ZooKeys 845: 1–97 (2019)
doi: 10.3897/zookeys.845.32428
http://zookeys.pensoft.net

RESEARCH ARTICLE

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Systematic re-structure and new species of Sphaerodoridae (Annelida) after morphological revision and molecular phylogenetic analyses of the North East Atlantic fauna

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Academic editor: *Greg Rouse* | Received 19 December 2018 | Accepted 25 February 2019 | Published 15 May 2019

http://zoobank.org/F05BDFEC-4C4A-4F22-9685-4AC2655B973D

Citation: Capa M, Nygren A, Parapar J, Bakken T, Meißner K, Moreira J (2019) Systematic re-structure and new species of Sphaerodoridae (Annelida) after morphological revision and molecular phylogenetic analyses of the North East Atlantic fauna. ZooKeys 845: 1–97. https://doi.org/10.3897/zookeys.845.32428

Abstract

Detailed morphological study of more than 2600 North East Atlantic (NEA) sphaerodorids (Sphaerodoridae, Annelida) and phylogenetic analyses of DNA sequences of representatives of several identified morphospecies enforced changing the current systematic classification within the family, allowed the discovery of new species, provided new information about the morphological and genetic characterisation of members of this group, and increased the species occurrence data to better infer their geographic and bathymetric distribution ranges. Phylogenetic analyses of nuclear (18S rRNA and 28S rRNA) and mitochondrial sequences (COI and 16S rRNA) of NEA short-bodied sphaerodorids revealed outstanding results including paraphyly of the genera *Sphaerodoropsis*, *Sphaerodoridium,* and *Sphaerephesia*. The number of longitudinal and transverse rows of dorsal macrotubercles is proposed as potential synapomorphies for the main clades, and are consequently herein used for the genera delimitation. The new classification proposed here implies nomenclatural changes and the erection of a new genus, *Geminofilum* **gen. n.**, to accommodate the species previously considered as *Sphaerodoropsis* with two transverse rows of dorsal macrotubercles per segment. Four species are being described herein: *Euritmia nordica* Capa & Bakken, **sp. n.**, *Sphaerephesia multichaeta* Capa, Moreira & Parapar, **sp. n.**, *Sphaerephesia ponsi* Capa, Parapar & Moreira, **sp. n.**, and *Sphaerodoridium celiae* Moreira, Capa & Parapar, **sp. n.** Characterisation of the other 21 species, including updated iconography, and an identification key to all NEA short-bodied sphaerodorids are provided.

Keywords

16S rRNA, 18S rRNA, 28S rRNA, classification, COI, identification key, integrative taxonomy, morphology, new genus, new species, phylogeny, systematics

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Introduction

Sphaerodoridae Malmgren, 1867 is a relatively small group (approximately 110–120 nominal species) of benthic marine worms, reported worldwide from intertidal to abyssal depths (Capa et al. 2014, 2016a). The monophyly of the group has been assessed recently and is evidenced by their well-defined external morphology (Capa et al. 2016a). Sphaerodorids are characterised by the presence of conspicuous epithelial tubercles arranged in more or less clear rows (longitudinal and transverse) and a thick cuticle without collagen (e.g., Ruderman 1911, Reimers 1933, Hausen 2005, Filippova et al. 2010, Capa et al. 2014, 2016a). Within Sphaerodoridae, two distinct groups with substantial morphological differences have been distinguished: the long-bodied forms (with elongate and slender bodies, clear segmentation, two longitudinal rows of macrotubercles with terminal papillae and presence of reduced dorsal cirri or microtubercles) and the short-bodied forms (usually measuring less than 5 mm long, with poorly delineated segments and a great variety of number and arrangement of epithelial dorsal tubercles) (Fauchald 1974, Helm and Capa 2015, Capa et al. 2016a).

Long-bodied sphaerodorids included members of *Ephesiella* Chamberlin, 1919, *Ephesiopsis* Hartman & Fauchald, 1971 and *Sphaerodorum* Ørsted, 1843, but it has recently been reviewed and all species transferred into the *Sphaerodorum* (Capa et al. 2018). Monophyly of some short-bodied genera (including *Clavodorum* Hartman

& Fauchald, 1971, *Commensodorum* Fauchald, 1974, *Euritmia* Sardá-Borroy, 1987, *Sphaerephesia* Fauchald, 1972, *Sphaerodoridium* Lützen, 1961, and *Sphaerodoropsis* Hartman & Fauchald, 1971) still need assessment (Capa and Bakken 2015, Capa et al. 2016a).

The North East Atlantic (NEA), which includes the European part of the Atlantic, is dominated by deep ocean basins, including the Greenland, Lofoten, and Norwegian Basins, with depths down to 5000 m, and a shallow continental shelf along the European coast (Celtic Sea, Bay of Biscay and Iberian coast). This marine region holds a large diversity of Sphaerodoridae (Annelida) compared with other world geographic areas, with 26 species described or reported herein to date (Table 1). This diversity may reflect the collecting effort put into this biogeographic region during the last two centuries and the taxonomic expertise gathered in European countries. Nevertheless, this species list needs revision.

Some of the species described and reported from the NEA have a wide distribution range. For instance, *Sphaerodoridium minutum* (Webster & Benedict, 1887) has been reported in both eastern and western coasts of the North Atlantic and in NEA, from the Arctic to temperate waters and from coastal and shelf habitats (Fauchald 1974).

Table 1. Species of Sphaerodoridae (Annelida) (with nomenclature as in Read and Fauchald 2018) reported from the North Eastern Atlantic, with type locality and depth.

Species	Type locality	Depth
Clavodorum fauchaldi Desbruyères, 1980	Banc Le Danois, Bay of Biscay	1913 m
Commensodorum commensalis (Lützen, 1961)	Kristineberg, Gullmarfjord, Sweden	35 m
Ephesiella abyssorum (Hansen, 1882)	Off Møre og Romsdal, Norway	960 m
Ephesiella ramosae Desbruyères, 1980	Meriadzek Terrace, Bay of Biscay	2156 m
Euritmia hamulisetosa Sardá-Borroy, 1986	Tarifa, Gibraltar Strait	0.5 m
Sphaerodoridium claparedii Greeff, 1866	Dieppe, English Channel	(?)
Sphaerodoridium fauchaldi Hartmann-Schröder, 1993	North Sea	172 m
Sphaerodoridium guerritai Moreira & Parapar, 2015	Iceland	600 m
Sphaerodoropsis amoureuxi Aguirrezabalaga & Ceberio, 2005	Capbreton Canyon, Bay of Biscay	984–1029 m
Sphaerodoropsis artabrensis Moreira & Parapar, 2007	Artabro Gulf, NW Iberian Peninsula	209 m
Sphaerodoropsis baltica Reimers, 1933	Kiel, Baltic Sea	6–8 m
Sphaerodoropsis chardyi Desbruyères, 1980	Bay of Biscay	2430 m
Sphaerodoropsis distichum (Eliason, 1962)	Skagerrak	460 m
Sphaerodoropsis garciaalvarezi Moreira et al., 2004	Baiona, NW Iberian Peninsula	7 m
Sphaerodoropsis gudmunduri Moreira & Parapar, 2012	North Iceland	97 m
Sphaerodoropsis halldori Moreira & Parapar, 2012	Western Iceland	1162 m
Sphaerodoropsis laureci Desbruyères, 1980	Meriadzek Terrace, Bay of Biscay	2325 m
Sphaerodoropsis longipapillata Desbruyères, 1980	Bay of Biscay	4150 m
Sphaerodoropsis martinae Desbruyères, 1980	Banc Le Danois, Bay of Biscay	1913 m
Sphaerodoridium cf. *minutum* (Webster & Benedict, 1887)	Off New England, USA,	continental shelf
Sphaerodoropsis philippi (Fauvel, 1911)	Kara Sea	0–220 m
Sphaerodoropsis sibuetae Desbruyères, 1980	Banc Le Danois, Bay of Biscay	1913 m
Sphaerodoropsis stellifer Aguirrezabalaga & Ceberio, 2005	Capbreton Canyon, Bay of Biscay	990
Sphaerodoropsis cf. *parva* (Ehlers, 1913)	Eastern Antarctica	380–3423 m
Sphaerodorum flavum Ørsted, 1843	Denmark	intertidal (?)
Sphaerodorum ophiuretos Martín & Alvà, 1988	Pas-de-Calais, English Channel	intertidal

Contrarily, there are other species that seem to be uncommon, and a few that only have been reported once or twice, such as *Clavodorum fauchaldi* Desbruyères, 1980, *Euritmia hamulisetosa* Sardá-Borroy, 1987, *Sphaerodoropsis distichum* (Eliason, 1962), *Sphaerodoropsis laureci* Desbruyères, 1980 or *Sphaerodoropsis stellifer* Aguirrezabalaga & Cebeiro, 2005. Some descriptions of the early-discovered species also need to be updated with additional morphological features and comments on intraspecific variation.

The aim of the present paper is to provide an accurate list of species of the so-called short- bodied sphaerodorids inhabiting the NEA sea floor, with updated descriptions, illustrations and a key for identification of morphospecies. DNA sequence data have been used to assess the evolutionary relationships between members of this family, evaluate the traditional classification, and better understand the boundaries between species and the genetic diversity within some of them.

Materials and methods

Access to the following museum collections have allowed the revision of the type material of all available species and examination of additional non-type material (a total of over 2600 specimens): NTNU University Museum, Norwegian University of Science and Technology, Trondheim (**NTNU-VM**); Natural History Collections, University of Bergen (**ZMBN**); Museo de Historia Natural, Universidade de Santiago de Compostela (**MHN-USC**); Museo Nacional de Ciencias Naturales, Madrid (**MNCN**); Museum national d'Histoire naturelle, Paris (**MNHN**); Zoological Museum Hamburg (**ZMH**); and Deutsches Zentrum für Marine Biodiversitätsforschung (**DZMB**), Hamburg; Senckenberg Museum Frankfurt (**SMF**); National Museum of Ireland (**NMI**); Icelandic Institute of Natural History, Reykjavik (**IINH**); Natural History Museum of Denmark, University of Copenhagen (**NHMD**, previously ZMUC).

Some of the contemporary expeditions that have contributed with material to this project are: BIOICE project (1991–2004) and the IceAGE project (ongoing since 2011) around Iceland (Omarsdottir et al. 2013), the MAREANO Programme (2005-present) in Norwegian waters (Buhl-Mortensen et al. 2015), and the "Brattegard-Sneli" sampling programme (1980–87) (Oug et al. 2017).

Morphological studies

Material examined was fixed in formalin and preserved in 70–80% ethanol or was directly preserved in 70–100% ethanol. Specimens were studied under dissecting and compound microscopes. Some dissected parapodia were mounted on a microscopic slide with glycerine. Drawings were made with an Olympus BX51 compound microscope with a drawing tube.

Micrographs were taken with a Dino-Lite digital microscope (AnMo Electronics Corporation, Taiwan) attached to the microscopes or with a LEICA DFC 420 camera attached to a Leica MZ 16A stereo microscope and a Leica DM 6000B compound microscopes (Leica Microsystems, Wetzlar, Germany). Stacks of multi-focus shots were merged into a single photograph to improve resolution with Leica APPLICATION SUITE v3.7 software (Leica Microsystems, Wetzlar, Germany).

Scanning electron micrographs were taken on specimens after dehydrating them in a series of 80, 90 and 100% ethanol before critical point or in a series of mixtures of absolute ethanol and Hexamethyldisilazane (HMDS) with the following ratios 2:1, 1:1, 1:2, and then into pure HMDS. The prepared samples were mounted on holders, sputter-coated with gold (10 nm thickness). The micromorphology and topography were determined using a Philips FEI INSPECT (Hillsboro, Oregon, USA) Scanning Electron Microscope (SEM) of the Museo Nacional Ciencias Naturales (Madrid, Spain), at the Cellular and Molecular Imaging Core Facility at NTNU. The samples were observed with the Back Scattering Electron Detector (BSED) with a resolution at high vacuum of 4.0 nm at 30 kV. Additional micrographs were taken in the Servicios de Apoio á Investigación-SAI (Universidade da Coruña-UDC, Spain); specimens were dehydrated in a graded ethanol series, prepared by critical-point drying using CO2, coated with gold in a BAL-TEC SCD 004 evaporator and examined and photographed under a JEOL JSM-6400.

Types of NEA species and others for comparison have been revisited when possible. This, together with the examination of additional material, provided additional information about the species distribution range.

Abbreviations used in figures:

al	acicular lobe
ap	antenniform papilla
bp	basal papillae
CH	chaetiger
dhp	dorsal head papilla
dp	dorsal papilla
go	genital opening
gp	genital pores
gs	genital structure
la	lateral antenna
ma	median antenna
mo	mouth
mt	macrotubercle
no	nuchal organ pits
pa	palp
pp	parapodial papilla
s	spur
st	stalked papilla
tc	tentacular cirrus
vc	ventral cirrus
1st	parapodia from first chaetiger

DNA sequence analyses

A selection of specimens (86) of a variety of morphospecies collected in different localities in the North East Atlantic and some other Atlantic localities, and fixed in 100% ethanol were included in the analyses. DNA was extracted with QuickExtract DNA Extraction (Epicentre); a small piece, usually one or two parapodia, were put in 50–100 µl QuickExtract, and treated with 65 °C for 45 min followed by 2 min in 95 °C in a dry block thermostat. We used the primers 16SANNF (GCGGTATCCTGACCGTRCWAAGGTA) (Sjölin et al. 2005) or 16SARL (CGCCTGTTTATCAAAAACAT), together with 16SBRH (CCGGTCTGAACTCAGATCACGT) (Palumbi 1996) for 16S rDNA; LCO1490 (GGTCAACAAATCATAAAGATATTGG) and HCO2198 (TAAACTTCAGGGTGACCAAAAAATCA) (Folmer et al. 1994) for COI; 28SC1 (ACCCGCTGAATTTAAGCAT) and 28SD2 (TCCGTGTTTCAAGACGG) (Lê et al. 1993) for 28S rDNA (D1-D2 region); and 18SAL (AACCTGGTTGATCCTGCCAGT and CCAACTACGAGCTTTTTAACTG), 18SBO (TGATCCTTCCGCAGGTTCACCT and AAGGGCACCACCAGGAGTGGAG), and 18SCY (CGGTAATTCCAGCTCCAATAG and CAGACAAATCGCTCCACCAAC) (Apakupakul et al. 1999), amplifying three overlapping fragments, for 18S rDNA. PCR mixtures contained 0.33 µl of each primer (10µM), 1 µl of DNA template, and 10 µl of RedTaq 1.1x MasterMix 2.0 mM MgCl2 (VWR). Temperature profile was as follows: 96 °C/1min – (95 °C/30s – 52 °C (for COI, 16S rDNA, and 18S rDNA) or 60 °C (for 28S rDNA)/30s – 72 °C/60s) x 29 cycles – 72 °C/7min. PCR products were visualized with UV-light (312 nm) following electrophoresis for c. 15 minutes on a 1% agarose gel (1 g Agarose DNA Pure Grade (VWR) in a TAE Buffer Ultra Pure Grade (Amresco)) containing 1 µl GelRed Nuclear Acid Stain (Bioticum) in 50 ml agarose. Each PCR product was purified with 2 µl cleaning solution made from 500 µl mQ-H20, 40 µl FastAP (EF0651), 45 µl Buffer FastAP, and 20 µl Exonuclease (EN0581) (ThermoScientific). PCR products with added cleaning solution were run for 37 °C in 60 minutes, followed by 75 °C in 15 minutes. Sequencing was performed at Eurofins Genomics, DNA Sequencing Department in Ebersberg, Germany.

Overlapping sequence fragments were merged into consensus sequences using Geneious version 7.0.6 available from http://www.geneious.com/. We used MAFFT v7.017 (Katoh et al. 2002) within Geneious 7.0.6 with the following settings: algorithm=E-INS-i, scoring matrix=200PAM / k=2, gap open penalty=1.53 to align the sequences. We used the online GBlocks server v. 0.91b (Castresana 2002), using the options 'Allow gap positions within the final blocks' and 'Allow less strict flanking positions', to detect alignment-ambiguous sites (Talavera and Castresana 2007). Analyses were performed both with and without these alignment-ambiguous sites. Gene partitions were concatenated using Mesquite v. 2.75 (Maddison and Maddison 2008).

The mitochondrial (COI and 16S rRNA) and nuclear data sets (18S rRNA and 28S rRNA) were analysed separately and combined using Bayesian inference (BA), and Maximum Likelihood (ML). Bayesian analyses (BAs) of separate and combined data sets were run in MrBayes 3.2 (Ronquist and Huelsenbeck 2003), and the best-fit models were selected using the Akaike information criterion in JModel (Darriba et al. 2012). The protein-coding gene COI was further divided into two partitions, one with the first and second positions, and one with the third positions. The selected best-fit models were a general time reversible model with gamma distributed rate across sites and a proportion of the sites invariable (GTR+I+G) for the COI-partition with first and second positions, 16S, 18S, and 28S, while a Hasegawa, Kishino and Yano model, with gamma distributed rate across sites (HKY+G) was selected for the COI-partition with third positions.

Partitions were unlinked for the parameters statefreq, revmat, shape, and pinvar. Rateprior for the partition rate multiplier was set to be variable. Number of generations was set to 3 million, with four parallel chains (three hot, one cold), sample frequency was set to 1000, and number of runs set to two. One fourth of the samples were discarded as burn-ins. Maximum likelihood analyses (ML) were performed in raxmlGUI (Silvestro and Michalak 2012). In RAxML, the analyses were run with the GTRGAMMAI model, the combined data set was partitioned as in BA, and clade support was assessed using 1000 bootstrap replicates.

Results

Phylogenetic analyses

The selected best-fit models were a general time reversible model with gamma distributed rate across sites and a proportion of the sites invariable (GTR+I+G) for the COI-partition with first and second positions, 16S, 18S, and 28S, while a Hasegawa, Kishino, and Yano model with gamma distributed rate across sites (HKY+G) was selected for the COI-partition with third positions.

The removal of poorly aligned positions from divergent regions of 16S, 18S and 28S from the alignments with GBLOCKS v. 0.91b did not affect the phylogenetic results, neither tree topology nor node supports (not shown); hence, all further analyses were conducted with the complete sequences for these markers.

