, Mt. Minomo; 4 May 1921; K. Takeuchi leg.; USNM.

Non-type material examined. JAPAN • 2 ♂; Honshu, Nagano, Ueda-shi, Sanada-machi-Osa, Kakuma Valley; 36.45378°N, 138.36592°E; alt. 1050 m; 16 May 2012; D. Kato leg.; BLKU. • 2 ♂; Honshu, Tokyo, near Tokyo, Mt. Mitake; 10 May 1931; B. Oda leg.; USNM. • 1 ♂; Honshu, Okayama, Maniwa-shi, Hiruzen-Shimotokuyama; 35.32931°N, 133.59725°E; alt. 780 m; 1 May 2016; D. Kato leg.; BLKU. • 1 ♀; Honshu, Hiroshima, Akiôta-chô, Yokogô; 34.59419°N, 132.14497°E; alt. 890 m; 18 May 2015; D. Kato leg.; BLKU. • 1 ♂; Shikoku, Tokushima, Mt. Tsurugi; alt. 1400–1950 m; 31 May 1950; Issiki and Ito leg.; USNM. • 1 ♂; Shikoku, Tokushima, Miyoshi-shi, Higashiiya-Ochiai, near Matsuogawa Dam; 33.96478°N, 133.93908°E; alt. 900 m; 15 May 2015; • 1 ♂, 1 ♀; same locality; 30 Apr. 2016; D. Kato leg., BLKU. • 6 ♂, 1 ♀; Shikoku, Tokushima, Miyoshi-shi, Higashiiya-Sugeoi, near Nagoro Dam; 33.85182°N, 134.0234°E; alt. 920 m; 29 Apr. 2016; • 3 ♂; same locality; 30 Apr. 2016; D. Kato leg. BLKU. • 4 ♂, 1 ♀; Shikoku, Ehime, Kumakogen, River Myogadani, springs; 33.56701°N, 132.9344 °E; 1420 m; 8 May 2022; L.-P. Kolcsár leg.; CKLP. • 1 ♂; Kyushu, Saga, Karatsu-shi, Kyuragi-Hirano, Mt. Sakurei-zan; 33.35701°N, 130.07038°E; alt. 860 m; 26 Apr. 2015; D. Kato leg.; BLKU.



Figure 1. Habitus of male **A** *Ormosia (Oreophila) confluenta* Alexander, 1922 **B** *Ormosia (Oreophila) komazawai* Kato & Kolcsár, sp. nov. Scale bars: 2 mm.

Diagnosis. General coloration yellow to pale brown (Fig. 1A). Vertex often pale brownish grey. Antenna dark brown except scape. Wing yellowish tinged, unpatterned. Legs distal to mid-tibiae gradually becoming dark brown towards tips. Male terminalia: tergite 9 bearing pair of triangular lobes at caudal margin. Gonocoxite slightly produced beyond base of clasper of gonostylus. Clasper of gonostylus wider apically, $3/4$ length of lobe of gonostylus, distal part $2\times$ as wide as that of lobe of gonostylus. Interbases fused medially into roundish sac-like plate, without mesal-apical lobe. Female terminalia with cercus almost straight, slightly upcurved on distal part. Genital frame with lateral arm of genital fork roughly triangular, situated at posterior $1/3$ of genital fork, with finger-shaped lobe on posterior end. Sternite 9 very small, fan-shaped.

Redescription. Male. Body length 2.9–4.2 mm, wing length 4.1–5.9 mm.

Head: covered with yellow to brown setae. Vertex dusky yellow to pale brownish grey, paler grey on anterior part, often widely dark brown on center of posterior part. Eyes small and widely separated, $\sim 1/2$ as wide as narrowest point of vertex, $\sim 1/3$ length of head including rostrum in dorsal view. Rostrum dusky yellow to pale brown, $\sim 1/2$ length of eye in lateral view. Palpus 5-segmented, $2/3$ length of head, dusky yellow on basal two segments, dark brown on succeeding segments, palpomere 1 small, globular, palpomere 2 cylindrical, palpomeres 3–5 globular. Labellum dark brown. Antenna 15 to 16-segmented, relatively short, $\sim 2\times$ length of head; scape dusky yellow to pale brown, $2\times$ as long as wide; pedicel dark brown, oval, $2/3$ length of scape; flagellomeres dark brown,

barrel-shaped, gradually decreasing in size toward apical segment; each flagellomere with ca. six verticils, longest one except in apical segment $\sim 1.5\times$ as long as each segment.

Thorax: covered with yellow setae. Antepnotum dusky yellow to pale brown; postpronotum pale yellow. Mesonotum subnitidous, pale brown to brown, lateral margin yellow, postero-outer corner of scutal lobe often yellow. Scutellum or mediotergite sometimes yellowish. Prescutal pit indistinctly present, oval to bacilliform. Tuberculate pit indistinctly present, situated slightly anterior to level of prescutal pit. Pleuron dusky yellow to yellow. Wing (Fig. 2) yellowish tinged, narrow, $3.5\text{--}4\times$ as long as wide; stigma absent; Sc ending between level of forks of Rs and R_{2+3+4} ; crossvein sc-r indistinct or absent, situated on level of basal $1/3$ of Rs if present; R_{2+3+4} $1/7\text{--}1/4$ length of R_3 ; R_2 situated between fork of R_{2+3+4} and length of itself distal to it; M_4 $1\text{--}1.5\times$ as long as M_{3+4} ; wing margin between tips of CuP and A_1 $1.3\text{--}2\times$ as long as that between tips of CuP and CuA; A_1 almost straight. Halter yellow, $\sim 2/3$ length of thorax. Legs yellow on coxae to femora; tibiae yellow basally, gradually turning to dark brown toward tips; tarsi dark brown (Fig. 1A).

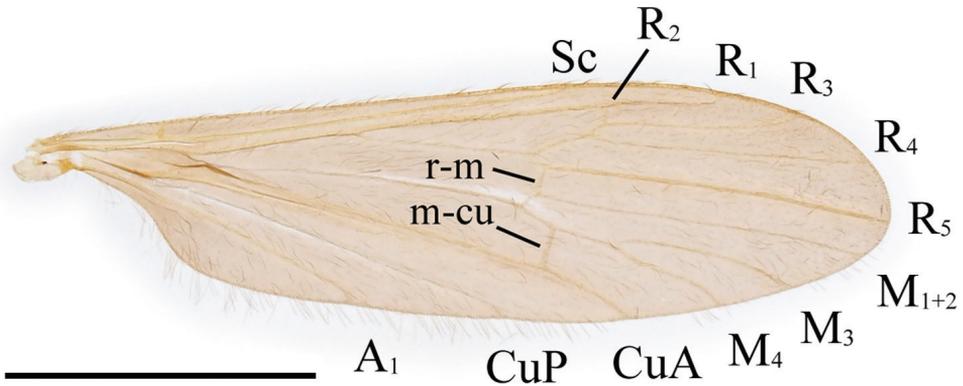


Figure 2. Wing of *Ormosia (Oreophila) confluenta* Alexander, 1922. Scale bar: 2 mm.

Abdomen: yellow to yellowish ochreous, densely covered with yellow setae.

Male terminalia (Fig. 3): Tergite 9 with pair of triangular lobes at caudal margin, $\sim 1/3$ length of middle of tergite 9; anterior margin of tergite 9 deeply and widely notched; tergite 9 slightly wider than long including caudal lobe (Fig. 3A). Sternite 9 almost straight at caudal margin (Fig. 3B). Gonocoxite almost same width in whole length, ca. as long as tergite 9, posteroventral margin slightly produced beyond base of clasper of gonostylus (Fig. 3A). Gonocoxal apodeme short, connected to anterolateral part of interbase (Fig. 3D). Clasper of gonostylus scabrous, darkened apically, $3/4$ length of lobe of gonostylus, gradually wide distally, rounded at tip, distal part $2\times$ as wide as that of lobe of gonostylus in apical view (Fig. 3C). Lobe of gonostylus long finger-shaped, $\sim 1/2$ length of gonocoxite, slightly curved, distal part flattened in apical view (Fig. 3C). Interbases fused medially into roundish sac-like plate, ca. as long as wide in dorsal view, posterior margin slightly concave, anterolateral part with short

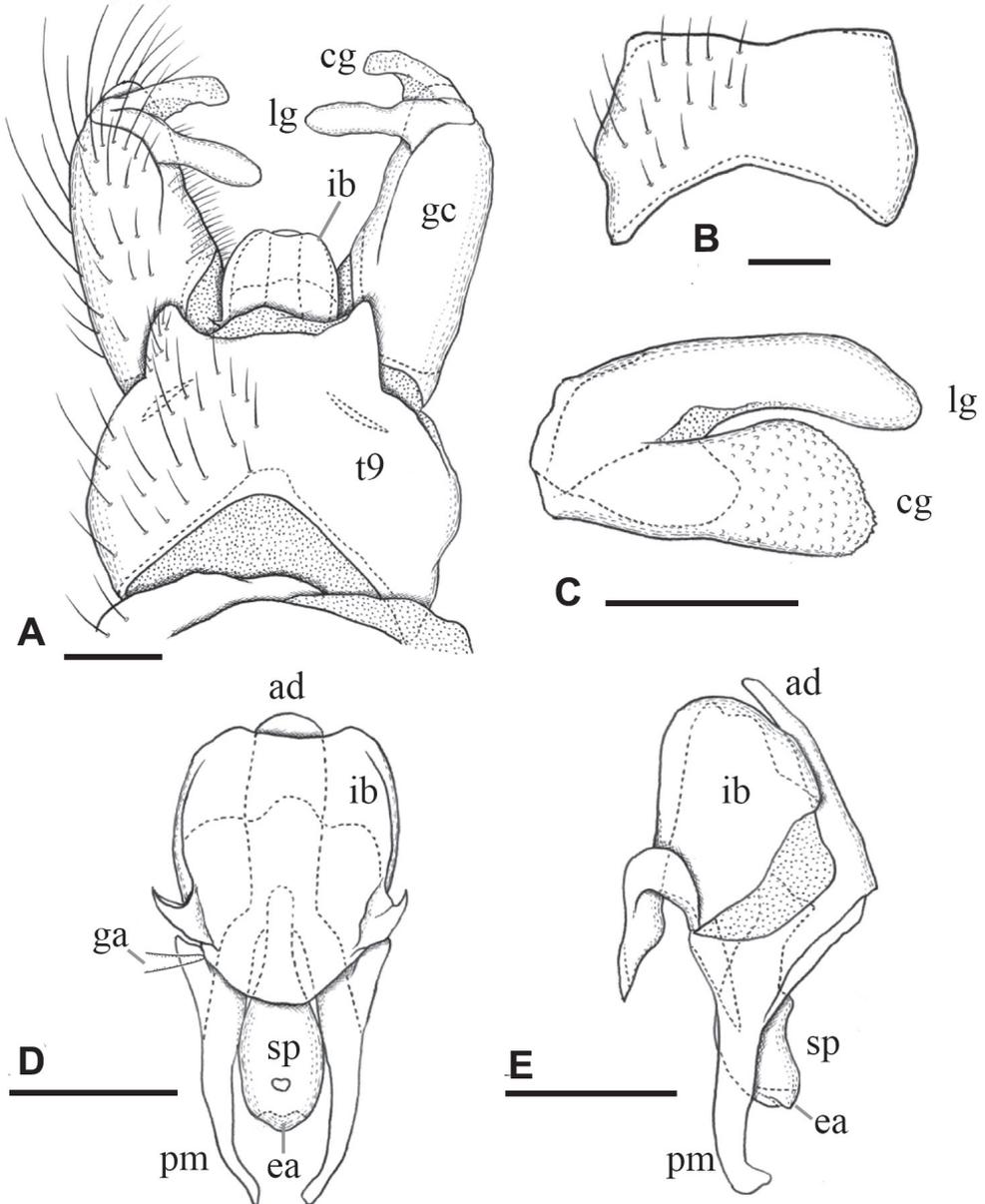


Figure 3. Male terminalia of *Ormosia* (*Oreophila*) *confluenta* Alexander, 1922 **A** dorsal view **B** sternite 9, ventral view **C** gonostylus, outer surface **D** aedeagal complex, dorsal view (left gonocoxal apodeme omitted) **E** aedeagal complex, lateral view (left = dorsal). Scale bars: 0.1 mm.

arm (Fig. 3D). Paramere roughly blade-shaped, ca. as long as interbase, anterior end curved inward (Fig. 3D). Aedeagus dorso-ventrally flattened, ~ 1/3 width of interbase, tip slightly beyond apex of interbase (Fig. 3D). Sperm pump long oval, anterior end

reaching at anterior 1/3 of paramere (Fig. 3D, E). Ejaculatory apodeme poorly developed (Fig. 3D, E).

Female. Body length 5.0–6.2 mm, wing length 5.6–6.7 mm. Generally resembling male.

Female terminalia (Fig. 4): yellow to yellowish ochreous, cercus and hypogynial valve amber-colored. Tergites 8 and 9 fused. Cercus almost straight, slightly upcurved on distal part, 1.5× as long as tergite 10; hypogynial valve ~ 1.7× as long as sternite 8, basal part distinctly wider than that of cercus, gradually narrowed on distal 1/2 toward tip, tip acute, ending near level of middle of cercus (Fig. 4A). Genital frame with genital fork, constricted at anterior 1/3, roughly heart-shaped on anterior end; lateral arm of genital fork roughly triangular distally, situated at anterior 2/3 of genital fork, with small finger-shaped lobe at posterior end; sternite 9 very small, narrower than posterior end of genital fork, fan-shaped distally, largely desclerotized on middle of posterior part. Three spermathecal ducts present, middle one very wide; spermathecae indistinct (Fig. 4B).

Distribution. Japan (Honshu, Shikoku, and Kyushu) (Fig. 5A), Russia (Far East), and Kuril Is.

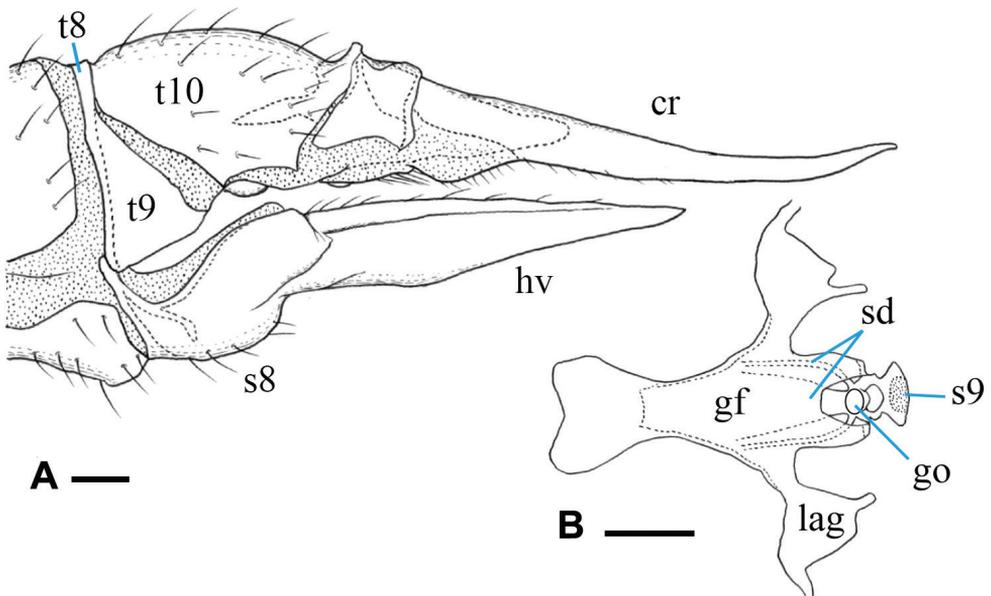


Figure 4. Female terminalia of *Ormosia (Oreophila) confluenta* Alexander, 1922 **A** lateral view **B** genital frame, ventral view (left = anterior). Scale bars: 0.1 mm.

Remarks. This species resembles a Nearctic species, *Ormosia (Oreophila) flaveola* (Coquillett, 1900) (Coquillett 1900), and an Eastern Palearctic species known from North Korea and China, *Ormosia (Oreophila) yankovskyi* Alexander, 1940 (Alexander 1940a), but is differentiated from them by the following characters: femora entirely yellow (yellow basally with darker apical parts in *Ormosia (Oreophila) flaveola* and *Ormosia (Oreophila) yankovskyi*).

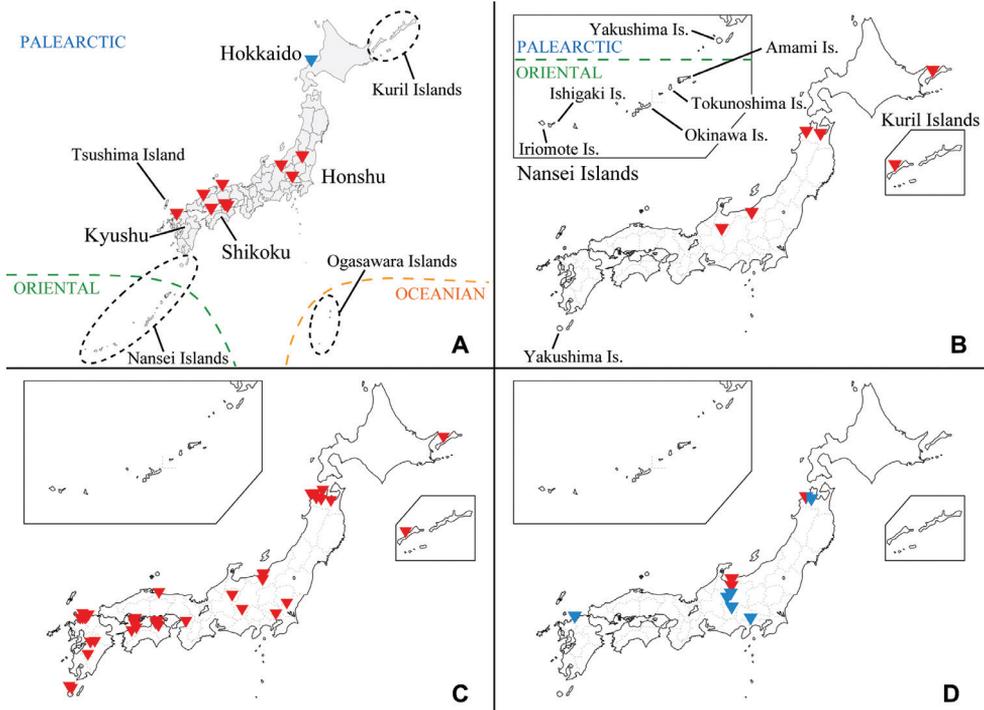


Figure 5. Distribution map of Japanese species of *Ormosia* (*Oreophila*) and *Ormosia* (*Parormosia*). **A** *Ormosia* (*Oreophila*) *confluenta* Alexander, 1922 (red), *Ormosia* (*Oreophila*) *komazawai* Kato & Kolcsár, sp. nov. (blue) **B** *Ormosia* (*Oreophila*) *sootryeni* Lackschewitz, 1935 **C** *Ormosia* (*Parormosia*) *diversipes* Alexander, 1919 **D** *Ormosia* (*Parormosia*) *nippoalpina* Alexander, 1941 (red), *Ormosia* (*Parormosia*) *phalara* Kato & Kolcsár, sp. nov. (blue).

***Ormosia* (*Oreophila*) *komazawai* Kato & Kolcsár, sp. nov.**

<https://zoobank.org/60D987FD-CE30-4CC5-A590-638024C82CA9>

Figs 1B, 5A, 6, 7

Type material examined. Holotype. ♂, pinned. Original label: “Hokkaido, Kucchan-chô-Iwaoto, tributary of Iou-gawa River; alt. 770 m; 42.88333°N, 140.65227°E; 6 Jul. 2015; M. Komazawa leg.” BLKU. “HOLOTYPE *Ormosia* (*Oreophila*) *komazawai* Kato & Kolcsár, sp. nov. [red label]”; BLKU.

Paratype. JAPAN: [Hokkaido] • 2 ♂; same data as holotype • 2 ♂; same data as holotype except 5 Jul. 2016, BLKU • 1 ♂; same data as previous, except CKLP. • 1 ♂; same data, except 2 July 2022; CMK; M. Komazawa leg.; • 3 ♂ same data as previous, except CKLP; • 6 ♂ same data as previous, except BLKU.

Diagnosis. General coloration yellow (Fig. 1B, 6). Vertex brown medially. Palpus 1-segmented. Antenna often brown on flagellum, very long, 1–1.4× as long as body in male. Wing reduced, ~ 2/3 length of thorax. Legs ochreous, yellowish proximal to basal parts of femora. Male terminalia: tergite 9 bearing pair of small triangular lobes at caudal margin. Gonocoxite distinctly produced beyond base of clasper of gonostylus.



Figure 6. Male *Ormosia (Oreophila) komazawai* Kato & Kolcsár, sp. nov. **A** habitus, living specimen **B** habitus, freshly killed specimen.

Clasper of gonostylus slightly shorter than lobe of gonostylus, almost same width in whole length, ca. as wide as lobe of gonostylus. Interbases fused medially into roundish sac-like plate, without mesal-apical lobe. Female unknown.

Description. Male. Body length 1.8–2.2 mm, wing length 0.6 mm.

Head: covered with yellow to brown setae. Vertex yellow, widely brown along medial longitudinal line (Fig. 6A), anterior part of vertex roundly convex (Figs 1B, 6B). Eyes small and widely separated, $1/2$ as wide as narrowest point of vertex, $\sim 1/3$ length of head including rostrum in dorsal view. Rostrum yellow, small, $\sim 1/4$ length of eye in lateral view. Palpus yellow, 1-segmented, roughly bacilliform, dilated distally, $1/4$ length of head. Labellum yellow. Antenna very long, $1\text{--}1.4\times$ as long as body length (Fig. 6), 15-segmented; scape yellow, $1.5\text{--}2\times$ as long as wide; pedicel yellow, oval, $1/2\text{--}2/3$ length of scape; flagellomeres yellow to brown, slender cylindrical, each segment as long as scape + pedicel or slightly longer, distal segments shorter, apical segment $1/2\text{--}2/3$ length of flagellomere 1; each flagellomere covered with abundant sensilla, and with 1–3 verticils present only on basal two flagellomeres, at most $1/5$ as long as each segment.

Thorax: covered with yellow setae. Anteprepronotum yellow, postprepronotum whitish. Mesonotum yellow, dorsoventrally flattened. Prescutal and tuberculate pits indistinct. Pleuron yellow. Wing greatly reduced, ~ 0.6 mm, $5\text{--}6\times$ as long as wide, $\sim 2/3$ length of thorax (Fig. 6B), dusky yellow, paler on basal part, covered with yellow setae. Veins vestigial except one stout vein, probably corresponding to vein R. Halter very slender, weakly dilated on knob, $\sim 2/3$ length of thorax. Legs with coxae and trochanters yellow, coxae relatively larger than those of non-flightless species; femora ochreous, basal parts more yellowish toward bases; tibiae and tarsi ochreous, sometimes slightly darker on distal one or two segments of tarsi (Figs 1B, 6B).

Abdomen: yellow (Fig. 1B), pale brown on living and freshly killed specimens (Fig. 6), densely covered with yellow setae.

Male terminalia (Fig. 7): Tergite 9 with pair of small triangular lobe at caudal margin, less than 1/4 length of middle of tergite 9; anterior margin of tergite 9 deeply and widely notched; tergite 9 slightly wider than long including caudal lobe (Fig. 7A).

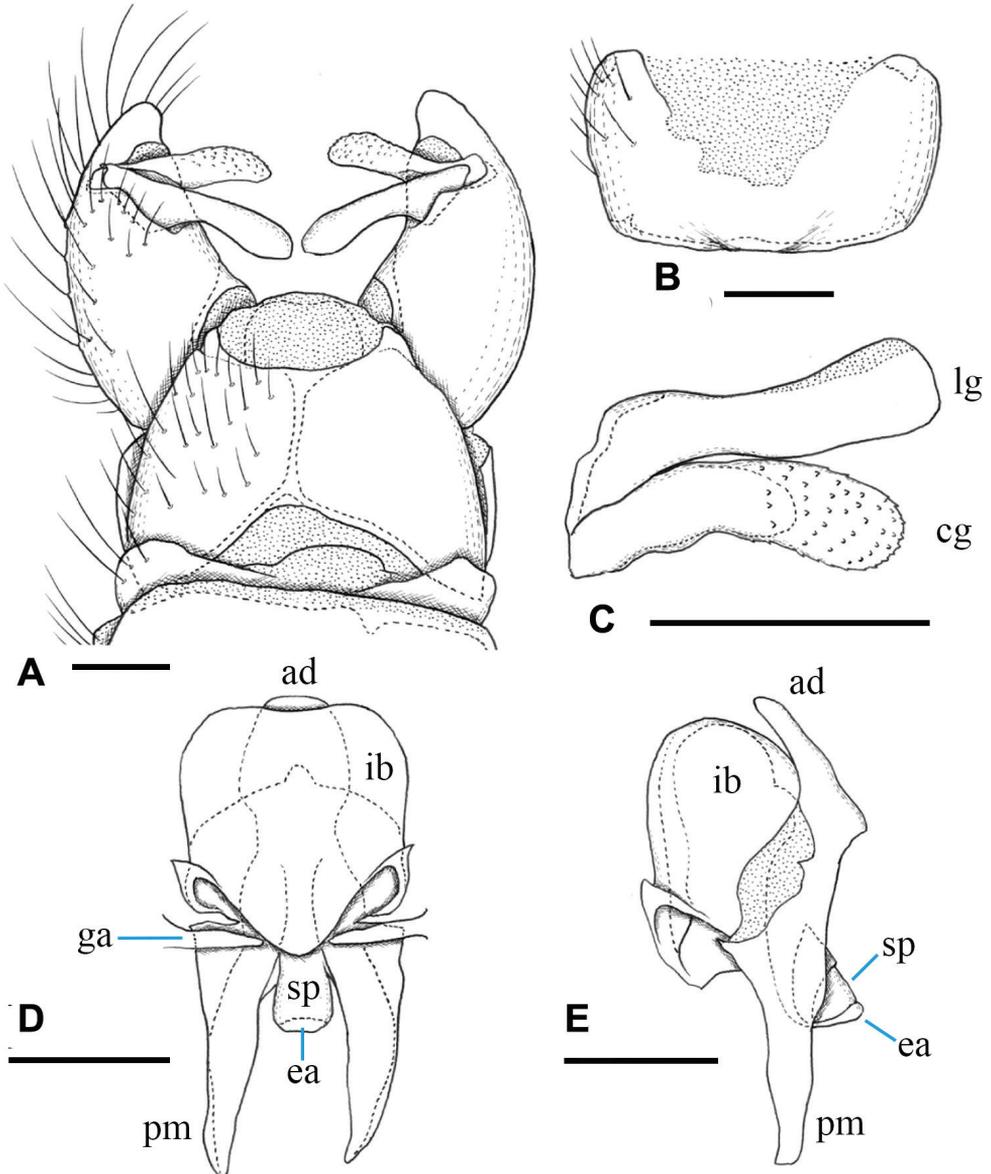


Figure 7. Male terminalia of *Ormosia (Oreophila) komazawai* Kato & Kolcsár, sp. nov. **A** dorsal view **B** sternite 9, ventral view **C** gonostylus, outer surface **D** aedeagal complex, dorsal view **E** aedeagal complex, lateral view (left = dorsal). Scale bars: 0.1 mm.

Sternite 9 largely membranous on posteromedial part (Fig. 7B), anteromedial part convex ventrally in lateral view. Gonocoxite gradually narrowing towards tip, slightly longer than tergite 9, posteroventral margin distinctly and roundly produced beyond base of clasper of gonostylus, produced part $\sim 1/2$ length of clasper of gonostylus (Fig. 7A). Gonocoxal apodeme short, connected to anterolateral part of interbase (Fig. 7D). Clasper of gonostylus dark and scabrous, slightly shorter than lobe of gonostylus, almost same width in whole length, rounded at tip, weakly curved dorsally on distal part, ca. as wide as lobe of gonostylus in apical view (Fig. 7C). Lobe of gonostylus long finger-shaped, slightly curved, $\sim 1/2$ length of gonocoxite, distal part flattened (Fig. 7C). Interbases fused medially into roundish sac-like plate, ca. as long as wide in dorsal view, posterior margin almost straight or slightly concave, anterolateral part with short arm (Fig. 7D). Paramere roughly blade-shaped, ca. as long as interbase (Fig. 7D, E). Aedeagus dorsoventrally flattened, $\sim 1/3$ width of sac-like interbase or slightly wider, weakly constricted near middle in dorsal view, tip slightly beyond apex of interbase (Fig. 7D). Sperm pump angular in dorsal view (Fig. 7D), anterior end situated at basal $1/3$ of paramere (Fig. 7D, E). Ejaculatory apodeme poorly developed (Fig. 7D, E).

Female. Unknown.

Etymology. This spectacular and unique species is named in honor of its collector, Masaki Komazawa.

Habitat and biology. Masaki Komazawa observed specimens walking on the surface of fallen leaves or on the surface of soil just after snow melt (Fig. 6A).

Distribution. Japan (Hokkaido) (Fig. 5A).

Remarks. The subapterous male of this species is unique in the subgenus, but brachypterous female is known in a Nearctic species, *Ormosia (Oreophila) parviala* Petersen & Gelhaus, 2004 (Petersen et al. 2004). This species is similar to *Ormosia (Oreophila) confluenta* in terms of body coloration, *Ormosia (Oreophila) longicornis* Savchenko, 1980 (Savchenko 1980) from Kazakhstan in terms of long antenna reaching (almost) apex of abdomen if bent backward, and *Ormosia (Oreophila) bergrothi* (Strobl, 1895) in terms of structure of male terminalia.

Ormosia (Oreophila) sootryeni Lackschewitz, 1935

Figs 5B, 8A, 9–11

Oreophila sootryeni in Lackschewitz 1935: 8: original description (type locality: Norway, Røsvik).

Ormosia (Ormosia) ducalis in Alexander 1938: 162: original description (type locality: North Korea, Ompo).

Ormosia ducalis in Alexander 1970: 77: faunistic record.

Ormosia (Oreophila) sootryeni in Savchenko 1983: 82: faunistic records, comparison; Nakamura 2014: 32: distribution; Oosterbroek 2022: distribution.

Type material examined. *Ormosia (Oreophila) ducalis* Alexander, 1938: **Holotype** • NORTH KOREA, ♂, Ompo; alt. 170 feet; 23 May 1937; A. Yankovsky leg.; USNM.

Non-type material examined. *Ormosia ducalis* Alexander, 1938: JAPAN • 1 ♂, Hida, On-take; 15 Jul. 1958, Mishima leg.; USNM. NORTH KOREA • 1 ♂; Ompo; alt. 100 feet; 19 May 1938; A. Yankovsky leg.; USNM.

Ormosia (Oreophila) sootryeni Lackschewitz, 1935: JAPAN • 3 ♂, 1 ♀; Honshu, Aomori, Nishimeya-mura, Kawaratai, Ôkawa-rindô Path; 40.50062°N, 140.20405°E; alt. 300 m; 30 May 2014; • 2 ♂; same locality; 3 Jun. 2014; D. Kato leg.; BLKU. • 1 ♂; Honshu, Aomori, Towada-shi, Okuse, Tsutanuma-rindô Path; 40.590842°N, 140.957052°E; alt. 460 m; 5 Jul. 2014; • 1 ♂; same locality; 30 Aug. 2014; • 1 ♂; same locality; 30 Sep. 2014; D. Kato leg.; BLKU. • 1 ♀; Honshu, Nagano, Sakae-mura, Sakai, Koakazawa-gawa River; 36.85352°N, 138.66358°E; alt. 1310–1500 m; 23 Jul. 2019; • 1 ♂; same locality; 19 Sep. 2019; D. Kato leg.; BLKU.

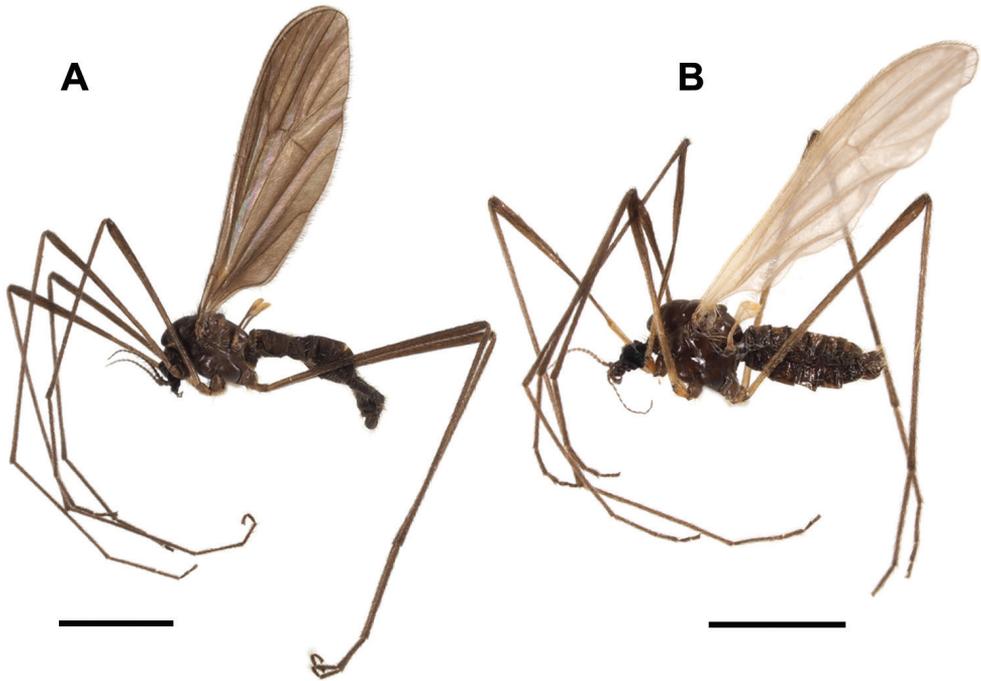


Figure 8. Habitus of male **A** *Ormosia (Oreophila) sootryeni* Lackschewitz, 1935 **B** *Ormosia (Parormosia) nipposalpina* Alexander, 1941. Scale bars: 2 mm.

Diagnosis. General coloration brownish black (Fig. 8A). Vertex often brownish grey. Antenna dark brown. Wing blackish tinged, stigmal region weakly dark. Halter yellow at base and knob. Legs entirely brownish black. Male terminalia: tergite 9 bearing of three small triangular lobes at caudal margin. Gonocoxite slightly produced beyond base of clasper of gonostylus. Clasper of gonostylus divided into two long arms, dorsal arm almost straight, strongly narrow and bent outward at tip, ventral arm slightly longer than dorsal arm, apical part strongly widened and rounded. Interbase with mesal-apical lobe long blade-shaped, curved at extreme tip, basal part of each in-

terbase fused with each other. Female terminalia with cercus stout, strongly upcurved. Hypogynial valve rounded at tip. Genital frame with lateral arm of genital fork roundish, situated at posterior end of genital fork. Sternite 9 slender, arched bridge-shaped.

Redescription. Male. Body length 3.8–5.9 mm, wing length 5.7–7.8 mm.

Head: covered with black setae. Vertex brownish black, brownish grey by pruinosity from certain angles. Eyes relatively large and widely separated, $\sim 4/5$ as wide as narrowest point of vertex, $\sim 1/2$ length of head including rostrum in dorsal view. Rostrum dark brown, $\sim 1/3$ length of eye in lateral view. Palpus dark brown, 5-segmented, $3/4$ length of head, palpomere 1 globular and small, palpomeres 2, 4, and 5 cylindrical, palpomere 3 oval. Labellum dark brown. Antenna dark brown, $\sim 3\times$ as long as head, 16-segmented; scape $2\times$ as long as wide; pedicel oval, $1/2$ length of scape; flagellomeres bacilliform, gradually slender toward apical segment; each flagellomere with ca. eight verticils, longest one except in apical segment $\sim 2.5\times$ as long as each segment.

Thorax: covered with black setae on dorsal part and partly with yellow setae on pleuron, coxae, and trochanters. Antep pronotum brownish black; postpronotum dusky yellow. Mesonotum subnitidous, brownish black, greyish ochreous by pruinosity from certain angles, weakly yellowish around humeral part. Prescutal pit black, long oval to long bacilliform. Tuberculate pit absent. Pleuron dark brown, slightly variegated with lighter brown. Wing (Fig. 9) tinged with black, stigmal region weakly dark; $3.3\text{--}3.5\times$ as long as wide; Sc ending between level of R_2 and fork of R_{2+3+4} ; crossvein sc-r distinct, situated between levels of basal $1/7\text{--}1/4$ of Rs; R_{2+3+4} $1/10$ length of R_3 or shorter; R_2 situated $1\text{--}2\times$ length of itself distal to fork of R_{2+3+4} ; M_4 $2\text{--}4\times$ as long as M_{3+4} ; wing margin between tips of CuP and A_1 $2\text{--}3\times$ as long as that between tips of CuP and CuA; A_1 almost straight. Halter dark brown, base and knob yellow, $\sim 2/3$ length of thorax. Legs brownish black (Fig. 8A).



Figure 9. Wing of *Ormosia (Oreophila) sootryeni* Lackschewitz, 1935. Scale bar: 2 mm.

Abdomen (Fig. 8A): brownish black, densely covered with black setae mainly on dorsal part and with yellow setae mainly on lateral and ventral parts.

Male terminalia (Fig. 10): Tergite 9 with three small triangular lobes at caudal margin, middle one $2\times$ longer as lateral one; lateral one $1/4$ length of middle of tergite 9 including middle lobe; anterior margin of tergite 9 widely notched; tergite 9 approximately $3\times$ wider than long including caudal lobe (Fig. 10A). Sternite 9 widely concave at middle

of posterior margin (Fig. 10B). Gonocoxite stout, 2× as long as tergite 9, posteroventral margin weakly and roundly produced beyond base of clasper of gonostylus, produced part less than 1/10 length of clasper of gonostylus (Fig. 10A). Gonocoxal apodeme short, connected to anterolateral part of interbase (Fig. 10D). Clasper of gonostylus dark

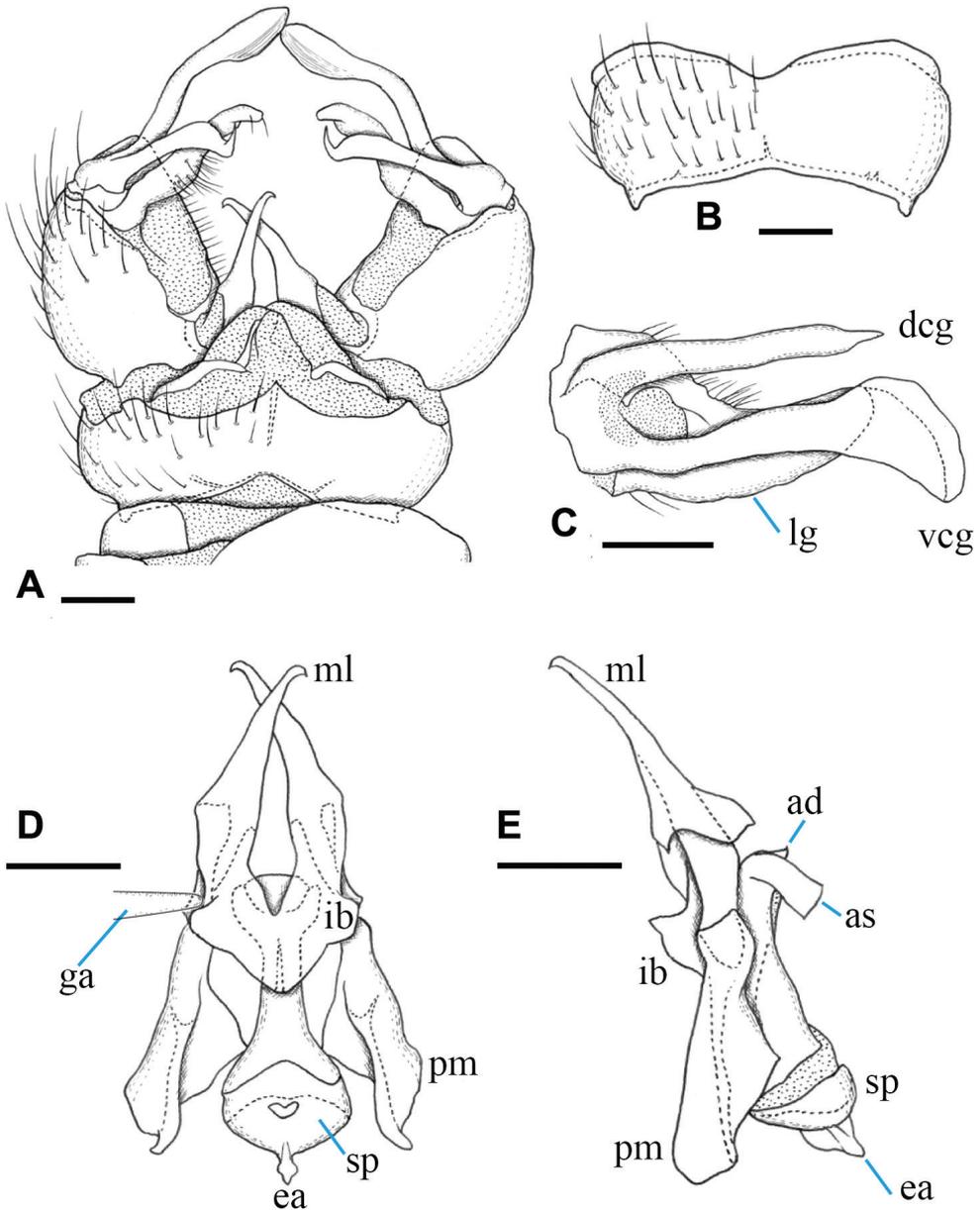


Figure 10. Male terminalia of *Ormosia* (*Oreophila*) *sootryeni* Lackschewitz, 1935 **A** dorsal view **B** sternite 9, ventral view **C** gonostylus, outer surface **D** aedeagal complex, dorsal view (left gonocoxal apodeme omitted) **E** aedeagal complex, lateral view (left = dorsal). Scale bars: 0.1 mm.

and smooth on surface, divided into two arms; dorsal arm roughly rod-shaped, almost straight in apical view, slightly shorter than gonocoxite, tip pointed, suddenly narrow and bent outward, claw-like in dorsal view; ventral arm slightly longer than gonocoxite, weakly sinuous, apical part strongly widened and rounded (Fig. 10C). Lobe of gonostylus slightly shorter than gonocoxite, flattened, gradually narrow and curved dorsally toward tip, rounded at tip, middle part 2× as wide as middle part of dorsal arm of clasper of gonostylus (Fig. 10C). Interbases with mesal-apical lobe long blade-shaped, gradually narrow distally, directed posterodorsally, curved at extreme tip, basal part fused with each other, anterolateral part roundly produced laterally (Fig. 10D). Paramere wide, roughly triangular, ca. as long as interbase (Fig. 10D). Aedeagus relatively flat, distinctly broad at tip in dorsal view (Fig. 10D), apical part ~ 1/3 width of basal part of interbase, tip slightly beyond furcation point of interbase (Fig. 10D), with short extension of aedeagal sheath directed ventrally (Fig. 10E). Sperm pump roundish in dorsal view, anterior end situated at level of anterior end of paramere (Fig. 10D). Ejaculatory apodeme developed, laterally compressed, fin-like plate, ~ 1/3 length of diameter of sperm pump (Fig. 10E).

Female. Body length 6.0–6.4 mm, wing length 7.4–8.1 mm. Generally resembling male.

Female terminalia (Fig. 11): brownish black, distal part of tergite 10 yellowish; cercus amber-colored, basal 1/2 dark; hypopygnal valve dusky yellow, base of lateral part brownish. Tergites 8 and 9 fused. Cercus stout, strongly upcurved, slightly shorter than tergite 10; hypopygnal valve ca. as long as sternite 8, finger-shaped in lateral view, rounded at tip, basal part ca. as wide as that of cercus, tip ending near level of middle of cercus (Fig. 11A). Genital frame with genital fork cross-shaped, extended laterally at posterior 1/4, weakly constricted medially, anterolateral corner of lateral extension pointed; lateral arm of genital fork roughly roundish, situated at posterior of genital fork; sternite 9 slender, arched bridge-shaped, arising from posterolateral corner of genital fork, middle part with small lobe (Fig. 11B). Two spermathecal ducts present, spermathecae indistinct.

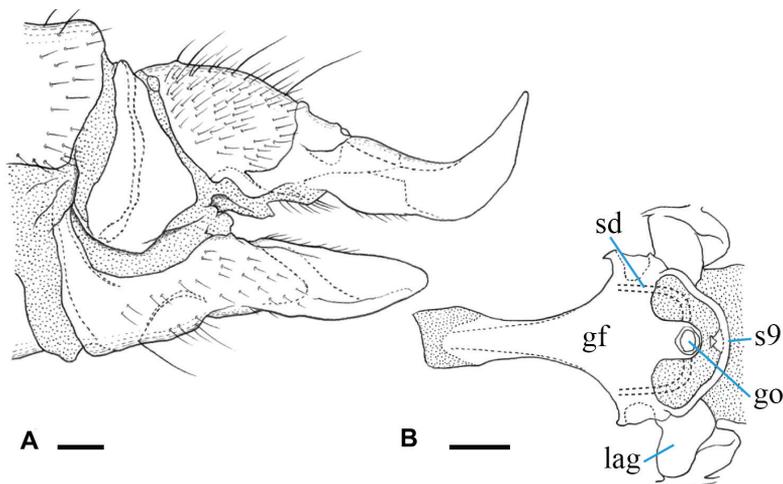


Figure 11. Female terminalia of *Ormosia (Oreophila) sootryeni* Lackschewitz, 1935 **A** lateral view **B** genital frame, ventral view (left = anterior). Scale bars: 0.1 mm.

Distribution. Japan (Honshu) (Fig. 5B), North Korea, Russia (FE), Kuril Islands, Kazakhstan (east), Finland, Norway, and Sweden.

Remarks. This species is similar to a Chinese species, *Ormosia (Oreophila) subducalis* Alexander, 1940 (Alexander 1940b), but is differentiated from it by the following characters: wing entirely blackish tinged (brownish yellow with clearer yellow base in *Ormosia (Oreophila) subducalis*); halter dark brown, base and knob yellow (orange yellow in *Ormosia (Oreophila) subducalis*).

Subgenus *Parormosia* Alexander, 1965

Type species. *Rypholophus nigripilus* Osten Sacken, 1869 (Osten Sacken 1869) by original designation.

Note. This subgenus includes 23 species, before this article (5 Palearctic, 9 Nearctic, and 9 Oriental species) (Oosterbroek 2022).

Ormosia (Parormosia) diversipes Alexander, 1919

Figs 5C, 12–15

BOLD ID: JPCOI003-22, JPCOI004-22

Ormosia diversipes in Alexander 1919: 334: original description (type locality: Japan, Honshu, Saitama, Chichibu); Alexander 1930: 508: faunistic record; Alexander 1936a: 193: comparison.

Ormosia atripes in Alexander 1919: 335: original description (type locality: Japan, Honshu, Tokyo, Meguro); Alexander 1936a: 193: suggestion of synonymy; Alexander 1965: 35: synonymy.

Ormosia (Ormosia) atripes in Alexander 1953b: 173: faunistic record; Alexander 1954: 31: faunistic record, distribution.

Ormosia (Parormosia) diversipes in Alexander 1965: 35: new subgeneric combination; Savchenko and Krivolutsкая 1976: 94: faunistic record; Savchenko 1979: 27: faunistic record; Savchenko 1983: 83: faunistic records; Pilipenko and Sidorenko 2006: distribution; Pilipenko 2009: 333: faunistic record; Nakamura 2014: 33: distribution; Oosterbroek 2022: distribution.

Type material examined. *Ormosia atripes* Alexander, 1919: **Paratype.** JAPAN • 1 ♀; Honshu; Tokio (Tokyo), Meguro; 9 Apr. 1919; R. Takahashi leg.; USNM.

Ormosia diversipes Alexander, 1919: **Paratype.** JAPAN • 1 ♂; Honshu; Tokio (Tokyo), Meguro; 26 Mar. 1919; R. Takahashi leg.; USNM.

Non-type material examined. *Ormosia (Parormosia) diversipes* Alexander, 1919: JAPAN • 1 ♂; Honshu, Aomori, Fukaura-machi, Okazaki, Fukaura House; 40.63684°N, 139.9116°E; alt. 130 m; 26 Aug. 2014; light trap; D. Kato leg.; BLKU. • 1 ♂; Honshu, Aomori, Fukaura-machi, Mt. Takaniô-yama; alt. 140 m; 11 May 2014; D. Kato leg.; BLKU. • 1 ♂; Honshu, Aomori, Hirosaki-shi, Koguriyama, Inekari-sawa River;

40.53658°N, 140.48701°E; alt. 170 m; 10 May 2013; • 1 ♂; same locality; 17 May 2013; D. Kato leg.; BLKU. • 1 ♂; Honshu, Aomori, Hirosaki-shi, Ichinowatari-Washinosu; 40.51923°N, 140.43889°E; alt. 205 m; 9 May 2013; • 1 ♂; same locality; 12 May 2013; • 1 ♂; same locality; 21 May 2013; • 1 ♂; same locality; 5 Sep. 2013; D. Kato leg.; BLKU. • 1 ♀; Honshu, Aomori, Nakadomari-machi, Ôsawanai, Ôsawanai-tameike Pond; 40.9464°N, 140.4623°E; alt. 35 m; 15 May 2014; • 1 ♂; same locality; 24 May 2014; D. Kato leg.; BLKU. • 1 ♂, 1 ♀; Honshu, Aomori, Nishimeya-mura, Kawaratai, Ôkawa-rindô Path; 40.50062°N, 140.20405°E; alt. 300 m; 18 Sep. 2013; • 1 ♂; same locality; 13 May 2014; D. Kato leg.; BLKU. • 1 ♀; Honshu, Aomori, Nishimeya-mura, Kawaratai, The Shirakami Natural Science Park, Hirosaki Univ.; 40.5188°N, 140.21488°E; alt. 255 m; 18 May 2014; • 2 ♂; same locality; 25 May 2014; • 2 ♂; same locality; 1 Jun. 2014; • 1 ♂; same locality; 28 Sep. 2014; light trap; D. Kato leg.; BLKU. • 2 ♂, 4 ♀; Honshu, Aomori, Towada-shi, Okuse, Tsutanuma-rindô Path; 40.59084°N, 140.95705°E; alt. 460 m; 14 May 2014; D. Kato leg.; BLKU. • 1 ♂; Honshu, Niigata, Tôkamachi-shi, Matsunoyama-Amamizukoshi, Mt. Amamizu-yama; alt. 920 m; 1 Oct. 2019; D. Kato leg.; BLKU. • 2 ♂; Honshu, Niigata, Tôkamachi-shi, Matsunoyama, Echigo-Matsunoyama Museum of Natural Science 'Kyororo'; 37.09956°N, 138.61631°E; alt. 310 m; 25 Apr. 2020; • 1 ♀; same locality; 5 May 2020; D. Kato leg.; BLKU. • 1 ♂; Honshu, Niigata, Tôkamachi-shi, Matsunoyama-Mizunashi, Step-in-plan; alt. 230 m; 2 Oct. 2020; D. Kato leg.; BLKU. • 1 ♂; Honshu, Nagano, Sakae-mura, Sakai, Koakazawa-gawa River; 36.85352°N, 138.66358°E; alt. 1320–1400 m; 21 Aug. 2020; D. Kato leg.; BLKU. • 1 ♂; Honshu, Gifu; 15 Nov. 1931; S. Kariya leg.; USNM. • 1 ♂; Honshu, Hida, Ontake; 26 Jul. 1959; Mishima leg.; USNM. • 1 ♀; Honshu, Ibaraki, Tsukuba-shi, Oda, Mt. Hôkyô-san; 36.15802°N, 140.12142°E; alt. 50 m; 14 Oct. 2011; • 1 ♂; same locality; 26 Mar. 2013; D. Kato leg.; BLKU. • 1 ♂; Honshu, Ôsaka, Izumisano-shi, Ôgi, Inunakisan Spa; 34.3398°N, 135.38375°E; alt. 250 m; 16 Apr. 2014; D. Kato leg.; BLKU. • 2 ♂; Honshu, Okayama, Okayama, Maniwa-shi, Hiruzen-Shimotokuyama; 35.3293°N, 133.59725°E; alt. 780 m; 17 May 2015; D. Kato leg.; BLKU. • 3 ♀; Shikoku, Kagawa, Mannô-chô, Katsuura, Myôjingu-gawa River; 34.09402°N, 134.0143°E; alt. 480 m; 21 Apr. 2014; D. Kato leg.; BLKU. • 1 ♂; Shikoku, Ehime, Kumakogen, Kuma River, dam; 33.68392°N, 132.87145°E; alt. 615 m; 10 Oct. 2021; L.-P. Kolcsár leg.; CKLP. • 2 ♂, 1 ♀; Shikoku, Ehime, Kumakogen, Omogo River; 33.56118°N, 133.00669°E; alt. 290 m; 13 Oct. 2021; light trap; L.-P. Kolcsár leg.; CKLP. • 1 ♂; Shikoku, Ehime, Kumakogen, Myogadani River; 33.54869°N, 132.94807°E; alt. 890 m; 17 Jun. 2019; L.-P. Kolcsár leg.; CKLP. • 1 ♂; Shikoku, Ehime, Kumakogen, small stream and concrete wall; 33.59423°N, 132.98385°E; alt. 640 m; 19 May 2019; L.-P. Kolcsár leg.; CKLP. • 1 ♂; Shikoku, Ehime, Matsuyama, bamboo forest and small stream; 33.86363°N, 132.76673°E; alt. 110 m; 24 Mar. 2021; L.-P. Kolcsár leg.; CKLP. • 1 ♂; Shikoku, Ehime, Matsuyama, fill up lake; 33.83858°N, 132.81399°E; alt. 100 m; 27 Apr-. 2019; L.-P. Kolcsár leg.; CKLP. • 1 ♂, 1 ♀; Shikoku, Ehime, Matsuyama, stream; 33.86152°N, 132.82591°E; alt. 180 m; 5 Apr. 2019; L.-P. Kolcsár leg.; CKLP. • 1 ♂; Shikoku, Ehime, Matsuyama, rocky stream and waterfall; 33.86801°N, 132.83482°E; alt. 240 m; 3 May 2019; L.-P. Kolcsár leg.; CKLP. • 1 ♂;

Shikoku, Ehime, Matsuyama, small ruderal stream; 33.863284°N, 132.771579°E; alt. 125 m; 10 Apr. 2020; • 7 ♂, 1 ♀; Shikoku, Ehime, Matsuyama, Takimoto, small lake; 33.96114°N, 132.82899°E; alt. 205 m; 10 Oct. 2021; light trap; L.-P. Kolcsár leg.; CKLP. • 8 ♂, 4 ♀; Shikoku, Ehime, Matsuyama, Tateiwa dam; 33.97129°N, 132.87542°E; alt. 310 m; 10 Oct. 2021; light trap; L.-P. Kolcsár leg.; CKLP. • 1 ♂; Shikoku, Ehime, Matsuyama, small waterfall in Japanese cedar forest; 33.85911°N, 132.83472°E; alt. 330 m; 17 May 2020; L.-P. Kolcsár leg.; CKLP. • 1 ♂; Shikoku, Ehime, Seiyo, Shirokawachō Noigawa; 33.44036°N, 132.81202°E; alt. 600 m; 11 May 2021; L.-P. Kolcsár leg.; CKLP. • 5 ♂ (1 ♂: BOLD ID: JPCOI003-22), 2 ♀ (1 ♀: BOLD ID: JPCOI004-22); Shikoku, Ehime, Toon, Kamihayashi Forest Park; 33.72146°N, 132.89012°E; alt. 1100 m; light trap; 3 Oct. 2021. • 2 ♀; Shikoku, Tokushima, Higashimiyoshi-chō, Higashiyama, Ogawadani-gawa River; alt. 340 m; 21 Apr. 2014; D. Kato leg.; BLKU. • 1 ♀; Shikoku, Tokushima, Miyoshi-shi, Higashiiya-Ochiai, near Matsuogawa Dam; 33.96478°N, 133.93908°E; alt. 900 m; 15 May 2015; • 1 ♂; same locality; 30 Apr. 2016; D. Kato leg.; BLKU. • 1 ♂; Shikoku, Tokushima, Miyoshi, Higashiiya, Mt. Tsurugi area; 33.86651°N, 134.08549°E; alt. 1315 m; light trap; 16 Oct. 2021; K. Kuroda leg.; CKLP. • 1 ♂; Kyushu, Fukuoka, Fukuoka-shi, Jōnan-ku, Katae, Mt. Abura-yama; 33.53046°N, 130.36594°E; alt. 220 m; 19 Apr. 2014; • 1 ♂, 1 ♀; same locality; 20 Oct. 2015; D. Kato leg.; BLKU. • 2 ♂; Kyushu, Fukuoka, Fukuoka-shi, Sawara-ku, Itaya, Mt. Sefuri-san; 33.43811°N, 130.36673°E; alt. 970 m; 23 May 2015; • 1 ♂, 2 ♀; same locality; 10 Jun. 2015; • 2 ♂; same locality; 4 Oct. 2015; D. Kato leg.; BLKU. • 1 ♀; Kyushu, Fukuoka, Itoshima-shi, Shimasakurai, Ōguchi seaside; 33.63249°N, 130.18094°E; alt. 5 m; 23 Oct. 2015; D. Kato leg.; BLKU. • 2 ♀; Kyushu, Fukuoka, Miyawaka-shi, Inunaki, Mt. Inunaki-san; 33.68112°N, 130.55317°E; alt. 300 m; 5 May 2015; D. Kato leg.; BLKU. • 1 ♀; Kyushu, Kumamoto, Yatsushiro-shi, Izumi-machi-Hagi, Momiki-gawa River; 32.51417°N, 130.93927°E; alt. 580 m; 11 May 2016; D. Kato leg.; BLKU. • 1 ♂; Kyushu, Kumamoto, Yatsushiro-shi, Izumi-machi-Momiki; alt. 1060 m; 22 Sep. 2015; • 1 ♂; same locality; alt. 1400 m; 17 Oct. 2015; D. Kato leg.; BLKU. • 1 ♀; Kyushu, Miyazaki, Gokase-chō, Kuraoka, Gokase ski area; alt. 1500 m; 28 Jun. 2015; D. Kato leg.; BLKU. • 1 ♂; Kyushu, Mt. Kirishima; alt. 2500 ft.; 3 May 1929; S. Issiki leg.; USNM. • 1 ♂; Kyushu, Saga, Karatsu-shi, Hamatama-machi-Torisu, Tsubakiyama-tameike Pond; 33.40414°N, 130.10641°E; alt. 630 m; 26 Apr. 2015; D. Kato leg.; BLKU. • 1 ♂; Kyushu, Saga, Saga-shi, Fuji-machi-Seiya, Kase-gawa River near Hokuzan Dam; 33.43322°N, 130.23212°E; alt. 320 m; 23 Apr. 2015; D. Kato leg.; BLKU. • 1 ♀; Kyushu, Kagoshima, Yakushima I, Mugio, close to Yakusugi Land; 30.30173°N, 130.58574°E; alt. 1100 m; 19 Oct. 2021; L.-P. Kolcsár leg.; CKLP. • 1 ♂; Kyushu, Kagoshima, Yakushima I, Nagata, Nagata River; 30.38757°N, 130.43528°E; alt. 40 m; 20 Oct. 2021; L.-P. Kolcsár leg.; CKLP.

Diagnosis. General coloration brown to dark brown (Fig. 12). Vertex greyish. Antenna yellowish on pedicel and at least basal segments of flagellum. Mesonotum sometimes barely greyish. Wing brownish tinged, stigmal region weakly dark. Cell dm usually closed. Halter dusky yellow. Legs dark brown in female (Fig. 12B), tibiae to tarsi mostly yellow in male (Fig. 12A). Male terminalia: tergite 9 bearing pair of long

membranous lobes at caudal margin. Clasper of gonostylus divided into two arms near base, ventral arm blade-shaped, gradually narrow toward tip, $\sim 2\times$ as long as curved stout dorsal arm. Lobe of gonostylus narrower and slightly shorter than clasper, weakly dilated at apical $1/4$, with long setae on ventral margin near tip. Interbase with mesal-apical lobe bearing two claws. Female terminalia with cercus slender, upcurved distally. Lateral arm of genital fork pointed and curved posteriorly. Sternite 9 rounded posteriorly, desclerotized medially.



Figure 12. Habitus of *Ormosia (Parormosia) diversipes* Alexander, 1919. **A** male **B** female. Scale bar: 2 mm.

Redescription. Male. Body length 3.2–4.5 mm, wing length 3.9–5.5 mm.

Head: covered with black setae. Vertex grey to dark grey. Eyes relatively large and widely separated, $\sim 4/5$ as wide as narrowest point of vertex, $\sim 1/2$ length of head including rostrum in dorsal view. Rostrum dark brown, $\sim 1/2$ length of eye in lateral view. Palpus dark brown, 5-segmented, slightly shorter than head, palpomere 1 globular and small, palpomeres 2–5 cylindrical, slenderer in palpomeres 2 and 5. Labellum dark brown. Antenna 16-segmented, $2.5\text{--}3\times$ as long as head (Fig. 12A); scape dark brown, $1.5\times$ as long as wide; pedicel dusky yellow, roughly globular, $3/4$ length of scape; flagellomeres dusky yellow, sometimes darker on distal segments, oval in flagellomere 1 and slender oval on succeeding segments; each flagellomere with one or two verticils, longest one $\sim 2\times$ as long as each segment, gradually shorter toward distal segment, sensilla abundant, at most as long as each flagellomere.

Thorax: covered with yellow setae, rarely brownish. Pronotum brown to dark brown, often yellowish on lateral side of postpronotum. Mesonotum brown to dark greyish brown, sometimes lighter brown around prescutal pit. Prescutal pit brown to black, oval to long bacilliform, often widened toward outer end. Tuberculate pit distinct, situated at anterior $2/5$ between anterior margin of mesonotum and prescutal pit. Pleuron subnitidous, dark brown. Wing (Fig. 13) relatively wide, $3.1\text{--}3.2\times$ as long as wide; tinged with brown, sometimes weakly yellowish on prearcular region, stigmal region weakly dark; Sc ending at level of R_2 or slightly distal to it; crossvein sc-r distinct, situated between levels of basal $1/3\text{--}1/2$ of R_s ; R_{2+3+4} $1/7\text{--}1/3$ length of R_3 ; R_2 situated between fork of R_{2+3+4} and length of itself distal to it; M_4 $1\text{--}2\times$ as long as M_{3+4} ; cell dm closed, $0.4\text{--}0.7\times$ as long as cell m_{1+2} , or sometimes open by atrophy of crossvein m-m; wing margin between tips of CuP and A_1 $2.5\text{--}3\times$ as long as that between tips of CuP and CuA; A_1 curved posteriorly near middle. Halter dusky yellow, $\sim 3/5$ length of thorax (Fig. 12A). Legs with coxae to femora dark brown, femora very narrowly pale at bases; tibiae to tarsi yellow to dusky yellow, tips of tibiae and distal segments of tarsi weakly dark (Fig. 12A).



Figure 13. Wing of *Ormosia* (*Parormosia*) *diversipes* Alexander, 1919. Scale bar: 2 mm.

Abdomen: dark brown, densely covered with yellow setae.

Male terminalia (Fig. 14): Tergite 9 with pair of long and flat, largely membranous lobes at caudal margin, $\sim 1/3$ length of remainder of tergite 9; tergite 9 slightly longer than wide including caudal lobe (Fig. 14A). Sternite 9 slightly and widely convex at posterior margin (Fig. 14B). Gonocoxite roundish, slightly shorter than tergite 9, posteroventral margin not produced beyond base of clasper of gonostylus. Gonocoxal apodeme long, connected to each other, forming bridge, central part jointed with anteromedial part of interbase (Fig. 14D). Clasper of gonostylus dark, slightly longer than gonocoxite, divided into two arms; dorsal arm short, stout and curved ventrally, rounded at tip, distal $1/2$ densely covered with black microscopic setae; ventral arm $\sim 2\times$ as long as dorsal arm, blade-shaped, weakly twisted, gradually narrow toward tip, acute at tip (Fig. 14C). Lobe of gonostylus slender, narrower, and slightly shorter than clasper, weakly dilated at apical $1/4$, with several long setae on ventral margin near tip, obtuse at tip (Fig. 14C). Interbase

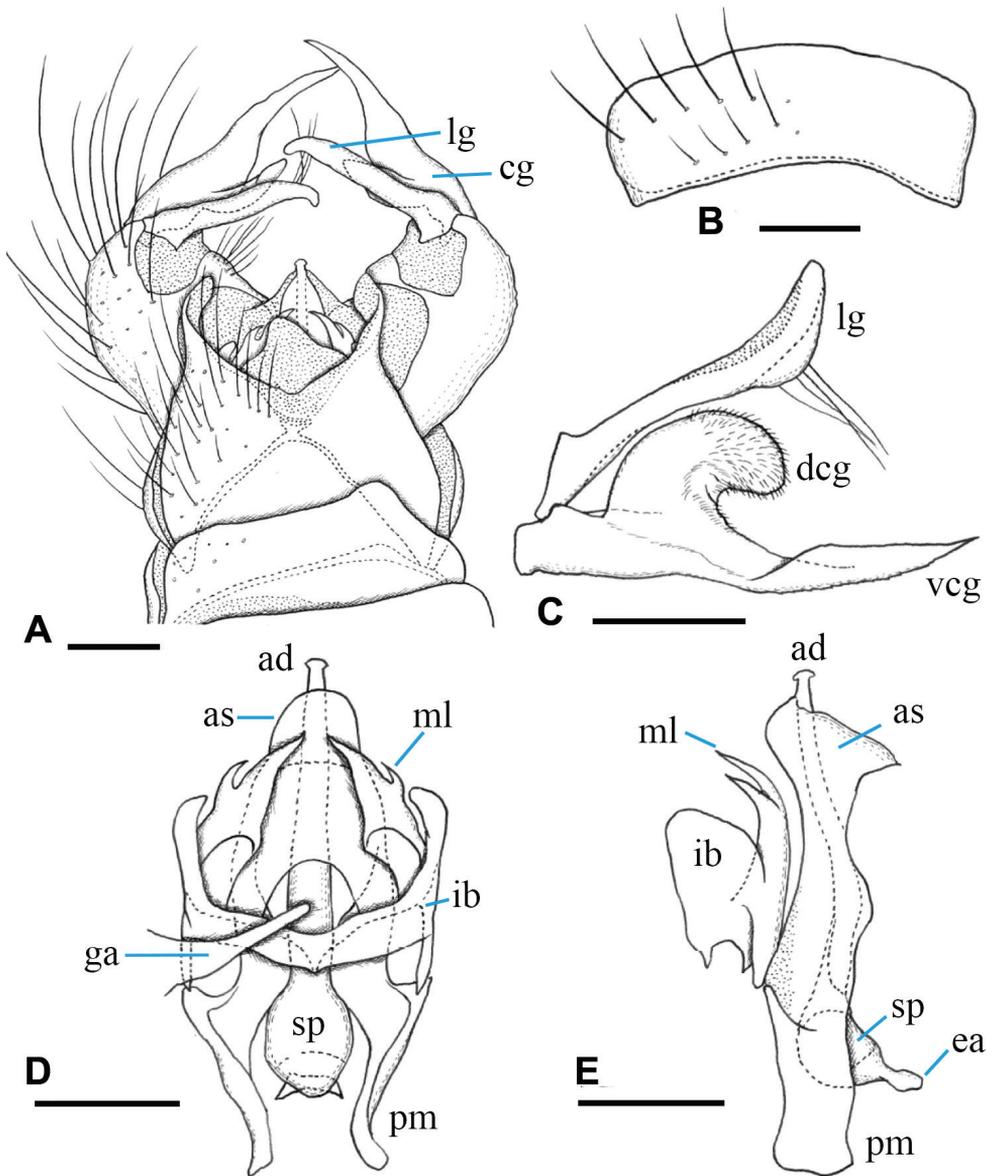


Figure 14. Male terminalia of *Ormosia* (*Parormosia*) *diversipes* Alexander, 1919 **A** dorsal view **B** sternite 9, ventral view **C** gonostylus, outer surface **D** aedeagal complex, dorsal view (tip of gonocoxal apodeme moved posteriorly and left gonocoxal apodeme omitted) **E** aedeagal complex, lateral view (left = dorsal). Scale bars: 0.1 mm.

with mesal-apical lobe claw-shaped, curved and directed posterodorsally, bearing smaller spine at middle of outer margin (Fig. 14D, E); basal part of each interbase fused and dorso-lateral part roundly produced in lateral view (Fig. 14E). Paramere wide, shorter than interbase (Fig. 14E). Aedeagus slender and cylindrical, extreme tip slightly widened, extending beyond tip of interbase (Fig. 14D, E). Aedeagal sheath covering aedeagus except

apical part, posterior end $\sim 4\times$ as wide as aedeagus at this point (Fig. 14D), strongly produced ventrally (Fig. 14E). Sperm pump roundish in dorsal view, anterior end situated at level of middle of paramere (Fig. 14D). Ejaculatory apodeme developed, dorsoventrally compressed, fan-like plate, $\sim 1/2$ length of diameter of sperm pump (Fig. 14D, E).

Female. Body length 3.6–5.0 mm, wing length 4.2–5.9 mm. Generally resembling male (Fig. 12B), except antenna shorter, $\sim 2\times$ as long as head; flagellomeres often dark brown entirely, with ca. eight verticils on each of basal segments, fewer on each of distal segments, longest one at most $1.5\times$ as long as each segment. Tibiae to tarsi dark brown, concolorous with femora (Fig. 12B).

Female terminalia (Fig. 15): dark brown, cercus turning to amber-color toward tip. Tergites 8 and 9 fused. Cercus slender, upcurved distally, $1.3\times$ longer than tergite 10; hypogynial valve slender, $1.5\times$ as long as sternite 8, gradually narrowed toward tip, basal part ca. as wide as that of cercus, tip ending at level of basal $2/3$ of cercus (Fig. 15A). Genital frame with genital fork widened posteriorly, anterior part slender; lateral arm of genital fork pointed at tip and curved posteriorly, situated at posterior end of genital fork; sternite 9 rounded posteriorly, middle part desclerotized; three membranous areas present at level of genital opening (Fig. 15B). Three spermathecal ducts present, basal parts blackened (Fig. 15B). Spermathecae indistinct.

Distribution. Japan (Honshu, Shikoku, Kyushu) (Fig. 5C), Russia (FE), and Kuril Islands.

Remarks. This species resembles a Chinese species, *Ormosia* (*Parormosia*) *nigripennis* Alexander, 1936 (Alexander 1936a), but this species has two-spined mesal-apical lobe of the interbase (Fig. 14D, E), while the latter species has a single pointed lobe on the interbase.

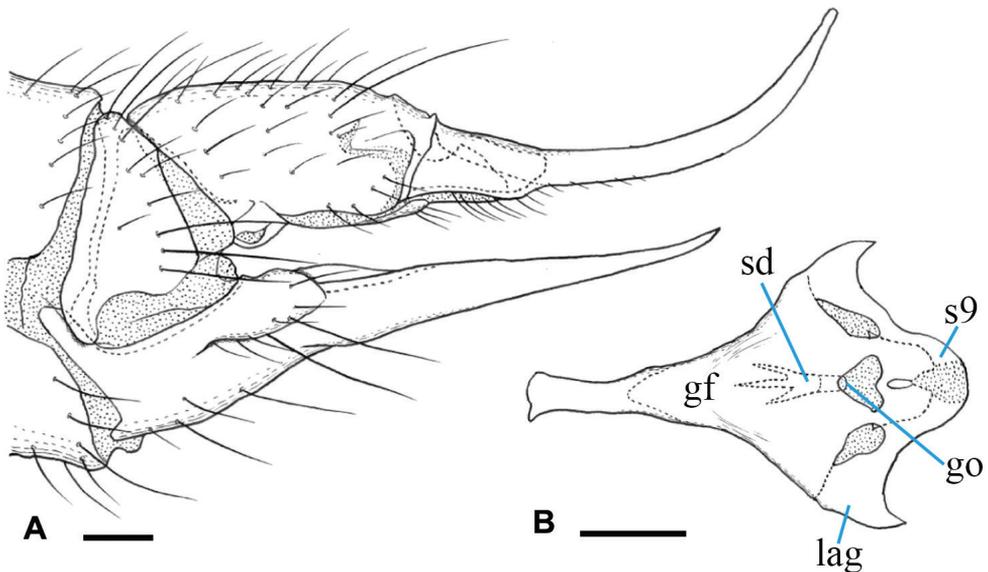


Figure 15. Female terminalia of *Ormosia* (*Parormosia*) *diversipes* Alexander, 1919 **A** lateral view **B** genital frame, ventral view (left = anterior). Scale bars: 0.1 mm.