Atlantic sphaerodorid relationships and subsequent nomenclatural changes

Analyses of combined mitochondrial (COI + 16S rDNA) and nuclear DNA sequence data (18S rDNA, and 28S rDNA) recover four main well-supported clades (Fig. 1, in different colours). These four groups are not congruent with the current sphaerodorid genera that mainly take into account the morphology of the dorsal tubercles (e.g., *Clavodorum* Hartman & Fauchald, 1971 and *Sphaerodoridium* Lützen, 1961 bearing stalked macrotubercles, and *Sphaerephesia* Fauchald, 1972 having macrotubercles with terminal papilla). Some of these traditional genera are therefore not recovered monophyletic herein. For instance, *Sphaerodoropsis* Hartman & Fauchald, 1971 is split into three, and *Sphaerodoridium* into two polyphyletic clades. These findings involve modifications in the current classification and also consequent nomenclatural changes. However, members of each of the four resulting clades in the molecular topology share the following morphological features related to the number of longitudinal and transverse rows of dorsal macrotubercles (Fig. 1):

Clade 1 (Fig. 1, in yellow) comprises sphaerodorids with four longitudinal rows of sessile macrotubercles, arranged in a single transverse row per segment, regardless if they have a smooth surface or a terminal papilla, or if they are spherical or hemispherical in shape. This clade is therefore merging members of the traditionally considered

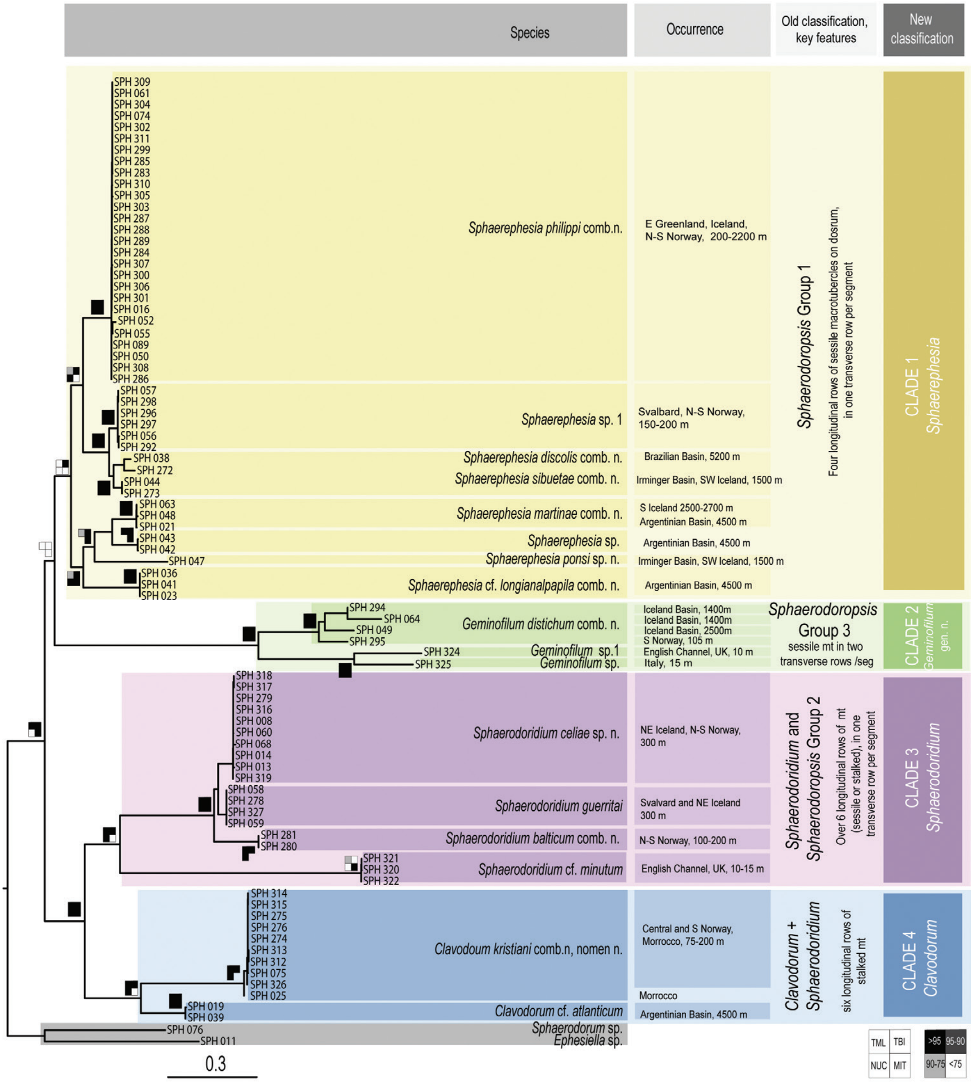

Figure 1. Consensus tree obtained after Bayesian analysis of the combined nuclear and mitochondrial dataset. Coloured squared on nodes (as indicated in the bottom of the figure) indicate (from top left to bottom right): TBI, Bayesian posterior probabilities of total dataset; TML, Maximum Likelihood Boostrap values of total dataset; NUC, Bayesian posterior probabilities of nuclear partition; MIT, Bayesian posterior probabilities of mitochondrial partition.

Sphaerodoropsis Group 1 according to Borowski (1994) (with four longitudinal rows of smooth macrotubercles), and also members of *Sphaerephesia* (with macrotubercles provided with a terminal papilla). In all analyses, the specimens bearing hemispherical macrotubercles with terminal papilla (e.g., *Sphaerephesia sibuetae* (Desbruyères, 1980), *Sphaerephesia ponsi* sp. n.) are scattered within the clade together with specimens with hemispherical and smooth tubercles (e.g., *Sphaerodoropsis martinae* Desbruyères, 1980) or with spherical or pear-shaped macrotubercles (e.g., *Sphaerodoropsis philippi* Fauvel, 1911). This provides evidence that the presence of a terminal papilla vs smooth and rounded/pear-shaped macrotubercles, has no phylogenetic implication.

The support values for Clade 1 are high after BI of the complete dataset, but moderate after ML analyses of the complete dataset or the partition of nuclear DNA. Analyses of only the mitochondrial sequence data (COI + 16S) did not recover Clade 1 as monophyletic and instead Clade 2 (Fig. 1, in green) was nested within, as sister to *S. philippi*.

The type species of both genera are not included in the present analyses, but it is expected that *Sphaerodoropsis sphaerulifer* Moore, 1909, type species of *Sphaerodoropsis*, would not be recovered within this clade as it bears more than four longitudinal rows of macrotubercles over dorsum (*Sphaerodoropsis* Group 2 according to Borowski, 1994). *Sphaerephesia longisetis* Fauchald, 1972, type species of *Sphaerephesia*, bears macrotubercles arranged in four longitudinal rows. It is therefore proposed herein that the members of this clade and other sphaerodorids not include in the analyses but sharing this morphological feature, including *S. longisetis*, keep the generic name *Sphaerephesia*. It is thus herein proposed that all members of *Sphaerodoropsis* group 1 are synonymised. The main diagnostic feature for the emended *Sphaerephesia* is the presence of four longitudinal rows of macrotubercles in one transverse row per segment.

Seven subclades, congruent with the identified morphospecies, are found within Clade 1. Of these, *Sphaerodoropsis philippi, Sphaerodoropsis* sp. 1, *S. sibuetae*, *S.martinae*, and *S. ponsi* sp. n. are present in the NE Atlantic, the other two species included in the analyses were collected from the Argentina Basin.

Clade 2 (Fig. 1, in green) consists of specimens bearing two transverse rows of sessile macrotubercles, corresponding to the *Sphaerodoropsis* Group 3 (according to Borowski 1994). This clade is well supported after analyses of the combined as well as separate nuclear and mitochondrial datasets. However, its position in the topology varied depending of the analyses performed. Nuclear genes alone, recover this clade branching off at the base of the tree (low support) while the mitochondrial dataset recovers this clade as sister to *S. philippi* (high support). The type species of *Sphaerodoropsis, S. sphaerulifer*, bears dorsal macrotubercles in a single transverse row per segments, not in two. Therefore, a new genus needs to be erected to accommodate sphaerodorids with this feature: *Geminofilum* gen. n.

Six genetically distinct terminals showing long branches were recovered after analyses of molecular data besides the small morphological differences between them. Four of these specimens are herein identified as *Geminofilum distichum* comb. n. (further analyses will need to determine species boundaries within this suspected species complex), and two as distinct unidentified species from the UK and Italy. All in all, this clade is morphologically homogenous, sharing the number and distribution of dorsal macrotubercles, chaetal morphology, and number and arrangement of parapodial papillae. Main differences rely on the number and distribution of epithelial papillae between dorsal transverse rows of dorsal macrotubercles. Differences in pigmentation in live specimens have been noticed (e.g., Fig. 8) and could provide valuable information for species distinction.

Clade 3 (Fig. 1, in purple) gathers sphaerodorids with 7–12 longitudinal rows of small macrotubercles, arranged in a single transverse row per segment. In this clade, some of the previously considered species of *Sphaerodoropsis* group 2 (sensu Borowski 1994) (with sessile macrotubercles) are nested within members of *Sphaerodoridium* (with 7–12 longitudinal rows of stalked macrotubercles). This clade is well supported after analyses of the combined and nuclear datasets. However, Bayesian analysis of the mitochondrial dataset recovers *Sphaerodoridium* cf. *minutum* branching off at the base of the ingroup (not in the ML analyses). On the basis of our findings we argue that the type species of *Sphaerodoridium*, *Sphaerodoridium claparedii* (Greeff, 1866), with eight longitudinal rows of macrotubercles would belong to this group. Since this name is older than the type species of *Sphaerodoropsis*, *S. sphaerulifer*, also with 7–8 longitudinal rows, we are consequently proposing to maintain the genus name *Sphaerodoridium* for members of this clade. Four species (morphospecies congruent with the lineages recovered), all from the NEA, form this clade, these are: *Sphaerodoridium celiae* sp. n., *Sphaerodoridium guerritai* Moreira & Parapar, 2015, *Sphaerodoridium balticum* (Reimers, 1933), comb. n., and *Sphaerodoridium* cf. *minutum* (Webster & Benedict, 1887).

Clade 4 (Fig. 1, in blue) consists of two well-defined lineages, corresponding to the diagnosis of the previously known species *Sphaerodoridium fauchaldi* Hartmann-Schröder, 1993, now re-named as *Clavodorum kristiani* (Hartmann-Schröder, 1993), comb. n., nom. n. for the reasons given below, and *Clavodorum* cf. *atlanticum* Hartman & Fauchald, 1971. The concept of *Sphaerodoridium,* as traditionally understood (sphaerodorids with stalked macrotubercles and a short median antenna), has here been shown invalid as members within this diagnosis are split into two different clades (Clades 3 and 4, Fig. 1), containing each *Sphaerodoropsis* and *Clavodorum* species respectively. We therefore propose that *Sphaerodoridium* species with six longitudinal rows of stalked macrotubercles (and by definition, sphaerodorids with a long median antenna) are transferred to *Clavodorum* (sphaerodorids with six longitudinal rows of stalked macrotubercles and a short median antenna) and keep the latter name since *Sphaerodoridium* is occupied by members of Sphaerodoridae with more than six rows of longitudinal macrotubercles in one single row per segment (Clade 3 above).

Taxonomic accounts

Clavodorum Hartman & Fauchald, 1971

Sphaerodoridium Lützen, 1961: 415 (in part); Fauchald 1974: 270; Capa et al. 2014: 15.
Clavodorum Hartman & Fauchald, 1971: 63; Fauchald 1974: 262; Bakken 2002: 198; Capa et al. 2014: 15.

Type species. *Clavodorum atlanticum* Hartman & Fauchald, 1971.

Diagnosis. Body generally short and ellipsoid. Head appendages smooth without spurs or basal papillae. Median antenna shorter, equal, or longer than lateral antennae;

antenniform papillae absent. Dorsal macrotubercles stalked, without terminal papilla, arranged in up to six longitudinal rows, one transverse row per segment; smaller tubercles, similarly stalked, may form irregular rows on ventrum. Microtubercles (small tubercles with collar and terminal papilla) absent. Stout hooks in the first chaetiger absent. Parapodia with large ventral cirri. All chaetae compound.

Remarks. The relative length of the median antenna with respect to the lateral ones was the single reported morphological feature separating the traditional *Clavodorum* (with a median antenna longer than the lateral, or similar in length) and *Sphaerodoridium* (with a shorter median antenna), the two genera considered to bear stalked dorsal macrotubercles prior to the present study (e.g., Hartman and Fauchald 1971, Fauchald 1974). However, there has been some debate if this character alone was enough to split species in these two genera (Hartmann-Schröder and Rosenfeldt 1990, Borowski 1994, Capa et al. 2016a).

After analyses of molecular data performed in this study (Fig. 1) species with sessile macrotubercles (e.g., *Sphaerodoropsis balticum*) were recovered nested within those with stalked macrotubercles (e.g., *Sphaerodoridium minutum* and *Sphaerodoridium guerritai*), requiring nomenclatural changes. Moreover, species with apparently shorter or longer median antenna are mixed in two different clades.

There seems to be some synapomorphies, related to the number of longitudinal rows of dorsal macrotubercles (Clade 3 and 4 in Fig. 1), characterizing these two clusters. In one clade, all the species bear up to six longitudinal rows of stalked macrotubercles (including the type species of *Clavodorum*, *Clavodorum atlanticum*), and in the other species bear more than six longitudinal rows of macrotubercles, regardless if they are sessile or stalked (including the type species of *Sphaerodoridium*, *Sphaerodoridium claparedii*). This pattern should be corroborated after including additional taxa in analyses, but it also requires some changes in the traditional classification.

Diagnostic features characterising *Clavodorum*, as traditionally understood, such as presence of postchaetal lobes (Fauchald 1974, Bakken 2002) or presence of nephridiopores in all chaetigers except for the first and the last three or four (Hartman and Fauchald 1971, Bakken 2002), have been omitted from the diagnosis as it has not been verified in some of the specimens examined nor are mentioned in the original description.

The species included in *Clavodorum* after this study are:

Clavodorum adriaticum Katzmann, 1973
    Type locality: Zlarin, Adriatic Sea, 20–60 m.
Clavodorum antarcticum Hartmann-Schröder & Rosenfeldt, 1990
    Type locality: Elephant Island, north of Antarctic Peninsula, 262 m.
Clavodorum atlanticum Hartman & Fauchald, 1971
    Type locality: northwest of Bermuda in 4700–3800 m.
Clavodorum clavatum Fauchald, 1972
    Type locality: Off El Segundo, California, 18–45 m.
Clavodorum fauchaldi Desbruyères, 1980
    Type locality: Banc Le Danois, Bay of Biscay, 1913 m.

Clavodorum fusum (Hartman, 1967)
  Type locality: Antarctic Peninsula, 128–165 m.
Clavodorum kristiani (Hartmann-Schröder, 1993), comb. n., nom. n.
  Type locality: North Sea, off Scotland, 172 m.
Clavodorum longipes Fauchald, 1974
  Type locality: Off Mozambique, 5119 m.
Clavodorum lutzeni (Kudenov, 1987), comb. n.
  Type locality: Off Florida, Gulf of Mexico, 37 m.
Clavodorum mexicanum Kudenov, 1987
  Type locality: Off Florida, Gulf of Mexico, 48 m.

***Clavodorum fauchaldi* Desbruyères, 1980**

Figs 2, 3, 4A, B, 5A

Clavodorum fauchaldi Desbruyères, 1980: 110–112, fig. 1.

Type locality. Banc Le Danois, Bay of Biscay, 44°05.2'N, 4°19.4'W, 1913 m.

Material examined. Holotype: MNHN POLY TYPE 1279, Bay of Biscay, Banc Le Danois, 44°05.2'N, 4°19.4'W, 1913 m, 1972.

Additional material. (141 specs) **Iceland**: IINH 38781 (55 specs,5 on SEM stub), 62°20.50'N, 16°59.30'W, 2074 m, 29 Aug 1995; IINH 38782 (25 specs -6 on SEM stub-), 61°50.22'N, 16°52.86'W, 2270 m, 29 Aug 1995; IINH 38783 (5 specs), 65°15.61'N, 28°50.15'W, 1300 m, 25 Aug 1996; IINH 38784 (2 specs), 60°02.03'N, 22°27.17'W, 2537 m, 29 July 2000; IINH 38785 (3 specs), 62°24.80'N, 19°48.60'W, 1780 m, 13 Sep 2001; IINH 38786 (1 spec.), 62°48.00'N, 16°14.80'W, 1813 m, 16 Sep 2001; IINH 38787 (30 specs), 62°02.40'N, 19°38.71'W, 1678 m, 3 Sep 2002; IINH 38788 (18 specs), 62°31.14'N, 17°09.87'W, 1940 m, 7 Sep 2002; IINH 38789 (1 spec.), 62°47.19'N, 17°20.37'W, 1662 m, 8 Sep 2002; IINH 38790 (1 spec.), 63°30.22'N, 29°38.40'W, 2233 m, 5 Sep 2003; ZMBN 127252 (1 spec.), South Iceland, 61°38.2'N16°27.7'W, 2355 m, 5 Jun 1983.

Diagnosis. Body ellipsoid. Median antenna similar in length to lateral antennae; lateral antennae with three or four basal papillae each; antenniform papillae absent; palps with 2–3 basal papillae each. Dorsal macrotubercles stalked, without terminal papilla, arranged in five longitudinal rows in first 2–3 and last chaetigers, and six longitudinal rows in middle chaetigers; stalk and tubercle of similar length. Additional hemispherical papillae (ca. 10–12) distributed over dorsum in two irregular transverse rows, following a zig-zag pattern. Two rows of stalked smaller tubercles along ventrum, with two tubercles near each parapodium. Parapodia with acicular lobe from chaetiger 1, and large ventral cirri, surpassing length of acicular lobe. One ventral papilla from chaetiger 2–4; and one terminal postchaetal papilla from chaetiger 7–10.

Re-description of holotype. *Measurements and general morphology.* Holotype oval in shape, measuring 2.7 mm long, 0.4 mm wide for 24 chaetigers.