***Ormosia (Parormosia) nippoalpina* Alexander, 1941**

Figs 5D, 8B, 16–18

Ormosia (Ormosia) nippoalpina in Alexander 1941: 63: original description (type locality: Japan, Honshu, Nagano, Kamikochi).

Ormosia (Parormosia) nippoalpina in Savchenko 1979: 27: faunistic records; Nakamura 2014: 33: distribution; Oosterbroek 2022: distribution.

Type material examined. *Holotype*. JAPAN • ♂; Honshu, Kamikochi, alt. 5000 feet; 23 Jun. 1939; E. Suenson leg.; USNM.

Paratype. JAPAN • 1 ♀; same locality and date as holotype; USNM.

Non-type material examined. JAPAN • 1 ♂; Honshu, Aomori, Nishimeya-mura, Kawaratai, Ōkawa-rindō Path; 40.50062°N, 140.20405°E; alt. 300 m; 13 May 2014. • 1 ♂; same locality; 20 May 2014; D. Kato leg.; BLKU. • 1 ♀; Niigata, Itoigawashi, Ōtokoro, near Udo-gawa River; alt. 1128 m; 36.84198°N, 137.82252°E; 14 June 2022; L.-P. Kolcsár leg.; CKLP.

Diagnosis. General coloration brown to dark brown (Fig. 8B). Vertex greyish. Antenna brown to dark brown. Mesonotum subnitidous. Wing brownish tinged, stigmal region barely dark. Cell dm open. Halter dusky yellow. Legs mostly dark brown, yellowish on trochanters and bases of femora. Male terminalia: tergite 9 bearing pair of large triangular lobes at caudal margin. Clasper of gonostylus divided into two arms; ventral arm ~ 1.5× as long as curved stout dorsal arm, roughly blade-shaped, wide at middle and narrow on distal part. Lobe of gonostylus flattened, slightly shorter than clasper, gradually widened distally, widest part ~ 1/3 length of lobe of gonostylus, pointed at apicodorsal corner, distal margin with several long setae. Interbases fused medially into large roundish plate, pointed at tip, mesal-apical lobe absent. Female terminalia with cercus relatively slender, upcurved distally. Lateral arm of genital fork pointed and curved posteriorly. Sternite 9 subacute at posterior end.

Redescription. Male. Body length 3.3–4.0 mm, wing length 4.8–5.8 mm.

Head: covered with yellow and black setae. Vertex grey to dark grey. Eyes relatively large and widely separated, ~ 3/4 as wide as narrowest point of vertex, ~ 1/2 length of head including rostrum in dorsal view. Rostrum dark brown, ~ 1/2 length of eye in lateral view. Palpus dark brown, 5-segmented, slightly shorter than head, palpomere 1 globular and small, palpomeres 2–5 cylindrical, slenderer in palpomeres 2 and 5. Labellum dark brown. Antenna 16-segmented, 2.5× as long as head; scape dark brown, 2× as long as wide; pedicel brown, roughly globular, 3/4 length of scape; flagellomeres brown, subglobular on basal segments, longer oval on distal segments; each flagellomere with two verticils, longest one ~ 2× as long as each segment, gradually shorter toward distal segment, sensilla abundant, at most 1/3 as long as each flagellomere.

Thorax: covered with yellow setae. Pronotum dark brown, yellowish on postpronotum. Mesonotum subnitidous, brown to dark brown, with small yellowish area just above lateral end of postpronotum. Prescutal pit dark brown, oval to long bacilliform.

Tuberculate pit distinct, situated at anterior $1/3$ to $1/2$ between anterior margin of mesonotum and prescutal pit. Pleuron subnitidous, dark brown, weakly yellowish on dorsal part of anepisternum. Wing (Fig. 16) tinged with brown, prearcular region more yellowish, stigmal region barely dark; $3.3\text{--}3.4\times$ as long as wide; Sc ending at level of R_2 or slightly distal to it; crossvein sc-r distinct, situated between levels of basal $1/5\text{--}2/5$ of R_3 ; R_{2+3+4} $1/9\text{--}1/6$ length of R_3 ; R_2 situated between $1/3\text{--}1\times$ lengths of itself distal to fork of R_{2+3+4} ; M_4 $3.5\text{--}10\times$ as long as M_{3+4} ; cell dm open by atrophy of crossvein m-m; wing margin between tips of CuP and A_1 $2\text{--}2.5\times$ as long as that between tips of CuP and CuA; A_1 curved posteriorly near middle. Halter yellow, slightly brownish at base, $\sim 3/5$ length of thorax. Legs with coxae dark brown; trochanters yellow to dusky yellow; femora to tarsi dark brown, basal parts of femora yellowish toward bases (Fig. 8B).



Figure 16. Wing of *Ormosia* (*Parormosia*) *nippostalpina* Alexander, 1941. Scale bar: 2 mm.

Abdomen: dark brown, densely covered with yellow setae.

Male terminalia (Fig. 17): Tergite 9 with pair of large triangular lobes at caudal margin, $\sim 1/2$ length of remainder of tergite 9; tergite 9 including caudal lobe slightly wider than long (Fig. 17A). Sternite 9 slightly and widely convex at posterior margin, anterior corner distinctly produced anteriorly (Fig. 17B). Gonocoxite roundish, slightly longer than tergite 9, posteroventral margin not produced beyond base of clasper of gonostylus (Fig. 17A). Gonocoxal apodeme short, connected to anterolateral part of interbase (Fig. 17D). Clasper of gonostylus dark, slightly longer than gonocoxite, divided into two arms; dorsal arm stout and curved ventrally in apical view (Fig. 17C), rounded at tip, tip directed distally (Fig. 17A), distal part densely covered with black microscopic setae; ventral arm $\sim 1.5\times$ as long as dorsal arm, roughly blade-shaped, wide at middle and narrow on distal part, acute at tip (Fig. 17C). Lobe of gonostylus flattened, slightly shorter than clasper, gradually broadened distally, widest part $\sim 1/3$ length of lobe of gonostylus, dorsal-apical corner pointed and ventral-apical margin rounded, distal margin with several long setae (Fig. 17C). Interbases fused medially into large roundish plate, almost straight at anterior margin and pointed at posterior

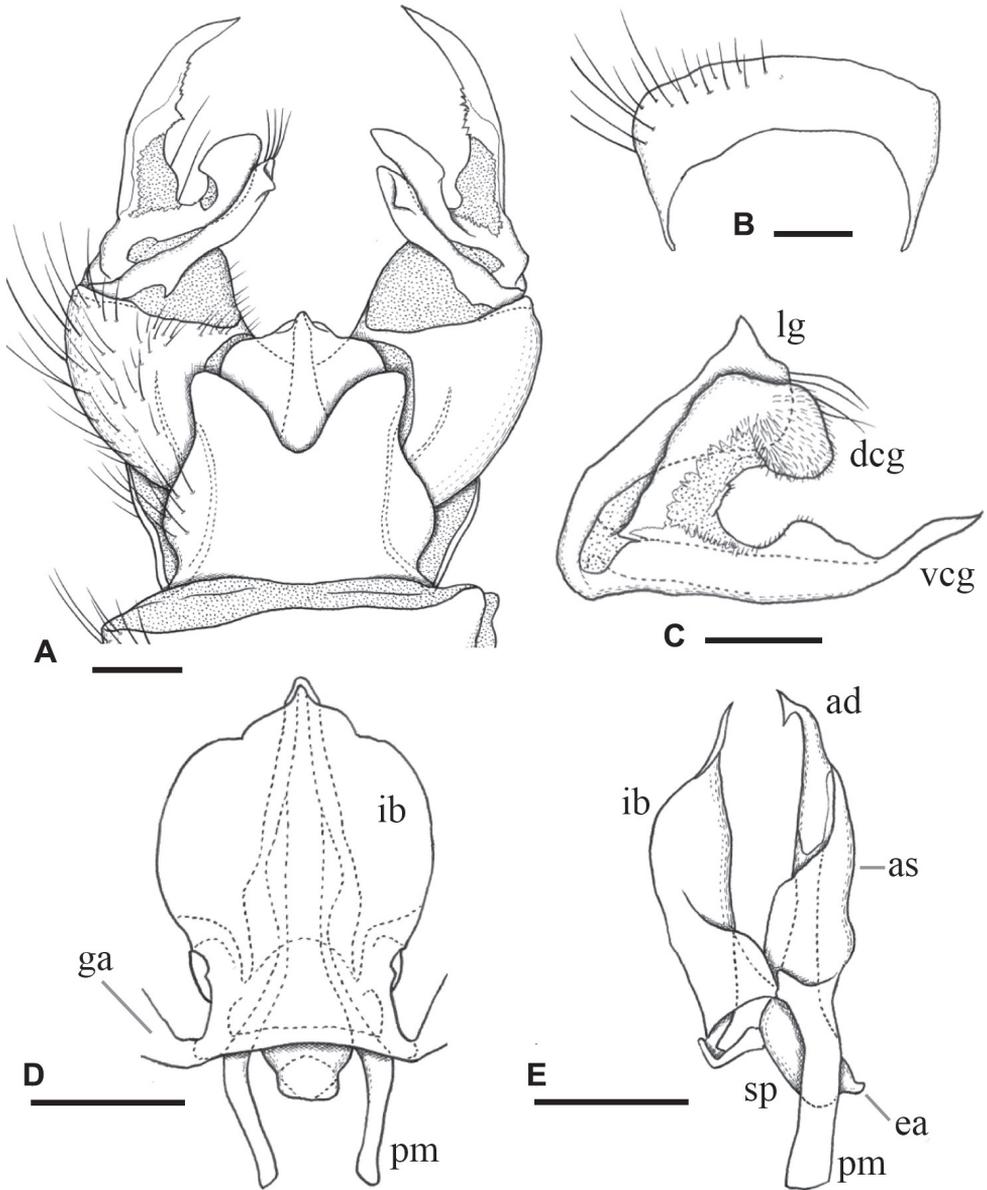


Figure 17. Male terminalia of *Ormosia (Parormosia) nippostalpina* Alexander, 1941 **A** dorsal view **B** sternite 9, ventral view **C** gonostylus, outer surface **D** aedeagal complex, dorsal view **E** aedeagal complex, lateral view (left = dorsal). Scale bars: 0.1 mm.

margin, basal 1/4 constricted; mesal-apical lobe absent (Fig. 17A, D). Paramere narrow rod-shaped, shorter than interbase (Fig. 17D, E). Aedeagus slender and cylindrical, extreme tip bent dorsally and widened, situated at level of tip of interbase (Fig. 17E). Aedeagal sheath covering basal 2/3 of aedeagus, not distinctly broadened (Fig. 17E).

Sperm pump roundish in dorsal view, anterior end situated at level of middle of paramere (Fig. 17D). Ejaculatory apodeme weakly developed (Fig. 17E).

Female. Body length 5.0–5.2 mm, wing length 5.7–6.0 mm. Generally resembling male.

Female terminalia (Fig. 18): dark brown, cercus amber-color. Tergites 8 and 9 fused. Cercus relatively slender, upcurved distally, 1.3× longer than tergite 10; hypogynial valve 1.8× as long as sternite 8, gradually narrowed toward tip, basal part 1.3× as wide as that of cercus, tip ending at level of basal 2/3 of cercus (Fig. 18A). Genital frame with genital fork gradually widened toward anterior and posterior ends, narrowest at anterior 1/4, lateral margin of posterior end produced into small lobe; lateral arm of genital fork pointed at tip and curved posteriorly, situated at posterior end of genital fork; sternite 9 relatively long, subacute at tip; one large membranous area present posterior to genital opening (Fig. 18B). Three spermathecal ducts present (Fig. 18B). Spermathecae indistinct.

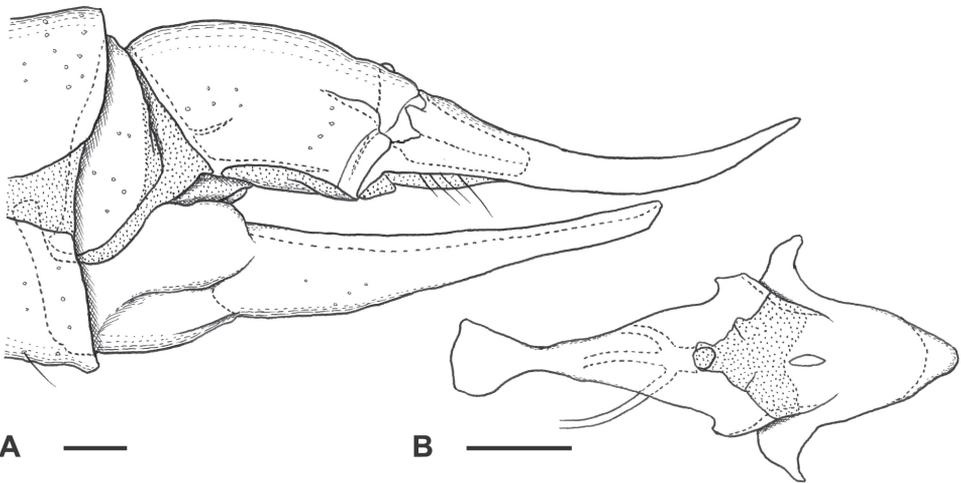


Figure 18. Female terminalia of *Ormosia* (*Parormosia*) *nippostalpina* Alexander, 1941 **A** lateral view **B** genital frame, ventral view (left = anterior). Scale bars: 0.1 mm.

Distribution. Japan (Honshu) (Fig. 5D) and Russia (FE).

Remarks. This species is similar to a Nearctic species, *Ormosia* (*Parormosia*) *divergens* (Coquillett, 1905) (Coquillett 1905), but is differentiated from it by the following characters: clasper of gonostylus without lobe at fork into dorsal and ventral arms (Fig. 17C) (with roundish lobe at fork in *Ormosia* (*Parormosia*) *divergens*); lobe of gonostylus with short pointed projection at dorsal-apical edge, width of lobe of gonostylus at this point ~ 1/3 length of lobe of gonostylus (dorsal-apical pointed projection long, width of lobe of gonostylus at this point ca. as long as lobe of gonostylus in *Ormosia* (*Parormosia*) *divergens*).

***Ormosia (Parormosia) phalara* Kato & Kolcsár, sp. nov.**

<https://zoobank.org/65BBAF0A-C395-4E8F-8CF5-D674396F44CA>

Figs 5D, 19–22

BoldSystems: JPCOI002-22

Type material examined. Holotype. ♂, pinned. Original label: “JAPAN, Fukuoka, Fukuoka-shi, Sawara-ku, Itaya, Mt. Sefuri-san; alt. 970 m; 10 Jun. 2015, D. Kato leg.” “HOLOTYPE *Ormosia (Parormosia) phalara* Kato & Kolcsár, sp. nov. [red label]”; BLKU.

Paratypes. JAPAN • 1♂; Honshu, Aomori, Hirosaki-shi, Ichinowatari-Yamashita; 40.53064°N, 140.44664°E; alt. 173 m; 25 Jul. 2014; light trap; D. Kato leg.; BLKU. • 1♀; Honshu, Aomori, Nishimeya-mura, Kawaratai, Ôkawa-rindô Path; 40.50062°N, 140.20405°E; alt. 300 m; 25 Jul. – 6 Aug. 2013; Malaise trap; D. Kato and T. Nakamura leg.; BLKU. • 1♂; Honshu, Nagano, Iida, Kamimurahodono; 35.45805°N, 138.01166°E; alt. 1415 m; 3 Aug. 2019; K. Kuroda et al. leg.; EUMJ. • 2♂, 1♀; Honshu, Nagano; Matsumoto, Azusa lake; 36.12889°N, 137.72512°E; alt. 1000 m; 21 Jul. 2020; L.-P. Kolcsár leg.; CKLP. • 1♀ (BOLD ID: JPCOI002-22); Honshu, Nagano, Kiso, Ohara Shinkai; 35.83739°N, 137.77346°E; alt. 1220 m, 19 Jul. 2020; L.-P. Kolcsár leg.; CKLP. • 1♂; Honshu, Kanagawa, Hakone; approximate coordinates: 35.23°N, 139.02°E; 25 Jul. 1957; light; S. Hisamatsu leg.; EUMJ. • 3♂, 1♀; Kyushu, Fukuoka, Fukuoka-shi, Sawara-ku, Itaya, Mt. Sefuri-san; alt. 970 m; 10 Jun. 2015; D. Kato leg.; BLKU.

Diagnosis. General coloration dark brown (Fig. 19). Vertex greyish. Antenna yellowish on pedicel and at least basal segments of flagellum. Mesonotum with ochreous to greyish brown parts. Wing dark brownish tinged, patterned with subhyaline spots on veins, spots free from veins absent. Cell dm closed. Halter yellow. Legs dark brown with narrow yellow areas at tips of femora and bases of tibiae in female, tibiae to tarsi mostly yellow in male. Male terminalia: tergite 9 bearing pair of long membranous lobes at caudal margin. Clasper of gonostylus divided into two arms, ventral arm ~ 3× as long as curved stout dorsal arm, slender blade-shaped, gradually narrow toward tip. Lobe of gonostylus slender and 3/5 length of clasper, tapered distally, with long setae on ventral margin at distal 2/5. Interbase with mesal-apical lobe bearing two claws. Female terminalia with cercus slender, weakly upcurved distally. Lateral arm of genital fork rounded. Sternite 9 rounded posteriorly.

Description. Male. Body length 3.2–3.6 mm, wing length 4.2–4.7 mm.

Head: covered with yellow and black setae. Vertex grey to dark grey, dark brownish on posterolateral part. Eyes relatively large and widely separated, ~ 4/5 as wide as narrowest point of vertex, ~ 1/2 length of head including rostrum in dorsal view. Rostrum dark brown, ~ 1/2 length of eye in lateral view. Palpus dark brown, 5-segmented, ca. as long as head, palpomere 1 globular and small, palpomeres 2–5 cylindrical, slenderer in palpomeres 2 and 5. Labellum dark brown. Antenna 3× as long as head; 16-segmented, scape dark brown, 2× as long as wide, narrower basally; pedicel pale to dusky yellow, roughly globular, 1/2 of length of scape; flagellomeres pale to dusky yellow, sometimes weakly dark on distal segments, oval on basal one or two segments, long cylindrical on distal segments, each flagellomere with one or two verticils, longest one at most 2× as long as corresponding segment, gradually shorter toward distal segment, sensilla abundant especially in ventral side, at most 1/2 as long as each flagellomere.

Thorax: covered with yellow to dark brown setae. Antep pronotum dark brown, pale at caudal margin; postpronotum dusky yellow. Mesonotum ochreous to greyish brown, dark brown at anterior and lateral margins, sometimes with three indistinctly dark stripes just anterior to transverse suture. Prescutal pit dark brown, roughly oval with narrower inner end. Tuberculate pit distinct, situated at anterior 1/3 to 1/2 between anterior margin of mesonotum and prescutal pit. Pleuron dark brown, variegated with grey pruinosity (Fig. 19A). Wing (Fig. 20) tinged with dark brown, subhyaline on prearcular region, patterned with subhyaline spots restricted to vicinity of veins, without ones free from veins; spot each at MA, Rs origin, crossvein sc-r, outer end of cell dm, and tips of all longitudinal veins; spot at each tip of R_1 , and R_4 to CuA smaller; cord seamed with subhyaline; relatively narrow, $3.3\times$ as long as wide; Sc ending at level of R_2 ; crossvein sc-r distinct, situated at level of middle of Rs; R_{2+3+4} $2/7$ length of R_3 ; R_2 situated between $1/2-1\times$ lengths of itself distal to fork of R_{2+3+4} ; M_4 $0.6-0.7\times$ as long as M_{3+4} ; cell dm closed, $0.7-0.8\times$ as long as cell m_{1+2} ; wing margin between tips of CuP and A_1 $2.5-3\times$ as long as that between tips of CuP and CuA; A_1 curved posteriorly near middle. Halter white to dusky yellow, slightly brownish at base, $\sim 1/2$ length of thorax (Fig. 19). Legs with coxae dark brown; trochanters dusky yellow on fore pair, brown to dark brown on mid and hind pairs; femora dark brown, bases and tips narrowly yellow; tibiae yellow, tips weakly brownish; tarsi yellow, turning to brown to dark brown toward tip distal to middle of tarsomere 1 (Fig. 19A).



Figure 19. Habitus of *Ormosia* (*Parormosia*) *phalava* Kato & Kolcsár, sp. nov. **A** male **B** female. Scale bar: 2 mm.



Figure 20. Wing of *Ormosia (Parormosia) phalara* Kato & Kolcsár, sp. nov. Scale bar: 2 mm.

Abdomen: dark brown, densely covered with brown setae; yellowish setae present on genital part.

Male terminalia (Fig. 21): Tergite 9 with pair of largely membranous, tongue-shaped lobes at caudal margin, $\sim 1/3$ length of remainder of tergite 9; tergite 9 slightly longer than wide including caudal lobe (Fig. 21A). Sternite 9 slightly and widely concave at middle of posterior margin (Fig. 21B). Gonocoxite oval, ca. as long as tergite 9, posteroventral margin not produced beyond base of clasper of gonostylus (Fig. 21A). Gonocoxal apodeme long, connected to each other, forming bridge, central part jointed with anteromedial part of interbase (Fig. 21D). Clasper of gonostylus dark, $\sim 1.4\times$ longer than gonocoxite, divided into two arms; dorsal arm stout, rounded at tip, curved ventrally in apical view (Fig. 21C) and tip directed distally in dorsal view (Fig. 21A), distal part densely covered with black microscopic setae; ventral arm $\sim 3\times$ as long as dorsal arm, slender blade-shaped, gradually narrow toward tip, acute at tip (Fig. 21C). Lobe of gonostylus slender, tapered distally and curved dorsally, $3/5$ length of clasper, ventral margin with several long setae at distal $2/5$ (Fig. 21C). Interbases fused basally, dorsolateral part roundly produced in lateral view; mesal-apical lobe slender claw-shaped, curved and directed posterodorsally, bearing smaller curved spine arising from ventral surface of mesal-apical lobe (Fig. 21D, E). Paramere wide, distinctly shorter than interbase (Fig. 21D, E). Aedeagus slender and cylindrical, extreme tip and subapical region slightly widened, tip extending beyond tip of interbase (Fig. 21D, E). Aedeagal sheath covering aedeagus except apical part, posterior end $\sim 5\times$ as wide as aedeagus (Fig. 21D) at this point and produced dorsally near tip and produced ventrally at distal $3/5$ (Fig. 21E). Sperm pump bacilliform in dorsal view, anterior end situated at level of $1/3$ of paramere (Fig. 21D). Ejaculatory apodeme developed, dorsoventrally compressed, fin-like plate, ca. as long as diameter of sperm pump (Fig. 21E).

Female. Body length 3.6–4.8 mm, wing length 4.2–5.0 mm. Generally resembling male (Fig. 19B) except, antenna shorter, $\sim 2\times$ length of head; each flagellomere

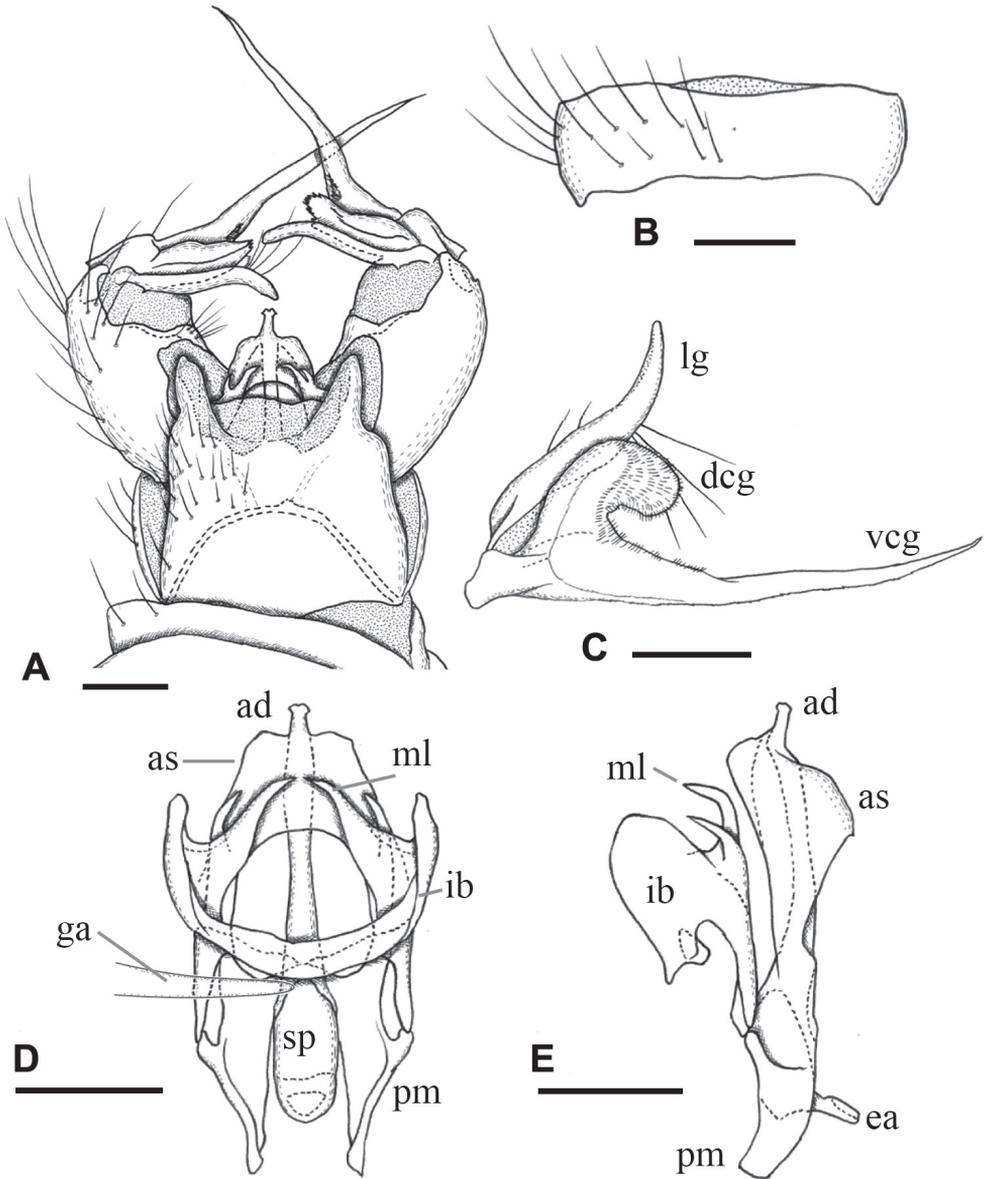


Figure 21. Male terminalia of *Ormosia* (*Parormosia*) *phalara* Kato & Kolcsár, sp. nov. **A** dorsal view **B** sternite 9, ventral view **C** gonostylus, outer surface **D** aedeagal complex, dorsal view (left gonocoxal apodeme omitted) **E** aedeagal complex, lateral view (left = dorsal). Scale bars: 0.1 mm.

with ca. eight verticils on each of basal segments, fewer on each of distal segments, longest one at most 1.5× as long as corresponding segment. Tibiae to tarsi dark brown, bases of tibiae narrowly yellow (Fig. 19B).

Female terminalia (Fig. 22): dark brown, cercus and hypogynial valve amber-colored, weakly dark on basal parts. Tergites 8 and 9 fused. Cercus weakly upcurved distally, 1.6× longer than tergite 10; hypogynial valve relatively stout, 1.5× as long as sternite 8, gradually narrowed toward tip, basal part 1.4× as wide as that of cercus, tip ending at level of basal 3/5 of cercus (Fig. 22A). Genital frame with genital fork widened posteriorly, anterior part slender; lateral arm of genital fork weakly produced, rounded, situated at posterior of genital fork; sternite 9 rounded posteriorly; long and arched groove present posterior to genital opening, lateral part curved anteriorly (Fig. 22B). Three spermathecal ducts present, basal parts blackened (Fig. 22B). Spermathecae indistinct.

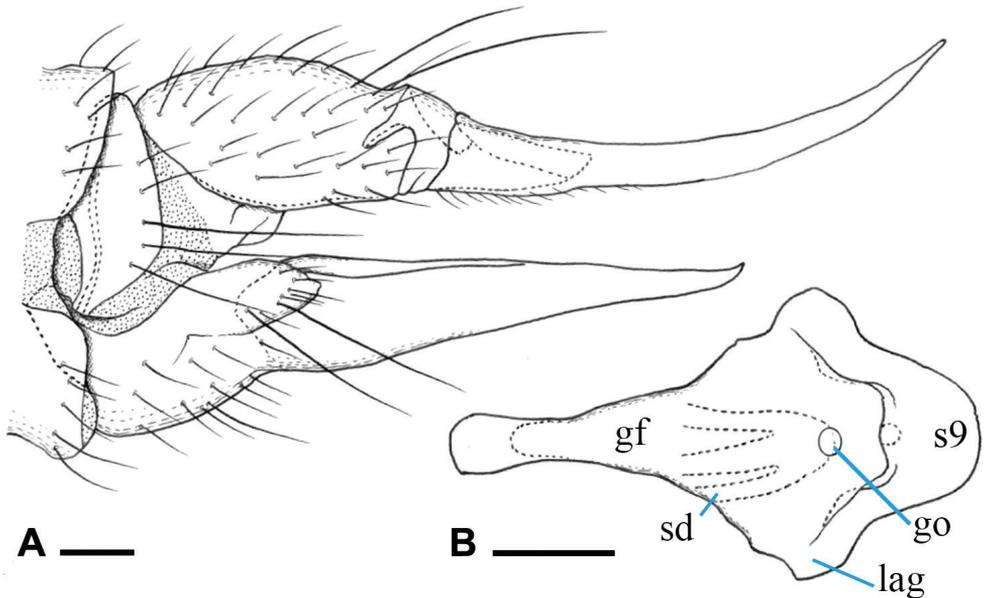


Figure 22. Female terminalia of *Ormosia (Parormosia) phalara* Kato & Kolcsár, sp. nov. **A** lateral view **B** genital frame, ventral view (left = anterior). Scale bars: 0.1 mm

Etymology. The name of this species, *phalara*, is from the Greek *phalaros*, meaning white-spotted. The name is deemed to be a Latinized feminine adjective in nominative singular.

Distribution. Japan (Honshu and Kyushu) (Fig. 5D).

Remarks. This species resembles a Chinese species, *Ormosia (Parormosia) angustaurata* Alexander, 1936 (Alexander 1936b), but is distinguished from it by the following characters: scape dark brown (yellow in *Ormosia (Parormosia) angustaurata*); wing with subhyaline spots restricted to vicinity of veins, without smaller spots free from veins (with at least a few smaller spots free from veins in addition to ones on veins in *Ormosia (Parormosia) angustaurata*); mesal-apical lobe slender with additional spine near tip (Fig. 21D, E) (stout and without additional spine in *Ormosia (Parormosia) angustaurata*).

Key to Japanese species of *Ormosia* (*Oreophila*) and *Ormosia* (*Parormosia*)

- 1 Wing with cell dm closed or open by atrophy of basal part of vein M_3 ; if cell dm closed, male terminalia with clasper of gonostylus simple, not forked near base..... **subgenus *Ormosia* s. s.**
- Wing with cell dm closed or open by atrophy of crossvein m-m; if cell dm closed, male terminalia with clasper of gonostylus bifid **2**
- 2 Cell dm closed (Figs 13, 20) or open (Fig. 16); clasper of gonostylus forked near base, dorsal arm stout and curved, distinctly shorter than ventral arm (Figs 14C, 17C, 21C) **3 (subgenus *Parormosia*)**
- Cell dm open (Figs 2, 9); clasper of gonostylus simple (Figs 3C, 7C), or forked near base with dorsal arm slender and nearly as long as ventral arm (Fig. 10C) **5 (subgenus *Oreophila*)**
- 3 Wing dark, with white maculae/spots (Fig. 20)
..... ***Ormosia* (*Parormosia*) *phalara* Kato & Kolcsár, sp. nov.**
- Wing unpatterned except barely with dark stigma (Figs 13, 16) **4**
- 4 Male flagellomeres brown to dark brown; mesonotum subnitidous; cell dm open (Fig. 16); tibiae dark brown in both sex (Fig. 8B); interbases fused medially into large roundish plate, without mesal-apical lobe (Fig. 17D)
..... ***Ormosia* (*Parormosia*) *nippoalpina* Alexander**
- Male flagellomeres yellowish on basal segments; mesonotum not nitidous; cell dm usually closed (Fig. 13); tibiae yellowish in male (Fig. 12A) and dark brown in female (Fig. 12B); interbase with mesal-apical lobe (Fig. 14D)
..... ***Ormosia* (*Parormosia*) *diversipes* Alexander**
- 5 Body almost entirely brownish black (Fig. 8A); clasper of gonostylus divided (Fig. 10C); cercus stout, strongly upcurved (Fig. 11A)
..... ***Ormosia* (*Oreophila*) *sootryeni* Lackschewitz**
- Body entirely yellowish or pale brownish (Figs 1, 6); clasper of gonostylus undivided (Figs 3C, 7C) **6**
- 6 Male antenna ca. as long as or slightly longer than body (Figs 1B, 6); subapterous in male (Figs 1B, 6); distal part of clasper of gonostylus ca. as wide as lobe of gonostylus (Fig. 7C); female unknown
..... ***Ormosia* (*Oreophila*) *komazawai* Kato & Kolcsár, sp. nov.**
- Antenna distinctly shorter than 1/2 length of body; wing fully developed (Fig. 1A); distal part of clasper of gonostylus 2× as wide as lobe of gonostylus (Fig. 3C) ***Ormosia* (*Oreophila*) *confluenta* Alexander**

Acknowledgements

We are grateful to Masaki Komazawa (Asahikawa City, Hokkaido) for giving us specimens of the fantastic new species of *Oreophila* and Keita Kuroda (Ehime University, Matsuyama) for the other valuable specimens of new *Parormosia* species and for helping examine specimens in EUMJ. We thank Jon Gelhaus (the Academy of

Natural Science of Drexel University, Philadelphia, USA) for helping examine specimens in USNM and Floyd Shockley and Torsten Dikow (USNM) for allowing us to examine their specimens. We are grateful to Jaroslav Starý and to Sigitas Podėnas for reviewing the manuscript. This study was supported by the International Research Fellow of the Japan Society for the Promotion of Science (JSPS) Grant Numbers: P21094 to L.-P. Kolcsár and the Ministry of Education, Culture, Sports, Science and Technology, Japan (MEXT) to a project on Joint Usage/Research Center, Leading Academia in Marine and Environment Pollution Research (LaMer).

References

- Alexander CP (1919) Undescribed species of Japanese crane-flies (Tipulidae, Diptera). *Annals of the Entomological Society of America* 12(4): 327–348. <https://doi.org/10.1093/aesa/12.4.327>
- Alexander CP (1920) The crane-flies of New York. Part II. Biology and phylogeny. *Memoirs. Cornell University Agricultural Experiment Station* 38: 691–1133. <https://doi.org/10.5962/bhl.title.33641>
- Alexander CP (1922) New species of Japanese crane-flies. Part III. (Diptera, Tipulidae). *Insecutor Inscitiae Menstruus* 10: 177–188.
- Alexander CP (1930) New or little-known Tipulidae from eastern Asia (Diptera). VII. *Philippine Journal of Science* 42: 507–535.
- Alexander CP (1936a) New or little-known Tipulidae from eastern Asia (Diptera). XXX. *Philippine Journal of Science* 60: 165–204.
- Alexander CP (1936b) New or little-known Tipulidae from eastern Asia (Diptera). XXXI. *Philippine Journal of Science* 60: 323–360.
- Alexander CP (1938) New or little-known Tipulidae from eastern Asia (Diptera). XL. *Philippine Journal of Science* 67: 129–166.
- Alexander CP (1940a) New or little-known Tipulidae from eastern Asia (Diptera). XLI. *Philippine Journal of Science* 71: 39–76.
- Alexander CP (1940b) New or little-known Tipulidae from eastern Asia (Diptera). XLII. *Philippine Journal of Science* 71: 169–204.
- Alexander CP (1941) New or little-known Tipulidae from eastern Asia (Diptera). XLIV. *Philippine Journal of Science* 76: 27–66.
- Alexander CP (1953a) Records and descriptions of Japanese Tipulidae (Diptera). Part I. The crane-flies of Shikoku. I. *Philippine Journal of Science* 82: 21–75.
- Alexander CP (1953b) Records and descriptions of Japanese Tipulidae (Diptera). Part II. The crane-flies of Shikoku. II. *Philippine Journal of Science* 82: 141–179.
- Alexander CP (1954) The Tipulidae of Mount Ishizuchi and the Omogo Valley, Iyo, Shikoku, Japan. First supplementary list. *Transactions of the Shikoku Entomological Society* 4: 23–31.
- Alexander CP (1965) Undescribed species of crane-flies from the Himalaya mountains (Diptera: Tipulidae). X. *Journal of the New York Entomological Society* 73: 33–38.
- Alexander CP (1970) Undescribed species of Japanese Tipulidae (Diptera). Part III. *Transactions of the Shikoku Entomological Society* 10: 67–78.

- Brinkmann R (1991) Zur Habitatpräferenz und Phanologie der Limoniidae, Tipulidae und Cylandrotomidae (Diptera) im Bereich eines norddeutschen Tieflandbaches. Faunistisch-Ökologische Mitteilungen (Supplement 11): 1–156.
- Coquillett DW (1900) Papers from the Harriman Alaska expedition. IX. Entomological results (3): Diptera. Proceedings of the Washington Academy of Sciences 2: 389–464.
- Coquillett DW (1905) New nematocerous Diptera from North America. Journal of the New York Entomological Society 13: 56–69.
- Cumming JF, Wood DM (2017) Adult morphology and terminology. In: Kirk-Spriggs AH, Sinclair BJ (Eds) Manual of Afrotropical Diptera. Volume 1. Introductory chapters and keys to Diptera families. Suricata. Vol. 4. South African National Biodiversity Institute, Pretoria, 89–133.
- de Jong H (2017) 14. Limoniidae and Tipulidae (crane flies). In: Kirk-Spriggs AH, Sinclair BJ (Eds) Manual of Afrotropical Diptera. Volume 2. Nematocerous Diptera and lower Brachycera. Suricata 5. South African National Biodiversity Institute, Pretoria, 427–477.
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3: 294–297.
- Krivosheina NP, Krivosheina MG (2011) Key to terrestrial crane-fly larvae (Diptera, Limoniidae, Peditiidae) of Russia. KMK Scientific Press, Moscow, 294 pp. [material, morphology, biology in Russian, keys to families, subfamilies, genera, species in Russian and English]
- Lackschewitz P (1935) Zur Kenntnis der polyneuren Nematoceren (Dipt.) des nordlichen Norwegens. Tromsø Museums Arshefter 53(4): 3–27.
- Macquart PJM (1826) Insectes Diptères du nord de la France. [Tome I.] Tipulaires. Recueil des Travaux de la Société d'Amateurs des Sciences, de l'Agriculture et des Arts à Lille 1823–1824, 59–224. <https://doi.org/10.5962/bhl.title.8146>
- Nakamura T (2002) Diptera of the Nasu Imperial Villa, Tochigi, Japan. In: Tochigi Prefectural Museum (Ed.) Flora and Fauna of the Nasu Imperial Villa. Tochigi Prefectural Museum, Tochigi, Japan, 167–170.
- Nakamura T (2014) Family Limoniidae. In: Nakamura T, Saigusa T, Suwa M (Eds) Catalogue of the Insects of Japan. Volume 8 Diptera (Part 1 Nematocera – Brachycera Aschiza). Touka Shobo, Fukuoka, Japan, 9–53.
- Oosterbroek P (2022) Catalogue of the Craneflies of the World (Diptera, Tipuloidea: Peditiidae, Limoniidae, Cylandrotomidae, Tipulidae). <https://ccw.naturalis.nl/index.php> [Accessed on 2022-4-12]
- Osten Sacken CR (1869) Monographs of the Diptera of North America. Part IV. Smithsonian Miscellaneous Collections 8(219): [i–xii] 1–345.
- Petersen MJ, Gelhaus JK, Bernard EC (2004) New species and records of crane flies (Diptera, Tipuloidea) from Great Smoky Mountains National Park, Tennessee and North Carolina, U.S.A. Transactions of the American Entomological Society 130: 439–455. <https://doi.org/10.11646/zootaxa.1013.1.1>
- Pilipenko VE (2009) Limoniidae. In: Biologo-pochvennyĭ institute (Ed.) Insects of Lazovsky Nature Reserve. Russian Academy of Science Far Eastern Branch, Institute of Biology and Soil Science, Dalnauka, Vladivostok: 331–335. [in Russian]

- Pilipenko VE, Sidorenko VS (2006) Crane-flies (Diptera: Pediciidae, Limoniidae) of Kedrovaya Pad Nature Reserve. In: Makarchenko EA (Ed.) The flora and fauna of Kedrovaya Pad Nature Reserve. Dalnauka, Vladivostok, 140–151. [in Russian]
- Podėnas S (1999) *Ormosia* Rondani crane flies (Diptera, Limoniidae) from the Baltic amber. Acta Zoologica Lituanica 9(1): 183–200. <https://doi.org/10.1080/13921657.1999.10512276>
- Ratnasingham S, Hebert PD (2007) BOLD: The Barcode of Life Data System (<http://www.barcodinglife.org>). Molecular Ecology Notes 7(3): 355–364. <https://doi.org/10.1111/j.1471-8286.2007.01678.x>
- Ribeiro GC (2008) Phylogeny of the Limnophilinae (Limoniidae) and early evolution of the Tipulomorpha (Diptera). Invertebrate Systematics 22(6): 627–694. <https://doi.org/10.1071/IS08017>
- Savchenko EN (1979) Supplements and corrections to the limoniid-flies fauna (Diptera, Limoniidae) of south Kuriles and south Sakhalin. Vestnik Zoologii 1979(1): 23–29. [in Russian with English summary]
- Savchenko EN (1980) New or little-known species of Limoniidae (Diptera) from the Zailiyskij Alatau. Entomologicheskoe Obozrenie 59: 391–403. [in Russian]
- Savchenko EN (1983) Limoniidae of South Primorye. Akademiy Nauk Ukrainskoy SSR, I.I. Schmalhausen Institute of Zoology of Academy of Sciences of Ukraine, Naukova Dumka, Kiev, 1–156. [in Russian]
- Savchenko EN, Krivolutskaya GO (1976) Limoniidae of the south Kuril Islands and south Sakhalin. Akademii Nauk Ukrainskoj SSR, Kiev, 160 pp. [in Russian]
- Starý J, Brodo F (2009) Arctic species of the subgenus *Symplecta* sensu stricto (Diptera: Limoniidae). Canadian Entomologist 141(1): 1–30. <https://doi.org/10.4039/n08-031>
- Strobl PG (1895) Die Dipteren von Steiermark. III. Theil. Diptera Nemocera. Mitteilungen des Naturwissenschaftlichen Vereines für Steiermark 31: 121–246.

Three new species of the genus *Perinereis* (Annelida, Nereididae) from Egyptian coasts

Asmaa Haris Elgetany^{1,2}, Torsten H. Struck², Christopher J. Glasby^{3,4}

1 Zoology Department, Faculty of Science, Damietta University, New Damietta, Central zone, 34517, Egypt **2** Natural History Museum, University of Oslo, P.O. Box 1172, Blindern, 0318 Oslo, Norway **3** Museum and Art Gallery of the Northern Territory, PO Box 4646, Darwin NT 0800, Australia **4** Currently, Australia Museum, 1 William Street, Darlinghurst NSW 2010, Australia

Corresponding author: Asmaa Haris Elgetany (Asmaa_Haris@du.edu.eg), (asmaa_haris222@yahoo.com)

Academic editor: Greg Rouse | Received 10 June 2022 | Accepted 9 October 2022 | Published 29 November 2022

<https://zoobank.org/E32A945F-C97D-4E42-8C8C-E0BF823B22DA>

Citation: Elgetany AH, Struck TH, Glasby CJ (2022) Three new species of the genus *Perinereis* (Annelida, Nereididae) from Egyptian coasts. ZooKeys 1132: 163–188. <https://doi.org/10.3897/zookeys.1132.87629>

Abstract

Despite being one of the most common groups of polychaetes on intertidal shores, the genus *Perinereis* (Nereididae) is comparatively poorly known taxonomically, with confusion still existing due to the lack of comprehensive systematic studies. The systematics of *Perinereis* species from the intertidal Egyptian coasts of the Red Sea, Gulf of Suez and Suez Canal have been investigated using morphology and the mitochondrial barcoding marker cytochrome oxidase subunit I (COI). New sequence data was obtained for 102 *Perinereis* specimens and analysis included all publicly available COI data from other *Perinereis* species. The COI data indicate that monophyly of the *P. nuntia* species group is doubtful, as specimens identified in this species group from south-eastern Asia and Australia form a monophyletic group exclusive of the three new species described in this study from the Red Sea region. A morphometric character set (26 characters) was used to identify and characterize each specimen in the study. Three distinct morphospecies belonging to the *P. nuntia* species group were found, each differentiated by the number and type of paragnaths on pharyngeal areas V and VI, relative sizes of parapodial lobes, type of notochaetae and neurochaetae, and form of the neurochaetal falciger blades. The three morphospecies were well supported by COI data: two of the three new species, *Perinereis suzezensis* **sp. nov.** and *Perinereis fayedensis* **sp. nov.**, are closely similar to *P. nuntia* *sensu stricto*, while the other, *Perinereis damietta* **sp. nov.**, is similar to *P. heterodonta*. The new species are described and illustrated, and bring the number of species in *Perinereis* to 97. The new species are compared and contrasted to the closely similar *P. heterodonta*, *P. nuntia* and other congeners from the region.

Keywords

Integrative taxonomy, morphometrics, *Perinereis damietta* *sp. nov.*, *Perinereis fayedensis* *sp. nov.*, *Perinereis nuntia* species complex, *Perinereis suzezensis* *sp. nov.*, systematics

Introduction

The family Nereididae includes several highly variable species characterized by high intra-specific morphological variation especially associated with the pharynx (e.g., number and arrangement of paragnaths) or associated with the parapodia (relative proportions of lobes/ligules and form of chaetae) and coloration. Often these morphologically variable species also show differences in reproductive biology (Yoshida 1984; Hardege and Bartels-Hardege 1995) and have widespread distributions. Such species were recognized in the old taxonomic literature as ‘forms’ or ‘varieties’ of a species (e.g., Fauvel 1932), but today most are recognized as full species (Read and Fauchald 2022). More than other nereidid genera, *Perinereis* contains a number of ‘species-groups’ or ‘species complexes’ (e.g. Wilson 1993; Glasby et al. 2013), which have served to group like forms, although none have been shown to be monophyletic.

Perinereis Kinberg, 1865 is the second most species-rich genus in the family. It includes approximately 94 worldwide-distributed valid species (Villalobos-Guerrero 2019, Villalobos-Guerrero et al. 2021; Bakken et al. 2022; Conde-Vela 2022). Bakken and Wilson (2005) found that the genus was likely to be polyphyletic based on morphology; specifically, that *P. nuntia* Lamarck, 1818 together with *P. variodentata* Augener, 1913, and *P. vallata* Grube, 1857 were more closely related to *Neanthes/Nereis* species than to the type species of the genus. Subsequent molecular studies have either supported non-monophyly (Glasby et al. 2013), or refuted it (Alves et al. 2020), but both studies lacked in-depth taxon sampling as they did not specifically set out to test *Perinereis* monophyly. Tosuji et al. (2019) found support for a clade among western Pacific members of the *P. nuntia* species group, suggesting biogeographic support for splitting the species group, although as *P. nuntia* s. s. was not included in the analysis, the question of whether the species group is monophyletic remained open.

Members of *Perinereis* have been long recognized based primarily on the number and type of paragnaths on areas V and VI (e.g., Kinberg 1865; Grube 1878; Horst 1889). Specifically, *Perinereis* have well-separated, mostly conical paragnaths on both pharyngeal rings and bar-shaped (which are shield-shaped) paragnaths on area VI (Villalobos-Guerrero et al. 2021). Other important characters are the number of paragnath bands on area VII-VIII, the presence of merged paragnaths on area IV, the presence of isolated paragnaths on area III, type and relative sizes of parapodial lobes (particularly dorsal ligule), type and form of the neurochaetal spinigers and falcigers, and presence of teeth on the jaws (Hutchings et al. 1991; Bakken and Wilson 2005; Santos et al. 2005; Sampértegui et al. 2013). Those species having more than two bars (often many more) on area VI have been considered traditionally as varieties of *P. nuntia* (Savigny in Lamarck, 1818) (e.g., Fauvel 1919, 1921, 1932, 1953; Augener 1931). Nowadays, they are all recognized as species belonging to the *Perinereis nuntia* species complex (Wilson 1993; Wilson and Glasby 1993; Glasby and Hsieh 2006; Villalobos-Guerrero 2019).

Until recently, the *Perinereis nuntia* species group comprised 15 valid species (Wilson and Glasby 1993; Glasby and Hsieh 2006; Tosuji et al. 2019). It is characterized by the presence of an arc of bar-shaped (including shield-shaped) paragnaths (or a

mixture of bars/shields and cones) on area VI (Tosuji et al. 2019). Subsequent revision involving a broader re-examination of the *P. nuntia* species group has revealed a further two members, historically referred to under *Neanthes* Kinberg, 1865 [*Nereis* (*Nereis*) *latipalpa* Schmarda, 1861 from Cape Town, South Africa, and *Nereis* (*Neanthes*) *larentukana* Grube in Peters, 1881 from Larantuka, Flores, Indonesia (Villalobos-Guerrero 2019)]. In total, Villalobos-Guerrero recognized five new combinations, bringing to 20 the number of valid species in the *P. nuntia* species group.

The present study investigates the taxonomy of three putative species belonging to the *P. nuntia* species group sampled from the Gulf of Suez, Suez Canal, and the northern Red Sea using a detailed morphological study and the mitochondrial barcoding marker cytochrome oxidase subunit I (COI). We compare our material with other members of the species group originally described from the region, including *Perinereis nuntia* (type locality: Gulf of Suez) and *P. heterodonta* Gravier, 1899 (type locality: Red Sea, Obock, Gulf of Aden, Djibouti). Our results show that all three species are new to science: two of them, *P. suezensis* sp. nov. and *P. fayedensis* sp. nov. from Gulf of Suez (part of Red Sea), are closely similar to *P. nuntia*, while the other one, *P. damietta* sp. nov., from Hurghada (northern Red Sea), is more similar to *P. heterodonta*. The three species are described below.

Material and methods

Data collection and preservation

Sampling was carried out during the period of January 2015 to July 2017 from four localities along the intertidal zone of Egyptian coasts of the Red Sea, Gulf of Suez and Suez Canal (Fig. 1).

A section of the mid body was removed from the Red Sea specimens and stored in 96% ethanol for molecular analysis. The rest of the animal was fixed in 4% seawater formalin and stored in 70% ethanol for morphological studies.

Morphological examination

Specimens were studied and photographed using a stereo microscope, Leica MZ16, with a Planapo 1.0X and Canon EOS 500D, as well as a compound microscope, Leica DFC420 connected to a Leica Computer CTR600 and a DM600B camera. For morphological characterization, we grouped specimens into three putative species, and recorded 26 morphometric characters for a subset of 45 of the 102 specimens in total (Suppl. material 1, Table 1). Measurements included number of chaetigers, total body length (cm), jaw length (mm), width at chaetiger 10 excluding parapodia (cm), number of paragnaths on area I, area II (left), area II (right), area III, area IV (left), area IV (right), area IV, area V, area VI (left), area VI (right), and area VII–VIII, length of dorsal cirri (DC; along its ventral edge from the proximal junction with the DNL to the distal extremity) at chaetiger 10 (mm), length of dorsal notopodial ligule (DNL; along its dorsal edge from the proximal



Figure 1. Map of *Perinereis* species localities referred to in this study. Colored squares indicate different species: red – *Perinereis heterodonta*, green – *P. nuntia*, yellow – *P. damietta* sp. nov., *P. suezensis* sp. nov. and *P. fayedensis* sp. nov. (see Table 1). Map based on URL: <https://www.google.com/eg/maps/@18.940384,68.1599381,10852298m/data=!3m1!1e3?hl=en>.

junction with the DC to the distal extremity, as per Villalobos-Guerrero (2019: fig. 4e)) at chaetiger 10 (mm), ratio DC/DNL, length of dorsal cirri of one chaetiger between chaetigers 75–90 (mm), length of dorsal notopodial ligule of one chaetiger between chaetigers 75–90 (mm), ratio DC/DNL, length of postero-dorsal tentacular cirrus (as indicated by chaetiger reached when posteriorly extended), occurrence of subacicular heterogomph spiniger at chaetiger 10, occurrence of subacicular heterogomph spiniger at chaetigers 75–90, chaetiger of first occurrence of subacicular heterogomph spiniger. We also recorded the form of the notopodial glands in posterior parapodia, and the color pattern in preserved species. Observation of features on the non-everted pharynx required a longitudinal dissection in the mid-ventral oral region. Characters reported in the taxonomic descriptions are those of the holotype, with those of the paratypes in parentheses. Terminology for nereidid features followed Hylleberg et al. (1986), Bakken and Wilson (2005), Bakken et al. (2009), Villalobos-Guerrero and Bakken (2018), and Villalobos-Guerrero (2019).

Institutional abbreviations

Samples are deposited in the Damietta University - Faculty of Science (**DUFS**), Damietta, Egypt, and the Senckenberg Forschungsinstitut und Naturmuseum (**SMZ**), Frankfurt, Germany.

Table 1. Species used in this study with Sample ID for the new specimens and accession numbers for all specimens.

Genus	Species	Sample ID	Accession #	Genus	Species	Accession #
<i>Perinereis</i>	<i>damietta</i> sp. nov.	5-1	OP610122	<i>Perinereis</i>	<i>aibubitensis</i>	KC800611
<i>Perinereis</i>	<i>damietta</i> sp. nov.	5-2	OP610123	<i>Perinereis</i>	<i>aibubitensis</i>	KC800612
<i>Perinereis</i>	<i>damietta</i> sp. nov.	5-8	OP610124	<i>Perinereis</i>	<i>aibubitensis</i>	KC800613
<i>Perinereis</i>	<i>damietta</i> sp. nov.	5-10	OP610125	<i>Perinereis</i>	<i>aibubitensis</i>	KC800614
<i>Perinereis</i>	<i>damietta</i> sp. nov.	12-1B	OP610126	<i>Perinereis</i>	<i>aibubitensis</i>	KC840698
<i>Perinereis</i>	<i>damietta</i> sp. nov.	12-2B	OP610127	<i>Perinereis</i>	<i>aibubitensis</i>	KF611806
<i>Perinereis</i>	<i>damietta</i> sp. nov.	12-3B	OP610128	<i>Perinereis</i>	<i>aibubitensis</i>	KY129885
<i>Perinereis</i>	<i>damietta</i> sp. nov.	12-4B	OP610129	<i>Perinereis</i>	<i>aibubitensis</i>	MN256534
<i>Perinereis</i>	<i>damietta</i> sp. nov.	12-5B	OP610130	<i>Perinereis</i>	<i>aibubitensis</i>	MN256535
<i>Perinereis</i>	<i>damietta</i> sp. nov.	12-6B	OP610131	<i>Perinereis</i>	<i>aibubitensis</i>	MN256536
<i>Perinereis</i>	<i>damietta</i> sp. nov.	12-8B	OP610132	<i>Perinereis</i>	<i>aibubitensis</i>	MT511716
<i>Perinereis</i>	<i>damietta</i> sp. nov.	12-10B	OP610133	<i>Perinereis</i>	<i>aibubitensis</i>	MT511717
<i>Perinereis</i>	<i>damietta</i> sp. nov.	16-1	OP610134	<i>Perinereis</i>	<i>aibubitensis</i>	MT511718
<i>Perinereis</i>	<i>damietta</i> sp. nov.	16-2	OP610135	<i>Perinereis</i>	<i>aibubitensis</i>	MT712474
<i>Perinereis</i>	<i>damietta</i> sp. nov.	16-3	OP610136	<i>Perinereis</i>	<i>aibubitensis</i>	MW593148
<i>Perinereis</i>	<i>damietta</i> sp. nov.	16-4	OP610137	<i>Perinereis</i>	<i>anderssoni</i>	MH143495
<i>Perinereis</i>	<i>damietta</i> sp. nov.	R4-1	OP610138	<i>Perinereis</i>	<i>anderssoni</i>	MH143497
<i>Perinereis</i>	<i>damietta</i> sp. nov.	R4-2	OP610139	<i>Perinereis</i>	<i>anderssoni</i>	MH143498
<i>Perinereis</i>	<i>damietta</i> sp. nov.	R4-3	OP610140	<i>Perinereis</i>	<i>anderssoni</i>	MH143502
<i>Perinereis</i>	<i>damietta</i> sp. nov.	R6-1	OP610141	<i>Perinereis</i>	<i>anderssoni</i>	MH143503
<i>Perinereis</i>	<i>damietta</i> sp. nov.	R6-2	OP610142	<i>Perinereis</i>	<i>anderssoni</i>	MH143504
<i>Perinereis</i>	<i>damietta</i> sp. nov.	R6-3	OP610143	<i>Perinereis</i>	<i>anderssoni</i>	MH143507
<i>Perinereis</i>	<i>damietta</i> sp. nov.	R8-1	OP610144	<i>Perinereis</i>	<i>anderssoni</i>	MH143508
<i>Perinereis</i>	<i>damietta</i> sp. nov.	R8-2	OP610145	<i>Perinereis</i>	<i>anderssoni</i>	MH143514
<i>Perinereis</i>	<i>damietta</i> sp. nov.	R8-3	OP610146	<i>Perinereis</i>	<i>anderssoni</i>	MH143516
<i>Perinereis</i>	<i>damietta</i> sp. nov.	R8-5	OP610147	<i>Perinereis</i>	<i>anderssoni</i>	MH143520
<i>Perinereis</i>	<i>damietta</i> sp. nov.	R8-6	OP610148	<i>Perinereis</i>	<i>anderssoni</i>	MH143522
<i>Perinereis</i>	<i>damietta</i> sp. nov.	R8-7	OP610149	<i>Perinereis</i>	<i>brevicirris</i>	JX503024
<i>Perinereis</i>	<i>damietta</i> sp. nov.	R8-8	OP610150	<i>Perinereis</i>	<i>brevicirris</i>	JX966314
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	1-9	OP612948	<i>Perinereis</i>	<i>brevicirris</i>	KC800628
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	2-3	OP612949	<i>Perinereis</i>	<i>brevicirris</i>	KC800630
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	2-4	OP612950	<i>Perinereis</i>	<i>brevicirris</i>	KC800632
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	2-5	OP612951	<i>Perinereis</i>	<i>camiguinoides</i>	KF850496
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	2-6	OP612952	<i>Perinereis</i>	<i>cultrifera</i>	KC800624
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	2-7	OP612953	<i>Perinereis</i>	<i>cultrifera</i>	KC800625
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	2-8	OP612954	<i>Perinereis</i>	<i>cultrifera</i>	KC800627
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	5-4	OP612955	<i>Perinereis</i>	<i>cultrifera</i>	KR916906
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	5-5	OP612956	<i>Perinereis</i>	<i>cultrifera</i>	KR916907
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	5-6	OP612957	<i>Perinereis</i>	<i>cultrifera</i>	KR916908
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	5-7	OP612958	<i>Perinereis</i>	<i>cultrifera</i>	KR916909
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	5-9	OP612959	<i>Perinereis</i>	<i>cultrifera</i>	KR916910
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	7-5B	OP612960	<i>Perinereis</i>	<i>cultrifera</i>	KR916911
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	7-7B	OP612961	<i>Perinereis</i>	<i>cultrifera</i>	KR916912
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	7-8B	OP612962	<i>Perinereis</i>	<i>cultrifera</i>	KY129882
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	7-9B	OP612963	<i>Perinereis</i>	<i>cultrifera</i>	KY129883
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	7-10B	OP612964	<i>Perinereis</i>	<i>cultrifera</i>	MN256544
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	8-1	OP612965	<i>Perinereis</i>	<i>cultrifera</i>	MN256545
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	8-2	OP612966	<i>Perinereis</i>	<i>cultrifera</i>	NC_051994
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	8-3	OP612967	<i>Perinereis</i>	<i>curvata</i>	MW277905

Genus	Species	Sample ID	Accession #	Genus	Species	Accession #
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	8-4	OP612968	<i>Perinereis</i>	<i>euini</i>	KY249122
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	8-5	OP612969	<i>Perinereis</i>	<i>euini</i>	KY249123
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	8-6	OP612970	<i>Perinereis</i>	<i>euini</i>	KY249124
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	8-7	OP612971	<i>Perinereis</i>	<i>falklandica</i>	HQ705184
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	8-8	OP612972	<i>Perinereis</i>	<i>falklandica</i>	HQ705185
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	8-9	OP612973	<i>Perinereis</i>	<i>gualpensis</i>	HQ705186
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	8-10	OP612974	<i>Perinereis</i>	<i>gualpensis</i>	HQ705187
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	10-3B	OP612975	<i>Perinereis</i>	<i>gualpensis</i>	HQ705188
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	10-4B	OP612976	<i>Perinereis</i>	<i>belleri</i>	JX420256
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	10-5B	OP612977	<i>Perinereis</i>	<i>linea</i>	MT511711
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	10-6B	OP612978	<i>Perinereis</i>	<i>linea</i>	MT511712
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	10-7B	OP612979	<i>Perinereis</i>	<i>linea</i>	MT511713
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	10-8B	OP612980	<i>Perinereis</i>	<i>linea</i>	MT511714
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	10-10B	OP612981	<i>Perinereis</i>	<i>linea</i>	MT511715
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	11-1B	OP612982	<i>Perinereis</i>	<i>longidonta</i>	HQ705190
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	11-3B	OP612983	<i>Perinereis</i>	<i>longidonta</i>	HQ705191
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	11-4B	OP612984	<i>Perinereis</i>	<i>nuntia</i>	JX420257
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	11-5B	OP612985	<i>Perinereis</i>	<i>nuntia</i>	JX644015
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	12-9B	OP612986	<i>Perinereis</i>	<i>nuntia</i>	MH337359
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	14-1	OP612987	<i>Perinereis</i>	<i>seridentata</i>	JF293314
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	14-2	OP612988	<i>Perinereis</i>	<i>singaporiensis</i>	EU835665
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	14-3	OP612989	<i>Perinereis</i>	sp.	EU352319
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	14-4	OP612990	<i>Perinereis</i>	sp.	KR916903
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	14-5	OP612991	<i>Perinereis</i>	sp.	KR916904
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	14-6	OP612992	<i>Perinereis</i>	sp.	KR916905
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	14-7	OP612993	<i>Perinereis</i>	sp.	KX525487
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	14-8	OP612994	<i>Perinereis</i>	sp.	KX525497
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	14-9	OP612995	<i>Perinereis</i>	sp.	KX525498
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	14-10	OP612996	<i>Perinereis</i>	sp.	KX525499
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	18-1	OP612997	<i>Perinereis</i>	sp.	KX840014
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	18-2	OP612998	<i>Perinereis</i>	sp.	MH143496
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	18-3	OP612999	<i>Perinereis</i>	sp.	MH143499
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	18-4	OP613000	<i>Perinereis</i>	sp.	MH143500
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	18-5	OP613001	<i>Perinereis</i>	sp.	MH143501
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	18-6	OP613002	<i>Perinereis</i>	sp.	MH143505
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	18-7	OP613003	<i>Perinereis</i>	sp.	MH143506
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	18-8	OP613004	<i>Perinereis</i>	sp.	MH143509
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	18-9	OP613005	<i>Perinereis</i>	sp.	MH143510
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	18-10	OP613006	<i>Perinereis</i>	sp.	MH143511
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	R5-1	OP613007	<i>Perinereis</i>	sp.	MH143512
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	R5-2	OP613008	<i>Perinereis</i>	sp.	MH143513
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	R5-3	OP613009	<i>Perinereis</i>	sp.	MH143515
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	R5-4	OP613010	<i>Perinereis</i>	sp.	MH143517
<i>Perinereis</i>	<i>suezensis</i> sp. nov.	R6-4	OP613011	<i>Perinereis</i>	sp.	MH143518
<i>Perinereis</i>	<i>fayedensis</i> sp. nov.	2-2	OP605755	<i>Perinereis</i>	sp.	MH143519
<i>Perinereis</i>	<i>fayedensis</i> sp. nov.	5-3	OP605756	<i>Perinereis</i>	sp.	MH143521
<i>Perinereis</i>	<i>fayedensis</i> sp. nov.	7-4B	OP605757	<i>Perinereis</i>	sp.	MH143523
<i>Perinereis</i>	<i>fayedensis</i> sp. nov.	7-6B	OP605758	<i>Perinereis</i>	sp.	MH143524
<i>Perinereis</i>	<i>fayedensis</i> sp. nov.	10-1B	OP605759	<i>Perinereis</i>	sp.	MH143525
<i>Perinereis</i>	<i>fayedensis</i> sp. nov.	10-2B	OP605760	<i>Perinereis</i>	sp.	MH143526
<i>Perinereis</i>	<i>fayedensis</i> sp. nov.	10-9B	OP605761	<i>Perinereis</i>	sp.	MN823962
<i>Perinereis</i>	<i>fayedensis</i> sp. nov.	11-2B	OP605762	<i>Perinereis</i>	sp.	MT528267

Genus	Species	Sample ID	Accession #	Genus	Species	Accession #
<i>Perinereis</i>	<i>fayedensis</i> sp. nov.	12-7B	OP605763	<i>Perinereis</i>	sp.	OK430976
<i>Perinereis</i>	<i>aibubitensis</i>		GU362686	<i>Perinereis</i>	<i>suluana</i>	JX392072
<i>Perinereis</i>	<i>aibubitensis</i>		JX503021	<i>Perinereis</i>	<i>suluana</i>	JX420245
<i>Perinereis</i>	<i>aibubitensis</i>		JX503022	<i>Perinereis</i>	<i>suluana</i>	JX420246
<i>Perinereis</i>	<i>aibubitensis</i>		JX503023	<i>Perinereis</i>	<i>suluana</i>	JX420247
<i>Perinereis</i>	<i>aibubitensis</i>		JX661442	<i>Perinereis</i>	<i>suluana</i>	JX420248
<i>Perinereis</i>	<i>aibubitensis</i>		JX661443	<i>Perinereis</i>	<i>suluana</i>	JX420250
<i>Perinereis</i>	<i>aibubitensis</i>		JX661444	<i>Perinereis</i>	<i>suluana</i>	JX420251
<i>Perinereis</i>	<i>aibubitensis</i>		JX661445	<i>Perinereis</i>	<i>suluana</i>	JX420252
<i>Perinereis</i>	<i>aibubitensis</i>		JX661446	<i>Perinereis</i>	<i>suluana</i>	JX420253
<i>Perinereis</i>	<i>aibubitensis</i>		JX661447	<i>Perinereis</i>	<i>suluana</i>	JX420254
<i>Perinereis</i>	<i>aibubitensis</i>		JX661448	<i>Perinereis</i>	<i>suluana</i>	JX420255
<i>Perinereis</i>	<i>aibubitensis</i>		JX661449	<i>Perinereis</i>	<i>vallata</i>	HQ705192
<i>Perinereis</i>	<i>aibubitensis</i>		JX661450	<i>Perinereis</i>	<i>vallata</i>	HQ705196
<i>Perinereis</i>	<i>aibubitensis</i>		JX661451	<i>Perinereis</i>	<i>vallata</i>	JX676119
<i>Perinereis</i>	<i>aibubitensis</i>		JX661452	<i>Perinereis</i>	<i>vallata</i>	JX676143
<i>Perinereis</i>	<i>aibubitensis</i>		JX661453	<i>Perinereis</i>	<i>vallata</i>	MT511721
<i>Perinereis</i>	<i>aibubitensis</i>		JX661454	<i>Perinereis</i>	<i>vallata</i>	MT511722
<i>Perinereis</i>	<i>aibubitensis</i>		JX661455	<i>Perinereis</i>	<i>vancaurica</i>	MT511719
<i>Perinereis</i>	<i>aibubitensis</i>		JX661456	<i>Perinereis</i>	<i>wilsoni</i>	KC800623
<i>Perinereis</i>	<i>aibubitensis</i>		JX661457	<i>Perinereis</i>	<i>wilsoni</i>	KC800629
<i>Perinereis</i>	<i>aibubitensis</i>		JX661458	<i>Perinereis</i>	<i>wilsoni</i>	KC800631
<i>Perinereis</i>	<i>aibubitensis</i>		JX661459	<i>Perinereis</i>	<i>wilsoni</i>	KY129887
<i>Perinereis</i>	<i>aibubitensis</i>		JX661460	<i>Perinereis</i>	<i>wilsoni</i>	KY129888
<i>Perinereis</i>	<i>aibubitensis</i>		JX661461	<i>Perinereis</i>	<i>wilsoni</i>	KY129889
<i>Perinereis</i>	<i>aibubitensis</i>		JX661462	<i>Perinereis</i>	<i>wilsoni</i>	MN256541
<i>Perinereis</i>	<i>aibubitensis</i>		JX661463	<i>Perinereis</i>	<i>wilsoni</i>	MN256542
<i>Perinereis</i>	<i>aibubitensis</i>		JX661464	<i>Perinereis</i>	<i>wilsoni</i>	MN256543
<i>Perinereis</i>	<i>aibubitensis</i>		JX661465	<i>Dendronereis</i>	<i>chipolini</i>	MW5320841
<i>Perinereis</i>	<i>aibubitensis</i>		JX661466	<i>Hediste</i>	<i>japonica</i>	MN876864
<i>Perinereis</i>	<i>aibubitensis</i>		JX661467	<i>Namalycastis</i>	<i>abiuma</i>	KU351089
<i>Perinereis</i>	<i>aibubitensis</i>		JX661468	<i>Platynereis</i>	<i>dumerilii</i>	AF178678
<i>Perinereis</i>	<i>aibubitensis</i>		JX661469			

Molecular study

Genomic DNA was extracted from three to four segments of the middle section of each worm using the DNeasy Tissue Kit (Qiagen) according to manufacturers' instructions with at least two elution steps to increase the amount of DNA. For each individual, the nucleotide sequences of the mitochondrial COI were amplified using the primer pair LCO1490JJ (forward, 5'-CHA CWA AYC ATA AAG ATA RYG G-3') and HCO2198JJ (reverse, 5'-AWA CTT CVG GRT GVC CAA ARA ATC A-3') (Astrin and Stuben 2008). The PCR was carried out in a reaction volume of a 20 µl solution each with 3.8 µl water, 2 µl Q solution, 10 µl Qiagen Multiplex-Solution, 1.6 µl 10 pmol/µl LCO1490JJ, 1.6 µl 10 pmol/µl HCO2198JJ and 1 µl template DNA. PCR parameters were 95 °C for 15min, 15 cycles of (94 °C for 35s, 55 °C for 90s with "−1 °C decrease per cycle", 72 °C for 90s), 25 cycle of (94 °C for 35s, 50 °C for 90s,

72 °C for 90s) and 72 °C for 10min. The PCR product was purified using ExoProStar (Qiagen, Hilden, Germany). Both strands were sequenced using Sanger sequencing at Macrogen Inc. (South Korea). Sequences were assembled into contigs using Codon-Code Aligner v. 6.0.2 (Centerville, MA). The 102 new COI sequences were deposited at National Center for Biotechnology Information (NCBI) (Table 1).

For the phylogenetic analyses, we included all publicly available COI data from other specimens of *Perinereis* as well as five nereidid species, who have a complete mitochondrial genome sequenced, as outgroup taxon (Table 1). The sequences were aligned using the multiple sequence alignment software MAFFT v. 7.310 (Katoh and Standley 2013) with an automatic selection of the best alignment method and the option ‘globalpair’. The selected alignment strategy was FFT-NS-i plus an iterative refinement method of two cycles. The 5' and 3' prime ends of the resulting aligned, where trimmed until the first position at each having at least 90% consensus (i.e., < 10% of taxa with missing data at the ends). The final dataset had 267 sequences and 583 nucleotide positions. A maximum likelihood (ML) analysis was conducted with IQ-TREE v. 1.6.12 using the automatically selecting the best-fitting substitution model and an ultrafast bootstrap analysis with 1000 pseudoreplicates (Nguyen et al. 2015; Kalyaanamoorthy et al. 2017; Thi Hoang et al. 2018). The selected model was GTR+F+I+G4 (GTR substitution model with ML estimated frequencies, a proportion of invariant sites and a Gamma distribution with four categories).