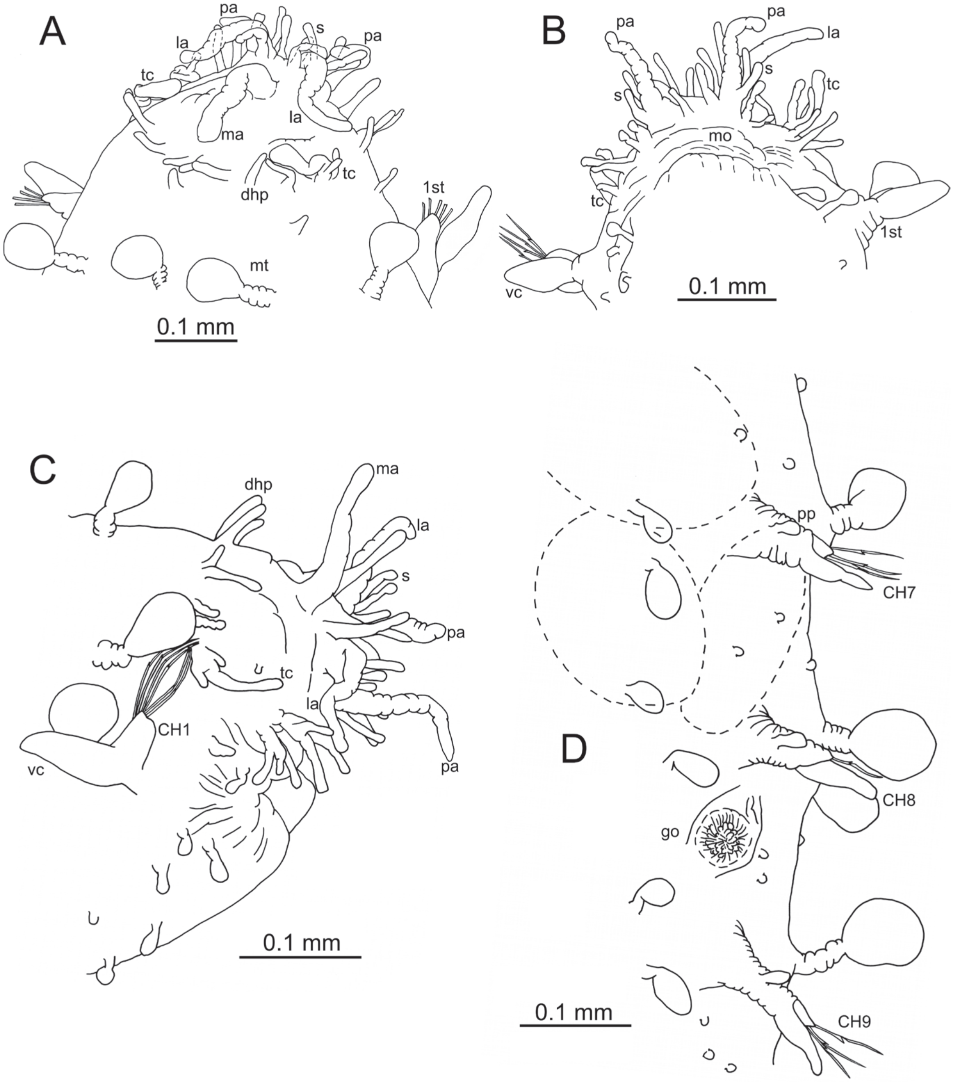

Figure 2. *Clavodorum fauchaldi* (IINH 38781: **A, D**; IINH 38786: **B, C**), line drawings. **A** Anterior end, dorsal view **B** anterior end, ventral view **C** anterior end, lateral view **D** female, chaetigers 7–9, ventral view, showing genital (?) opening.

Head. Head fused to first chaetiger, with elongated and digitiform prostomial appendages, reaching the end of head (Figs 2A–C, 3A). Palps and lateral antennae similar in length, with 2–4 digitiform, shorter and slightly thinner basal papillae. Median antenna, similar in length to lateral, lacking spurs or basal papillae (Fig. 2B). Tentacular cirri ca. half of the length of prostomial appendages and thinned. Some elongated papillae distributed randomly on posterior part of head (Fig. 3B). Proboscis retracted in holotype and muscular pharynx through segments 3–6.

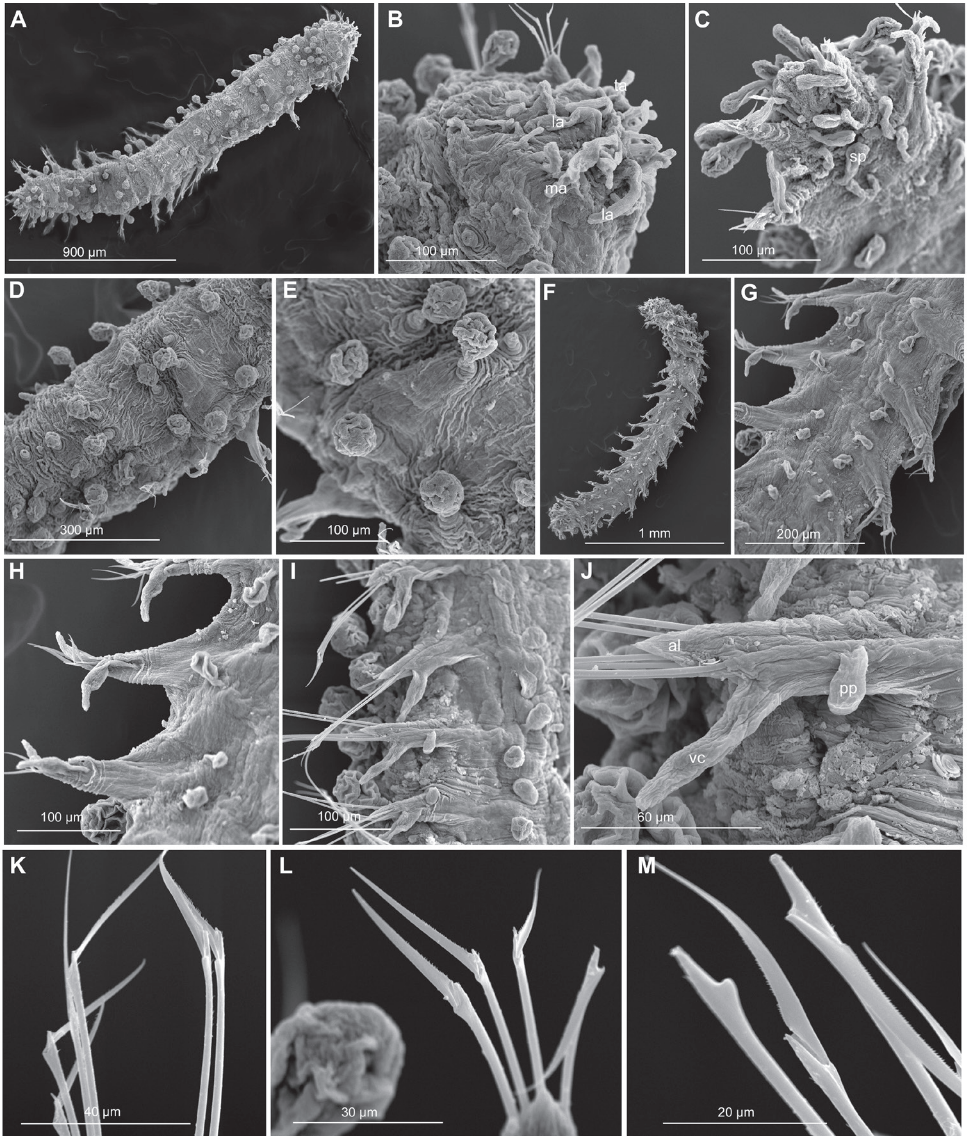

Figure 3. *Clavodorum fauchaldi* (IINH 38781: **A–E, K–M**; IINH 38782: **F–J**), scanning electron micrographs. **A** Complete specimen, lateral view **B** anterior end, dorsal view **C** anterior end, ventral view **D** mid-body chaetigers, arrangement of dorsal macrotubercles and papillae **E** dorsal macrotubercles and papillae, detail **F** complete specimen, ventral view **G** mid-body chaetigers, arrangement of ventral tubercles **H, I** mid-body chaetigers, parapodia and ventral tubercles **J** mid-body parapodium, anterior view **K–M** compound chaetae.

Tubercles. Body with stalked dorsal macrotubercles distributed in five longitudinal rows, on three anterior and two posterior segments and six rows in segments in between, although some detached in holotype; one transverse row per segment (Figs 3A, D, E, 4A). Stalk ca. the length of the macrotubercle, the latter oval, smooth, lacking terminal papilla

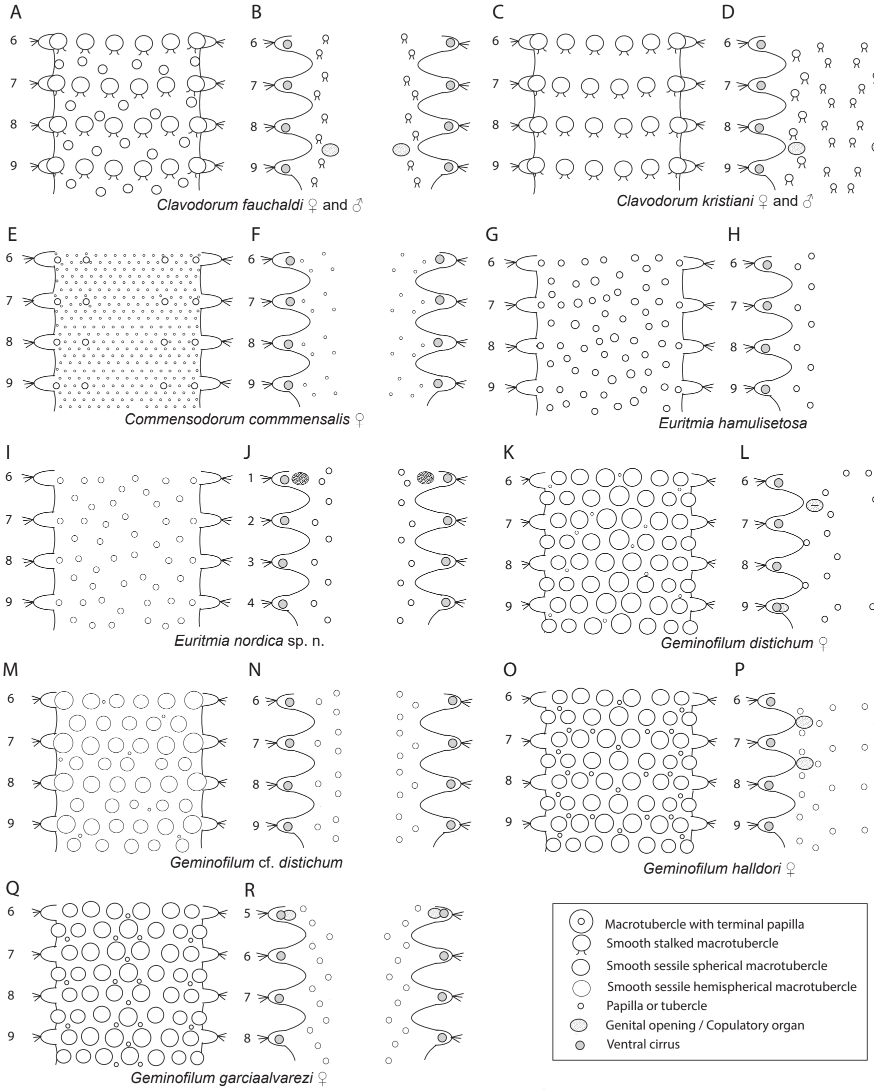

Figure 4. Stylized drawings of selected dorsal (left) and ventral (right) segments of species of *Clavodorum*, *Commensodorum*, *Euritmia* and *Geminofilum* gen. n., showing number and arrangement of epithelial tubercles and papillae.

(Figs 2A, D, 3D, E). Dorsal papillae in two irregular transverse rows, 4–6 papillae each per segment, rounded in shape (Fig. 4A). Ventral surface with two longitudinal rows of oval and stalked tubercles, arranged in two transverse rows per segment; anterior row with smaller tubercles than those of posterior row within each segment (Figs 2D, 3F–I, 4B).

Parapodia. Parapodia cylindrical, longer than wide, similar in length along body, with almost similar in length ventral cirri, digitiform or slightly tapering in width distally, well surpassing length of acicular lobe (Figs 2D, 3G–J). One large and rounded parapodial papilla from segment 2, located on the distal half of the antero-ventral surface of parapodia. One terminal papilla present from chaetiger 8, digitiform (Fig. 5A), and increasing its size to posterior chaetigers. One straight acicula supporting each parapodia, curved in first chaetigers.

Chaetae. All chaetae compound, ca. six in first segment to eight in middle chaetigers; with long, straight, unidentate and finally serrated blades. Blades similar in length between and within chaetigers, ca. ten times longer than maximum blade width (Fig. 3K–M).

Pygidium. Paired anal cirri similar to dorsal macrotubercles and ventral digitiform anal papilla similar in length to lateral cirri.

Reproductive features. Gametes or sexual structures not observed in holotype.

Variation. Intraspecific variation was assessed by examining a number of samples collected during the BIOICE project, in Iceland. Largest specimen examined 3.75 mm long, 1 mm wide and 28 chaetigers. Most Icelandic specimens measuring ca. 2 mm in length, 0.65 mm in width with 18–24 chaetigers. Median antenna usually as long as lateral antennae, depending on the state of contraction of specimens. Tentacular cirri shorter than prostomial appendages and provided each with two short papillae near the base. One dorsal transverse row of eight longer papillae (clavate or digitiform) behind median antenna and running at level of tentacular cirri; several digitiform papillae surrounding the mouth at each side (usually including one bifid and sometimes one trifid). Muscular pharynx extending over three chaetigers (5–7). In some elongated specimens stalk seems slightly longer than macrotubercle. Postchaetal papilla present from chaetiger 7 to last chaetiger. Parapodial antero-ventral papilla present from chaetigers 2–4, becoming more lateral in chaetigers 8–10; rounded to elongated in shape. Acicula is straight and chaetae blades show some gradation in length, being ventral ones slightly shorter in middle and posterior chaetigers. Several females with oocytes and males observed; both sexes show genital openings near the base of parapodia between chaetigers 8 and 9 (Fig. 4B).

Remarks. The original description indicates that at least two specimens were found (holotype and another used for SEM) but only the holotype has been deposited in a museum collection (MNHN). All the specimens examined from Iceland bear three basal papillae on lateral antennae, variation that has been added into the diagnoses, at least one or two emerge directly from the base of antennae and the rest probably from the surroundings of the base. This species was described as new due to the uniqueness of its parapodia, with postchaetal lobe absent on anterior segments. However, we consider here that the postchaetal lobe is a postchaetal papilla. Furthermore, both females and males from Iceland samples show a pair of ventral genital openings (Fig. 2D); these may be interpreted as sexual structures and therefore this is the first mention for the genus of such features.

Distribution. Iceland (present study), Bay of Biscay (Desbruyères 1980).

Habitat. Bathyal soft bottoms (1300–2537 m) (Desbruyères 1980; this study).

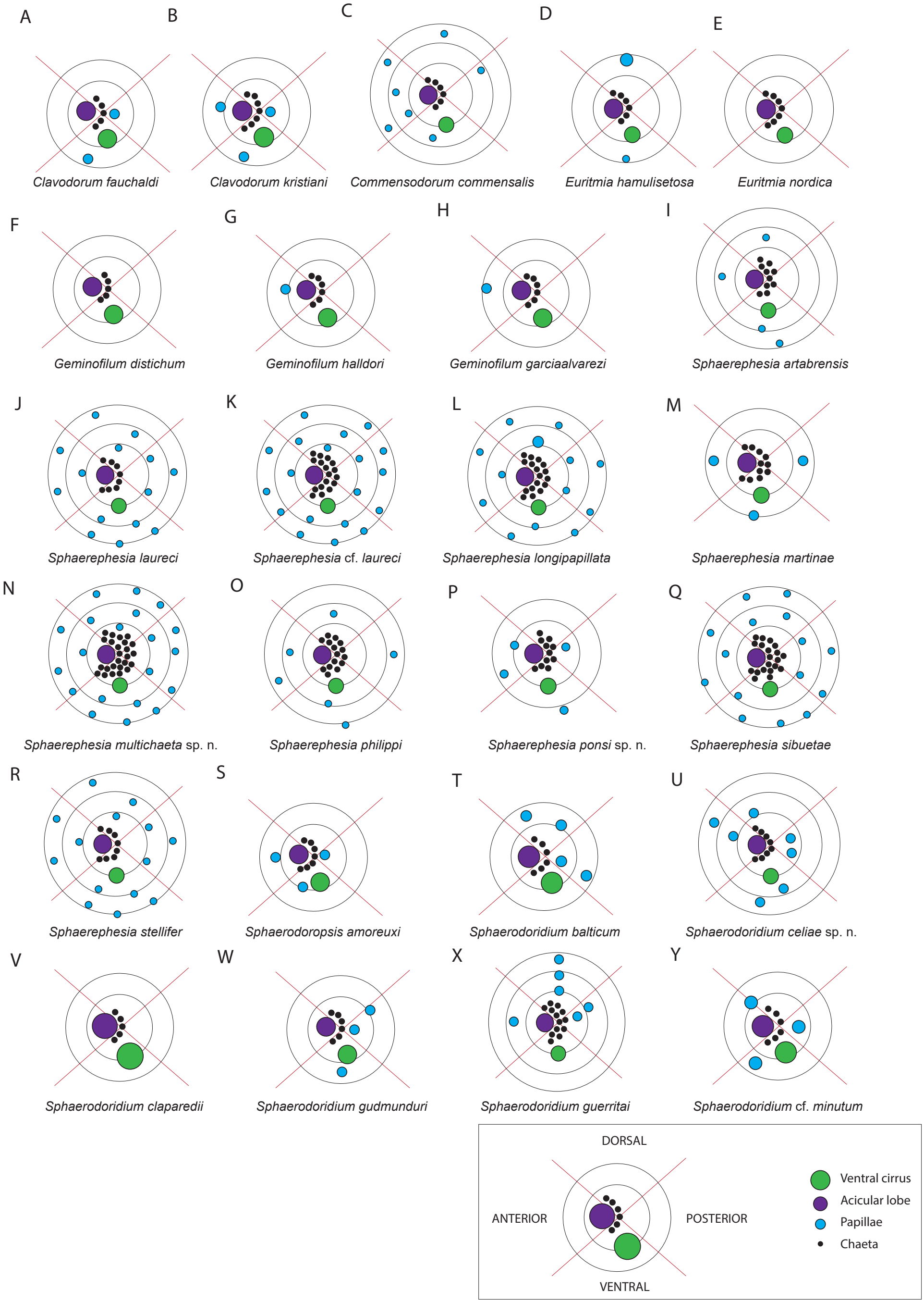

Figure 5. Stylized drawings of parapodia, showing the relative position and arrangement of parapodial lobes, cirri, and papillae, in mid-body chaetigers of all sphaerodorid species reported in the North East Atlantic waters.