Results

Phylogenetic analysis

The ML tree (logL = -11297.8710) showed that the genus *Perinereis* is probably not monophyletic as the outgroup *Hediste japonica* Izuka, 1908 grouped within the genus (Fig. 2), but bootstrap support is low for most basal nodes with values below 95. While the monophyly of several *Perinereis* species is strongly supported with values equal to or more than 95, the monophyly of the *P. nuntia* species group and of several other species seem to be doubtful or, alternatively, specimens have been wrongly assigned to species. For example, the specimen JX644015 of *P. nuntia* is placed within *P. brevicirris* (Grube, 1866) (see Remarks for *Perinereis suzezensis* sp. nov.). Other cases comprise species, for example, of *P. aibuhitensis* (Grube, 1878), *P. suluana* (Horst, 1924), *P. brevicirris*, *P. wilsoni* (Glasby & Hsieh, 2006), *P. cultrifera* (Grube, 1840), or *P. euiini* (Park & Kim, 2017). Hence, the requirement for a thorough taxonomic revision of the genus is further supported. The specimens collected for this study were grouped into three strongly supported clades, which were supported with bootstrap values of 99, 99 and 100, respectively (boxes in Fig. 2A, C). Herein, we describe them as new species, *P. suzezensis* sp. nov., *P. fayedensis* sp. nov. and *P. damietta* sp. nov. Moreover, *P. suzezensis* sp. nov. and *P. fayedensis* sp. nov. are sister groups to each other with a maximal bootstrap of 100.

A

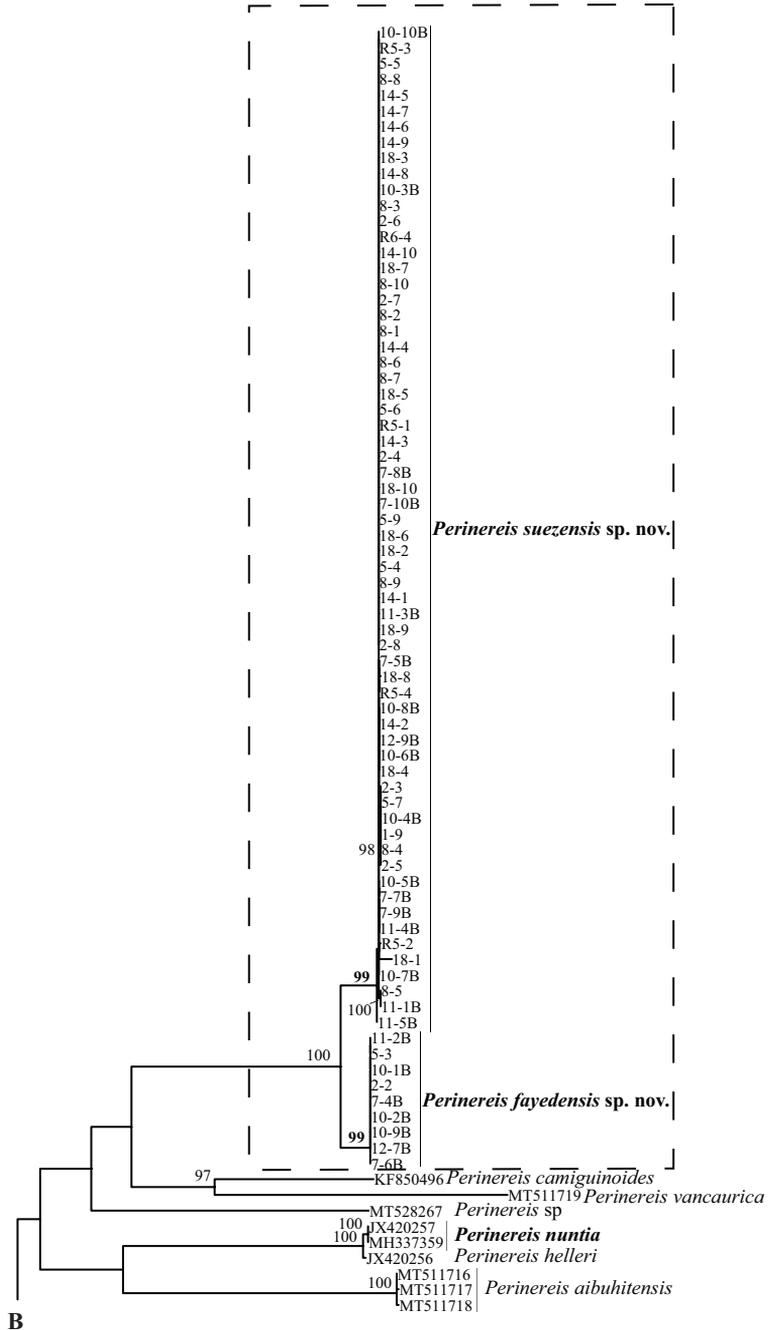


Figure 2. ML tree (logL = -11297.8710) of the *Perinereis* species in this analysis shown in three parts (A, B, C). The points, where we cut the branches, are indicated by letters. The new species *P. suezensis* sp. nov., *P. fayedensis* sp. nov., and *P. damietta* sp. nov. are highlighted by boxes and in bold. *Perinereis nuntia* is also highlighted in bold. Bootstrap values equal to and more than 95 indicating strong support are given at the branches. The three relevant bootstrap values are highlighted in bold. The scale bar shows substitutions/position.

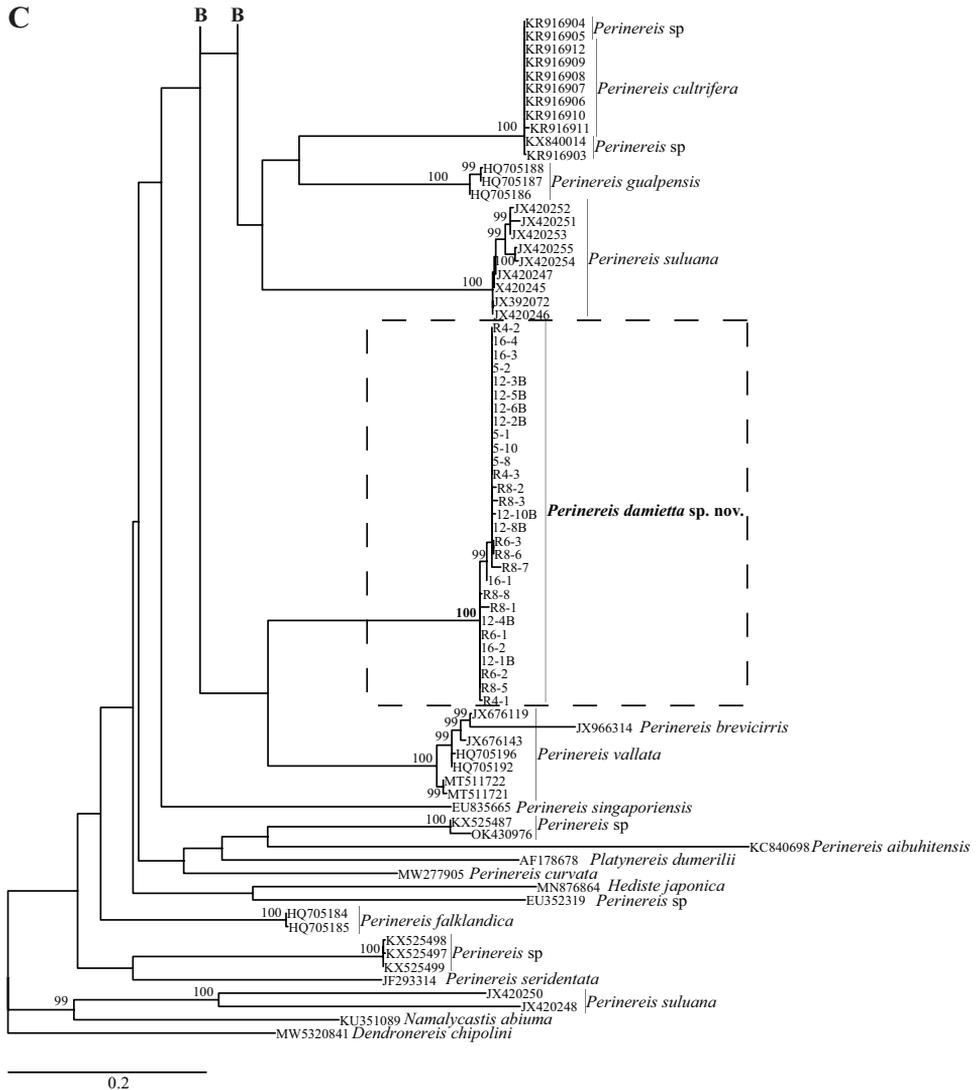


Figure 2. Continued.

Taxonomic account

Nereididae Blainville, 1818

Nereidinae Blainville, 1818

Perinereis Kinberg, 1856

Perinereis nuntia species complex

Perinereis nuntia species complex Wilson & Glasby, 1993: 259. – Glasby and Hsieh 2006: 558. – Villalobos-Guerrero 2019: 468.

Diagnosis. *Perinereis* species having conical paragnaths on all areas (rarely absent on area V), except area VI with long bars, which can be shield-shaped or pyramidal paragnaths, arranged in a single-arched row; area V with paragnaths displaced posteriorly (on everted proboscis) to those on area VI; area IV rarely with merged paragnaths.

Remarks. We have restricted the diagnosis of the species complex to include only unique diagnostic features. Some new characters introduced by Villalobos-Guerrero (2019) describing the faint ridges and furrows of the dorsal oral ring may prove to be useful when broader comparisons can be made. However, at this stage we consider that the form of the pharyngeal ridges and furrows is too closely allied to underlying musculature, and therefore could be unduly influenced by the fixation process and length of time in preservative. Similarly, the form (and length) of the deeply embedded paired nuchal organs may prove to be useful when more comparative data are available. However, observation of that character depends heavily on state of preservation (e.g., they are seen more clearly in specimens relaxed before preservation); in the present specimens the nuchal organs were hidden under the anterior edge of the apodous segment and thus not visible externally. Pharyngeal morphologies are reported herein by describing the form and arrangement of paragnaths on the ridges and in the furrows of the pharynx. The form and arrangement of paragnaths on area VI is unique to the genus (and family) and serves as the easiest way to recognize a member of the species complex. However, Tosuji et al. (2019) have demonstrated that in at least two East Asian species of the complex, the number of bars increases with the growth of individuals (fragmentation of the long bars produces multiple shorter bars (= shield-shaped paragnaths)). Therefore, this character should be used cautiously for species identification across the group, and comparisons are best made between individuals of similar size until we have a better understanding of the processes involved.

***Perinereis suezensis* sp. nov.**

<https://zoobank.org/E765642E-72D6-41FD-AB9D-C9607F3E48CB>

Fig. 3

Material examined. Holotype: DUF5 067 Al-Adabiya; west of Port Taofik, Gulf of Suez (Red Sea), intertidal, under coarse sands, at 29°56'06.0"N, 32°28'36.6"E, collection date (15.01.2015) **Paratypes:** 13 specimens (DUF5 057-066, 068-070) from Al-Qantara, Suez Canal, intertidal, muddy sand bottom, at 30°50'31.5"N, 32°18'54.8"E, Fayed, western shore of Great Bitter Lake, intertidal, silty mud bottom at 30°20'18.0"N, 32°18'14.9"E, and Al-Adabiya (same collection details as holotype). Collection dates (18.02.2015/ 15.01.2015/ 01.07.2017).

Non-type material. 2 specimens (SMZ unregistered), Hurghada, Egypt (northern Red Sea), at 27°15'42.0"N, 33°48'44.7"E, intertidal, under stones, St. 9a, '3192', det. as *Nereis* sp., collected 9.01.1992

Description. Holotype (DUF5 067) not complete, 53 chaetigers, 50 mm in length, 2 mm wide at chaetiger 10 **Paratypes** with 33–88 chaetigers, 32–81 mm long,

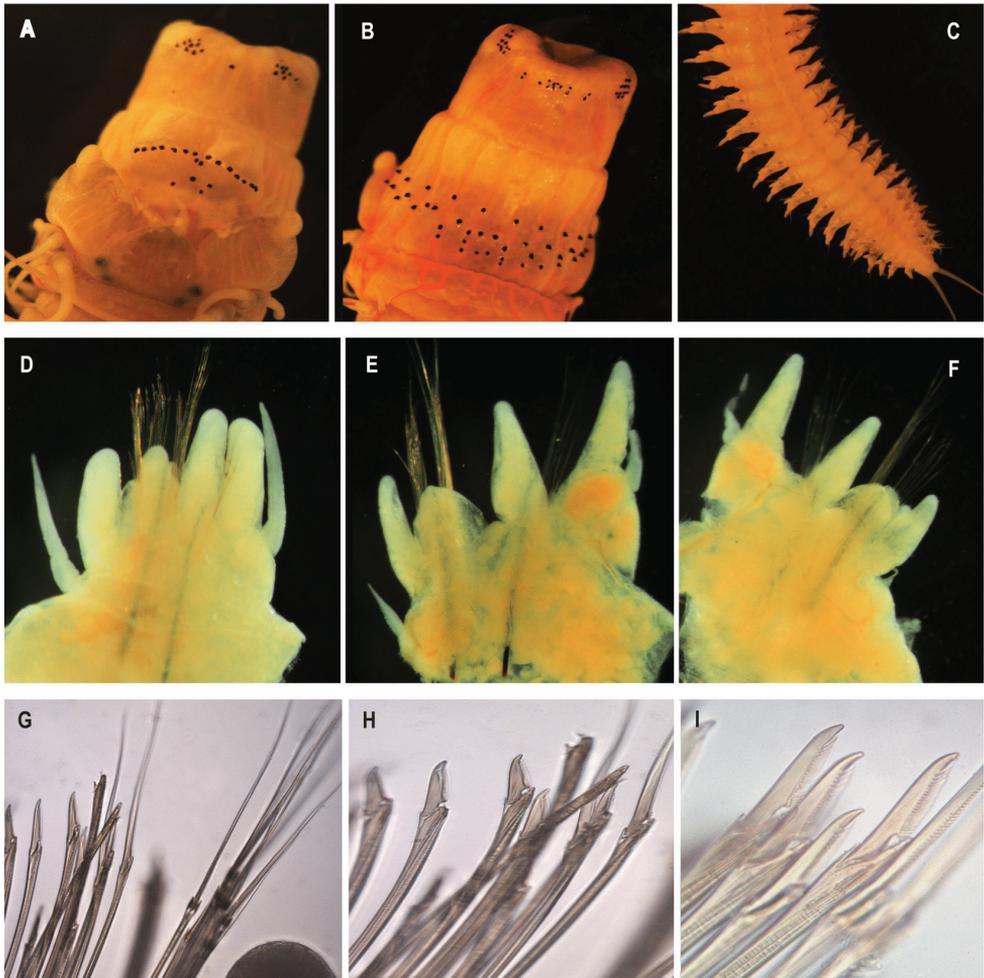


Figure 3. *Perinereis suezensis* sp. nov. All pictures are from the holotype if not stated otherwise **A** anterior end, maxillary apparatus, dorsal view **B** anterior end, maxillary apparatus, ventral view **C** posterior end, ventral view **D** right parapodium, posterior view, chaetiger 7 **E** right parapodium, anterior view, chaetiger 33 **F** right parapodium, anterior view, chaetiger 64 **G** chaetal bundle of a right parapodium homogomph spiniger, heterogomph spiniger & heterogomph falciger, chaetiger 7 **H** neuropodial sub-acicular heterogomph falciger, chaetiger 7 **I** heterogomph falciger, chaetiger 7.

2.0–4.5 mm wide at chaetiger 10. Epidermis with orange pigmentation on anterior dorsum in some preserved paratypes.

Prostomium with entire anterior margin; as wide as long. Antennae closely set, as long as $\sim 1/3$ length of prostomium. Eyes black, anterior pair set slightly further apart than posterior pair; lenses not obvious.

Apodous segment $\sim 1.2\times$ or $1.6\times$ longer than chaetiger 1. Posterodorsal tentacular cirri extending back to chaetiger 6 (6–7).

Pharynx with jaws translucent, red-brown, with 7 (7–8) teeth. Paragnaths black. Area I with 2 (1–5) conical paragnaths; area II conical paragnaths with 5 (5–10) on left and 8 (7–10) on right, in a triangular patch; area III with 10 (9–17) conical paragnaths in 2–3 rows, with two laterally isolated paragnaths; area IV conical paragnaths with 16 (11–19) on left, 13 (9–16) on right, in two or three rows, in elongated triangle; area V with 4 (2–4) conical paragnaths interspersed with one or two bars, set well proximal (on everted proboscis) to line of area VI paragnaths; area VI with 15 (14–21), shield-shaped bars with pointed tips (very close in appearance to cones), arranged in one arc, with the right and left rows almost touching; area VII–VIII with 44 (37–44) conical paragnaths arranged in a single band of two rows laterally to three or four rows deep medially (Fig. 3A, B; Table 2). Paragnath-free region between areas VI and VII–VIII broad, ca. as wide as palpopore; paragnaths of VII–VIII not visible in dorsal view (Fig. 3A).

Anterior notopodia with conical dorsal and median ligules of equal length in anterior body; dorsal ligule slightly longer in mid- and posterior body. Superior lobes absent. DC length 1.1 (1.0–1.2) × DNL length anteriorly (chaetigers 10–20); posteriorly DC length 1.09 (1.0–1.3) × length of DNL length (chaetigers 75–90). DC and DNL of mid-body parapodia proportionally similar to those of posterior parapodia (Fig. 3D–F).

Dorsal notopodial ligule larger than ventral notopodial ligule anteriorly and posteriorly. Neuropodia with inferior and postchaetal lobes, ventral ligule and ventral cirri. Neuropodial postchaetal lobe lowly rounded, not projecting beyond end of acicular ligule. Ventral neuropodial ligule subconical, ca. as long as median ligule throughout. Ventral cirri extending laterally to reach tip of ventral neuropodial ligule anteriorly, extending to ~ 1/4 length of ventral neuropodial ligule posteriorly (Fig. 3D–F).

Notochaetae with homogomph spinigers throughout, blades long; teeth short. Neurochaetae in upper fascicle with homogomph spinigers with long blades; one heterogomph falciger with short blades throughout, blades serrated. Neurochaetae in lower fascicle with heterogomph falcigers, blades short and thick, teeth long; and two or three heterogomph spinigers, median long blades, teeth short present throughout body. Aciculae black, single in each ramus (Fig. 3G–I).

Pygidium with anal cirri extending to last 6 (6–7) chaetigers, 5 (5–7) mm long, whitish cream without any pigmentation (Fig. 3C).

Variation (non-type material). Two specimens: one complete with 105 chaetigers, 57 mm long and 2.8 mm wide, and another with regenerating tail, 107 chaetigers, 71 mm long and 4.3 mm wide. Apodous segment ~ 1.3–1.8× longer than chaetiger 1. Posterodorsal tentacular cirri extending back to chaetigers 5 and 6. Jaws with 4–7 teeth. Paragnaths count: area I with 2; area II with 8–17 on left and 9–17 on right; area III with 11 or 12 in two or three rows; area IV with 17 or 18 on both sides, in two or three rows; area V with three or four; area VI with 8–12 on left and 8–11 on right, shield-shaped bars with pointed tips and cones arranged in one row with the right and left side rows almost touching each other; area VII–VIII with 47 or 48, arranged in a single band of two rows laterally to three or four rows deep medially. Dorsal cirrus length ~ 0.8× length of dorsal notopodial ligule anteriorly and 0.7–0.9× length of dorsal notopodial ligule posteriorly. Ventral cirri extending laterally to reach tip or half-length of ventral

Table 2. Comparison of key characters between forms resembling *P. heterodonta* (pale grey) and *Perinereis nuntia* (dark grey) in the Red Sea, the Gulf of Aden, and the Arabian (= Persian) Gulf. Abbreviations: AIII = Area III; AV = Area V; AVI Area VI; AVII-VIII = Areas VII and VIII; p-dTC = posterior extension of postero-dorsal tentacular cirri (chaetiger); ratio of lengths of dorsal cirri v dorsal notopodial lobe in posterior chaetigers; HS, presence (p) or absence (a) of heterogomph spinigers in anterior neuropodia; NA = data not available.

Species	Type locality	AIII (lateral group p/a)	AV	AVI	AVII-VIII	p-dTC	p-DC:DNL	HS	Reference
<i>heterodonta</i> sensu stricto	Djibouti	6-7 irregular cluster	0	10-16	18	5	NA	a	Gravier (1899)
<i>heterodonta</i> sensu stricto	Gulf of Oman	8-14 (p) cluster	0-1	14-24	20-35	1-6	0.6-1x	a	Yousefi et al. (2011); CJG pers. obs. 2021
<i>Perinereis damietta</i> sp. nov.	Gulf of Suez	3-9 (one transverse row)	0-1	24-40	16-32	2-4	1.1-1.2	a	Present paper
<i>djiboutiensis</i>	Djibouti	small rectangular patch (p)	0	6-7	NA (3 rows)	10-15	NA (DC > DNL)	NA	Fauvel (1919)
<i>nuntia</i> sensu stricto	Gulf of Suez, Red Sea	15	3(2-4)	10-12 (8-10)	41 (36-50)	(4-6)	4-5X (3-4X)	p	Savigny in Lamarck (1818); Villalobos-Guerrero (2019) [in parentheses]
<i>nuntia</i> sensu Wilson and Glasby 1993	'Red Sea'	8-14 (p)	3-4	8-13	24-31	6-14	~1.2	p	Wilson and Glasby (1993)
<i>nuntia</i> sensu Yousefi et al. 2011	Gulf of Oman	9-15	3	13-20	36-58	8-14	2X	p	Yousefi et al. (2011); CJG pers. obs. 2021
<i>Perinereis suzezensis</i> sp. nov.	Gulf of Suez, Red Sea	9-17 (p)	2-4	14-21	37-44	6-7	1.0-1.3X	p	Present paper
<i>Perinereis fayedensis</i> sp. nov.	Gulf of Suez, Red Sea	2-5 (one transverse row)	1-4	14-17	28-40	6-8	1.1-1.2X	p	Present paper

neuropodial ligule anteriorly. Neurochaetae in upper fascicle with 1-3 heterogomph falcigers. Neurochaetae in lower fascicle with 1-4 heterogomph spinigers, rarely absent.

Distribution and habitat. Gulf of Suez, Suez Canal including Great Bitter Lake, northern Red Sea; intertidal sand and mud, under stones.

Etymology. The new species is named after the port city of Suez (Egyptian Arabic pronunciation: (سويسل)) located on the north coast of the Gulf of Suez.

Remarks. The molecular data place *P. suzezensis* sp. nov. clearly apart from all other species and the monophyly of the species is very well supported by a bootstrap value of 99 (Fig. 2A). Not considering identical sequences between specimens within each species, the average genetic distance based on the branch length in the tree to its sister-taxon, *P. fayedensis* sp. nov., is 6.65% ($\pm 0.60\%$), while the average genetic distance within *P. suzezensis* is only 0.24% ($\pm 0.37\%$). Hence, there is a clear gap in the genetic distances.

In addition to our sequences, only three additional COI sequences for *P. nuntia* have been published: JX420257 (Indonesia), JX644015 (South Korea), and MH337359 (Andaman and Nicobar Islands). JX420257 and MH337359 are identical (boot-

strap value of 100; Fig. 2A), however, they are distantly related to *P. suezensis* sp. nov. (Fig. 2A). Glasby et al. (2013) found that *P. nuntia* JX420257 clustered with *P. helleri* (Grube, 1878), and together was the sister group of *P. suluana*, both relationships with a high Bayesian posterior probability (> 0.95). This confirms the distant relationship between material identified as *P. nuntia* from the Australasian region. JX644015 nested within a group comprising otherwise only *P. brevicirris* with a bootstrap value of 100 (Fig. 2B). Together they clustered with the East Asian-restricted *P. wilsoni*. Hence, it is also dubious whether JX644015 is a *P. nuntia* specimen and perhaps should be considered to belong to a species related to other East Asian *Perinereis* based on the molecular data. Reports of *P. brevicirris*, which was considered a synonym of *P. vallata* by Wilson and Glasby (1993) but is now accepted as valid (see key in Villalobos-Guerrero 2019), are widespread throughout the Indo-Pacific but most tropical and northern hemisphere records are unlikely to represent this species, which was originally described from Ile Saint Paul, Southern Ocean.

The new species is most similar to *P. nuntia*, which was also described from the Gulf of Suez. Although the exact location of Savigny's specimens has never been established, it is very likely to be from shallow waters of the port city of Suez, as for Savigny's other polychaetes (see Villalobos-Guerrero 2019 and references therein). *Perinereis nuntia* was recently redescribed by Villalobos-Guerrero (2019), and based on his redescription and Lamarck's type description, we have found two key differences between the two species (values in parentheses those of Villalobos-Guerrero). The number and shape of paragnaths in area VI: 14–21 shield-shaped paragnaths in the new species, compared to 8–10 (10–12) short bars in *P. nuntia*; and the relative length of the posterior dorsal cirri, which are 1.0–1.3 \times the DNL in the new species and 4–5 (3–4) \times the DNL in *P. nuntia*. The new species also shows similarities with *P. heterodonta* from Djibouti in having a high number of paragnaths on area VI and short dorsal cirri in the posterior end; however, the new species can be differentiated from *P. heterodonta* by the greater number of paragnaths on areas V (24 vs. 0–1) and VII–VIII (37–44 vs. 18–35) (Table 2).

The larger-sized, non-type specimens generally had more paragnaths in each area compared to the type material, except for area VI. The fewer paragnaths in area VI in the non-type specimens is most likely due to loss, as the ones present were irregularly spaced, with some gaps large enough to accommodate a lost shield-shaped bar or two cones. Another reflection on the condition of the non-type specimens is the unusually short dorsal and ventral cirri; on this point, the cirri appeared withered and many were missing, which we attribute to damage or a fixation artifact.

***Perinereis fayedensis* sp. nov.**

<https://zoobank.org/92062163-4B3D-46B3-9D2D-9DC669BD73F5>

Fig. 4

Material examined. Holotype: DUFS 0123 Al-Adabiya, west of Port Taofik, Gulf of Suez (Red Sea), intertidal, under coarse sands, at 29°56'06.0"N, 32°28'36.6"E.

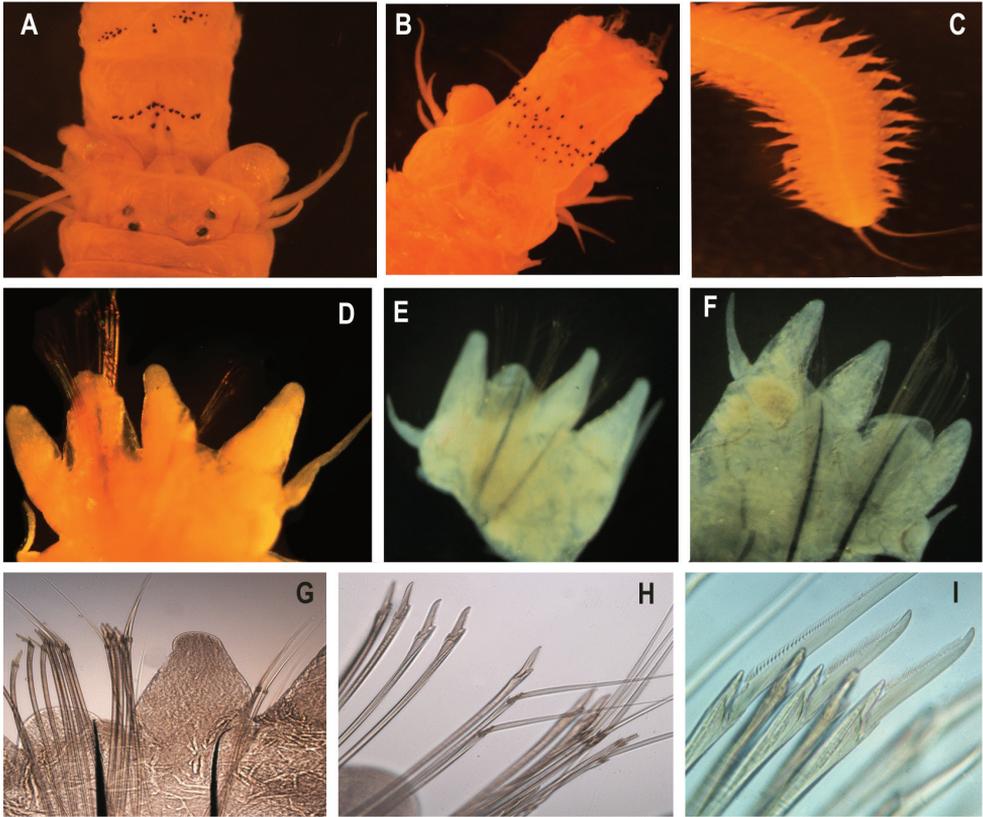


Figure 4. *Perinereis fayedensis* sp. nov. All pictures are from the holotype if not stated otherwise **A** anterior end, maxillary apparatus, dorsal view **B** anterior end, maxillary apparatus, ventral view **C** posterior end, ventral view **D** right parapodium, anterior view, chaetiger 16 **E** right parapodium, posterior view, chaetiger 32 **F** right parapodium, posterior view, chaetiger 67 **G** chaetal bundle of a right parapodium, homogomph spiniger and heterogomph falcigers, chaetiger 17 **H** neuropodial chaetal bundle of a right parapodium, homogomph spiniger & heterogomph falciger, chaetiger 33 **I** heterogomph falciger, chaetiger 33.

Paratypes (DUFS 120–122, 124–128): 8 specimens from El-Qantara, Suez Canal, intertidal, muddy sand bottom, at 30°50'31.5"N, 32°18'54.8"E, Fayed, western shore of Great Bitter Lake, intertidal, silty mud bottom, at 30°20'18.0"N, 32°18'14.9"E, Al-Adabiya (same collection details as holotype).

Description. **Holotype** (DUFS 0123) not complete, 49 chaetigers, 35 mm in length, 3 mm wide at chaetiger 10. **Paratypes** with 37–88 chaetigers, 30–70 mm long, 1.5–4.5 mm wide at chaetiger 10. Epidermis whitish cream with a longitudinal beige pigmentation stripe on ventral side of posterior chaetigers in some preserved.

Prostomium with entire anterior margin; wide as long. Antennae closely set, as long as ~ 1/3 length of prostomium. Eyes black, anterior pair set slightly further apart than posterior pair; lenses not obvious.

Apodous segment ~ 1.5× longer than chaetiger 1. Posterodorsal tentacular cirri with distinct cirrophores, extend back to chaetiger 7 (6–8).

Pharynx with jaws translucent red-brown, with 8 (7–8) teeth. Maxillary ring of pharynx with paragnaths, arranged in discrete areas, areas II–IV arranged in regular comb-like rows. Area I with 2 (1–2) conical paragnaths in vertical arrangement; area II with 9 (7–10) in left and 9 (7–10) in right conical paragnaths, three or four rows in a triangular patch; area III with 2 (2–5) conical paragnaths in vertical arrangement; area IV with 13 (12–15) in left, 14 (12–15) in right, conical paragnaths without bars; area V with 4 (1–3) conical paragnaths; area VI with 17 (14–17), shield-shaped bars with pointed tip present, cones paragnaths absent; area VII–VIII with 38 (28–40) conical paragnaths with small p-bars interspersed arranged in a single band of 3–5 rows (Fig. 4A, B; Table 2). Paragnath-free region between areas VI and VII–VIII broad, ca. as wide as palpophore; paragnaths of VII–VIII not visible in dorsal view (Fig. 4A).

Notopodia with conical dorsal and median ligules of equal length throughout. Superior lobes absent. DC length 1.2 (0.9–1.2) × length of DNL length anteriorly (chaetigers 10–20); posteriorly, DC length 1.2 (1.1–1.2) × length of DNL length (chaetigers 75–90). DC and DNL of mid-body parapodia proportionally similar to those of posterior parapodia (Fig. 4D–F).

Neuropodia with inferior and postchaetal lobes, ventral ligule and ventral cirri. Neuropodial postchaetal lobe lowly rounded, not projecting beyond end of acicular ligule. Ventral neuropodial ligule subconical, ca. as long as median ligule throughout. Ventral cirri extending laterally to halfway to tip of ventral neuropodial ligule in anterior and midbody, extending to ~ 1/3 length of ventral neuropodial ligule posteriorly (Fig. 4D–F).

Aciculae black, single in each ramus (Fig. 4G). Notochaeta with homogomph spinigers throughout, spinigers of long blades; teeth short. Neurochaetae with homogomph spinigers and heterogomph falcigers in the supra and sub-acicular fascicle (Fig. 4G–I). Acicula black, single in each ramus.

Pygidium with anal cirri fine, tapering, extending to last 7 (6–8) chaetigers, 50 (45–55) mm long (Fig. 4C).

Remarks. The molecular data place the new species, *P. fayedensis*, clearly apart from all other species and as sister to *P. suzezensis* (Fig. 2A). The monophyly is well supported by a bootstrap value of 99. Not considering identical sequences between specimens within each species, the average genetic distance to its sister-taxon, *P. suzezensis*, is 6.65% (\pm 0.60%), while the average genetic distance within *P. fayedensis* is substantially lower with a value of 0.01% (\pm 0.00%). Hence, there is again a clear gap in the genetic distances.

Morphologically, *P. fayedensis* is intermediate between *P. nuntia* and *P. heterodonta* described from Obock, Djibouti, Gulf of Aden. It differs from the former most notably in the number of paragnaths in area III (2–5 vs. ~ 15 in *P. nuntia*) and area VI (14–17 vs. 8–12 in *P. nuntia*), and the relative length of the DC (1.1–1.2× DNL in the new species vs. 3–5× DNL in *P. nuntia*; Table 2). *Perinereis fayedensis* can be distinguished from *P. heterodonta* by having fewer paragnaths in area III (2–5 in one row vs. a cluster of 6–7 in *P. heterodonta*) and more paragnaths in area VII–VIII (28–40 vs. 18 in *P. heterodonta*) (see Table 2).

Distribution and habitat. Gulf of Suez, Suez Canal including Great Bitter Lake; intertidal sand and mud, under stones.

Etymology. The new species is named after the Egyptian city of Fayed on the western shore of Great Bitter Lake approximately halfway along the Suez Canal.

***Perinereis damietta* sp. nov.**

<https://zoobank.org/32CCF83E-CDF3-4A3E-802A-E5C1EDD8B851>

Fig. 5

Material examined. Holotype: DUFS 055, Hurghada (northern Red Sea), Grand Aquarium beach, subtidal area, clay bottom, at 27°07'59.2"N, 33°49'51.2"E.

Paratypes: 22 specimens (DUFS 027–048) and non-type material 6 specimens (DUFS 049–054) from Al-Adabiya, west of Port Taofik, Gulf of Suez (Red Sea), intertidal, under coarse sands, at 29°56'06.0"N, 32°28'36.6"E and from Hurghada, National institute of Oceanography beach, intertidal and upper subtidal area, from muddy and sand bottoms, at 27°17'03.1"N, 33°46'19.8"E (Egypt).

Description. Holotype (DUFS 055) not complete, 94 chaetigers, 62 mm in length, 4.5 mm wide at chaetiger 10. **Paratypes** with 42–96 chaetigers for 30–115 mm long and 1.5–7 mm wide at chaetiger 10. Epidermis with orange and gold pigmentation on anterior dorsum and ventrum in some preserved samples.

Prostomium with entire anterior margin; relatively large, longer than wide, two pairs of eyes, dark green with black lenses, and two large palps longer than antennae, palpostyles conical. Antennae closely set, as long as $\sim 1/3$ length of prostomium. Lenses not obvious.

One apodous anterior segment, $\sim 1.6\times$ longer than chaetiger 1. Tentacular cirri with distinct cirrophores, longest tentacular cirri extend back to chaetiger 2 (2–4).

Pharynx with jaws black, 4 (4–5) reddish brown teeth. Paragnaths black with light brown base; those of maxillary ring pointed conical paragnaths. Paragnath counts: area I with 0 (0–2); area II with 2 (1–5) on the left side and 3 (2–5) on the right side; area III with 4 (3–9) in one transverse row; area IV with 14 (10–21) on the left side and 16 (10–20) on the right side; arranged in irregular row of unequal paragnaths. Area V with 0 (0–1); area VI with 24 (24–40) conical paragnaths arranged in one arc; area VII–VIII with 24 (16–32), similar in size, arranged in two rows (Fig. 5A, B). Paragnath-free region between areas VI and VII–VIII broad, ca. as wide as palpophore; paragnaths of VII–VIII not visible in dorsal view (Fig. 5A).

Anterior notopodia with conical dorsal and median ligules of equal length in anterior body; dorsal ligule slightly longer in mid- and posterior body. DC length 0.8 (0.7–1.0) \times length of DNL length anteriorly (chaetigers 10–20); posteriorly, DC length 1.1 (0.9–1.2) \times length of DNL (chaetigers 75–90). DC and DNL of mid-body parapodia proportionally similar to those of posterior parapodia (Fig. 5D).

Dorsal notopodial ligule; triangular with conical tip, slightly longer than notopodial ventral ligule throughout. Ventral notopodial ligule rounded triangular. Dorsal and ventral notopodial ligules marked decreasing in size on posterior chaetigers. Neuropodium with dorsal rounded lobe in anterior chaetigers, with one black acicula,

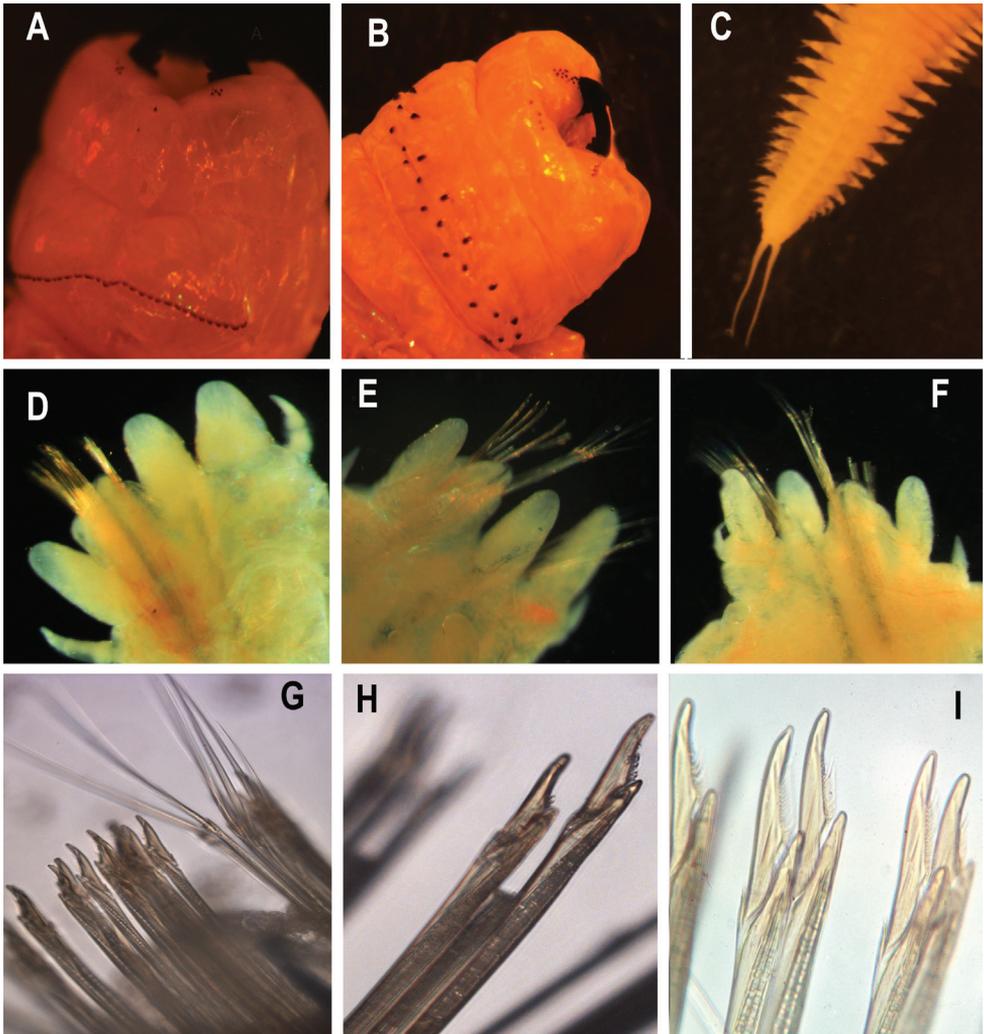


Figure 5. *Perinereis damietta* sp. nov. All pictures are from the holotype if not stated otherwise **A** anterior end, maxillary apparatus, dorsal view **B** anterior end, maxillary apparatus, ventral view **C** posterior end, ventral view **D** right parapodium, posterior view, chaetiger 9 **E** right parapodium, posterior view, chaetiger 41 **F** right parapodium, anterior view, chaetiger 56 **G** chaetal bundle of a right parapodium, homogomph spiniger & heterogomph falciger chaetiger 56 **H** neuropodial chaetal bundle of a right parapodium, heterogomph falciger, chaetiger 56 **I** heterogomph falciger, chaetiger 67.

less developed posteriorly. Ventral neuropodial ligule digitiform, similar in length to acicular ligule on anterior chaetigers; slightly longer than acicular ligule in posterior chaetigers. Ventral cirri extending to ~ 1/3 length of ventral neuropodial ligule anteriorly and posteriorly (Fig. 5D–F).

Notochaetae with homogomph spinigers, long and thin serrated blade throughout. Neurochaetae dorsal fascicle: homogomph spinigers; median thick serrated blade

present and heterogomph falcigers present on anterior and posterior chaetigers, blades serrated. Neurochaetae ventral fascicle: heterogomph falcigers with median long and wide blades with a single terminal tooth, in anterior and posterior chaetigers (Fig. 5G–I). Aciculae black with red-brown base, single in each ramus.

Pygidium with anal cirri cirriform, cirri extending to last 2 (2–4) chaetigers (Fig. 5C).

Distribution and habitat. Gulf of Suez, northern Red Sea; intertidal and subtidal, sand and mud, under stones.

Etymology. The new species is named after the university of the first author, Damietta University, a noun in apposition. Damietta (Egyptian Arabic: *Dumyāt* (طايمة)) is also a port city located on an eastern distributary of the Nile Delta, ~ 15 km from the Mediterranean Sea.

Remarks. *Perinereis damietta* sp. nov. is well supported by the highest bootstrap value of 100 (Fig. 2C) and clearly set apart from the other *Perinereis* species in the tree. According to the present molecular phylogeny, the sister group to *P. damietta* is *P. vallata*, which is also a former variety of *P. nuntia* (Wilson and Glasby 1993; Glasby and Hsieh 2006). Not considering identical sequences between specimens within each species, the average genetic distance to its sister group is 42.57% (\pm 6.72%), while the average genetic distance within *P. damietta* is 1.12% (\pm 0.74%) and hence substantially lower. Hence, there is again a clear gap in the genetic distances.

Herein, *P. vallata* also includes one specimen (JX966314) assigned to *P. brevicirris* (Fig. 2C). This is probably a misidentification given the very strong bootstrap support values of 100 for both the monophyly of *P. vallata* and the group of *P. brevicirris* specimens mentioned above (Fig. 2A, C).

Perinereis damietta is morphologically most similar to *P. heterodonta* (type locality: Obock, Djibouti, Gulf of Aden). Both species belong to the group of the *P. nuntia* complex that lack heterogomph spinigers in anterior parapodia, which is unlike *P. nuntia*. Other key differences between *P. damietta* / *P. heterodonta* and *P. nuntia* are the shorter tentacular cirri and the fewer paragnaths in area V (0–1) (Table 2). *Perinereis damietta* differs from *P. heterodonta* most notably in having 24–40 pyramidal paragnaths in area VI (vs. 10–16 in *P. heterodonta*). In this regard, it has the highest number of area VI paragnaths of any species in the *P. nuntia* species complex, exceeding the next highest (12–16 bars) found in *P. vallata* (Wilson and Glasby 1993).

Another species originally described from Djibouti, *Perinereis djiboutiensis*, is unfortunately poorly known, especially in respect to the presence or absence of heterogomph spinigers in anterior parapodia and numbers of paragnaths in areas III and VII–VIII (Table 2). Although it resembles the new species in having one, or no, paragnaths in area V, it may be differentiated from the new species in having only six or seven short bars (may also include cone-shaped paragnaths) in area VI, which is the lowest of all species of the *Perinereis nuntia* species group in the region (Table 2), and in this regard it is closer to material described as *Perinereis nuntia* from the Red Sea by Wilson and Glasby (1993).

A novel character introduced by Villalobos-Guerrero (2019), the size of the gap between areas VI and VII–VIII, may also set this new species (and others in this study)

apart from other members of the *P. nuntia* complex. The gap in all three species described here is about ‘as wide as palpophore’, which is similar to *P. nuntia* according to Villalobos-Guerrero (2019), but differs from the Southern Ocean species *P. latipalpa* (Schmarda, 1861) from South Africa and *P. vallata* from Chile in which the gap is only as wide as the palpostyle (Wilson and Glasby 1993; Villalobos-Guerrero 2019).

Discussion

The present study supports the finding of Bakken and Wilson (2005) of the non-monophyly of *Perinereis* and the ‘*P. nuntia*’ species complex. Bakken and Wilson (2005) found that the clade containing the type species, *P. novaehollandiae* Schmarda, 1861 (a junior synonym *P. amblyodonta* Schmarda, 1861) does not group with the clade *P. nuntia*+*P. vallata*, suggesting that the characteristic arc of bars on area VI, may not be homologous between the two groups. Nevertheless, the presence of a large number (> 10) of uniform, very short bars in area VI may be found as an autapomorphy for some subgroups within the species group, for example, in the sister grouping of *P. damietta* and the Southern Ocean species, *P. vallata*. Possibly, fine details of paragnath form and pattern may be found to delineate natural groups within *Perinereis*, which would lend support to Villalobos-Guerrero’s (2019) recognition of the taxonomic importance of faint ridges and furrows of the dorsal oral ring. Microstructures of the pharyngeal surface probably reflect underlying muscular and therefore may play a role in the form and function of paragnaths.

Despite recent advancements in integrative studies in many groups of polychaetes, taxonomic confusion still exists in many groups of Nereididae. *Perinereis* species are especially problematic due to difficult morphological species differentiation and a lack of detailed systematic studies. This has led to informal denomination of the species complex and recognition of geographic morphs and varieties such as *P. cultrifera* (Scaps et al. 2000) and the *P. nuntia* species group (Wilson and Glasby 1993; Glasby and Hsieh 2006; Sampértegui et al. 2013). Today, genetic assessment in combination with morphology is considered an effective tool for redescription of several species principally focused on population differentiation (Rouabah and Scaps 2003) and species delimitation (Chen et al. 2002; Park and Kim 2007; Sampértegui et al. 2013; Villalobos-Guerrero et al. 2021). The present study confirms the utility of such an approach, and moreover demonstrates that the specific combination of the barcoding gene and selected morphometric characters is an effective way to delineate cryptic species.

Finally, this study has uncovered further examples of sympatry among polychaetes. All three new species described here were found in the same habitat, viz., intertidal sand and mud, under stones, at the same location. *Perinereis damietta* appears to have a slightly wider habitat preference as it also occurs sub-tidally, but more intense sampling including exploration of potential microhabitat differences, is required to confirm our observations. Assuming sympatry, identification of the specific isolation mechanism(s) would be interesting. Several studies have suggested the importance of reproductive

isolation as an important speciation mechanism in the species group (e.g., Yoshida 1984; Hardege and Bartels-Hardege 1995). This idea merits further investigation as an explanation for the phenotypic similarity of the three cohabiting nereidid species described in this study.

Acknowledgements

This work was funded by the Egyptian Government to AHE for a research stay at the NHM of University of Oslo. THS received additional support by the Norwegian Metacenter for Computational Science (NOTUR; project numbers NN9408K & NS9408K). This is NHM Evolutionary Genomics lab contribution No #18. We gratefully acknowledge the use of Google map. CG thanks Dr Dieter Fiege (SMZ) for the loan of specimens from Hurghada, Egypt. The authors are also grateful to Tulio F. Villalobos-Guerrero and Robin S. Wilson for their detailed suggestions and helpful comments to improve the manuscript.

References

- Alves PR, Halanych KM, Santos CSG (2020) The phylogeny of Nereididae (Annelida) based on mitochondrial genomes. *Zoologica Scripta* 49(3): 366–378. <https://doi.org/10.1111/zsc.12413>
- Astrin JJ, Stuben PE (2008) Phylogeny in cryptic weevils: molecules, morphology and new genera of western Palaearctic *Cryptorhynchinae* (Coleoptera: *Curculionidae*). *Invertebrate Systematics* 22(5): 503–522. <https://doi.org/10.1071/IS07057>
- Augener H (1931) Die bodensässigen Polychaeten nebst einer Hirudinee der Meteor-Fahrt. *Mitteilungen des Zoologischen Staatsinstituts und zoologischen Museums, Hamburg* 44: 279–313.
- Bakken T, Wilson RS (2005) Phylogeny of nereidids (Polychaeta, Nereididae) with paragnaths. *Zoologica Scripta* 34(5): 507–547. <https://doi.org/10.1111/j.1463-6409.2005.00200.x>
- Bakken T, Glasby CJ, Wilson RS (2009) A review of paragnath morphology in Nereididae (Polychaeta). *Zoosymposia* 2(1): 305–316. <https://doi.org/10.11646/zoosymposia.2.1.21>
- Bakken T, Glasby CJ, Santos CSG, Wilson RS (2022) Nereididae Blainville, 1818. In: *Handbook of Zoology. Volume 4: Pleistoannelida, Errantia II. Phyllodocida*. De Gruyter, Berlin, 259–307. <https://doi.org/10.1515/9783110647167-010>
- Chen CA, Chen CP, Fan TY, Yu JK, Hsieh HL (2002) Nucleotide sequences of ribosomal internal transcribed spacers and their utility in distinguishing closely related *Perinereis* polychaetes (Annelida; Polychaeta; Nereididae). *Marine Biotechnology* 4(1): 17–29. <https://doi.org/10.1007/s10126-001-0069-3>
- Conde-Vela VM (2022) Reinstatement of *Perinereis bairdii* (Webster, 1884) and description of *P. websteri* sp. nov. from Bermuda, including the reproductive morphology of two Atlantic *Perinereis* species (Annelida: Errantia: Phyllodocida). *European Journal of Taxonomy* 787: 104–145. <https://doi.org/10.5852/ejt.2021.787.1619>

- Fauvel P (1919) (19 19) Annélides polychètes de Madagascar, de Djibouti et du Golfe Persique. Archives de Zoologie Expérimentale et Générale 58: 315–473. <https://doi.org/10.5962/bhl.part.8154>
- Fauvel P (1921) Polychètes de Madagascar, du Museum d'Histoire naturelle recueillies par M. le Dr. W.kaudern. Arkiv för Zoologi 13: 1–32. <https://doi.org/10.5962/bhl.part.20151>
- Fauvel P (1932) Annelida Polychaeta of the Indian Museum, Calcutta. Memoirs of the Indian Museum 12: 1–262.
- Fauvel P (1953) Annelida Polychaeta. The Fauna of India, including Pakistan, Ceylon, Burma and Malaya. The Indian Press, Allahabad, 507 pp.
- Glasby CJ, Hsieh HL (2006) New species and new records of the *Perinereis nuntia* species group (Nereididae: Polychaeta) from Taiwan and other Indo-West Pacific shores. Zoological Studies 45(4): 553–577. <https://zoolstud.sinica.edu.tw/Journals/45.4/553.html>
- Glasby CJ, Wei NWV, Gibb KS (2013) Cryptic species of Nereididae (Annelida: Polychaeta) on Australian coral reefs. Invertebrate Systematics 27(3): 245–264. <https://doi.org/10.1071/IS12031>
- Gravier C (1899) Contribution à l'étude des Annélides Polychètes de la Mer Rouge. Bulletin du Muséum d'Histoire Naturelle, Paris 5: 234–244. <https://www.biodiversitylibrary.org/part/6290>
- Grube AE (1878) Untersuchungen uber die Familie Eunicea. Schlesische Gesellschaft für vaterländische Cultur. Jahres- Bericht 55: 79–104. <https://www.biodiversitylibrary.org/page/37206794>.
- Hardege JD, Bartels-Hardege HD (1995) Spawning behaviour and development of *Perinereis nuntia* var. *brevicirrus* (Annelida: Polychaeta). Invertebrate Biology 114(1): 39–45. <https://doi.org/10.2307/3226951>
- Horst R (1889) Contribution towards the knowlegde of the Annelida Polychaeta. On species of *Nereis*, belonging to the sub-genus *Perinereis*. Notes from the Leyden Museum 11: 161–186. <https://repository.naturalis.nl/pub/509452>
- Hutchings PA, Reid A, Wilson RS (1991) *Perinereis* from Australia (Polychaeta, Nereididae) from Australia, with redescrptions of six additional species. Records of the Australian Museum 43(3): 241–274. <https://doi.org/10.3853/j.0067-1975.43.1991.47>
- Hylleberg J, Nateewathana A, Bussarawit S (1986) Polychaetes of Thailand, Nereidae (Part 1), *Perinereis* and *Pseudonereis*, with notes on species of commercial value. Phuket Marine Biological Center Research Bulletin 43: 1–22. <https://cir.nii.ac.jp/crid/1573387448936054912>
- Kalyaanamoorthy S, Minh BQ, Wong TK, Haeseler Av, Jermini LS (2017) ModelFinder: Fast model selection for accurate phylogenetic estimates. Nature Methods 14: 587–589. <https://www.nature.com/articles/nmeth.4285>
- Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. Molecular Biology and Evolution 30(4): 772–780. <https://doi.org/10.1093/molbev/mst010>
- Kinberg JGH (1865) Annulata Nova (Nereidum Dispositio Nova. Leonnatidea, Nereidea, Aretidea, Pisenoida, Niconidea). Öfversigt af Kongelige Vetenskaps-Akademiens Förhandlingar 22(2): 167–179. <https://www.biodiversitylibrary.org/page/32339443>

- Nguyen LT, Schmidt HA, von Haeseler A, Minh BQ (2015) IQ-TREE: A Fast and Effective Stochastic Algorithm for Estimating Maximum-Likelihood Phylogenies. *Molecular Biology and Evolution* 32(1): 268–274. <https://doi.org/10.1093/molbev/msu300>
- Park TS, Kim W (2007) A taxonomic study on *Perinereis nuntia* species group (Polychaeta: Nereididae) of Korea. *Korean Journal of Systematic Zoology* 23(1): 75–85. <https://doi.org/10.5635/KJSZ.2007.23.1.075>
- Park T, Kim W (2017) Description of a New Species for Asian Populations of the “Cosmopolitan” *Perinereis cultrifera* (Annelida: Nereididae). *Zoological Science* 34(3): 252–260. <https://doi.org/10.2108/zs160154>
- Peters W (1881) Beschreibungen von neuen Anneliden des zoologischen Museums zu Berlin. *Sitzungsberichte der Gesellschaft der naturforschende Freunde zur Berlin* 7: 109–117. <https://www.biodiversitylibrary.org/item/35574#page/121>
- Read G, Fauchald K (Eds) (2022) World Polychaeta Database. *Perinereis* Kinberg, 1865. Accessed through: World Register of Marine Species. <https://www.marinespecies.org/aphia.php?p=taxdetails&id=129380> [on 2022-04-04]
- Rouabah A, Scaps P (2003) Life cycle and population dynamics of the polychaete *Perinereis cultrifera* from the Algerian Mediterranean coast. *Marine Ecology* 24(2): 85–99. <https://doi.org/10.1046/j.1439-0485.2003.03796.x>
- Sampértegui S, Rozbaczylo N, Canales-Aguirre CB, Carrasco F, Hernández CE, Rodríguez-Serrano E (2013) Morphological and molecular characterization of *Perinereis gualpensis* (Polychaeta: Nereididae) and its phylogenetic relationships with other species of the genus off the Chilean coast, Southeast Pacific. *Cahiers de Biologie Marine* 54: 27–40.
- Santos CSG, Pleijel F, Lana P, Rouse GW (2005) Phylogenetic relationships within Nereididae (Annelida: Phyllococida). *Invertebrate Systematics* 19(6): 557–576. <https://doi.org/10.1071/IS05001>
- Savigny IC (1818) Les Annelides. In: de Lamarck JB. *Histoire Naturelle des Animaux sans Vertèbres*. Paris vol 5: 612. <http://biodiversitylibrary.org/page/12886879>
- Scaps P, Rouabah A, Lepêtre A (2000) Morphological and biochemical evidence that *Perinereis cultrifera* (Polychaeta: Nereididae) is a complex of species. *Journal of the Marine Biological Association of the United Kingdom* 80(4): 735–736. <https://doi.org/10.1017/S0025315400002587>
- Thi Hoang D, Chernomor O, Haeseler AV, Minh BQ, Vinh LS (2018) UFBoot2: Improving the Ultrafast Bootstrap Approximation. *Molecular Biology and Evolution* 35(2): 518–522. <https://doi.org/10.1093/molbev/msx281>
- Tosuji H, Nishinosono K, Hsieh H-L, Glasby CJ, Sakaguchi T, Sato M (2019) Molecular evidence of cryptic species diversity in the *Perinereis nuntia* species group (Annelida: Nereididae) with first records of *P. nuntia* and *P. shikueii* in southern Japan. *Plankton & Benthos Research* 14(4): 287–302. <https://doi.org/10.3800/pbr.14.287>
- Villalobos-Guerrero TF (2019) Redescription of two overlooked species of the *Perinereis nuntia* complex and morphological delimitation of *P. nuntia* (Savigny in Lamarck, 1818) from the Red Sea (Annelida, Nereididae). *Zoosystema* 41(1): 465–496. <https://doi.org/10.5252/zoosystema2019v41a24>
- Villalobos-Guerrero TF, Bakken T (2018) Revision of the *Alitta virens* species complex (Annelida: Nereididae) from the North Pacific Ocean. *Zootaxa* 4483(2): 201–257. <https://doi.org/10.11646/zootaxa.4483.2.1>

- Villalobos-Guerrero TF, Park T, Idris I (2021) Review of some *Perinereis* Kinberg, 1865 (Annelida: Nereididae) species of Group 2 *sensu* Hutchings, Reid & Wilson, 1991 from the Eastern and South-eastern Asian seas. *Journal of the Marine Biological Association of the United Kingdom* 101(2): 279–307. <https://doi.org/10.1017/S0025315421000126>
- Wilson RS (1993) Systematics of the *Perinereis nuntia* complex (Polychaeta: Nereididae) from south-eastern Australia. *Records of the Australian Museum* 45(3): 241–252. <https://doi.org/10.3853/j.0067-1975.45.1993.22>
- Wilson RS, Glasby CJ (1993) A revision of the *Perinereis* species group (Polychaeta: Nereididae). *Records of the Australian Museum* 45(3): 253–277. <https://doi.org/10.3853/j.0067-1975.45.1993.23>
- Yoshida S (1984) Studies on the biology and aquaculture of a common polychaete, *Perinereis nuntia* (Grube). *Bulletin of the Osaka Prefectural Fisheries Experimental Station* 6: 1–63. <https://cir.nii.ac.jp/crid/1570854174379996160>
- Yousefi S, Rahimian H, Nabavi SMB, Glasby CJ (2011) Nereididae (Annelida: Polychaeta) from intertidal habitats in the Gulf of Oman, Iran. *Zootaxa* 3013(3): 48–64. <https://doi.org/10.11646/zootaxa.3636.3.8>

Supplementary material I

Supplementary data

Authors: Asmaa Haris Elgetany, Torsten H. Struck, Christopher J. Glasby

Data type: excel file.

Explanation note: Morphometric characterization of 45 specimens of three putative species of *Perinereis*, identified by voucher number and sample identification (as for Table 1). Abbreviations: p, present; NP, not present.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zookeys.1132.87629.suppl1>

Scorpiops lourencoi sp. nov., the revalidation of *Scorpiops atomatus* Qi, Zhu & Lourenço, 2005, and the redescription of *Scorpiops tibetanus* Hirst, 1911 (Scorpiones, Scorpiopidae) from China

Heyu Lv^{1,2}, Zhiyong Di^{1,2}

1 Key Laboratory of Zoological Systematics and Application of Hebei Province, College of Life Sciences, Hebei University, Baoding, Hebei 071002, China **2** Institute of Life Sciences and Green Development, Hebei University, Baoding 071002, Hebei, China

Corresponding author: Zhiyong Di (zydi@ustc.edu.cn)

Academic editor: Wilson Lourenço | Received 9 June 2022 | Accepted 28 October 2022 | Published 30 November 2022

<https://zoobank.org/B4388BBD-BD51-40F6-8341-ADA7CF276E4B>

Citation: Lv H, Di Z (2022) *Scorpiops lourencoi* sp. nov., the revalidation of *Scorpiops atomatus* Qi, Zhu & Lourenço, 2005, and the redescription of *Scorpiops tibetanus* Hirst, 1911 (Scorpiones, Scorpiopidae) from China. ZooKeys 1132: 189–214. <https://doi.org/10.3897/zookeys.1132.87364>

Abstract

Scorpiops lourencoi sp. nov. is described from Shigatse, Xizang. *Scorpiops atomatus* Qi, Zhu & Lourenço, 2005 and *Scorpiops pococki* Qi, Zhu & Lourenço, 2005 were synonymized by Kovařík et al. (2020) as two junior synonyms of *Scorpiops tibetanus* Hirst, 1911 but based on several field surveys in Xizang in recent years, and a careful survey of the literature, *S. atomatus* is reaffirmed as a valid species and *S. tibetanus* is redescribed, both based on newly collected specimens. This brings the total number of species of *Scorpiops* recorded in China to 32.

Keywords

China, new species, *Scorpiops*, Xizang

Introduction

Kovařík et al. (2020) and Štáhlavský et al. (2020) revised the family Scorpiopidae Kraepelin, 1905 and synonymized the previously accepted genera of the family Scorpiopidae, excepting *Parascorpiops* Banks, 1928, with the genus *Scorpiops* Peters, 1861.

Lourenço and Ythier (2022) reclassified the genera of the family Scorpiopidae, proposed six subgenera of the genus *Scorpiops* (including *Alloscorpiops* Vachon, 1980, *Dasyscorpiops* Vachon, 1974, *Euscorpiops* Vachon, 1980, *Neoscorpiops* Vachon, 1980, *Plethoscorpiops* Lourenço, 2017 and *Scorpiops*), and maintained *Parascorpiops* as a distinct genus of *Scorpiops*.

Scorpiops is the main member of the family Scorpiopidae, distributed mainly in south and southeast Asia, and currently includes 104 species (Lourenço and Ythier 2022; Tang 2022). In China, thirty species are found in Hubei, Xinjiang, Xizang, and Yunnan (Lv and Di 2022; Tang 2022).

Hirst (1911) erected *S. tibetanus*, based on specimens from “Tsangpo Valley, Chak-sam Ferry”, Xizang. This appears to be the first species of the genus *Scorpiops* found in China. Kovařík (2000) reported new additions to the distribution range of *S. tibetanus*: Kambu basti, Lhasa, and Shigatse, and provided outline drawings of the chelae of both sexes. The figures are not accurate, but the remarkable thickness, nearly square, and distinctly rectangular dimorphism of the chelae of both sexes is clear. Kovařík (2000) examined the holotype (male) and collected new materials of *S. tibetanus*, recording some important new information: the ventral trichobothria on the patella number 7–10 (but usually 9; in one young of 37 specimens, 7 on one side).

Qi et al. (2005) reported one small species, *S. atomatus*, and two medium species, *Scorpiops langxian* Qi, Zhu & Lourenço, 2005 and *S. pococki* and one large species, *Scorpiops luridus* Qi, Zhu & Lourenço, 2005. The type locality of *S. atomatus* is Lang County, and other localities include Chayu and Gyaca counties. The type locality of *S. pococki* is Gyaca County, and other localities include Chayu and Nêdong counties, Lhasa, Nyingchi, and Shigatse cities.

Kovařík and Ahmed (2009) provided a list of taxa of the *S. hardwickii* (Gervais, 1843) complex, which contains 12 species, widely distributed in Asia, including five species distributed in China: *S. atomatus*, *S. hardwickii*, *S. langxian*, *S. pococki*, and *S. tibetanus*. However, following the reports of Kovařík (2000), Kovařík and Ahmed (2009), Qi et al. (2005), and Di et al. (2011) thought that *S. atomatus* and *S. tibetanus* should be excluded from *S. hardwickii* complex. Di et al. (2013) described the female of *S. tibetanus* and revised the key for Chinese *Scorpiops* species. Kovařík et al. (2020) proposed *S. atomatus* and *S. pococki* as two junior synonyms of *S. tibetanus* and provided figures of freshly collected *S. tibetanus*.

In this work, we analyze species information from the literature in tandem with newly collected material, and confirm that *S. atomatus* is a valid species; additionally, we redescribe *S. tibetanus* based on new material and describe *S. lourencoi* as a new species.

Materials and methods

Specimens were collected by hand and preserved in 75% ethanol. Type series of the new species are deposited in the Museum of Hebei University, Baoding, China (MHBU).

Illustrations and measurements were produced using a Leica M205 stereomicroscope. The photographs were taken with a Canon 650D camera and a Leica M205FA stereomicroscope (with a digital color microscope camera Leica DFC495). Measurements (in mm) follow Sissom (1990). Trichobothrial notations are done according to Vachon (1974), and the morphological terminology mostly follows Hjelle (1990). The terminology of metasomal carination is that of Vachon (1952), and the terminology of pedipalp chelal carinae follows Soleglad and Sissom (2001).

Movable finger dentition abbreviations used in the text are as follows: **ID**, inner denticles; **IAD**, inner accessory denticles; **MD**, median denticles; **OD**, outer denticles.

Taxonomic treatment

Family Scorpiopidae Kraepelin, 1905

Genus *Scorpiops* Peters, 1861

Type species. *Scorpiops hardwickii* Gervais, 1843.

Type locality. India Himalaya.

Scorpiops atomatus Qi, Zhu & Lourenço, 2005

Figs 1–32, Table 1

Scorpiops atomatus Qi, Zhu & Lourenço, 2005: 6, 10, figs 16–31; Kovařík and Ahmed 2009: 10; Di et al. 2013: 59–61, figs 1–21, tab. 1; Di et al. 2014: 11.

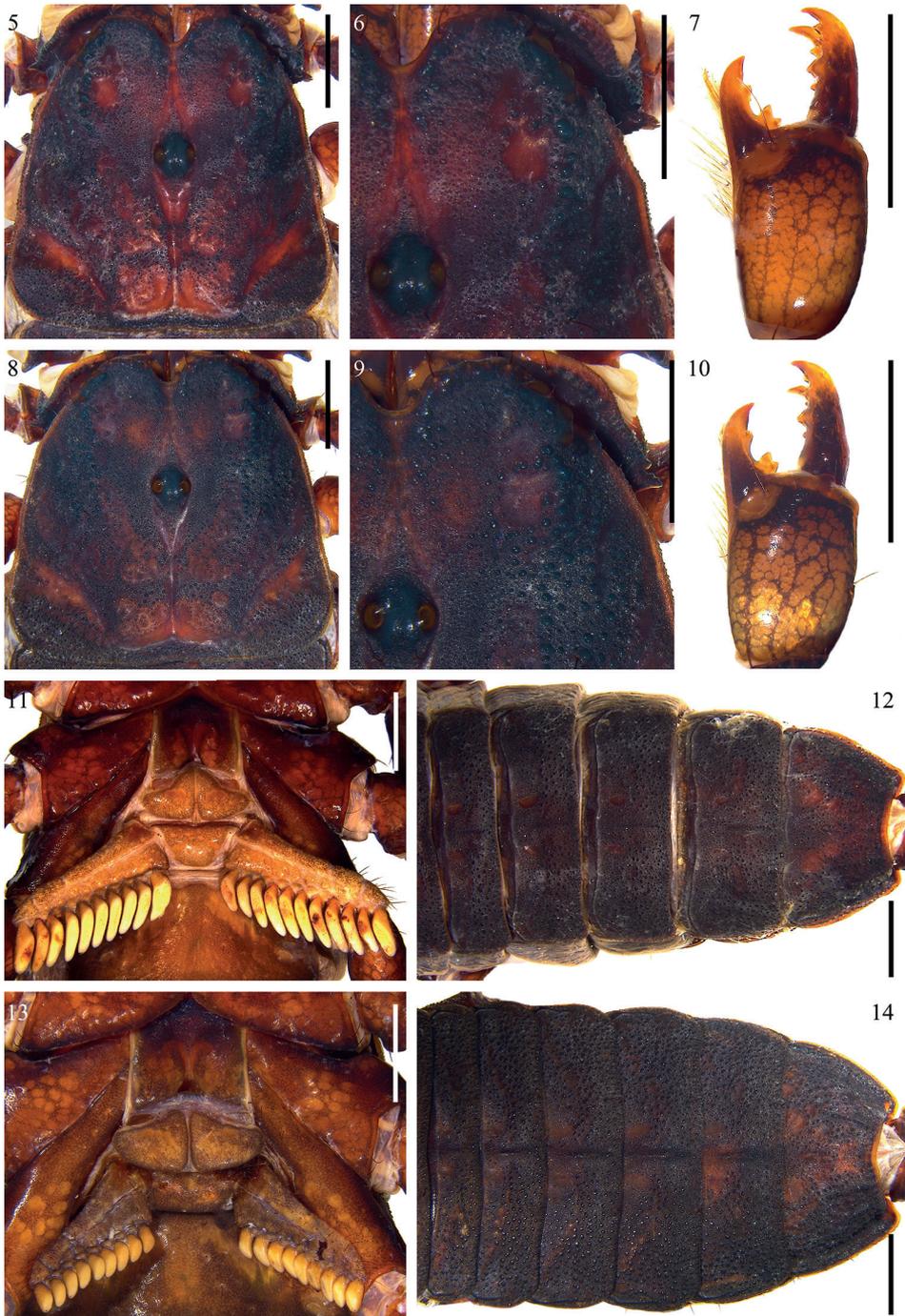
Type locality. China, Xizang, Lang County (29.02°N, 93.08°E).

Material examined. 2 males and 3 females, China, Xizang (Tibet), Linzhi City (Nyingchi City), Lang County (Nang County), Dongga Town (Tonga Town), 06/5/2017, Zhiyong Di leg. (Ar.-MHBUScXZLX17050601, 01–05).

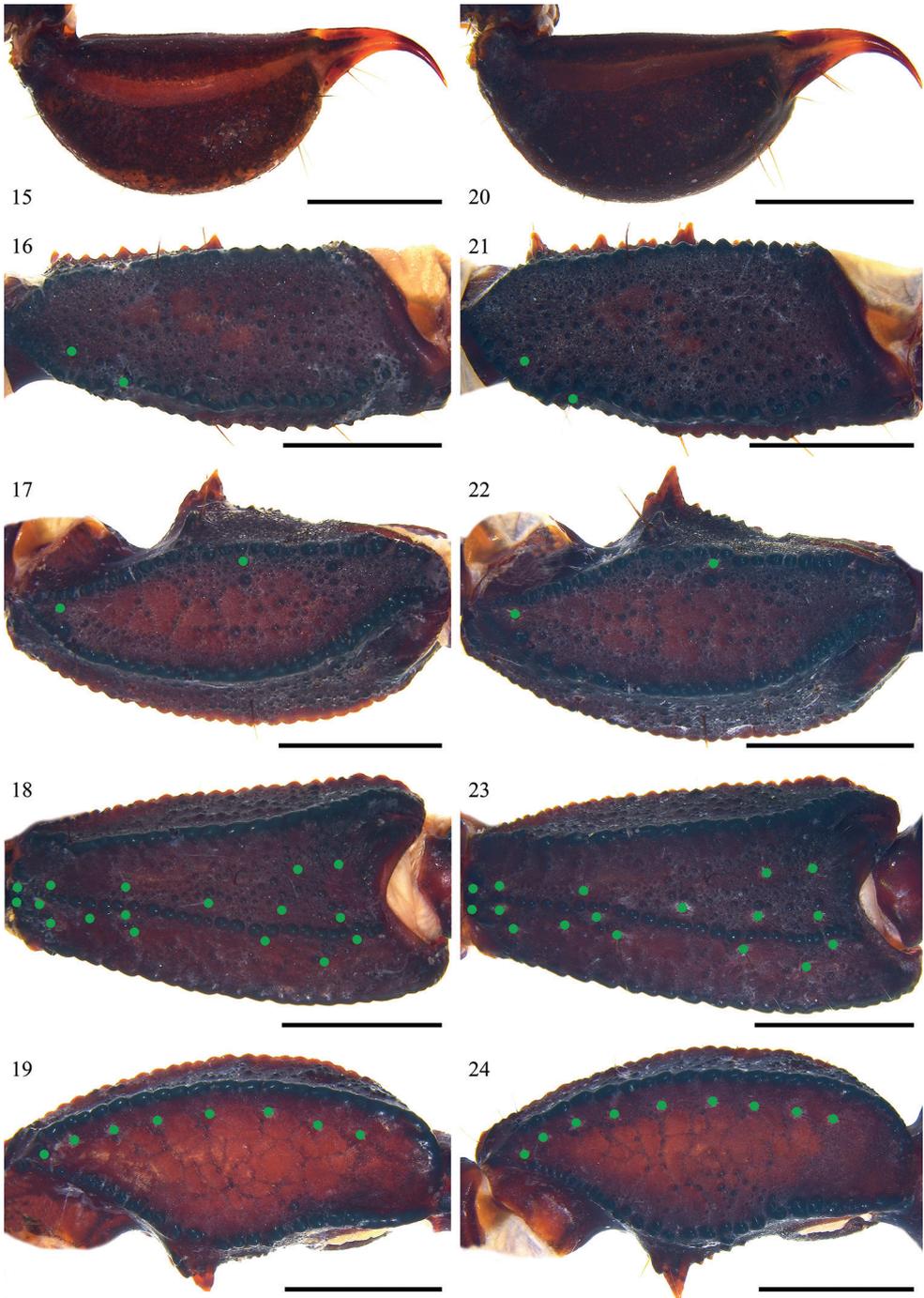
Diagnosis (modified from Qi et al. 2005). Adult body length 35–45 mm. Base color uniformly brown. Patella of pedipalp with 17 (5 *eb*, 2 *esb*, 2 *em*, 4 *est*, 4 *et*) external and 8–10 (usually nine) ventral trichobothria. Chelal trichobothria *Eb*₃ is located in proximal half of manus between trichobothria *Dt* and *Db*. Chela with four ventral trichobothria. Chela with an average length/width ratio of 2.3 in males ($n = 2$ adults) and 2.5 in females ($n = 3$ adults); pedipalp movable finger with ca. five ID, eight or nine IAD, 58–62 MD, and 7–9 OD present, chela fingers on adult males and females scalloped, usually more strongly in male. Pectinal teeth count 10–11 in males ($n = 2$ adults) and eight or nine in females ($n = 3$ adults), fulcra present. Pectinal with three marginal and six middle lamellae. Telson bulbous and granulate, annular ring absent.