Clavodorum kristiani (Hartmann-Schröder, 1993), comb. n., nom. n.

Figs 4C, D, 5B, 6, 7, 8A

Sphaerodoridium fauchaldi Hartmann-Schröder, 1993: 123–125, figs 1–9; Hartmann-Schröder 1996: 234–235, fig. 104; Aguirrezabalaga and Cebeiro 2005: 16–19, figs 5, 6; Moreira and Parapar 2007: 377–378, fig. 3 B–E; Moreira et al. 2011: 26, fig. 3; Moreira 2012: 28–29, fig. 6.

Type locality. North Sea, 58°16.98'N, 0°58.31'W, 172 m.

Material examined. Holotype: ZMH P21082, North Sea, (N. Scotland) 58°16.98'N, 0°58.31'W, 172 m.

Additional material. (140 specs) **Norwegian Sea**: NTNU-VM 74198 (3 specs in SEM stub), Sandsfjord, 62°12.3'N, 5°26.7'E, 85 m, 18 Oct 1987; ZMBN 127253 (1 spec.), Sandsfjord, 62°12.3'N, 5°26.7'E, 85 m, 18 Oct 1987; ZMBN 127256 (1 spec. for DNA sequencing, SPH274), Møre og Romsdal, 63°18.81'N, 6°39.24'E, 226 m, 26 Sep 2012; ZMBN 127257 (1 spec. for DNA sequencing, SPH275), Norwegian Sea, Møre og Romsdal, 63°18.81'N, 6°39.24'E, 226 m, 26 Sep 2012; NTNU VM 68172 (1 spec. used for DNA sequencing, SPH276), Ytre Mørebanken, 004°29.74'N, 62°36.86'E, 203 m, 03. Oct. 2012; ZMBN 103139 (1 spec. used for DNA sequencing, SPH075), 62°36.858'N, 4°29.742'E, Møre og Romsdal, 203 m, 3 Oct. 2012; NTNU VM 65127 (5 spec.), Halsafjord, Ytterfjorden, 63°10.17'N, 7°43.9'E, 150 m, 25 May 1884; ZMBN 127254 (1 spec. used for DNA sequencing, SPH314), Bergen, 60°16.181'N, 5°11.865'E, 120 m, 25 Jul 2014; ZMBN 127255 (1 spec. used for DNA sequencing, SPH315), Bergen, 60°16.181'N, 5°11.865'E, 120 m, 25 Jul 2014; ZMBN 125433 (1 spec. used for DNA sequencing, SPH312), Rogaland, Kvitsøy, 59°1.791'N, 5°26.929'E, 58 m, 10 Jun 2014; ZMBN 127258 (1 spec. used for DNA sequencing, SPH313 photographed alive, Fig. 8A), Rogaland, Karmøysundet, 59°17.273'N, 5°19.504'E, 74 m, 08 Jun 2014; ZMBN 127259 (1 spec. used for DNA sequencing, SPH326), Rogaland, Karmøysundet, 59°17.273'N, 5°19.504'E, 74 m, 08 Jun 2014. **Continental shelf, Galicia, NW Spain**: MNCN 16.01/18456 (27 specs), 43°35.45'N, 08°34.43'W, 152 m, 8 Sep 2002; MNCN 16.01/18457 (52 specs), 43°34.13'N, 8°36.56'W, 152 m, 14 Sep 2003; MNCN 16.01/18458 (42 specs), 42°30.39'N, 09°19.52'W, 147 m, 17 Sep 2004; MNCN 16.01/18459 (41 specs), 42°15.82'N, 09°22.68'W, 260 m, 23 Oct 2009. **Morocco**, ZMBN 103140 (1 spec. used for DNA sequencing, SPH025), Atlantic Ocean, 28°0.04836'N, 13°16.32'W, 100 m, 4 Dec 2011.

Diagnosis. Body ellipsoid. Median antenna shorter than lateral antennae; lateral antennae and palps with 1–2 basal papillae each; antenniform papillae absent. Dorsal macrotubercles stalked, without terminal papilla, arranged in five longitudinal rows in first three chaetigers, and six longitudinal rows in following chaetigers; stalk and tubercle of similar length. Additional epithelial papillae on dorsum absent. Six to eight longitudinal rows of smaller tubercles with short stalk on ventrum; two tubercles near each parapodium slightly larger than others. Parapodia with long, oval acicular lobe from chaetiger 4; ventral cirri large, reaching or surpassing length of acicular lobe. Three

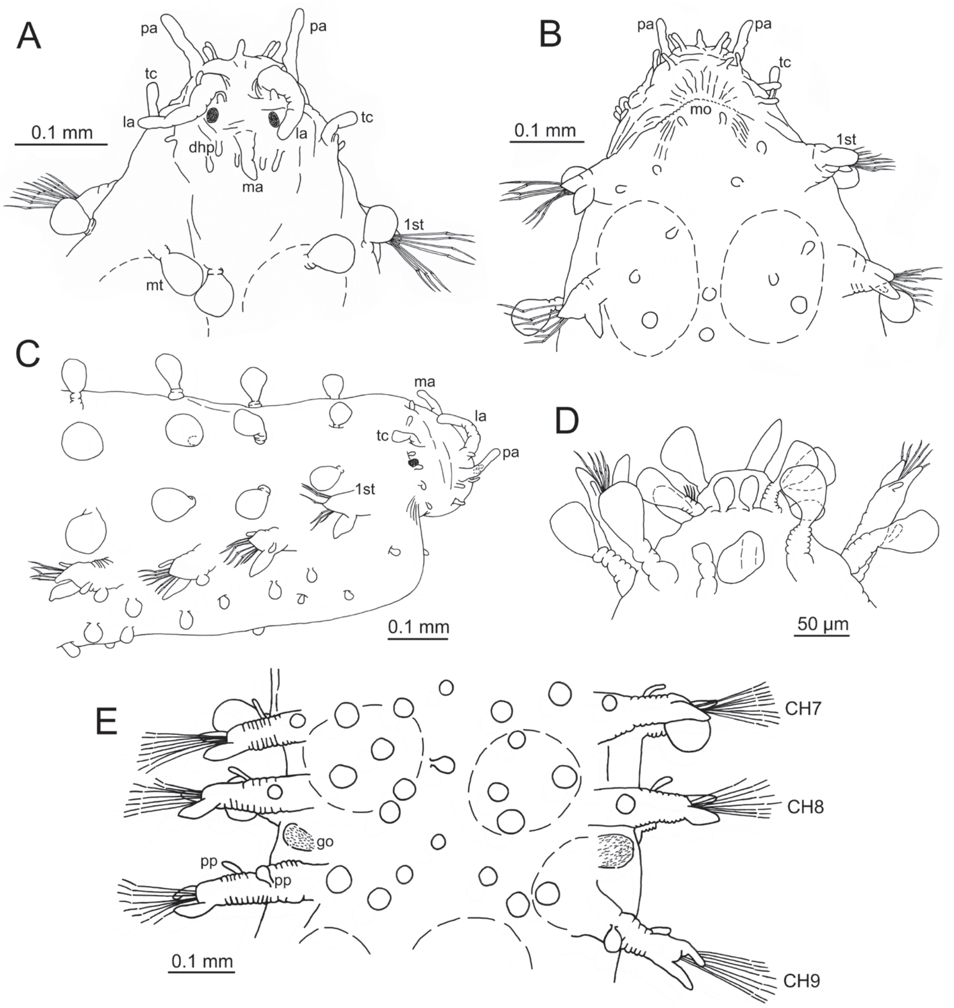

Figure 6. *Clavodorum kristiani* comb. n., nom. n. (MNCN 16.01/18458: **A, B**; MNCN 16.01/18459: **C, D**; MNCN 16.01/18457: **E**), line drawings. **A** Anterior end, dorsal view **B** same, ventral view **C** anterior end, lateral view **D** posterior end, ventral view **E** mid-body chaetigers, ventral view.

parapodial papillae: one on antero-lateral surface from chaetiger 2, one ventral from chaetiger 3–4 and one terminal digitiform papilla from chaetiger 1, behind chaetae.

Re-description of holotype. *Measurements and general morphology*. Body ellipsoid, measuring 1.0 mm long, 0.4 m wide, with nine segments; with rounded anterior and posterior ends, with slightly flat ventrum. Segmentation inconspicuous and pigmentation absent in preserved specimen (Fig. 8A).

Head. Head fused to first chaetiger, with elongated and digitiform prostomial appendages, reaching the end of peristomium (Figs 6A, 7C). Lateral antennae slightly longer than palps, with 1–2 digitiform, shorter and thinner basal papillae each. Me-

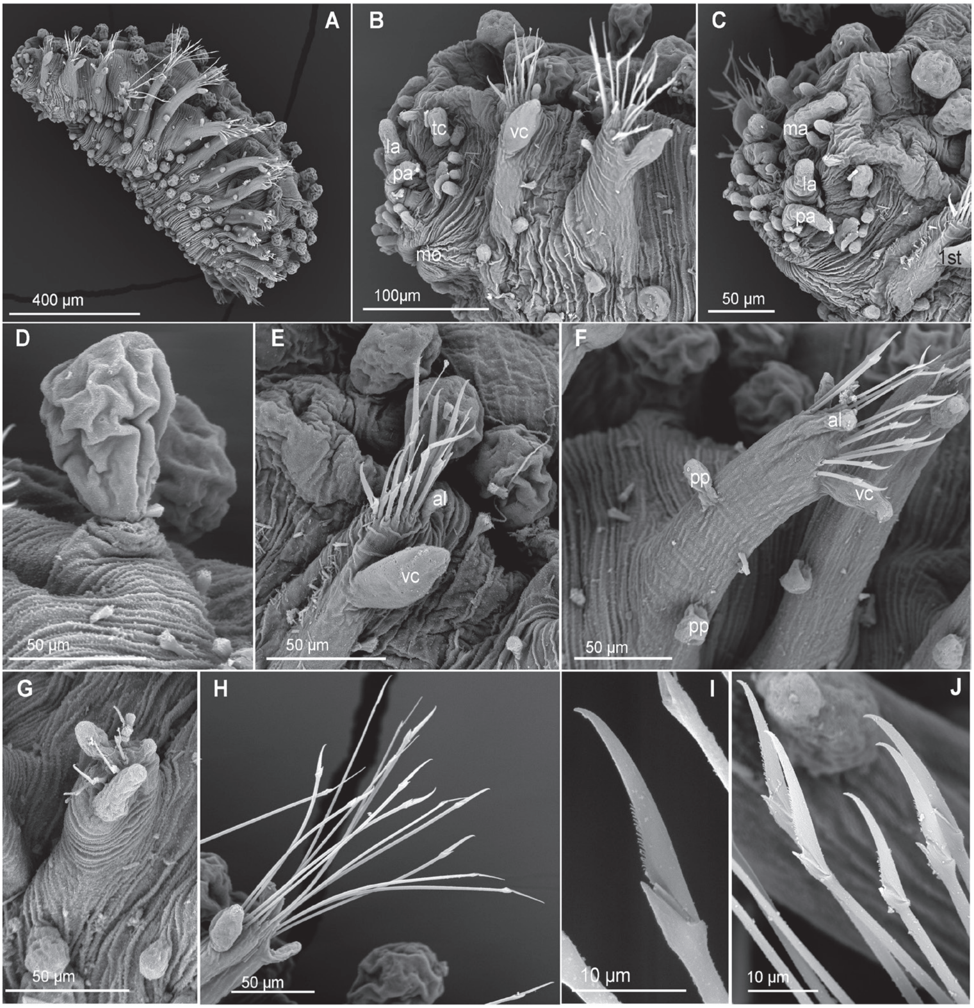

Figure 7. *Clavodorum kristiani* comb. n., nom. n. (Norway, NTNU-VM 74198). **A** Complete specimen, lateral view **B** anterior end, lateral view **C** same, slightly frontal **D** dorsal stalked macrotubercle, detail **E** left parapodium, chaetiger 1, latero-ventral view **F** same, chaetiger 7 **G** same, posterior chaetiger **H** chaetae fascicle, mid-body parapodium **I, J** chaetae, mid-body parapodium, detail.

dian antenna shorter than lateral, lacking spurs or basal papillae. Five prostomial papillae between lateral antennae and palps (Figs 6A, B, 7C). Tentacular cirri approx. half of length of prostomial appendages and thinner, with a basal papilla each (Figs 6A, C, 7C). An irregular transverse row of ca. 6–10 elongated papillae behind median antenna and tentacular cirri. Up to eight elongated papillae surrounding mouth (Fig. 6B, C).

Tubercles. Body with stalked dorsal macrotubercles distributed in five longitudinal rows on three anterior segments and six rows in following segments; one transverse row per segment (Figs 4C, 6A, 8A). Stalk shorter or as long as macrotubercle, the later oval, smooth, and lacking terminal papilla (Fig. 7D). Ventral surface with 6–8 longi-

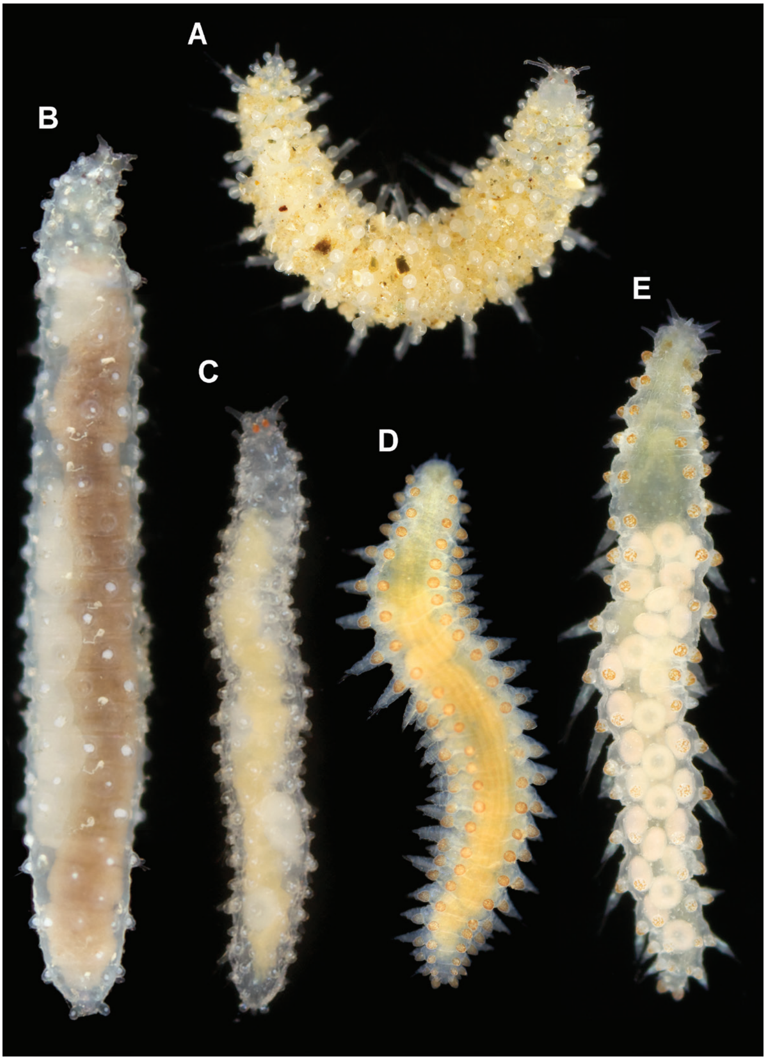

Figure 8. Photographs of live specimens (included in analyses shown in Fig. 1). **A** *Clavodorum kristiani* comb. n., nom. n. (ZMBN 127258, SPH313) **B** *Geminofilum distichum* comb. n. from Skagerrak (ZMBN 127263, SPH295) **C** *Geminofilum* sp. 1, from UK (SPH324) **D** *Sphaerephesia philippi* comb. n., from Skagerrak (ZMBN 125432, SPH297) E *Sphaerephesia philippi* comb. n., from Finnmark (ZMBN 127311, SPH304).

tudinal rows of oval to rounded smaller tubercles with short stalk (Figs 4D, 6E); one (sometimes two) tubercles in between parapodia areas and six in parapodial areas; two tubercles closer to each parapodium slightly larger than others. Dorsum and lateral surfaces lacking papillae (Fig. 6C).

Parapodia. Parapodia cylindrical, longer than wide, increasing in length in midbody. Acicular lobe long, oval from chaetiger 4 (Fig. 6C, E). Ventral cirri digitiform to conical, slightly tapering in width distally; as long or slightly shorter than parapodia in chaetigers 1–3; in following chaetigers at least reaching distal end of acicular lobe

(Fig. 7E, G). Parapodial papillae numbering usually up to three: one terminal digitiform papilla ("postchaetal lobe") present from chaetiger 1 (sometimes two papillae in a few mid-body chaetigers); one large spherical to ellipsoid papilla from chaetiger 3–4, on proximal half of ventral surface of parapodia; one digitiform papilla from chaetiger 2, centred on anterior surface of parapodia (Figs 5B, 6E, 7E–G). One straight acicula supporting each parapodium.