Figures 1–4. *Scorpions atomatus* from Lang County **1, 2** male (Ar.-MHBU-ScXZLX1705060101), dorsal and ventral views **3, 4** female (Ar.-MHBU-ScXZLX1705060102), dorsal and ventral views. Scale bars: 12.0 mm.



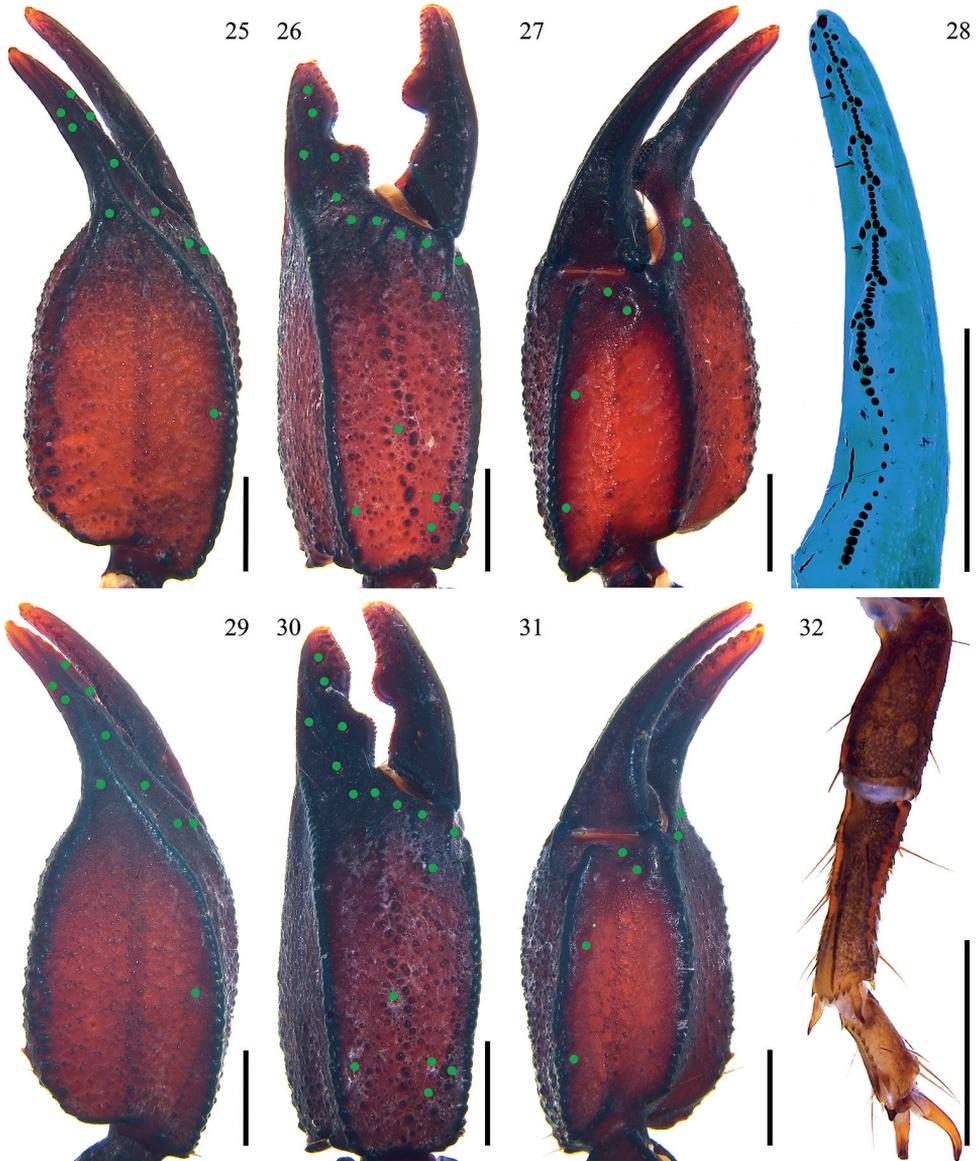
Figures 5–14. *Scorpiops atomatus* from Lang County **5, 6, 7, 11, 12** male (Ar.-MHBUScXZLX1705060101) **8, 9, 10, 13, 14** female (Ar.-MHBUScXZLX1705060102) **5, 8** carapace **6, 9** eyes and nearby area **7, 10** chelicera dorsal surface **11, 13** sternum, genital operculum, and pectines **12, 14** tergites. Scale bars: 2.0 mm.



Figures 15–24. *Scorpions atomatus* from Lang County. **15–19** male (Ar.-MHBU-ScXZLX1705060101) **20–24** female (Ar.-MHBU-ScXZLX1705060102) **15, 20** telson, lateral surface **16, 21** femur dorsal surface **17–19, 22–24** patella dorsal, external, and ventral surfaces. Green dots showing trichobothrial patterns of pedipalps. Scale bars: 2.0 mm.

Table I. Measurements (in mm) of *S. atomatus*, *S. tibetanus*, and *S. lourencoi* sp. nov.

Species Contents	<i>S. atomatus</i>		<i>S. tibetanus</i>		<i>S. lourencoi</i> sp. nov.		
	Sex	Male ScXZLX 1705060101	Female ScXZLX 1705060102	Male ScXZQS 1907200101	Female ScXZQS 1907200102	Male (holotype) ScXZRKZ 2107260101	Female (paratype) ScXZRKZ 2107260102
Total length:		42.5	40.3	57.3	52.7	46.7	47.3
Carapace:							
– Length		6.6	6.8	7.7	7.3	6.5	6.7
– Anterior width		4.1	4.1	3.9	3.9	3.6	3.7
– Posterior width		6.9	7.3	7.8	7.6	6.7	6.9
Mesosomal segments:							
– Length		11.6	10.9	14.7	15.0	14.1	14.9
Metasomal segment I:							
– Length		2.5	2.4	3.6	3.0	2.7	2.7
– Width		2.5	2.4	4.1	3.6	3.0	2.8
– Depth		2.1	2.0	2.9	2.5	2.1	2.0
Metasomal segment II:							
– Length		2.9	2.6	4.3	3.7	3.2	3.1
– Width		2.1	2.1	3.6	3.2	2.7	2.6
– Depth		2.0	2.0	3.4	3.0	2.3	2.1
Metasomal segment III:							
– Length		3.0	2.8	5.0	4.4	3.7	3.7
– Width		2.1	2.0	3.6	3.0	2.7	2.6
– Depth		2.2	2.1	3.2	2.7	2.3	2.1
Metasomal segment IV:							
– Length		3.5	3.3	5.5	5.2	3.9	3.8
– Width		2.0	1.9	3.2	2.8	2.4	2.4
– Depth		1.9	1.9	2.9	2.7	2.2	2.1
Metasomal segment V:							
– Length		6.0	5.6	8.3	7.4	6.1	5.9
– Width		2.0	1.9	2.6	2.1	2.1	2.0
– Depth		1.9	1.7	2.7	2.2	1.8	1.8
Telson:							
– Length		6.4	5.9	8.2	7.3	6.5	6.5
– Width		2.4	2.4	3.3	2.8	2.7	2.2
– Depth		2.4	2.2	3.1	2.8	2.5	2.2
Pedipalp femur:							
– Length		5.6	5.6	5.4	4.8	4.9	4.8
– Width		2.5	2.6	2.6	2.3	2.5	2.4
– Depth		1.5	1.5	2.2	2.1	1.9	1.8
Pedipalp patella:							
– Length		5.3	5.7	6.2	5.8	5.2	5.4
– Width		3.2	3.3	2.7	2.6	2.7	2.1
– Depth		2.4	2.2	2.6	2.6	2.5	2.4
Chela:							
– Length		11.3	11.3	11.5	10.9	9.9	10.4
– Width (manus)		4.9	4.5	5.6	5.3	5.3	4.4
– Depth (manus)		3.1	2.9	4.0	3.9	3.6	3.3
Movable finger:							
– Length		4.3	3.8	4.6	4.4	3.6	3.1
Pectinal teeth		10/11	9/9	7/7	5/4	8/9	7/8



Figures 25–32. *Scorpiops atomatus* from Lang County **25–28, 32** male (Ar.-MHBU-ScXZLX1705060101) **29–31** female (Ar.-MHBU-ScXZLX1705060102) **25–27, 29–31** chela dorsal, external, and ventral surfaces **28** dentate margin of movable finger under UV light, showing rows of granules **32** right leg I retrolateral surface. Green dots showing trichobothrial patterns of pedipalps. Scale bars: 2.0 mm.

Description (based on male specimen: Ar.-MHBU-ScXZLX1705060101).

Coloration (Figs 1, 2; after five years of preservation in alcohol): Carapace, reddish brown. Median and lateral ocular tubercles dark brown. Tergites and metasomal segments dark brown. Vesicle brown, with yellowish brown aculeus. Chelicerae yellow-

brown, with black-brown fingers. Pedipalps dark brown. Legs brown. Tarsal claws yellowish brown. Sternum dark reddish brown. Genital operculum and sternites brown. Pectinal teeth yellowish.

Morphology. *Prosoma* (Figs 5, 6): Entire surface of carapace with fine granules. Anterior median furrow broad and shallow; lateral furrow broad and flat; posterior median furrow deep. Median ocular tubercle high and smooth, with single shallow median furrow, situated anterior to center of carapace. Lateral ocular tubercle with some large granules, three pairs of lateral ocelli, posterior smallest; smooth oval area behind lateral ocular tubercle.

Mesosoma: Tergites densely covered with fine granules; tergites III–VI with median carina; tergite VII with two pairs of lateral carinae (outside lateral carinae degenerated) with large granules (Fig. 12). Pectinal teeth count 10/11, fulcra present (Fig. 11). Genital operculum subtriangular with genital protruding papillae (Fig. 11). Sternum pentagonal (Fig. 11). Sternite segments III–VI entirely smooth and shiny with few setae; segment VII with four ventral carinae and few setae.

Metasoma: Integument coarse with few setae. Metasoma segments II–V are longer than wide; segments I–V have 10-8-8-8-7 granular carinae. All dorsal carinae granular on segment I, and gradually become strongly serrated from II–IV; segment V carinae with smaller serration dorsally and larger serration ventrally. Vesicle coarse with few setae (Fig. 15).

Pedipalps: Integument with smooth granules and few setae. Femur with all dorsointernal, dorsoexternal, external, ventroexternal, ventrointernal carinae granulated, and internal carinae crenulated (Fig. 16). Patella with large granules on dorsointernal, dorsoexternal, ventrointernal, ventroexternal, and external carinae; two spinoid granules present on internal surface (Figs 17–19). Trichobothrial pattern C, neobothriotaxic (Vachon, 1974); patella with 17 external trichobothria (5 *eb*, 2 *esb*, 2 *em*, 4 *est*, 4 *et*), 8 (right) and 9 (left) ventral trichobothria (Figs 18, 19). Chela with four ventral trichobothria, all carinae are granular and coalesced except the dorsal secondary, subdigital, dorsal internal, interomedian, and ventromedian carinae vestigial, movable and fixed fingers with scalloped margins, single pronounced lobe in movable finger, and a corresponding notch in fixed finger (Figs 25–28).

Legs: Integument coarse with few setae, except ventral aspects of coxae, trochanters, femurs, and patellae smooth. Trochanter dorsally with few granules. Femur dorsally densely granular. Patella dorsally densely granular, with dorsoexternal granular carinae. Tibiae without spurs (Fig. 32). Basitarsus with setae, spurs, and two lateral pedal spurs (Fig. 32). Tarsus ventrally with single row of spinules (Fig. 32). Tarsal ungues curved and hook-like (Fig. 32).

Chelicerae (Fig. 7): Integument smooth, dorsally with an irregular pattern, ventrally with long hairs. Fixed finger of chelicera with three large triangular teeth on inner margin. Ventral of movable finger with five teeth on inner margin. Dorsal of movable finger with three teeth on inner margin.

Variations. Figures of adult females are provided (Figs 3, 4, 8–10, 13, 14, 20–24, 29–31). Number (left/right) of trichobothria on the ventral surface of the pedipalp

patellae: females with 9/9 ($n = 2$) and 10/9 ($n = 1$), males with 8/9 ($n = 1$) and 8/8 ($n = 1$). Number of pectinal teeth: females with 9/9 ($n = 2$) and 8/8 ($n = 1$), males with 10/11 ($n = 1$) and 11/11 ($n = 1$). Chela with an average length/width ratio of 2.3 in males ($n = 2$) and 2.5 in females ($n = 3$), male pedipalp chela fingers more strongly curved than females. All measurements are provided in Table 1. Holotype (male, not examined; Qi et al. 2005): patella with 17 external and nine ventral trichobothria, pectinal teeth count 11/11; paratype (female): some of the segments are slightly bulkier than that of the male, pectinal teeth count 9/9.

Distribution. China (Xizang) (Fig. 97).

Remarks. Body size is an important feature in distinguishing between the *Scorpiops* species. In China, *S. atomatus* (Xizang), *Scorpiops jendeki* Kovařík, 2000 (Yunnan), *Scorpiops lhasa* Di & Zhu, 2009 (Xizang), and *Scorpiops taxkorgan* Lourenço, 2018 (Xinjiang) are undoubtedly small species. In this work, we tried to separate the small-type species: usually < 50 mm, such as *S. atomatus*; the medium-sized species, usually 50–70 mm, such as *S. pococki* and *S. langxian*; and the larger species, usually > 70 mm, including *S. luridus* and *S. ingens* Yin, Zhang, Pan, Li & Di, 2015.

Di et al. (2011) thought that *S. atomatus* should be excluded from the *S. hardwickii* complex previously proposed by Kovařík and Ahmed (2009) due to the following reasons: (i) pectinal teeth count is 9–11 in *S. atomatus* and 4–8 in *S. hardwickii*; (ii) ventral trichobothria on patella are nine in *S. atomatus* and 6–8 in *S. hardwickii*; (iii) fulcra are present in *S. atomatus* but absent in *S. hardwickii*. In addition, *S. atomatus* has clearly thinner chela than *S. pococki* and *S. langxian*.

The most important morphological difference is that the body length of *S. tibetanus* holotype is 60.4 mm, and Kovařík (2000) recorded *S. tibetanus* as 50–65 mm; although there may be different measurement methods used by different authors, it suggested *S. tibetanus* significantly longer than *S. atomatus*. Here, we reaffirm the validity of *S. atomatus* based on newly collected materials.

***Scorpiops tibetanus* Hirst, 1911**

Figs 33–64, Table 1

Scorpiops tibetanus Hirst, 1911: 472–473; Kovařík 2000: 196, figs 47, 68, 69, tab. 1–3;

Fet 2000: 495; Kovařík et al. 2020: 126, figs 46, 143, 239–240, 799, tab. 9.

Scorpiops pococki Qi, Zhu & Lourenço, 2005: 14, figs 47–61; Di et al. 2013: 72, 75, figs 64–84, tab. 3; Di et al. 2014: 12.

Type locality. China, Xizang, Tsangpo Valley, Chaksam Ferry.

Material examined. 1 male and 1 female, China, Xizang, Lasa City (Lhasa City), Qushui County (Chushur County), Caina Town (Saena Town), 20/7/2019, Zhiyong Di leg. (Ar.-MHBUScXZQS1907200101, Ar.-MHBUScXZQS1907200102); 1 male and 2 females, China, Xizang, Shannan City (Lhoka City), Jiacha County (Gyaca County), Jiacha Town (Gyaca Town), 12/8/2021, Zhiyong Di leg. (Ar.-MHBUScXZJC21081206, 01–03).

Diagnosis. Adult body length 50–57 mm. Base color uniformly reddish black. Patella of pedipalp with 17 (5 *eb*, 2 *esb*, 2 *em*, 4 *est*, 4 *et*) external and 6–8 (usually seven) ventral trichobothria. Chelal trichobothria *Eb*₃ is located in proximal half of manus between trichobothria *Dt* and *Db*. Chela with four ventral trichobothria. Chela with an average length/width ratio of 2.0 in both sexes, pedipalp movable finger with ca. four or five ID, 10–25 IAD, 45–62 MD, and eight or nine OD present, chela fingers on adult males and females scalloped, usually more strongly in males. Pectinal teeth count 4–7, fulcra absent. Pectinal with two marginal and one middle lamellae. Telson bulbous and granulate, annular ring present.

Description (based on male specimen: Ar.-MHBUScXZQS1907200101).

Coloration (Figs 33, 34; after three years of preservation in alcohol): Carapace reddish black. Median and lateral ocular tubercles dark brown. Tergites and metasomal segments dark brown. Vesicle dark brown, with dark brown aculeus. Chelicerae unevenly dark brown and fingers uniformly dark reddish. Pedipalps dark reddish brown. Legs dark brown. Tarsal claws brown. Sternum reddish brown. Genital operculum and sternites brown. Pectinal teeth light brown.

Morphology. Prosoma (Figs 37, 38): Integument coarse, carapace with dense, fine granules; anterior median furrow broad and deep; lateral furrow broad; posterior median furrow broad and deep. Median eyes situated anteriorly compared to center of carapace; three pairs of lateral ocelli with posterior-most the smallest. Median ocular tubercle with granules and median furrow. Lateral ocular tubercle with some coarse granules around lateral eyes.

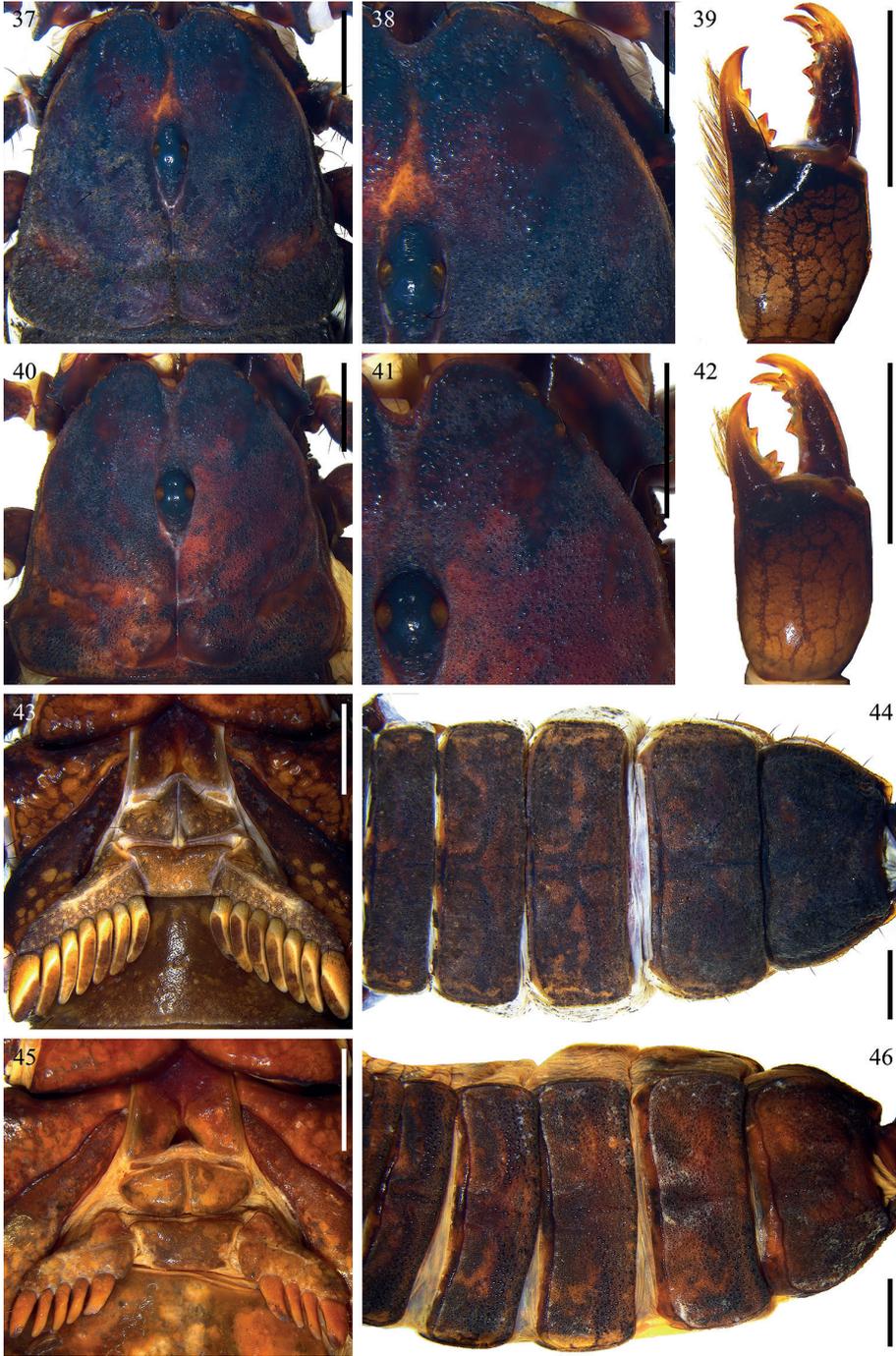
Mesosoma: Tergites densely covered with fine granules, tergites II–VII with median carina barely visible at first and gradually becomes distinct; tergite VII with two pairs of lateral carinae with large granules present only on posterior half (Fig. 44). Pectinal teeth count 7/7, fulcra absent (Fig. 43). Genital operculum subtriangular with genital papillae protruding (Fig. 43). Sternum pentagonal (Fig. 43). Sternite segments III–VI entirely smooth and shiny with few setae; segment VII with four ventral carinae and few setae.

Metasoma: Integument coarse, segments II–V longer than wide; segments I–V with respectively 10–8–8–8 granular carinae; segment V with pair of vestigial lateral carinae; all ventral carinae crenulated, gradually becoming more strongly crenulated. Vesicle with dense granules and few setae (Fig. 47).

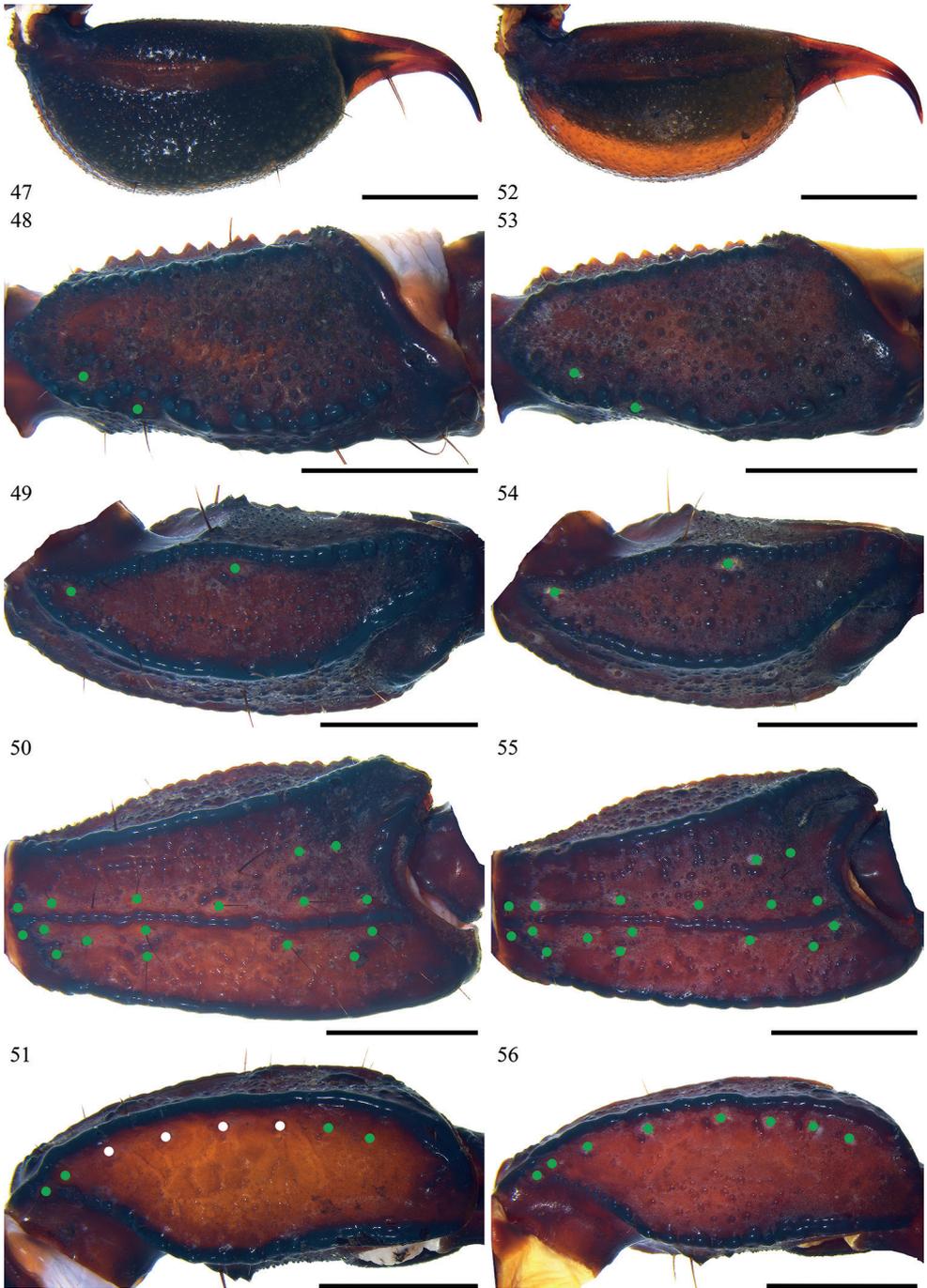
Pedipalps: Integument smooth with smooth granules and few setae. Femur with dorsointernal, dorsoexternal, external, ventroexternal, ventrointernal carinae granulated, and internal carinae crenulated (Fig. 48). Patella with large granules on dorsointernal, dorsoexternal, ventrointernal, ventroexternal, and smooth external carinae; two spinoid granules present on internal surface (Figs 49–51). Trichobothrial pattern C, neobothriotaxitic (Vachon, 1974); patella with 17 external trichobothria (5 *eb*, 2 *esb*, 2 *em*, 4 *est*, 4 *et*), 4 (right, dysplastic) and 7 (left) ventral trichobothria (Figs 50, 51). Chela with granules forming the indistinct reticulated pattern, ventral with four trichobothria, all carinae are granular and coalesced except the subdigital, dorsal internal, interomedian, and ventromedian carinae vestigial; movable and fixed fingers with scalloped margins, a pronounced lobe in movable finger and corresponding notch in fixed finger (Figs 57–60).



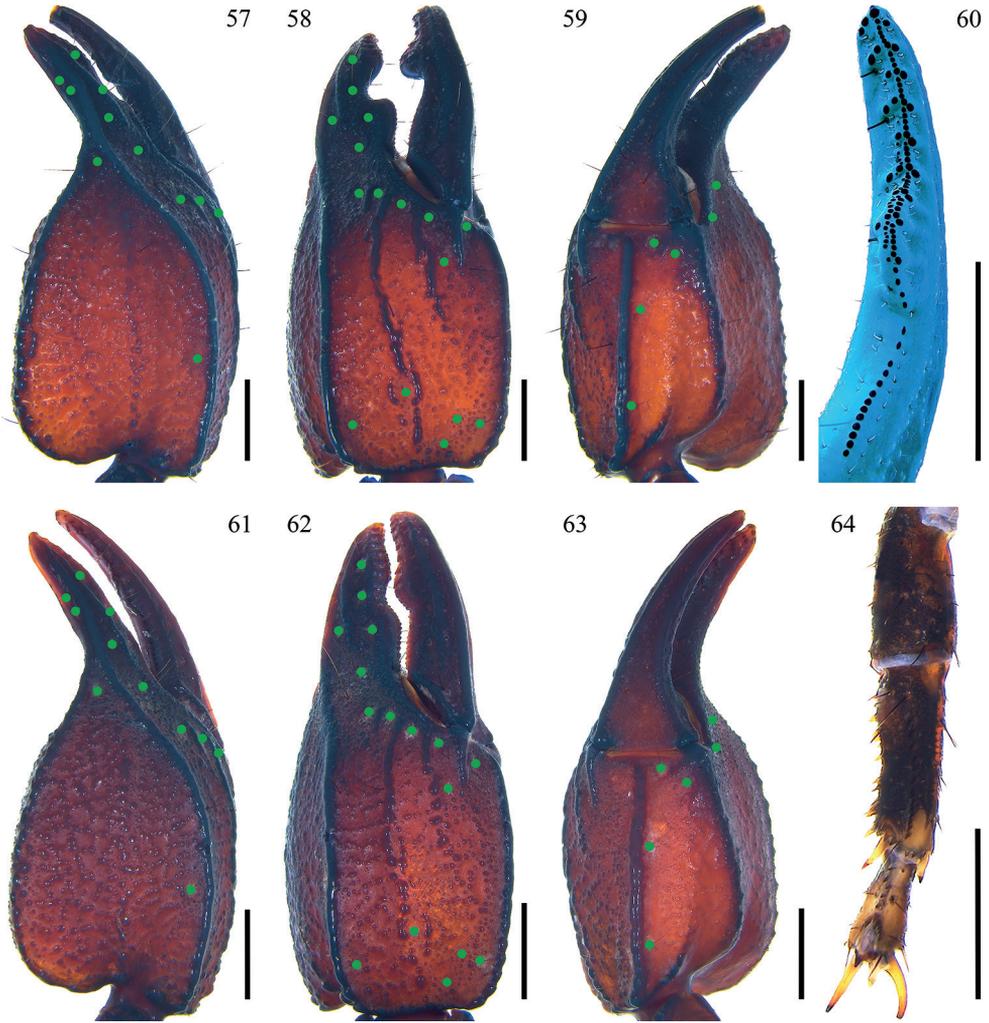
Figures 33–36. *Scorpiops tibetanus* from Qushui County **33, 34** male (Ar.-MHBUScXZQS1907200101), dorsal and ventral views **35, 36** female (Ar.-MHBUScXZQS1907200102), dorsal and ventral views. Scale bars: 12.0 mm.



Figures 37–46. *Scorpiops tibetanus* from Qushui County **37, 38, 39, 43, 44** male (Ar.-MHBUScXZQS1907200101) **40, 41, 42, 45, 46** female (Ar.-MHBUScXZQS1907200102) **37, 40** carapace **38, 41** eyes and nearby area **39, 42** chelicera dorsal surface **43, 45** sternum, genital operculum and pectines **44, 46** tergites. Scale bars: 2.0 mm.



Figures 47–56. *Scorpiops tibetanus* from Qushui County **47–51** male (Ar.-MHBU-ScXZQS1907200101) **52–56** female (Ar.-MHBU-ScXZQS1907200102) **47, 52** telson, lateral surface **48, 53** femur dorsal surface **49–51, 54–56** patella dorsal, external, and ventral surfaces. Green dots showing trichobothrial patterns of pedipalps (the white dots representing dysplasia caused trichobothrial absence). Scale bars: 2.0 mm.



Figures 57–64. *Scorpiops tibetanus* from Qushui County and Jiacha County **57–59, 64** male (Ar.-MHBU-ScXZQS1907200101) **61–63** female (Ar.-MHBU-ScXZQS1907200102) **60** male (Ar.-MHBU-ScXZJC2108120601, from Jiacha County) **57–59, 61–63** dorsal, external, and ventral surfaces of chela **60** dentate margin of movable finger under UV light, showing rows of granules **64** right leg I retrolateral surface. Green dots showing trichobothrial patterns of pedipalps. Scale bars: 2.0 mm.

Legs: Integument coarse with few setae. Trochanter dorsal surface with few granules. Femur dorsal surface densely granular. Patella dorsal surface densely granular, with dorsoexternal and dorsal granular carinae. Tibiae without spurs (Fig. 64). Basitarsus with more setae, spurs, and two lateral pedal spurs (Fig. 64). Tarsus ventrally with single row of spinules (Fig. 64). Tarsal ungues curved and hook-like (Fig. 64).

Chelicerae (Fig. 39): Dorsally with irregular pattern, ventrally with long hairs. Fixed finger of chelicera with three large triangular teeth on inner margin; ventral of

movable finger with five teeth on inner margin, dorsal of movable finger with four teeth on inner margin.

Variation. Figures of adult females are provided (Figs 35, 36, 40–42, 45, 46, 52–56, 61–63). Number (left/right) of trichobothria on the ventral surface of the pedipalp patellae: females with 8/8 ($n = 1$), 7/7 ($n = 1$), and 6/6 ($n = 1$), males with ?/7 ($n = 1$) and 7/7 ($n = 1$). Number of pectinal teeth: females with 5/4 ($n = 2$) and 6/5 ($n = 1$), males with 7/7 ($n = 2$). Chela with an average length/width ratio of 2.0 in males ($n = 2$) and 2.0 in females ($n = 3$), male pedipalp chela fingers stronger curved than females. The measurements are provided in Table 1. Holotype (male, not examined; Kovařík, 2000): body length 60.4 mm, patella with eight ventral trichobothria, pectinal teeth count seven or eight. Holotype (male) of *S. pococki* (= *S. tibetanus*): patella with 17 external and eight ventral trichobothria, pectinal teeth count 8/7; paratype (female) of *S. pococki* (= *S. tibetanus*): pectinal teeth count 6/6, telson is smaller than that of male in Qi et al. (2005).

Distribution. China (Xizang) (Fig. 97).

Remarks. Hirst (1911) erected *S. tibetanus* based on a male specimen from “Tsangpo Valley, Chaksam Ferry”, for which the species information is brief, and no figures provided.

The type locality is therefore the most crucial information on the species. Followed the Internet and literature information for “Chaksam Ferry”: “Chaksam” means “iron bridge”, located in Dagar village and under the Quwori Mountain, Qushui County. It was created by the famous bridge designer, Tangdongjiebu, and is the first cable bridge across the Brahmaputra River, completed in 1420 or 1430. “Chaksam Ferry” subsequently became a famous place, also called “Qushui Ferry” or “Daga Ferry” in ancient times (Fig. 97). However, with the disappearance of the “iron bridge” and the construction of Qushui Bridge (Qushuidaiao) near where the ancient “iron bridge” used to be in 1966, “Chaksam Ferry” has now been replaced by Qushui Bridge and is the probable type locality of *S. tibetanus*.

In recent years, we found *S. atomatus* distributed near the “iron bridge”, and found *S. pococki* 28 km away from this “iron bridge” (Fig. 97).

The list of taxa included in the *S. hardwickii* “complex” proposed by Kovařík and Ahmed (2009) included *S. tibetanus*. Kovařík (2000) examined the holotype (male) of *S. tibetanus* and recorded some important information: “length 60.4 mm, ventral trichobothria on the patella number 8, and pectinal teeth number 7 or 8”. Kovařík (2000) concluded that the characters of *S. tibetanus* were “length 50–65 mm, ventral trichobothria on the patella number 7–10 (usually 9, in one young of 37 specimens, 7 on one side), pectinal teeth number 5–11”. In his revision, the new localities of *S. tibetanus* included Lhasa, Shigatse, and Kambu batsi. Kovařík et al. (2020) proposed *S. pococki* as a junior synonym of *S. tibetanus* and provided figures of *S. tibetanus* (one male identified as “*S. pococki*” and donated by Di).