Chaetae. All chaetae compound, ca. 7–8 in first segment to 12–13 in middle chaetigers; with long, straight, unidentate and finally serrated blades (Fig. 7H–J). Blades similar in length within chaetigers, slightly shorter in mid-body to posterior chaetigers; ca. 6–7 times longer than maximum width (Fig. 7I, J).

Pygidium. Paired anal cirri similar to dorsal macrotubercles and ventral digitiform anal papilla similar in length to lateral cirri (Figs 6D, 7A).

Internal structures. Muscular pharynx between segments 2 and 4. Eyes or nuchal organs not seen in holotype.

Reproductive features. Gametes or sexual structures not observed in holotype.

Variation. Additional material measuring 1.0–3.5 mm in length and 0.33–0.37 mm wide; with 10–20 (usually 17–18) chaetigers. Live specimens unpigmented, with dorsum covered with small sediment particles, except for dorsal macrotubercles (Fig. 8A). Two oval eyes at level of median antenna or chaetiger 1–2, in some specimens (Fig. 8A). Stalk of dorsal macrotubercle is as long as the tubercle but in many specimens is contracted and therefore seems much shorter (e.g., Fig. 6C vs 6D). Usually, up to seven ventral stalked papillae in mid-body chaetigers but first two and last 2–3 chaetigers may show six (rarely five) papillae. Some specimens show the inter-parapodial tubercle displaced to parapodial areas. Ventral parapodial papilla usually appears in chaetiger 3–4 but in one specimen first appears in chaetiger 7. Otherwise, postchaetal papilla, lateral papilla, and acicular lobe appear constantly in chaetigers 1, 2, and 4 respectively. Muscular pharynx through segments 3–5. Genital openings distinguished in larger females and males (> 2 mm long) as swallowing of the tissue near the base of parapodia between chaetigers 8 and 9 (Figs 4D, 6E).

Etymology. This species, originally described as *Sphaerodoridium fauchaldi* was dedicated to our colleague and prolific annelid systematist Kristian Fauchald (Hartmann-Schröder, 1993). The new name given to it, after the genus *Sphaerodorum* is synonymised with *Clavodorum* and therefore the species is homonym to the previously described *Clavodorum fauchaldi* Desbruyères, 1980, aims to maintain tribute to Kristian, and therefore *kristiani* is proposed.

Remarks. The present diagnosis is based in the original description of *Sphaerodoridium fauchaldi* by Hartmann-Schröder (1993), additional observations (Aguirrezabalaga and Ceberio 2005, Moreira and Parapar 2007) and examination of the holotype, and several specimens from NW Spain and Nordic Seas. This species was described based on one small specimen (1.0 mm long, Fig. 2D, E); several minor differences were reported in material from the Bay of Biscay and NW Spain (Aguirrezabalaga and Ceberio 2005, Moreira and Parapar 2007) but these can be due to the size and state of maturity of the holotype. For instance, Hartmann-Schröder

(1993) did not mention the presence of a ventral parapodial papilla, that is present in specimens reported by Aguirrezabalaga and Ceberio (2005) and Moreira and Parapar (2007) and in those examined in this study; however, this papilla could have been mistaken with a ventral small tubercle by Hartmann-Schröder (1993), and in fact one ventral papilla seems half-drawn in the original description (Hartmann-Schröder 1993: Fig. 8). Otherwise, this species is well characterized and can easily be distinguished from other *Clavodorum-Sphaerodoridium* species from the NE Atlantic, based on the number and arrangement of small ventral tubercles and lack of additional epithelial papillae.

Distribution. We are reporting the species for the first time for the Norwegian Sea and Morocco. Previous records of the species include: North Sea (Hartmann-Schröder 1993); Bay of Biscay (Aguirrezabalaga and Ceberio 2005); NW Iberian Peninsula (Moreira and Parapar 2007, Moreira et al. 2011).

Habitat. Continental shelf, sandy sediments (70–1000 m) (Moreira et al. 2011, and present study).

Commensodorum Fauchald, 1974

Commensodorum Fauchald, 1974: 265–266; Capa et al. 2014: 16.

Type species. *Sphaerodoridium commensalis* Lützen, 1961.

Diagnosis. Body ellipsoid. Head with a median and a pair of lateral antennae; antenniform papillae absent; all appendages short. Tubercles sessile, conical, or pear-shaped, in four longitudinal rows, one transverse row per segment, except for first chaetiger with only two. Minute epithelial papillae on dorsal and ventral surfaces, in ca. 5–6 transverse rows per segment. Parapodia with rounded and small ventral cirri, not surpassing tip of acicular lobe. Stout hooks in anterior chaetigers absent. All chaetae simple, unidentate chaetae, enlarged subdistally, with serrated edge.

Remarks. Referring to the main dorsal tubercles in *Commensodorum* as macrotubercles (e.g., Fauchald 1974) is herein avoided due to their smaller size compared to other members of the family. Members of this group have not been included in molecular analyses due to absence of material properly fixed for DNA extraction and sequencing and therefore relationships with other sphaerodorids remains unknown. The number of longitudinal rows of dorsal tubercles resembles the arrangement of macrotubercles in members of *Sphaerephesia* (as redefined in this study). However, tubercles in *Commensodorum* are smaller than in any other sphaerodorid. Shape of simple chaetae somehow resembles those of *Euritmia,* but they are thinner in the only species described in the genus, *Commensodorum commensalis* (Lützen, 1961).

The genus is monotypic.

Commensodorum commensalis (Lützen, 1961).

Type locality: Gullmarfjord, Sweden, 35 m.

Commensodorum commensalis (Lützen, 1961)

Figs 4E, F, 5C, 9

Sphaerodoridium commensalis Lützen, 1961: 409–416, fig. 1.

Type locality. Blåbergsholmen Island, Gullmarfjord, Sweden, 35 m.

Material examined. Holotype: ZMUC-POL-1984, Sweden: Gullmarfjord, Blåbergsholmen Island, 35 m, 30 Oct 1960.

Additional material. (2 specs) **Skagerrak**, NTNU-VM 73780 (1 spec. on SEM stub) (1 spec.), Lindön, 58°47.90'N, 11°09.52'E, 46 m, 7 May 2008. ZMBN 127260 (1 spec.), Tvedestrand, 58°33.929'N, 9°0.215'E, 34 m, 27 May 2011.

Diagnosis. Body ellipsoid, up to 2.5 mm long. Head with short appendages, without spurs or basal papillae; antenniform papillae absent. Tubercles sessile, conical or pear-shaped, small, arranged in four longitudinal rows on dorsum, one transverse row per segment; except for first chaetiger with only two. Additional epithelial papillae minute over dorsal and ventral surfaces, in ca. 5–6 transverse rows per segment. Parapodia lacking papillae, acicular lobe, and ventral cirrus small and ellipsoid. Stout hooks in anterior chaetigers absent. All chaetae simple, unidentate, with broadened distal end, and serrated edge.

Re-description of holotype. *Measurements and general morphology.* Holotype 2.5 mm long, 0.7 mm wide, with 17 chaetigers; body ellipsoid, with convex dorsum and flattened ventrum; segmentation slightly noticeable, especially on ventral side (Fig. 9A, F). Pigmentation absent on preserved material.

Head. Head fused to first chaetiger (Fig. 9A, B). Prostomial appendages conical, slightly longer than wide. A pair of palps, bigger than lateral and median antennae (Fig. 9B). Dorsal antenniform papillae absent. Few small hemispherical papillae scattered on head surface (only noticeable under SEM, Fig. 9B). Tentacular cirri ellipsoid, smaller than palps, similar in size and shape to median antenna (Fig. 9B). Eyes not observed.

Tubercles. Dorsum with four longitudinal rows of larger tubercles; in one transverse row per segment (Figs 5E, 9A, C). First chaetiger only with two tubercles. Distance between dorsalmost rows larger than there and lateral rows of tubercles. Tubercles sessile, ellipsoid or pear shaped (Fig. 9C–E), with some pores on distal end (Fig. 9D). Dorsal papillae minute, hemispherical, arranged in ca. six transverse rows per segment (Figs 4E, 9C, E). Ventrum with fewer and larger papillae, more abundant near parapodial bases, than in mid-ventral line; with no clear arrangement pattern (Figs 4F, 9F).

Parapodia. Parapodia conical, as long as wide in three or four anterior chaetigers, 2–3 times longer in medium and posterior chaetigers. Acicular lobes ellipsoid, from first chaetiger (Fig. 9G, H). Ventral cirri similar in shape and size as acicular lobe (Fig. 9H). Parapodial papillae absent (Fig. 5C).

Chaetae. All parapodia with 4–5 simple chaetae (Fig. 9G–I); blade serrated on cutting edge and slight recurved distal tip; distal framed by thickened edges (Fig. 9I–K). One straight acicula per parapodium. Large, recurved hooks in the first chaetiger absent.

Pygidium. Pygidium with two dorsolateral and one mid-ventral ellipsoid cirri, similar in size.

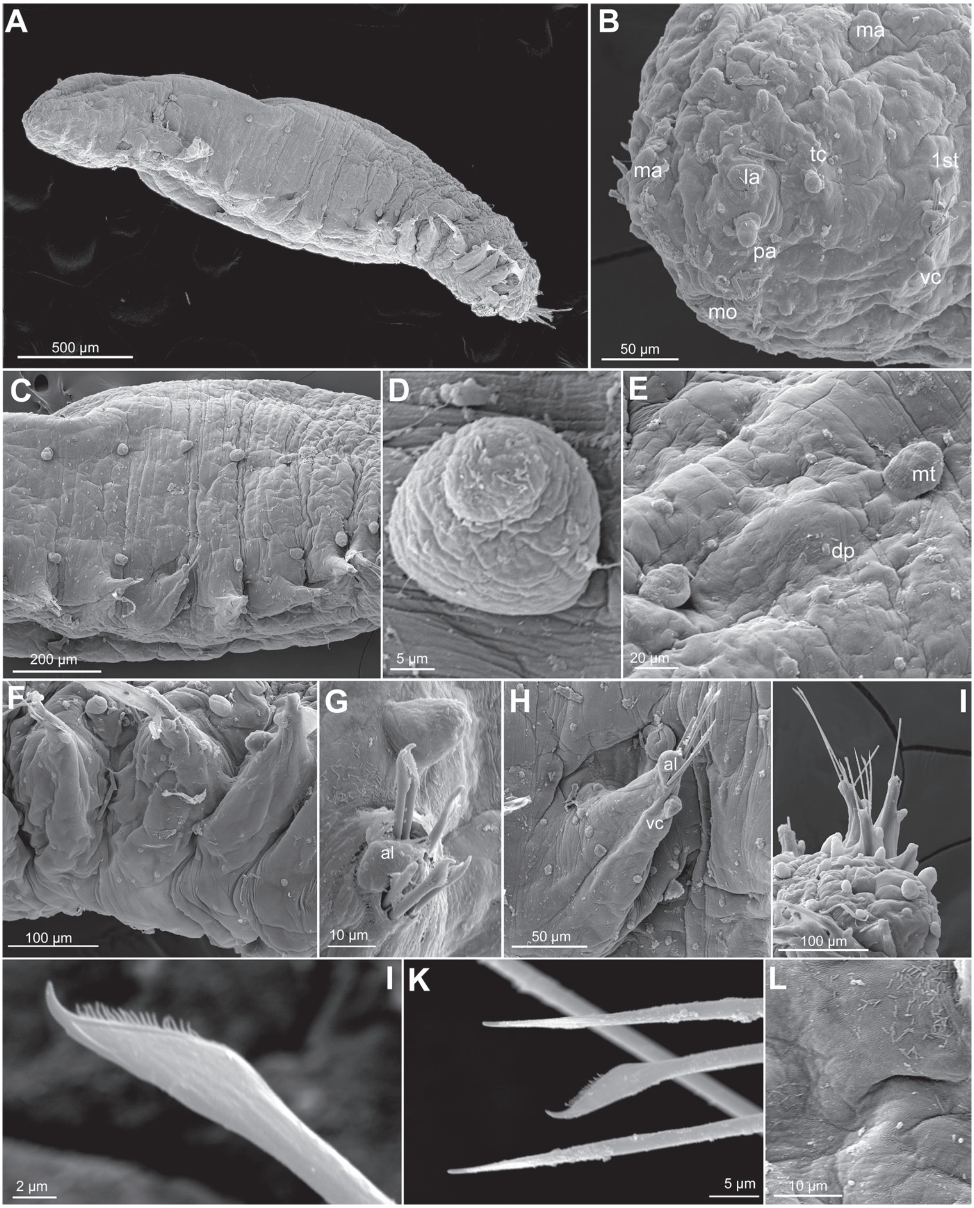

Figure 9. *Commensodorum commensalis* (Skagerrak, NTNU VM 73780). **A** Complete specimen, lateral view **B** anterior end, lateral view **C** mid-body chaetigers, lateral view **D** dorsal tubercle, mid-body chaetiger, detail **E** epithelium between dorsal tubercles, detail **F** parapodia, chaetigers 12–14, lateral view **G** parapodium, anterior chaetiger, lateral view **H** parapodium, mid-body chaetiger, anterior view **I** parapodium, posterior chaetiger **J, K** simple chaetae, anterior and posterior chaetigers **L** epithelium, detail, showing granules.

Reproductive features. Holotype, gravid female, with oocytes measuring ca. 200 µm. Largest specimen also with oocytes, but smaller. Sexual structures or genital openings not observed.

Variation. Largest specimens examined 4 mm long, 0.9 mm wide and 22 chaetigers. Smallest specimens with 19 chaetigers, 0.5 mm long. General morphology is homogenous among material studied. All specimens bear short prostomial appendages, ellipsoid or pear-shaped dorsal tubercles and minute epithelial papillae barely noticeable under stereomicroscope. One specimen (ZMUB 127260) is a gravid female with spheroid eggs occupying most of the body. Genital openings not observed in specimens examined.

Remarks. Epithelium described as transparent in live specimens (Lützen 1961), allowing the observation of the nuchal organs (as pharyngeal glands) and the coiled gut. These are not visible in currently preserved specimens, with opaque epithelium. Original drawings of specimen with 22 chaetigers, does not correspond with the holotype. The body shape is ellipsoid, with blunt anterior and posterior ends, unlike the original description with tapering anterior end, probably due to contraction of specimens after fixation. Head appendages are short and ellipsoid in all specimens examined, not digitiform as in original description (Lützen 1961), also probably due to contraction. The main dorsal tubercles, four per chaetiger, were described as clavate ('forme de massue'), additionally other mid-dorsal 'capsules' were described in anterior chaetigers, but they were not spotted in the material examined. Additional minute papillae are displayed forming ca. six transverse rows per segment.

Commensodorum commensalis differs from other sphaerodorids in the presence of a unique combination of morphological features: four longitudinal rows of small dorsal tubercles, arranged in a single transverse row per segment, and the presence of simple chaetae. Sphaerodorids with simple chaetae comprise members of *Euritmia*, including the recently synonymised *Amacrodorum* (Capa et al. 2016b), lacking large epithelial tubercles but with epithelium covered with small papillae. In addition, members of *Sphaerodorum* typically bear simple chaetae, but macrotubercles are arranged in two longitudinal rows and have clearly defined terminal papillae, absent in *Commensodorum,* and bear in addition two longitudinal rows of dorsal microtubercles (small tubercles also provided with a terminal papilla).

Distribution. Skagerrak, ? United Kingdom (Lützen 1961, Howson and Picton 1997, Frid et al. 2009, present study).

Habitat. Originally described as commensal of *Terebellides stroemii* Sars, 1835 (Lützen 1961), at 35 m. The species has only a few times been reported in the literature since and is not necessarily associated exclusively with *Terebellides* (Frid et al. 2009).

Euritmia Sardá-Borroy, 1987

Euritmia Sardá-Borroy, 1987: 48; Moreira 2012: 41; Capa et al. 2014: 16; Capa et al. 2016a: 9.

Amacrodorum Kudenov, 1987: 917–918.

Type species. *Euritmia hamulisetosa* Sardá-Borroy, 1987

Diagnosis. Body short and ellipsoid. Head with short appendages, without spurs or basal papillae; antenniform papillae absent. Small tubercles or papillae spherical, sessile, smooth, without a terminal papilla, scattered over body surface and parapodia with apparent random distribution (over eight dorsal irregular longitudinal rows, and three or more transverse rows). Parapodia with short, rounded, ventral cirri, not surpassing the tip of acicular lobe. Stout hooks in anterior chaetigers absent. All chaetae simple unidentate, enlarged subdistally, with serrated edge.

Remarks. The genus *Euritmia* was erected to gather sphaerodorids with tubercles scattered over the dorsum and simple chaetae, differing in morphology from chaetae present in other sphaerodorids (Sardá-Borroy 1987, Capa et al. 2014) (i.e., *Sphaerodorum* and *Commensodorum*). The lack of morphological differences across members of *Euritmia* and *Amacrodorum*, a genus erected in the same year (Kudenov 1987) concluded in the recent synonimization of *Amacrodorum* (Capa et al. 2016b). The presence of the characteristic simple chaetae is also shared by species of *Sphaerodoropsis* species belonging to the informal Group 4, sensu Borowski (1994), whose dorsal tubercles are also small compared to other sphaerodorids, but similar to those present in *Euritmia*, and arranged in several transverse rows per segment. No sequences of members of *Euritmia* or this group of *Sphaerodoropsis* have been produced to date to assess their relationships and position within the sphaerodorid tree, but it will be most interesting to test if these two groups (*Euritmia* and *Sphaerodoropsis* Group 4) are closely related. Members of this group of *Sphaerodoropsis* are not reported in the NEA, or found in the present study.

The species currently considered in the genus are:

Euritmia bipapillata (Kudenov, 1987)
  Type locality: Akutan Island, Alaska, 59 m.
Euritmia capense (Day, 1963)
  Type locality: Cape Town, South Africa, unknown depth.
Euritmia carolensis Capa, Osborn & Bakken, 2016.
  Type locality: Off South Carolina, USA, 799 m.
Euritmia hamulisetosa Sardá-Borroy, 1987.
  Type locality: Cádiz, Spain, 0.5–10 m.
Euritmia nordica sp. n.
  Type locality: Greenland, Denmark Strait, 321 m.

Euritmia hamulisetosa Sardá-Borroy, 1987

Figs 4G, H, 5D

Euritmia hamulisetosa Sardá-Borroy, 1987: 48–49, fig. 1, 2; Moreira 2012: 41–43, fig. 12F, 14.

Type locality. Cádiz, South of Iberian Peninsula, 0.5–10 m.

Diagnosis. Body short and ellipsoid, up to 0.6 mm long. Head with short appendages, without spurs or basal papillae; antenniform papillae absent. Epithelial papillae sessile, spherical, arranged in four transverse rows per segment. Ventrum with a pair of papillae near the parapodial bases and two additional longitudinal rows. Ventral papillae, in four transverse rows per segment. Microtubercles (small tubercles with a collar and terminal papillae) absent. Parapodia with a large dorsal papilla, digitiform acicular lobe, and spherical ventral cirrus. Stout hooks in anterior chaetigers absent. Six simple chaetae with serrated edge, enlarged subdistally, with a distal spine and filament in opposite directions.

Material examined. No specimens were available for this study.

Remarks. In the original description, the dorsal epithelial tubercles were termed macrotubercles (Sardá-Borroy 1987). These have later been interpreted as papillae due to their size and arrangement in comparison to other sphaerodorids (e.g., Capa et al. 2016b). The parapodia were originally described with double parapodial lobes and a small globular cirrus (Sardá-Borroy 1987). These were interpreted differently as it was clear the large lobes represent the acicular lobe and ventral cirrus, and ventral papillae placed at the base of parapodia (Fig. 5D; Capa et al. 2014).

Euritmia hamulisetosa is distinguished from other congeners by the unique combination of two features: the arrangement of dorsal papillae in four transverse rows per segment (Fig. 4G) and the presence of parapodial papillae on the anterior and posterior surfaces (Fig. 5D). *Euritmia capense* (Day, 1963) bears two transverse rows of papillae per segment and five parapodial papillae (one dorsal, one ventral and three smaller ones on anterior and posterior parapodial surfaces). *Euritmia bipapillata* (Kudenov, 1987) has three transverse rows of dorsal papillae and one papilla on anterior surface of parapodia; *Euritmia carolensis* (Capa, Osborn & Bakken, 2016) has three transverse rows of papillae and no parapodial papillae (Capa et al. 2016b). *Euritmia nordica* sp. n. bears three transverse rows per segment (with a characteristic longitudinal mid-dorsal bare area) and no papillae on parapodia (present study).

Distribution. Gibraltar Strait and Mediterranean coast of the Iberian Peninsula (Sardá-Borroy 1987, Moreira 2012).

Habitat. Littoral algae and dentritic bottoms to 10 m (Moreira 2012).

Euritmia nordica Capa & Bakken, sp. n.

http://zoobank.org/77E0A063-122F-46C9-93CB-E7DDD04DA297
Figs 4I–J, 5E, 10

Type locality. Greenland Sea, off eastern Greenland in Denmark Strait, 321 m.

Material examined. Holotype: SMF 25281, Greenland, Denmark Strait, 67°38.77'N, 26°44.78'W, 321 m, 14 Sep 2011. **Paratype**: ZMBN 127261 (1 spec. on SEM stub), Norwegian Sea, 63°2.232'N, 4°41.34'E, 760 m, 30 Sep 2013.

Diagnosis. Body short and ellipsoid, up to 1.5 mm long. Head with short appendages, without spurs or basal papillae; antenniform papillae absent. Dorsum with sessile

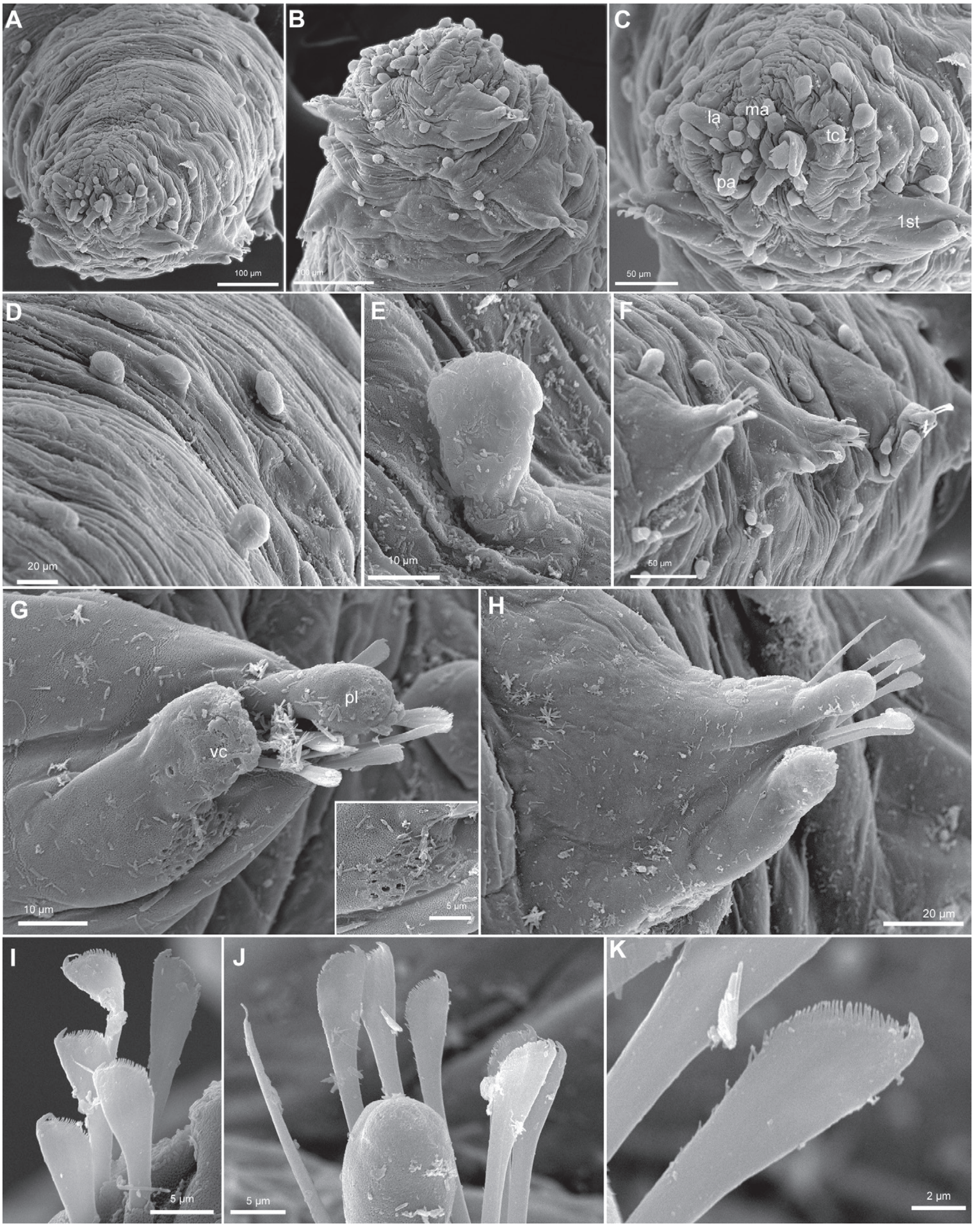

Figure 10. *Euritmia nordica* sp. n., paratype (ZMBN 127261), scanning electron micrographs. **A** Anterior end, frontal view **B** anterior end, ventral view **C** anterior end with head appendages, frontal view **D** epithelial dorsal papillae, chaetiger 3, detail **E** dorsal papilla, chaetiger 2 **F** parapodia, left side, chaetigers 3–5, anterior view **G** parapodium, left side, chaetiger 1, anterior view (insert: detail of pores ventral to ventral cirrus) **H** parapodium, left side, chaetiger 2, anterior view **I** simple chaetae, anterior chaetiger **J** simple chaetae, anterior chaetiger **K** simple chaetae, detail of distal spines on blade.

spherical papillae arranged in three transverse rows, and up to 18, per segment. Ventrum with a pair of papillae near each parapodial bases and two additional longitudinal rows. Parapodia without papillae; digitiform acicular lobe and spherical ventral cirrus. Six or seven simple chaetae with serrated edges, enlarged subdistally, with a distal spine and filament in opposite directions.

Description. *Measurements and general morphology*. Holotype 0.9 mm long, 0.5 mm wide, with 12 chaetigers. Body ellipsoid, with strongly convex dorsum and flattened ventrum (Fig. 10A). Epithelium with transverse wrinkles, segmentation not noticeable (Fig. 10A, D). Pigmentation absent on preserved material.

Head. Head fused to first chaetiger (Fig. 10B, C). Prostomial appendages digitate, with a pair of palps, a pair of lateral antennae slightly longer than palps, a median antenna half as long as lateral antennae (Fig. 10B, C). Dorsal antenniform papillae absent or not conspicuous. Few small hemispherical papillae scattered on head surface, ca. 5–6 confined among palps and antennae. Tentacular cirri, digitate, shorter than palps, similar in size and shape to median antenna (Fig. 10C). Eyes not observed.

Tubercles. Dorsum with about eight rows of similar sized and ellipsoid papillae, in three irregular transverse rows of per segment (Fig. 10A, D–F); adding up to ca. 15–18 per segment on mid-body chaetigers (Fig. 4I). Ventrum with fewer spherical papillae, arranged at base of parapodia with two parallel papillae (Fig. 10B, F), and additional two longitudinal rows (10B, C), in total ca. six papillae per segment (Figs 4J, 10B, C). Mid-dorsal body bare of papillae (Fig. 10B).

Parapodia. Parapodia conical, as long as wide in all chaetigers (Fig. 10F, H), similar throughout. Acicular lobe digitate longer than ventral cirri; ventral cirri ellipsoid (Fig. 10F–H). Most segments with no additional papillae or parapodial appendages, exceptionally one or two small parapodial papillae near the base of ventral cirrus (Fig. 5E, 10F).

Chaetae. Large, recurved hooks in the first chaetiger absent. All parapodia with 6–7 simple chaetae; blade serrated on cutting edge and a recurved distal tip (Fig. 10C, G–K).

Pygidium. Pygidium with two small and spherical tubercles and a small digitiform ventral cirrus.

Internal features. A pair of rounded eyes observed under the epithelium, in the head. Muscular pharynx not observed.

Reproductive features. Two large eggs are visible in the coelom of the holotype.

Variation. Paratype 1.5 mm long, 0.6 mm wide, with 19 chaetigers (anterior end on SEM stub). Papillae on ventrum in three transverse rows per segment, positioned as two parallel at base of parapodia and one towards mid-body (Fig 10B). Parapodia are smooth in most chaetigers of both holo- and paratype but variation has been observed, with one parapodium with one small papilla and the following with two papillae, located at the base of the ventral cirrus (Fig. 10F). Sexual structures (unknown gender) observed as inflated ventral cirri with pore openings in first chaetiger in the paratype (Figs 4J, 10G).

Etymology. The epithet of this species, *nordica*, refers to the geographical region where this species has currently been found. Nordic or The North gathers the north-western European countries, including Scandinavia and Fennoscandia.

Remarks. *Euritmia nordica* sp. n. is characterized by a unique combination of features: dorsum provided with similar sized, ellipsoid tubercles arranged in three transverse rows per segment, leaving a conspicuous longitudinal bare mid-dorsal area; two longitudinal zig-zag rows of small and ellipsoid papillae on ventrum (with ca. six papillae per segment); parapodia lacking papillae (with some exceptions). *Euritmia nordica* sp. n. resembles *E. carolensis* due to the arrangement of dorsal papillae in three transverse rows per segment and the absence of parapodial papillae. Differences between members of these two species rely on size and number of dorsal epithelial papillae, larger and more abundant in *E. carolensis* (covering most of the dorsum, while in *E. nordica* sp. n. the dorsum is mainly smooth); chaetae in *E. nordica* sp. n. are broader subdistally and recurved at the distal end, while *E. carolensis* has a slim appearance and a straighter distal tip. Moreover, *E. nordica* sp. n. presents an inflated cirrus in the first chaetiger, with pore openings on its base (Fig. 10G), similar to what was described in *Sphaerodoropsis halldori*, on chaetiger 6 of males (Moreira and Parapar 2012). This is the first time that potentially sexual structures are described in members of *Euritmia*, and therefore it is unknown if the attributes described herein are species specific.

Euritmia nordica sp. n. is distinguished from *E. bipapillata*, described from Alaska, in the absence of parapodial papillae, while *E. bipapillata* has one papilla on anterior surface of parapodia (Kudenov, 1987). *Euritmia hamulisetosa* from southern Spain has dorsal papillae in four transverse rows per segment and parapodial papillae (Sardá-Borroy 1987), unlike *E. nordica* sp. n. with three transverse rows of dorsal papillae and smooth parapodia. *Euritmia capense*, from South Africa, bears two transverse rows of papillae per segment and five parapodial papillae (Day 1963).

Distribution. The species is known from Denmark Strait, East of Greenland (holotype), and the Norwegian Sea.

Habitat. The specimens were found in soft bottom, in areas influenced with cold water (approximately 0 °C). The paratype was found inside the tube of an undescribed species of *Ampharete*.

***Geminofilum* gen. n.**

http://zoobank.org/35550293-C24E-44D9-8748-D56C437BCB97

Sphaerodoropsis Hartman & Fauchald, 1971: 69 (in part); Fauchald 1974: 261 (in part); Borowski 1994: 23 (in part); Moreira 2012: 30 (in part); Capa et al. 2014: 18 (in part).

Type species. *Sphaerodorum distichum* Eliason, 1962.

Diagnosis. Body short and cylindrical. Head with a median and a pair of lateral antennae; antenniform papillae absent or present; all appendages short. Tubercles sessile, spherical or hemispherical, arranged in two transverse rows per segment. Additional epithelial papillae on dorsal (sometimes absent) and ventral surfaces. Parapodia with elongated ventral cirri, as long as acicular lobe. Stout hooks in anterior chaetigers absent. All chaetae compound, unidentate, with serrated edge.

Remarks. Analyses of molecular data presented here reveal that members of previously considered *Sphaerodoropsis* Group 3, according to Borowski (1994), form a monophyletic group, morphologically quite distinct (with dorsal macrotubercles, arranged in two transverse rows per segment and genetically (long branch compared to other clades; Fig. 1). This clade is sister to *Sphaerephesia sensu stricto* in the present study (sphaerodorids with four dorsal longitudinal rows of sessile macrotubercles). Since the type species of *Sphaerodoropsis, Sphaerodoropsis sphaerulifer* does not possess the main diagnostic features of this clade, and instead bears dorsal macrotubercles in a single transverse row (e.g., Moore 1909, Kudenov 1987), the erection of a new genus for accommodating these other species is needed. *Geminofilum distichum* (Eliason, 1962), comb. n., is the selected type species of the new genus because it is the oldest described species in the group that has been included in the present molecular analyses.

It is here assumed that *Geminofilum* gen. n. includes all sphaerodorids presenting two transverse rows of macrotubercles, but confirmation of this hypothesis is needed, since several of the species with this morphological feature have not been included in the analyses. *Geminofilum* gen. n. would therefore be represented by the following 15 species, all of which require nomenclatural changes:

Geminofilum arctowskyensis (Hartmann-Schröder & Rosenfeldt, 1988), comb. n.
Type locality: South Shetland Islands, Antarctica, 265 m.
Geminofilum bisphaeroserialis (Hartmann-Schröder, 1974), comb. n.
Type locality: South of Durban, South Africa, 20 m.
Geminofilum distichum (Eliason, 1962), comb. n.
Type locality: Skagerrak, North East Atlantic, 460 m.
Geminofilum fauchaldi (Hartmann-Schröder, 1979), comb. n.
Type locality: Pt. Hedland, Western Australia, shallow depth.
Geminofilum garciaalvarezi (Moreira, Cacabelos & Troncoso, 2004), comb. n.
Type locality: Baiona, NW Spain, 7 m.
Geminofilum halldori (Moreira & Parapar, 2012), comb. n.
Type locality: Western Iceland, 1162 m.
Geminofilum heteropapillatum (Hartmann-Schröder, 1987), comb. n.
Type locality: Geelong, Victoria, Australia, shallow depth (coralline algae).
Geminofilum multipapillatum (Hartmann-Schröder, 1974), comb. n.
Type locality: Mtwara, Tanzania, shallow depth (in coral reef).
Geminofilum oculatum (Fauchald, 1974), comb. n.
Type locality: Antarctic Peninsula, 412 m.
Geminofilum paracapense (Hartmann-Schröder, 1974), comb. n.
Type locality: Diaz Point, Namibia, SW Africa, unknown depth.
Geminofilum pycnos (Fauchald, 1974), comb. n.
Type locality: Antarctic Peninsula, 650 m.
Geminofilum sexantennellum (Kudenov, 1993), comb. n.

Type locality: Southern California, ca. 150 m.

Geminofilum solis (Reuscher & Fiege, 2015), comb. n.

Challenger Plateau, Tasman Sea, 1523–1526 m.

Geminofilum spissum (Benham, 1921), comb. n.

Type locality: Macquarie Island, Southern Ocean, unknown depth.

Geminofilum translucidum (Borowski, 1994), comb. n.

Type locality: Peru Basin, 4162 m.

Etymology. The name of this genus, *Geminofilum,* refers to the particular organization of macrotubercles in members of this genus in double (*Geminus* in Latin, gender: masculine) rows (*filum*, in Latin, gender: neuter).

Geminofilum distichum (Eliason, 1962), comb. n.

Figs 4K–N, 5F, 8B–C, 11, 12

Sphaerodorum distichum Eliason, 1962: 247–248, fig. 12.

Sphaerodoropsis distichum (Eliason, 1962). Hartmann-Schröder 1996: 236.

? *Sphaerodoropsis chardyi* Desbruyères, 1980: 115–117, fig. 4; ? Böggemann 2009: 388–389, fig. 120, 123, 124, 137.

Type locality. Skagerrak, 58°05'N, 8°32'E, 460 m.

Material examined. Holotype: UUZM 203, Skagerrak, 58°05'N, 8°32'E, 460 m, 4 July 1933.