During several surveys in Shigatse and the surrounding counties, we found *S. lourencoi* sp. nov. and *S. luridus*. The body length of *S. lourencoi* sp. nov. is no more than 50 mm, while *S. luridus* is a distinctive species. *Scorpiops pococki* (from Chaksam

Ferry 28 km away) has the diagnosis as followed: fulcra absent, body length ~ 55 mm, the ventral trichobothria on the patella number seven or eight, and the pectinal teeth number 4–7. *Scorpiops pococki* fits the characteristics of *S. tibetanus*, and we agree that *S. pococki* is a synonym of *S. tibetanus*.

***Scorpiops lourencoi* sp. nov.**

<https://zoobank.org/92D21DC0-794E-4D76-B2F8-28AB9D88520B>

Figs 65–96, Table 1

Scorpiops tibetanus Di et al., 2013: 75, 77, 80, 81, 83, 85, figs 102–118, tab. 2.

Type material. **Male holotype**, China, Xizang, Rikaze City (Shigatse City), 26/7/2021, Zhiyong Di leg. (Ar.-MHBU-ScXZRKZ2107260101); 3 male and 3 female paratypes (Ar.-MHBU-ScXZRKZ21072601, 02–06; Ar.-MHBU-ScXZRKZ2107270501), same location data as holotype.

Diagnosis. *Scorpiops lourencoi* sp. nov. differs from all other species in the genus based on the following combination of characters: reddish black color, length 45–50 mm; patella of pedipalp with 17 (5 *eb*, 2 *esb*, 2 *em*, 4 *est*, 4 *et*) external and eight or nine (usually nine) ventral trichobothria. Chelal trichobothria *Eb*₃ located in proximal half of manus between trichobothria *Dt* and *Db*, chela with four ventral trichobothria; chela with an average length/width ratio of 1.9 in males ($n = 4$ adults) and 2.4 in females ($n = 3$ adults); pedipalp movable finger with ca. four or five ID, 10–14 IAD, 44–45 MD, and seven or eight OD present; pedipalp chelal fingers on adult males and females scalloped, usually more strongly in male. Pectinal teeth count 8–11 (usually 10) in four males and seven or eight (usually seven) in three females, fulcra present; pectinal with three marginal and five or six middle lamellae. Telson bulbous and granulate, annular ring present.

Etymology. Patronym in honor of Prof. Wilson R. Lourenço, who significantly contributed to scorpion research.

Description (based on holotype: Ar.-MHBU-ScXZRKZ2107260101).

Coloration (Figs 65, 66; after one year of preservation in alcohol): Carapace, dark red-brown. Median and lateral ocular tubercles dark brown. Tergites and metasomal segments dark red-brown to dark brown. Vesicle dark brown, with brown aculeus. Chelicerae dark brown; with the fingers dark brown and gradually lighter toward the tip. Pedipalps dark red-brown. Legs dark brown. Tarsal claws yellowish brown. Sternum, genital operculum, and sternites yellowish brown. Pectinal teeth yellowish.

Morphology. Prosoma (Figs 69, 70): Carapace with dense, coarse granules; shallow anterior median furrow; broad and flat lateral furrow; posterior median furrow broad and deep. Median ocular tubercle high and coarse, with a shallow median furrow, median eyes situated anteriorly compared to center of carapace; three pairs of lateral ocelli, posterior smallest, some large granules near lateral ocelli, and presence of smooth oval area behind the lateral ocular tubercle.

Mesosoma: Integument coarse. Tergites sparsely covered with large coarse granules, posterior part of tergites with larger granules; tergites III–VI with a median carina; tergite VII with two pairs of lateral carinae (outside lateral carinae degenerated) (Fig. 76). Sternum quinquangular with few setae (Fig. 75). Genital operculum subtriangular with genital papillae protruding (Fig. 75). Pectinal teeth count 8/9, fulcrum present (Fig. 75). Sternites, segments III–VI are smooth and shiny with few setae, segment VII with four smooth carinae of big granules and few setae.

Metasoma: Integument coarse with few setae. Segments II–V longer than wide; segments I–V with respectively 10-8-8-8-7 granular carinae, segments II–IV all dorsal carinae gradually become strongly serrated; segment V carinae with smaller granules dorsally and larger serration ventrally. Vesicle with few setae and granules (Fig. 79).

Pedipalps: Integument with smooth granules and few setae, especially the granules are larger on dorsal and external surfaces of chelae. Femur with external, dorsointernal, dorsoexternal, ventrointernal, ventroexternal carinae granulated, and internal carinae crenulated (Fig. 80). Patella with dorsointernal, ventrointernal, ventroexternal, and external carinae with smooth granules; two spinoid granules present on the internal aspect, the ventral internal spinoid granule being much larger than the dorsointernal one (Figs 81–83). Trichobothrial pattern C, neobothriotaxic (Vachon, 1974); patella with 17 external trichobothria (5 *eb*, 2 *esb*, 2 *em*, 4 *est*, 4 *et*), 9 (right) and 9 (left) ventral trichobothria (Figs 82, 83). Chela very thick, with four ventral trichobothria, all carinae are granular and coalesced except the dorsal secondary, subdigital, dorsal internal, interomedian, and ventromedian carinae vestigial; fingers scalloped, with a pronounced lobe in the movable finger and a corresponding notch in the fixed finger (Figs 89–92).

Legs: Integument coarse with few setae except ventral aspects of coxae, trochanters, femurs, and patellae smooth. Trochanter dorsal with few granules and few setae. Femur dorsal with few granules. Patella internally with a dentate carina. Tibiae without spurs (Fig. 96). Basitarsus with spurs and two lateral pedal spurs (Fig. 96). Tarsus ventrally with a row of spinules (Fig. 96). Tarsal ungues curved and hook-like (Fig. 96).

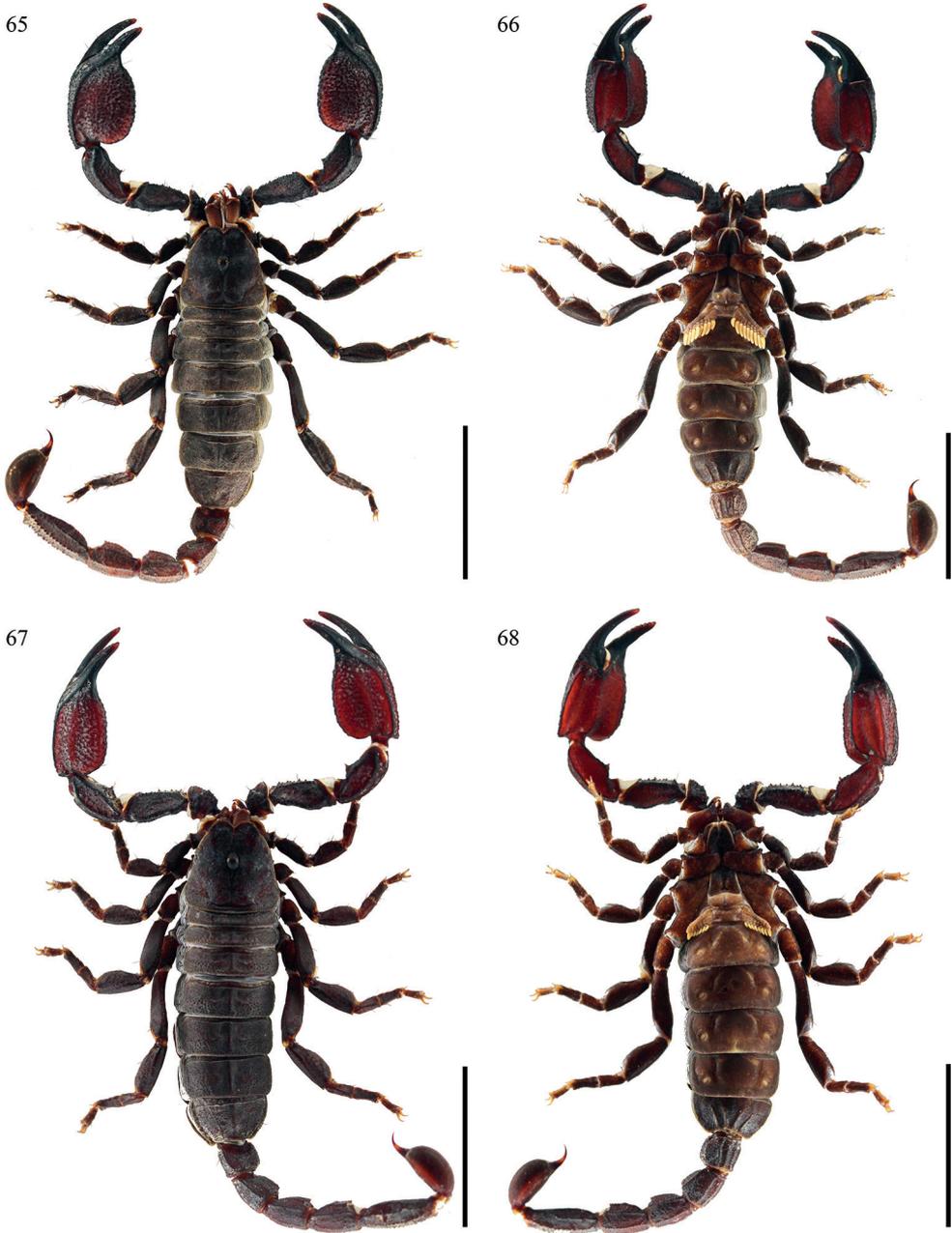
Chelicerae (Fig. 71): Integument smooth and shiny, dorsal with irregular pattern, ventrally with long hairs. Fixed finger of chelicera with three large triangular teeth on inner margin; ventral of movable finger with six teeth on inner margin, dorsal of movable finger with four teeth on inner margin.

Variation. Feature figures of adult females are provided (Figs 67, 68, 72–74, 77, 78, 84–88, 93–95). Number (left/right) of trichobothria on the ventral surface of the pedipalp patellae: females with 9/9 ($n = 2$) and 8/9 ($n = 1$), males with 9/9 ($n = 4$). Number of pectinal teeth: females with 7/7 ($n = 2$) and 7/8 ($n = 1$), males with 8/9 ($n = 1$), 10/10 ($n = 2$), and 10/11 ($n = 1$). Chela with an average length/width ratio of 1.9 in males ($n = 4$) and 2.4 in females ($n = 3$), male pedipalp chela fingers stronger curved than females, lobe and corresponding notch reduced in females. Measurements provided in Table 1. One female specimen (mistakenly identified as *S. tibetanus* in Di et al. (2013); not examined): body length 45.2 mm, patella with nine ventral trichobothria, pectinal teeth count 7/7.

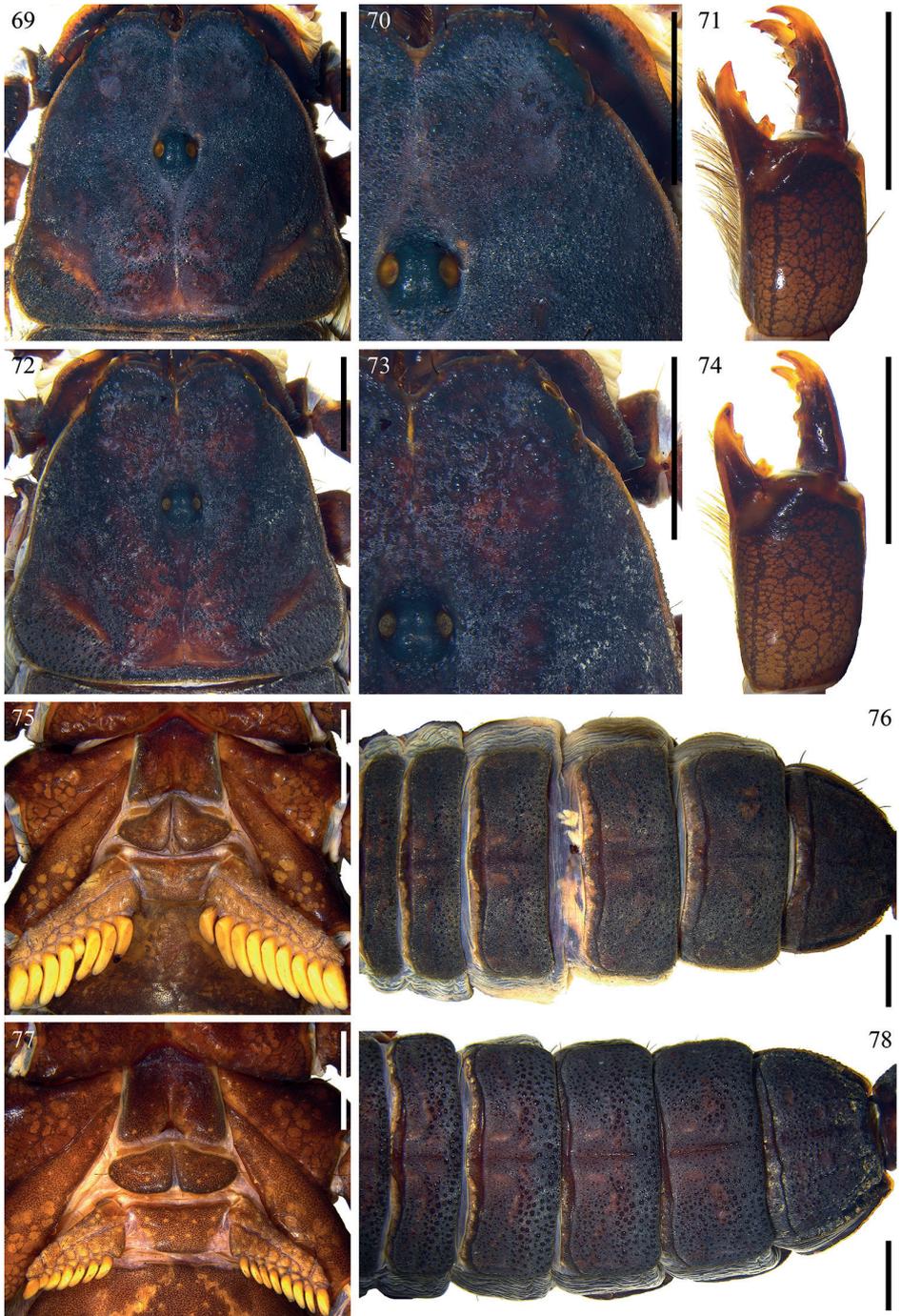
Habitat. Found under stones in dry mountain boscage in Shigatse City, ~ 3889 m elevation.

Distribution. Rikaze City, Xizang, China (Fig. 97).

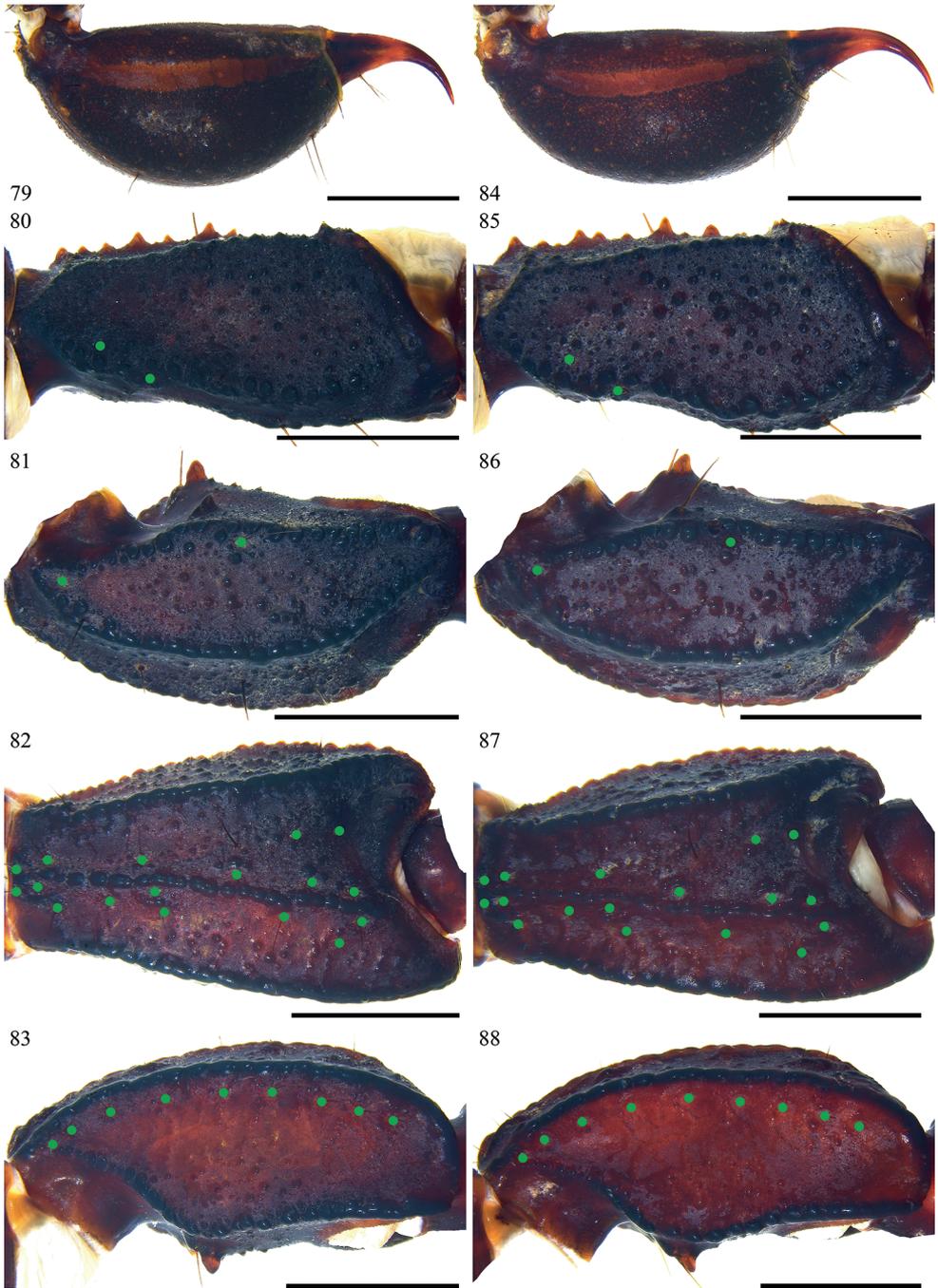
Remarks. *Scorpiops atomatus* is similar to the new species, but can be readily distinguished based on the following combination of characters: (i) the pectinal teeth count



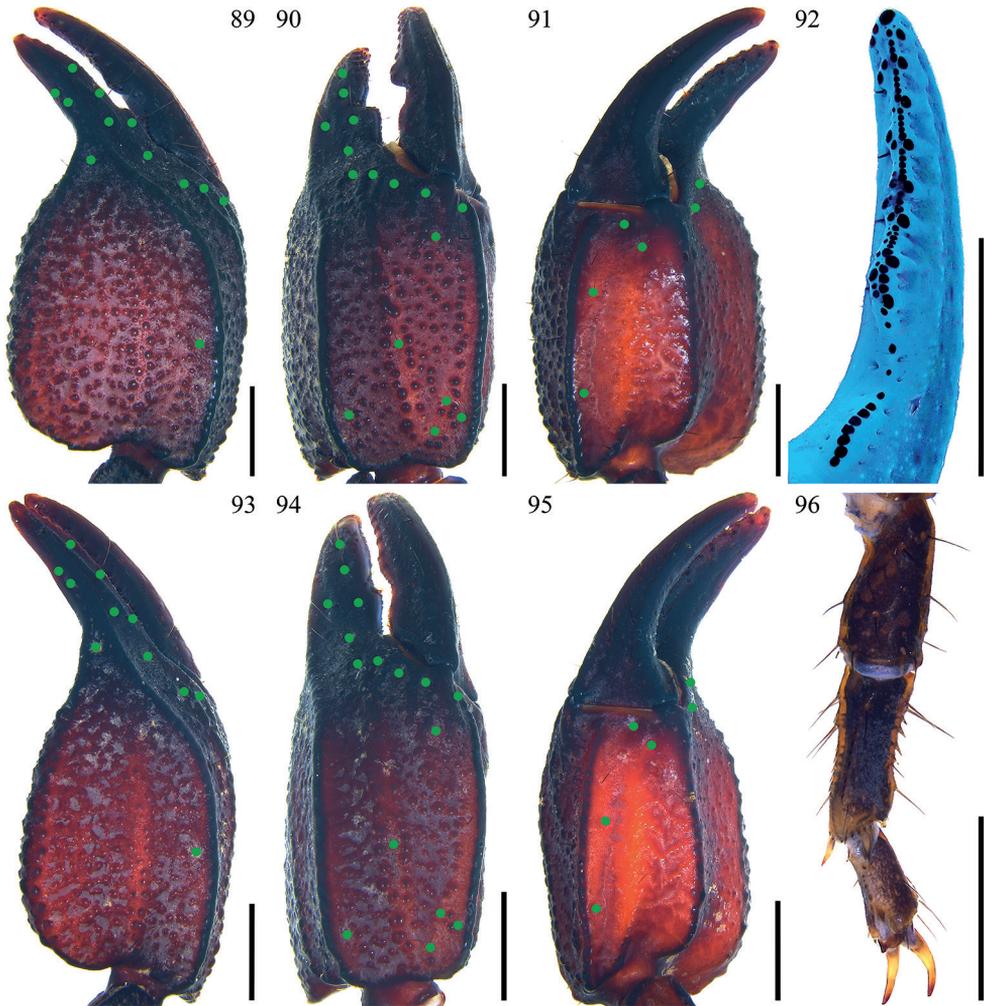
Figures 65–68. *Scorpiops lourencoi* sp. nov. from Rikaze City **65, 66** male (Ar.-MHBU-ScXZ-RKZ2107260101), dorsal and ventral views **67, 68** female (Ar.-MHBU-ScXZRKZ2107260102), dorsal and ventral views. Scale bars: 12.0 mm.



Figures 69–78. *Scorpiops lourencoi* sp. nov. from Rikaze City **69, 70, 71, 75, 76** male (Ar.-MHBU-ScXZRKZ2107260101) **72, 73, 74, 77, 78** female (Ar.-MHBU-ScXZRKZ2107260102) **69, 77** carapace **70, 73** eyes and nearby area **71, 74** chelicera dorsal surface **75, 77** sternum, genital operculum, and pectines **76, 78** tergites. Scale bars: 2.0 mm.



Figures 79–88. *Scorpiops lourencoi* sp. nov. from Rikaze City **79–83** male (Ar.-MHBUScXZ-RKZ2107260101) **84–88** female (Ar.-MHBUScXZ-RKZ2107260102) **79, 84** telson, lateral surface **80, 85** femur dorsal surface **81–83, 86–88** patella dorsal, external, and ventral surfaces. Green dots showing trichobothrial patterns of pedipalps. Scale bars: 2.0 mm.



Figures 89–96. *Scorpiops lourencoi* sp. nov. from Rikaze City **89–92, 96** male (Ar.-MHBUScXZ-RKZ2107260101) **93–95** female (Ar.-MHBUScXZ-RKZ2107260102) **89–91, 93–95** chela dorsal, external, and ventral surfaces **92** dentate margin of movable finger under UV light, showing rows of granules **96** right leg I retrolateral surface. Green dots showing trichobothrial patterns of pedipalps. Scale bars: 2.0 mm.

8–11 (with 10–11 (usually 11) in males and eight or nine (usually nine) in females) in *S. atomatus*, while there are 7–11 (with 8–11 (usually 10) in males and seven or eight (usually seven) in females) in *S. lourencoi* sp. nov. (ii) length of adults 40–45 mm in *S. atomatus*, while the length of adults 45–50 mm in *S. lourencoi* sp. nov. (iii) chela with an average length/width ratio of 2.3 in males ($n = 2$ adults) and 2.5 in females ($n = 3$ adults) in *S. atomatus*, while 1.9 in males ($n = 4$ adults) and 2.4 in females ($n = 3$ adults) in *S. lourencoi* sp. nov. (iv) chela surface with small granules in *S. atomatus*, while large granules in *S. lourencoi* sp. nov.

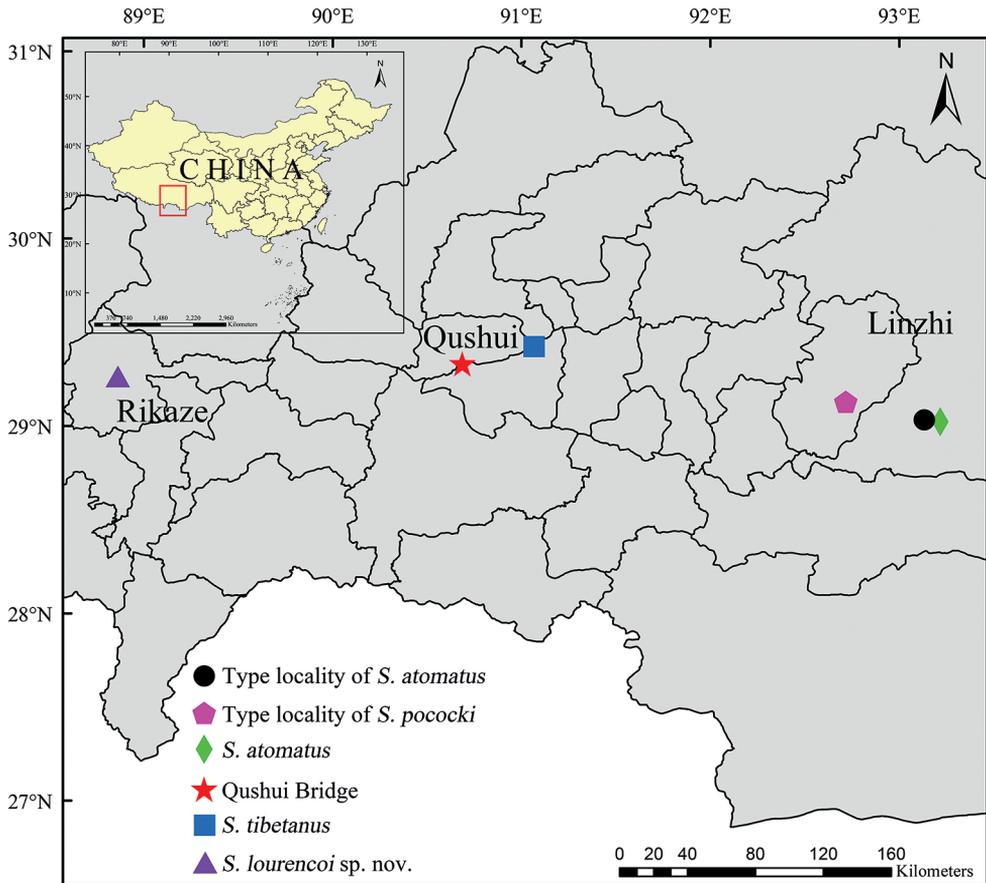


Figure 97. Distribution of *S. atomatus* (circle and diamond), *S. tibetanus* (pentagon and square), *S. lourencoi* sp. nov. (triangle), and the location of Qushui Bridge and Chaksam Ferry (star) in Xizang, China.

Discussion

Kovařík (2000), Kovařík and Ahmed (2009), and Kovařík et al. (2020) examined the type specimen of *S. tibetanus*, however, they provided confusing information that led to *S. pococki* and *S. atomatus* being considered synonyms of *S. tibetanus*. Influenced by this, Qi et al. (2005) incorrectly erected *S. pococki*. The precise information on Chaksam and Chaksam Ferry was not easily available in 2005, and the revision of the family Scorpiopidae by Kovařík (2000) was undoubtedly the most important basis for Qi et al. (2005). Di et al. (2011, 2013, 2014), Di and Qiao (2020), Li et al. (2016), and Yin et al. (2015) also relied on Kovařík’s (2000) information when reviewing the *Scorpiops* species from China. This led to mistakes in the keys related to *Scorpiops* from China by Di et al. (2011, 2013, 2014), Di and Qiao (2020), Li et al. (2016), and Yin et al. (2015). Those keys of *Scorpiops* species from China should be corrected and the new revised key is presented below.

Updated key to Chinese species of the genus *Scorpiops* with chelal trichobothria Eb_3 located in the proximal half of the manus between trichobothria *Dt* and *Db* (modified from Di and Qiao 2020)

- 1 Pedipalp chela fingers with non-scalloped (nearly straight) margins in both sexes.....2
 – Pedipalp chela fingers with scalloped margins in male adults.....4
- 2 Chela length-to-width ratio > 3.03
 – Chela length-to-width ratio < 3.0 *S. jendeki*
- 3 Total length 40.0–58.0 mm, chela length-to-width ratio ~ 3.3–3.5
 *S. leptochirus*
 – Total length 35.2 mm (male holotype), chela length-to-width ratio ~ 3.2
 *S. taxkorgan*
- 4 Manus length-to-width ratio visibly > 15
 – Manus with similar length and width12
- 5 Total length > 61.0 mm usually6
 – Total length < 61.0 mm usually8
- 6 Red brown, ventral patella of pedipalps with 7 (rarely 6 or 8) trichobothria..
 *S. petersii*
 – Lighter than red brown7
- 7 Ventral patella of pedipalps with 7 or 8 trichobothria, pectinal teeth count 7
 in males and 6 in females *S. songi*
 – Ventral patella of pedipalps with 9 trichobothria, pectinal teeth count 9/10 in
 male holotype and 8 in female paratype *S. luridus*
- 8 Dorsally flat manus of pedipalps and chela of both sexes, with length/width
 ratio: 2.1–2.2 (~ 2.1 in males and 2.2 in females), total length 40.0–50.0 mm
 in adults..... *S. margerisonae*
 – Dorsally round manus of pedipalps or at least the chela of one sex, with
 length-to-width ratio > 2.2 or total length > 50.0 mm9
- 9 Body length ~ 45.0 mm–61.0 mm10
 – Body length < 40.0 mm.....11
- 10 Patella of pedipalp with 17 (5 *eb*, 2 *esb*, 2 *em*, 4 *est*, 4 *et*) external trichobo-
 thria *S. lourencoi* sp. nov.
 – Patella of pedipalp with 18–20 (5 *eb*, 2 *esb*, 2 *em*, 5 *est*, 4–6 *et*) external tricho-
 bothria..... *S. wrzecionkoi*
- 11 Chela of pedipalp length-to-width ratio ~ 2.6–3.0..... *S. lhasa*
 – Chela of pedipalp length-to-width ratio < 2.5 *S. atomatus*
- 12 Yellow-brown color, length of adults > 70.0 mm *S. ingens*
 – Red-brown to red-black color, length of adults < 65.0 mm *S. hardwickii*
complex (*S. hardwickii*, *S. jingshanensis*, *S. langxian*, *S. tibetanus*)

Acknowledgements

This work was supported in part by grants from the National Natural Sciences Foundation of China (31970403 and 31601871), the Hebei Provincial Natural Science Foundation (C2019201273), and the Advanced Talents Incubation Program of the Hebei University (801260201276) to Zhiyong Di. We thank the editors for all the editorial work and anonymous reviewers for their comments.

References

- Di ZY, He YW, Cao ZJ, Wu YL, Li WX (2011) The first record of the family Euscorpiidae (Arachnida: Scorpiones) from Central China, with a key of Chinese species of the genus *Scorpiops*. *Euscorpius* 118(118): 1–9. <https://doi.org/10.18590/euscorpius.2011.vol2011.iss118.1>
- Di ZY, Qiao S (2020) *Scorpiops songi* sp. n. and key to species of *Scorpiops* from China (Scorpiones: Scorpipidae). *Arthropoda Selecta* 29(3): 316–324. <https://doi.org/10.15298/arth-sel.29.3.03>
- Di ZY, Xu XB, Cao ZJ, Wu YL, Li WX (2013) Notes on the scorpions (Arachnida, Scorpiones) from Tibet with the redescription of *Scorpiops jendeki* Kovařík, 2000 (Scorpiones, Euscorpiidae) from Yunnan (China). *ZooKeys* 301: 51–99. <https://doi.org/10.3897/zookeys.301.4608>
- Di ZY, Yang ZZ, Yin SJ, Cao ZJ, Li WX (2014) History of study, updated checklist, distribution and key of scorpions (Arachnida: Scorpiones) from China. *Zoological Research* 35(1): 3–19. <https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5042949/pdf/ZoolRes-35-1-3.pdf>
- Hjelle JT (1990) Anatomy and morphology. In: Polis GA (Ed.) *The Biology of Scorpions*. Stanford University Press, Stanford, California, 9–63.
- Hirst S (1911) Descriptions of new scorpions. *Annals and Magazine of Natural History* 8(8): 462–473. <https://doi.org/10.1080/00222931108693056>
- Kovařík F (2000) Revision of family Scorpipidae (Scorpiones), with descriptions of six new species. *Acta Societatis Zoologicae Bohemicae* 64: 153–201.
- Kovařík F, Ahmed Z (2009) Three new species of *Scorpiops* Peters, 1861 (Scorpiones: Euscorpiidae: Scorpipinae) from Pakistan. *Euscorpius* 88(88): 1–11. <https://doi.org/10.18590/euscorpius.2009.vol2009.iss88.1>
- Kovařík F, Lowe G, Stockmann M, Štáhlavský F (2020) Revision of genus-group taxa in the family Scorpipidae Kraepelin, 1905, with description of 15 new species (Arachnida: Scorpiones). *Euscorpius* 325: 1–140. <https://mds.marshall.edu/cgi/viewcontent.cgi?article=1356&context=euscorpius>
- Li WX, Wu YL, Cao ZJ, Di ZY (2016) *Scorpion Biology and Toxins*. Science Press, Beijing, China, 235–239.

- Lourenço WR, Ythier E (2022) A new species of the genus *Scorpiops* Peters, 1861, subgenus *Euscorpiops* Vachon, 1980 from Laos (Scorpiones: Scorpipidae). *Faunitaxys* 10(27): 1–9. [https://doi.org/10.57800/faunitaxys-10\(27\)](https://doi.org/10.57800/faunitaxys-10(27))
- Lv HY, Di ZY (2022) The first record of *Scorpiops bhutanensis* Tikader & Bastawade, 1983 from China, with the first report of its female (Scorpiones: Scorpipidae). *Euscorpius* 358: 1–8. <https://mds.marshall.edu/euscorpius/vol2022/iss358/1>
- Qi JX, Zhu MS, Lourenço WR (2005) Eight new species of the genera *Scorpiops* Peters, *Euscorpiops* Vachon, and *Chaerilus* Simon (Scorpiones: Euscorpiidae, Chaerilidae) from Tibet and Yunnan, China. *Euscorpius* 32(32): 1–40. <https://doi.org/10.18590/euscorpius.2005.vol2005.iss32.1>
- Sissom WD (1990) Systematics, biogeography and paleontology. In: Polis GA (Ed.) *The Biology of Scorpions*. Stanford University Press, Stanford, California, 64–160.
- Soleglad ME, Sissom WD (2001) Phylogeny of the family Euscorpiidae Laurie, 1869 (Scorpiones): a major revision. In: Fet V, Selden PA (Eds) *Scorpions 2001*. In Memoriam Gary A. Polis. British Arachnological Society, 25–111.
- Štáhlavský F, Kovařík F, Stockmann M, Opatova V (2020) Karyotype evolution and preliminary molecular assessment of genera in the family Scorpipidae (Arachnida: Scorpiones). *Zoology* 144(2021): 125882. <https://doi.org/10.1016/j.zool.2020.125882>
- Tang V (2022) Reanalysis of the Yunnan population of *Scorpiops kubani* with a description of a new species, *Scorpiops lowei* sp. n. (Scorpiones: Scorpipidae). *Euscorpius* 361: 1–22. <https://mds.marshall.edu/euscorpius/vol2022/iss361/1>
- Vachon M (1952) *Études sur les Scorpions*. Publications de l'Institut Pasteur d'Algérie. Algérie, 482 pp.
- Vachon M (1974) Étude des caractères utilisés pour classer les familles et les genres de Scorpions (Arachnides). 1. La trichobothriotaxie en arachnologie. Sigles trichobothriax et types de trichobothriotaxie chez les Scorpions. *Bulletin du Muséum national d'Histoire naturelle*, Paris, 3 sér., 140: 857–958.
- Yin SJ, Zhang YF, Pan ZH, Li SB, Di ZY (2015) *Scorpiops ingens* sp. n. and an updated key to the *Scorpiops* from China (Scorpiones, Euscorpiidae, Scorpipinae). *ZooKeys* 495: 53–61. <https://doi.org/10.3897/zookeys.495.9085>