Holotype of *Sphaerodoropsis chardyi*: MNHN TYPE 1282, Bay of Biscay, 44°11.3'N, 4°15.4'W, 2430 m.

Additional material. (6 specs) **Iceland**: DZMB-HH 28574 (1 spec. used for DNA sequencing, SPH 294), South Iceland, Iceland Basin, 62°33.50'N, 020°21.18'W, 1390 m, 02 Sep 2011; SMF 23898 (1 spec., used for SEM and DNA sequencing, SPH 064), Iceland Basin, 62°33.1'N, 20°23.71'W, 1384 m, 2 Sep 2011; SMF 23899 (1 spec. used for DNA sequencing, SPH 049) South Iceland, Irminger Basin, 61°36.19'N, 031°22.60'W, 2537 m, 07, Sep 2011. **Norwegian Sea**: ZMBN 127262 82.11.27.1 (1 spec.), 62°59.1'N, 3°13.1'E, 804 m, 27 Nov 1982; **Skagerrak**: ZMBN 127263 (1 spec. used for SEM and DNA sequencing, SPH295, photographed alive Fig. 8B), Drøbak, 59°38.664'N, 10°37.152'E, 106 m, 24 Oct 2014.

Diagnosis. Body short and cylindrical, up to 2.5 mm long. Prostomial appendages smooth, lacking spurs or basal papillae. Dorsal macrotubercles sessile, hemispherical, arranged in two transverse rows per segment, with five and six macrotubercles each, from segment 2. Dorsum with 4–6 additional papillae per segment in mid body. Ventrum with 6–8 hemispherical papillae per segment, arranged in nearly Λ-shaped. Females with a pair of large ventral papillae, or sexual structures, between chaetigers 6 and 7. Parapodia without papilla. Acicular lobe from chaetiger 2. Stout hooks absent in anterior chaetigers. Compound chaetae in all parapodia, 4–7, with short blades (up to four times as long as wide).

Re-description of holotype. *Measurements and general morphology.* Holotype short and cylindrical, 2.2 mm long and 0.4 mm wide, with 16 chaetigers. Dorsum convex, ventrum flattened. Segmentation inconspicuous, tegument smooth. Live specimens with some whitish macrotubercles (Fig. 8B); preserved specimen lacking pigmentation.

Head. Anterior end bluntly rounded. Prostomium and peristomium indistinct, appendages not observed in holotype, due to contraction of specimen. Additional material with small and digitiform prostomial appendages, without spurs or basal papillae (Figs 11A, B, 12A–C). Antenniform papillae could be considered present (due to the position behind lateral antennae), but similar in shape and size to other prostomial papillae (Fig. 12B). Tentacular cirri, similar in size and shape to prostomial appendages. Either five or six rounded prostomial papillae between antennae (Figs 11B, 12B).

Tubercles. Dorsal macrotubercles sessile and ovoid (Figs 11C, 12D). First chaetiger with two anterior macrotubercles and a posterior with four (Figs 11B, 12B). Following chaetigers with double transverse rows of macrotubercles per segment, with five and six tubercles on each of the anterior and posterior rows, arranged in zig-zag pattern; lateralmost tubercles smaller (Fig 4K). Few additional hemispherical papillae scattered on dorsum in no clear pattern, maximum of five or six papillae on mid segments (Fig. 12A). Ventrum with 6–8 small, hemispherical papillae arranged in a more or less Λ-shaped, on each segment (Figs 4L, 11D, 12E). One hemispherical papilla between parapodia, larger than ventral papillae, forming one row on each side on some segments (Fig. 11A).

Parapodia. Parapodia sub-conical, slightly longer than wide. Chaetigers with digitiform acicular lobe, present from chaetiger 2, projecting as long as ventral cirrus (Fig. 11B); ventral cirri bluntly rounded (Figs 11D–F, 12F). Parapodia lacking papillae (Figs 5F, 11D–F, 12F).

Chaetae. Compound chaetae present in all chaetigers, arranged in a straight or curved row posterior to acicular lobe, numbering 4–7 per fascicle (Fig. 11E, F). Shaft with slender distal end, blades slender, ranging 3–4 times longer than maximum width (Figs 11G, H, 12G).

Pygidium. Pygidium blunt with a pair of rounded terminal papillae (Fig. 11H).

Internal features. Eyes or muscular pharynx not seen in opaque holotype.

Reproductive features. Holotype female with few oblong eggs measuring 200 µm in length. A female with a flat tubercle (genital opening) between parapodia 6 and 7 (Figs 4L, 11F).

Variation. Specimens studied measured between 1.5 and 2.5 mm long and 0.3–0.5 mm wide. Live specimens translucent with white spots in macrutubercles (Fig. 8B, C). Eyes seen (dark red) in one live specimen (Fig. 8B), pigmented (bright orange) nuchal organs observed in another similar specimen (Fig. 8C). Fixed specimens lacking any pigmentation pattern. Muscular pharynx, occupying ca. three segments, observed in translucent live specimens. All specimens identified as *Geminofilum distichum* comb. n. bear a similar pattern of dorsal hemispherical-oval macrotubercles (5+6), on each midbody segment, but in one individual, and also in the holotype of *S. chardyi* the lateral most tubercles are larger than the mid-dorsal ones, contrary to the holotype and some

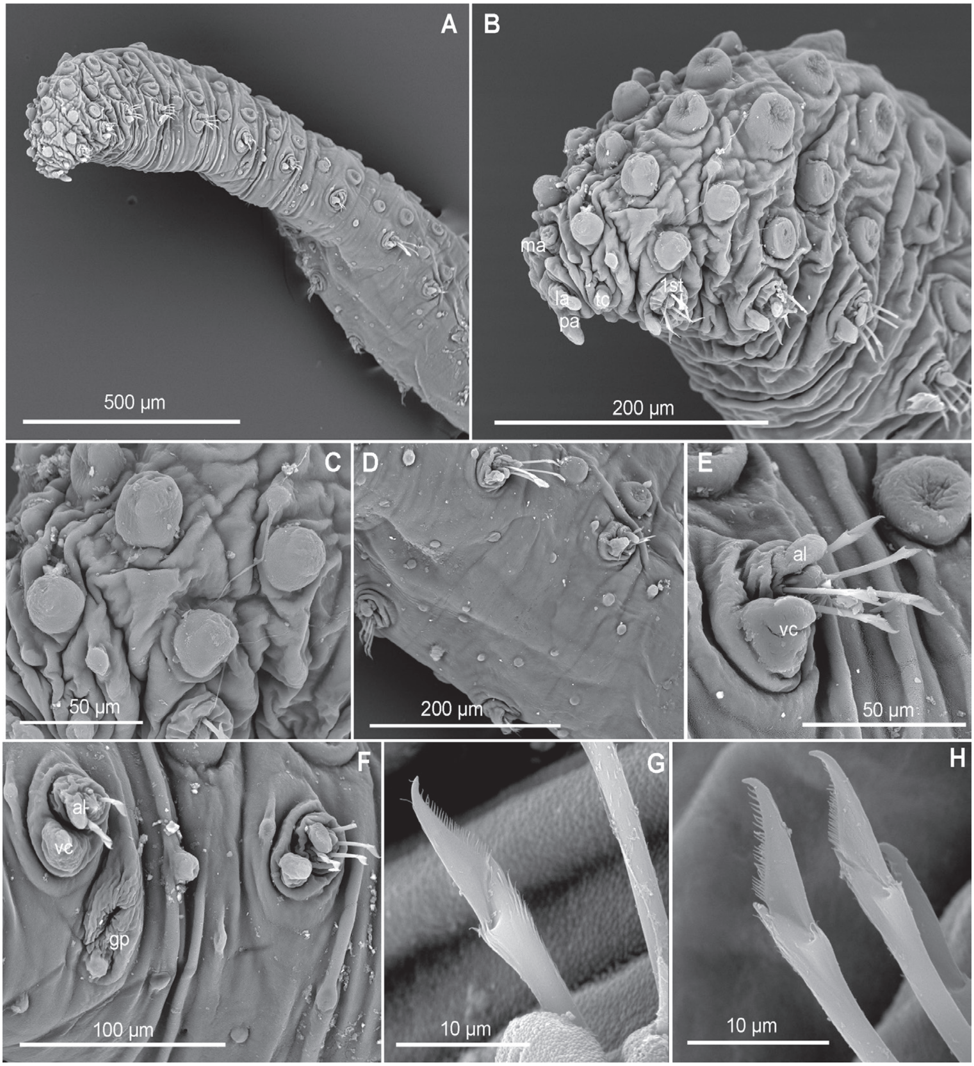

Figure 11. *Geminofilum distichum* comb. n. (ZMBN 127263), scanning electron micrographs. **A** Anterior end, lateral view **B** head and anterior segments, dorsal view **C** dorsal macrotubercles, anterior chaetigers **D** chaetigers 9 and 10, ventral view **E** parapodium, chaetiger 5, anterior view **F** genital opening between parapodia of chaetiger 6 and 7 **G** chaeta, chaetiger 5 **H** chaetae, mid-body chaetiger.

other specimens with smaller macrotubercles near parapodia (Fig. 4K). This specimen also presented a slightly different arrangement of ventral papillae, more aligned into four longitudinal rows (Fig. 4L).

Remarks. *Sphaerodoropsis distichum* was described from 450 m depth in the Skagerrak (Eliason 1962), and has never been found again. The single specimen acknowledged, the holotype, is not in optimal condition and some of the features referred to in the original description (Eliason 1962) may be inaccurate. For example, the ante-

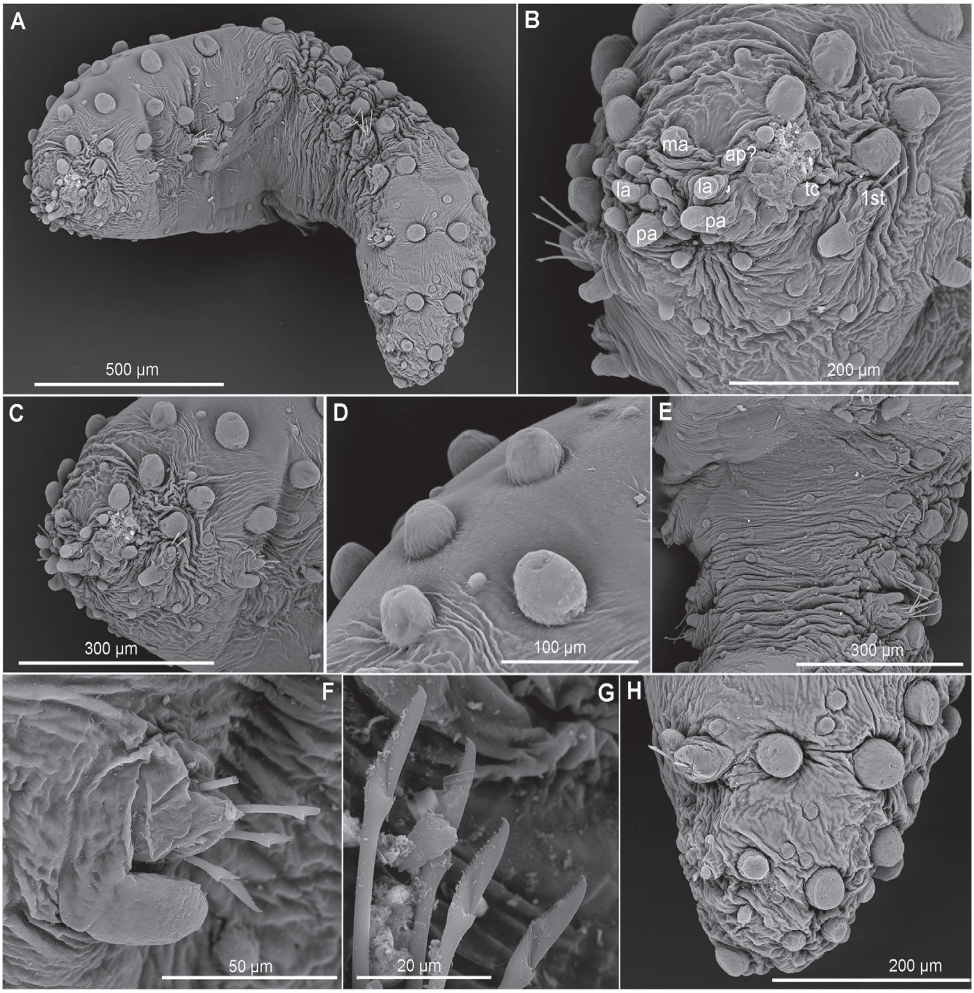

Figure 12. *Geminofilum distichum* comb. n. (SMF 23898), scanning electron micrographs. **A** complete specimen, lateral view **B** head, frontal view **C** head and anterior segments, lateral view **D** dorsal macrotubercles, chaetiger 2 **E** mid-body chaetigers, ventral view **F** parapodium, chaetiger 2, anterior view **G** chaetae, mid-body chaetigers **H** posterior end and pygidium, lateral view.

rior appendages were reported as absent even if the specimen looked like presenting a contracted anterior end. Re-examination of the holotype indicates parapodia lack papillae (although reported as bearing one papilla in the posterior surface), and instead there seem to be some papillae over the ventrum of the specimen, that was reported as smooth, except for a longitudinal row near parapodia. Additional material collected nearby the type locality confirmed these new findings: the specimen presents head appendages, that are short and digitiform; parapodia do not bear papillae; dorsum has a few scattered papillae in addition to the hemispherical macrotubercles and ventrum has 6–8 small spherical papillae. With these changes, the description of *G. distichum* comb. n. resembles that of *S. chardyi* Desbruyères, 1980 described from the Bay of Biscay, ca. 2500 m depth. Differences would be the presence of a curved acicula in *S. chardyi,* a feature that is herein questioned as it has not been observed in any sphaerodorid. Moreover, Desbruyères (1980) most likely unintentionally overlooked the existence of *S. distichum* and did not compare both species. It is the first time that sexual structures are reported in members of these two species.

Additional individuals found at 1400 m in Iceland (Fig. 12) also match the description of *G. distichum* comb. n. It is therefore here proposed the synonymy of *S. chardyi* and *G. distichum* (with some caution), based on morphological similarity between the types and additional material reported herein. There is, however, considerable genetic difference between specimens collected at different localities and depths (Fig. 1) that may indicate a large population structure within the species, or else that we are dealing with a species complex with clear geographical or bathymetrical boundaries between them. Furthermore, this species was reported from the Angola Basin also lacking parapodial papillae, apart from a globular papilla near anterior base (Böggemann 2009). In order to assess the species boundaries of *G. distichum* comb. n., and the distribution range more material, and DNA sequences, will be needed.

Geminofilum distichum comb. n. is clearly recognised from other congeners, by the arrangement of macrotubercles in the first segment (2+4), the scarce and randomly arranged additional papillae over dorsum and the lack of parapodial papillae.

Distribution. This is the first record for this species in Iceland and the Norwegian Sea. It had previously been reported from Skagerrak and English Channel (Eliason 1962, Desbruyères 1980). Species reported also in Angola and Guinea Basins, 3900–5500 m (Böggemann 2009).

Habitat. Sediments from 100 to 2500 m (at least) (Eliason 1962, Desbruyères 1980, and present study)

***Geminofilum halldori* (Moreira & Parapar, 2012), comb. n.**

Figs 4O, P, 5G, 13A–F

Sphaerodoropsis halldori Moreira & Parapar, 2012: 588–591, figs 1B, 4–5, 6D–F.

Type locality. West Iceland, 64°26'N, 28°15'W, 1162 m.

Material examined. Iceland (13 specs): IINH 38791 (3 specs), 65°15.61'N, 28°50.15'W, 1300 m, 28 Aug 1996; IINH 38792 (8 specs), 65°11.01'N, 29°04.18'W, 1456 m, 25 Aug 1996; IINH 38793 (2 spec. on SEM stub), 62°23.15'N, 28°16.91'W, 1558 m, 7 Sep 2003.

Diagnosis. Body short and cylindrical, up to 3.5 mm long. Prostomial appendages smooth, lacking spurs or basal papillae. Dorsal macrotubercles sessile, almost spherical, arranged in two transverse rows per segment, with six and seven macrotubercles each, from segment 3. Dorsum with seven additional rounded papillae per segment in mid body, arranged in seven longitudinal rows. Ventrum with up to eight papillae per segment in mid body, arranged in six longitudinal rows and forming a V on each segment. Females with a pair of larger tubercles in chaetigers 7–9. Parapodia with one papilla on anterior surface from chaetiger 3. Acicular lobe from chaetiger 1–2. Compound chaetae, 4–8, with short blades (up to five times as long as wide), showing some intrafascicle variation in size.

Reproductive features. Some males filled with sperm and females with oocytes. Sexual structures of males as ventral cirri basally inflated, and with pores on ventral surface on chaetiger 6. Females with pair of oval, distally opened tubercle located ventrolaterally to parapodia on chaetigers 6–7 (Fig. 4P); in addition, ventral cirri of chaetigers 4–7 basally inflated and with ventral pores.

Variation. Size range (type series): 2.5–3.1 mm long, 0.4 mm wide, with 17–20 chaetigers. Pigmentation absent in fixed specimens.

Remarks. *Geminofilum halldori* comb. n. resembles *G. bisphaeroserialis* (Hartmann-Schröder, 1974), comb. n., *G. arctowskyensis* (Hartmann-Schröder & Rosenfeldt, 1988), comb. n., and *G. garciaalvarezi* (Moreira et al. 2004), comb. n. in the general appearance, number and arrangement of dorsal macrotubercles (Fig. 13A, B), and the presence of one papilla on the anterior surface of parapodia (Fig. 5G). However, they can be distinguished by the number and arrangement of dorsal and ventral papillae. *Geminofilum halldori* comb. n. is characterised by presenting seven small and hemispherical papillae per segment from chaetiger 3 arranged in a transverse row between segments (Fig. 4O), and three in a row between parapodia (these features are not visible in Fig 13, probably due to the contraction of animal and wrinkled epithelium). Chaetae show slight variation in size of blades within parapodia, but anterior chaetigers bear longer blades (Fig. 13E, F).

Distribution. West Iceland (Moreira and Parapar 2012, present study).

Habitat. Sandy sediments, at depths of 1162–1558 m (Moreira and Parapar 2012, this study).

Geminofilum garciaalvarezi (Moreira, Cacabelos & Troncoso, 2004), comb. n.

Figs 4Q, R, 5H, 13G–I

Sphaerodoropsis garciaalvarezi Moreira, Cacabelos & Troncoso, 2004: 995–999, figs 1–3, 4A, D.

Type locality. Ensenada de Baiona, NW Iberian Peninsula, 42°08.83'N, 8°50.25'W, 7 m.

Material examined. (2 specs) **NW Spain:** MNCN 16.01/18460 (2 specs, on SEM stub), Ría de Ferrol, 08°14.37'N, 43°27.88'W, 15 m, 19 Jul 2010.

Diagnosis. Body short and cylindrical, up to 2.5 mm long. Head appendages short, smooth, lacking spurs or basal papillae. Median antenna shorter than lateral antennae and palps. Antenniform papillae absent. Dorsal macrotubercles sessile, almost spherical, arranged in two transverse rows per segment, with six and seven macrotubercles each in midbody segments. Additional five papillae, hemispherical and small, per

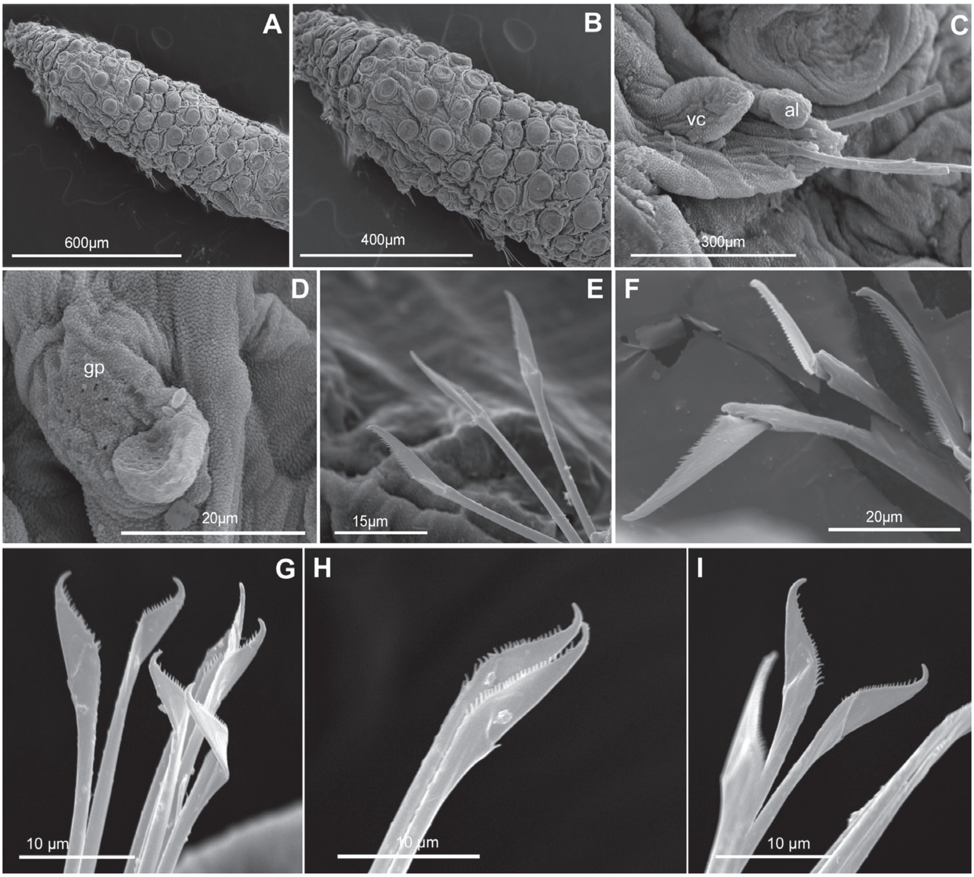

Figure 13. *Geminofilum halldori* comb. n., scanning electron micrographs (IINH 38793). **A** anterior end, dorsal view **B** disposition of dorsal macrotubercles, anterior chaetigers **C** parapodium, mid-body chaetiger, ventral view **E, F** chaetae, mid-body chaetiger. *Geminofilum garciaalvarezi*, scanning electron micrographs (MNCN 16.01/18460, NW Spain) **G–I** chaetae, mid-body chaetiger.

segment. Ventrum with six papillae per segment, hemispherical and small, arranged in a V-shape. Parapodia with one papilla on anterior surface. Acicular lobe from chaetiger 2, digitiform. Ventral cirri digitiform reaching acicular lobe tip. Compound chaetae (3–6) with short blades (up to five times as long as wide); all similar. Females with large tubercle near ventral edge of parapodia of chaetiger 6 and inflated ventral cirri of chaetigers 4–7. Males with a pair of oval tubercles, ventral cirri of chaetiger 6 also basally inflated.

Remarks. The recent description of this species is complete and re-examination of material, even under the SEM did not provide further information about morphological features. Range of variation among chaetae of different specimens and segments show moderate variation and all studied blades range between 3–5 times as long as wide, are unidentate, and finely serrated (Fig. 13G–I). *Geminofilum garciaalvarezi* comb. n.

is similar to *G. bisphaeroserialis* (Hartmann-Schröder, 1974), comb. n. (South Africa), *G. arctowskyensis* (Hartmann-Schröder & Rosenfeldt, 1988), comb. n. (Antarctica), and *G. halldori* (Moreira & Parapar, 2012), comb. n. (Iceland) but they can be distinguished according to the number and arrangement of ventral papillae (Moreira et al. 2004, Moreira and Parapar 2012).

Distribution. NW Iberian Peninsula (Moreira et al. 2004, Cacabelos et al. 2008).

Habitat. From gravel to muddy sand and sandy mud and seagrass (*Zostera marina* L.), 7–28 m depth (Moreira et al. 2004, Cacabelos et al. 2008).

***Sphaerephesia* Fauchald, 1972, emended**

Sphaerodoropsis Hartman & Fauchald, 1971: 69 (in part); Fauchald 1974: 261 (in part); Borowski 1994: 23 (in part); Moreira 2012: 30 (in part); Capa et al. 2014: 18 (in part).

Sphaerephesia Fauchald, 1972: 197 (in part); Fauchald 1974: 271 (in part); Capa and Bakken 2015: 238 (in part), Capa et al. 2016b: 14 (in part).

Type species. *Sphaerephesia longisetis* Fauchald, 1972.

Diagnosis. Body generally short and ellipsoid, some species slender. Head with short appendages, with or without spurs or basal papillae; antenniform papillae absent or present. Four longitudinal rows of dorsal macrotubercles, one transverse row per segment. Macrotubercles sessile, spherical or hemispherical, pear-shaped or with terminal papilla. Microtubercles (small tubercles with a collar and terminal papillae) absent. Additional papillae over body surface and parapodia. Parapodia with cylindrical or pear-shaped ventral cirri, not surpassing the tip of acicular lobe. Stout hooks in anterior chaetigers absent. All chaetae compound.

Remarks. *Sphaerephesia* has been, up to know, diagnosed by the presence of terminal papillae on dorsal macrotubercles (e.g., Fauchald 1972, 1974, Capa et al. 2014). These papillae are not discrete nor separated by a constriction. Instead, they appear to be as a continuous thinner tip of the tubercles, in most cases. The most conspicuous example of well-developed terminal papillae is the recently described *Sphaerephesia amphorata* Capa, Osborn & Bakken, 2016. There were nine species considered within this genus (Capa et al. 2016b). Some members of *Sphaerodoropsis* (prior to this study) present pear-shaped macrotubercles on some dorsal tubercles, or even with subtle terminal papillae. It was previously indicated that the validity of both genera and their boundaries are unclear and require assessment (Capa and Bakken 2015, Capa et al. 2016b). Analyses of molecular data in this study recover *Sphaerephesia* and members of *Sphaerodoropsis* Group 1 (Borowski 1994) both paraphyletic and together forming Clade 1 (Fig. 1). We are proposing the transfer of members of *Sphaerodoropsis* group 1 to *Sphaerephesia* and expanding the diagnosis of the latter to incorporate those sphaerodorids with four longitudinal rows of sessile macrotubercles, regardless their shape (hemispherical, spherical, pear-shaped or with terminal papilla). Members of

Sphaerephesia were described lacking antenniform papillae and with four longitudinal rows of dorsal macrotubercles. However, there are congeners presenting antenniform papillae. *Sphaerephesia gesae* Moreira & Parapar, 2011, provided with eight longitudinal rows of macrotubercles, needs validation and it is for the time being considered with an uncertain position.

The species included in the genus after this study are:

Sphaerephesia amphorata Capa, Osborn & Bakken, 2016
  Type locality: North Carolina, USA, 640 m.
Sphaerephesia anae (Aguado & Rouse, 2006), comb. n.
  Type locality: Pacific Antarctic Ridge, 2216–2334 m.
Sphaerephesia artabrensis (Moreira & Parapar, 2007), comb. n.
  Type locality: Artabro Gulf, NW Iberian Peninsula, 209 m.
Sphaerephesia biserialis (Berkeley & Berkeley, 1944), comb. n.
  Type locality: Dease Strait, northern Canadian Arctic, 82 m.
Sphaerephesia chilensis Fauchald, 1974
  Type locality: Seno and Estero de Reloncaví, Chile, intertidal to 80 m.
Sphaerephesia corrugata (Hartman & Fauchald, 1971), comb. n.
  Type locality: Off New England, USA, 400–1500 m.
Sphaerephesia discolis (Borowski, 1994), comb. n.
  Type locality: Peru Basin, 4152 m.
Sphaerephesia elegans (Hartman & Fauchald, 1971), comb. n.
  Type locality: Off Brazil, 3730–3783 m.
Sphaerephesia exmouthensis (Hartmann-Schröder, 1981), comb. n. Type locality: Exmouth, Western Australia, ? intertidal.
Sphaerephesia fauchaldi Kudenov, 1987
  Type locality: Florida, Gulf of Mexico, 54 m.
Sphaerephesia furca (Fauchald, 1974), comb. n.
  Type locality: Chile-Peru Trench, Peru, 1296–1317 m.
Sphaerephesia gesae Moreira & Parapar, 2011.
  Type locality: Bellingshausen Sea, Antarctica, 612–620 m.
Sphaerephesia hutchingsae Capa & Bakken, 2015
  Type locality: East of Malabar, Sydney, Australia, 82 m.
Sphaerephesia kitazatoi (Shimabukuro et al., 2017), comb. n.
  Type locality: São Paulo Ridge, South Atlantic, 4204 m.
Sphaerephesia laevis (Fauchald, 1974), comb. n.
  Type locality: Chile-Peru Trench, Peru, 1296–1317 m.
Sphaerephesia laureci (Desbruyères, 1980), comb. n.
  Type locality: Terrasse de Meriadzek, Bay of Biscay, 2325 m.
? Sphaerephesia longesetosa (Averincev, 1972), comb. n. (incertae sedis)
  Type locality: Antarctica, 1000 m.
Sphaerephesia longipalpa (Hartman & Fauchald, 1971), comb. n.
  Type locality: Off Bermuda, NW Atlantic, 1700 m.

Sphaerephesia longipapillata (Desbruyères, 1980), comb. n.
Type locality: Bay of Biscay, 4150 m.
Sphaerephesia longiparapodium (Katzmann, 1973), comb. n.
Type locality: Adriatic Sea, 20–60 m.
Sphaerephesia longisetis Fauchald, 1972
Type locality: Baja California, 957 m.
Sphaerephesia malayana (Augener, 1933), comb. n.
Type locality: Banda, Indonesia, unknown depth.
Sphaerephesia mamalaensis Magalhães, Bailey-Brock & Barrett, 2011
Type locality: Oahu Island, Hawaii, 68 m.
Sphaerephesia martinae (Desbruyères, 1980), comb. n.
Type locality: Banc Le Danois, Bay of Biscay, 1913 m.
Sphaerephesia parva (Ehlers, 1913), comb. n.
Type locality: Eastern Antarctica, 380–3423 m.
Sphaerephesia philippi (Fauvel, 1911), comb. n.
Type locality: Kara Sea, Artic Ocean, 220 m.
Sphaerephesia protuberanca (Böggemann, 2009), comb. n.
Type locality: Guinea Basin, South Atlantic, 5048–5443 m.
Sphaerephesia regularis Böggemann, 2009
Type locality: Guinea and Angola basins, South Atlantic, 5048–5051 m.
Sphaerephesia sibuetae (Desbruyères, 1980), comb. n.
Type locality: Banc Le Danois, Bay of Biscay, 1913 m.
Sphaerephesia similisetis Fauchald, 1972.
Type locality: Baja California, 461 m.
Sphaerephesia stellifer (Aguirrerezabalaga & Ceberio, 2005), comb. n.
Type locality: Capbreton Canyon, Bay of Biscay, 990–1040 m.
? Sphaerephesia simplex (Amoureux, Rulllier & Fishelson, 1978), comb. n.
Type locality: Gulf of Suez, 30 m.
Sphaerephesia triplicata (Fauchald, 1974), comb. n.
Type locality: off Durban, South Africa, 715–675 m.
Sphaerephesia vittori (Kudenov, 1987), comb. n.
Type locality: Gulf of Mexico, USA, 37–121 m.
Sphaerephesia wilsoni (Capa & Bakken, 2015), comb. n.
Type locality: Jervis Bay, Australia, 1–40 m.

Sphaerephesia artabrensis (Moreira & Parapar, 2007), comb. n.

Figs 5I, 14, 15A, B

Sphaerodoropsis artabrensis Moreira & Parapar, 2007: 374–377, figs 1–2, 3A; Moreira et al. 2011: 30.

Type locality. Ártabro Gulf, NW Iberian Peninsula, 43°40.192'N, 8°43.760'W, 209 m.

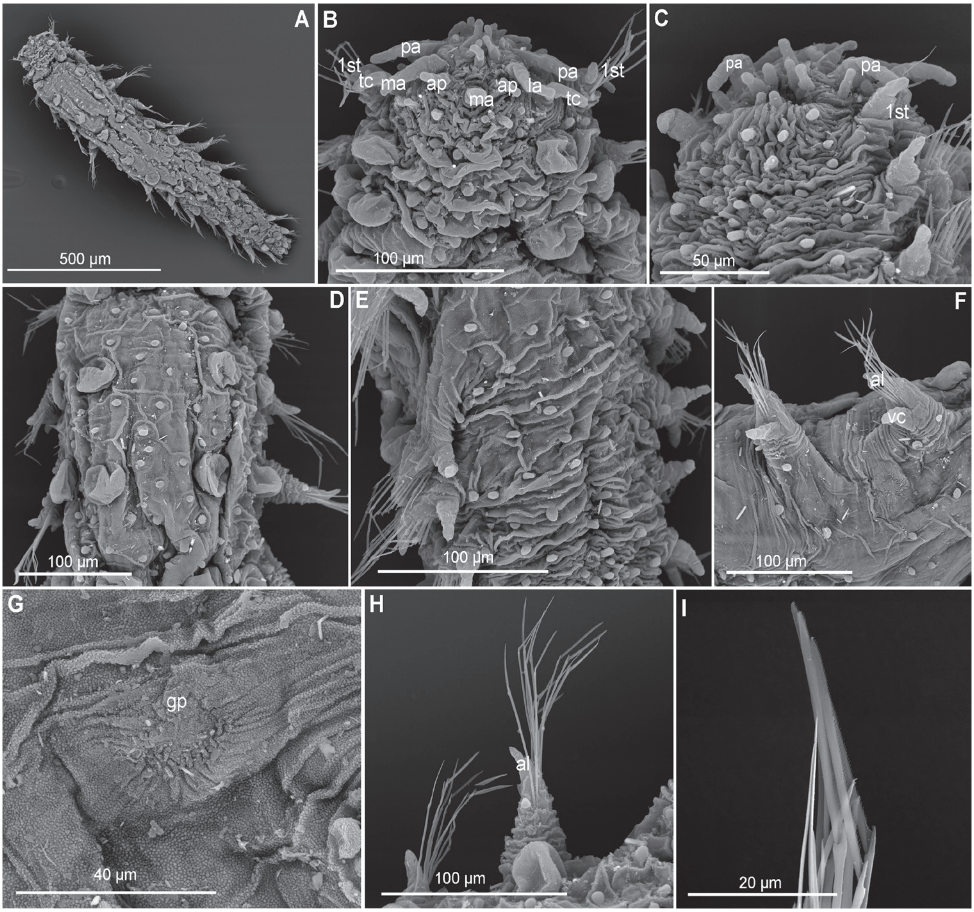

Figure 14. *Sphaerephesia artabrensis* comb. n., scanning electron micrographs (MNCN 16.01/18461). **A** Complete specimen, dorsal view **B** head and chaetiger 1, dorsal view **C** anterior end, ventral view **D** chaetigers 4 and 5, dorsal view **E** anterior chaetigers, ventral view **F** parapodia, chaetigers 7 and 8, ventral view (female) **G** genital opening, between chaetigers 7 and 8, detail (female) **H** parapodium, chaetiger 4, dorsal view **I** chaetal fascicle, mid-body chaetiger.

Material examined. Paratypes: (3 specs) SMF 16881/3, Golfo Ártabro, NW Spain, DIVA-Artabria I-02, sample EBS-250, 43°41.11'N, 08°44.23'W, 257 m, 14 Sep 2002.**Additional material** (119 specs): **NW Spain**: MNCN 16.01/13270 (40 specs), Golfo Ártabro, 43°40.25'N, 08°43.75'W, 197–207 m, 12 Sep 2003. MNCN 16.01/18461 (79 specs), 42°30.39'N, 09°19.52'W, 147 m, 17 Sep 2004.

Diagnosis. Body short and ellipsoid, up to 1.75 mm long. Palps and antennae smooth, lacking spurs or basal papillae. Median antenna shorter than palps and lateral antennae. Antenniform papillae present. Four longitudinal rows of macrotubercles in a single transverse row per segment. Macrotubercles sessile, small, spherical to pear shaped. Additional small spherical papillae on dorsum (arranged in four irregular transverse rows with ca. 20 papillae per segment) and ventral surfaces. Parapodia coni-

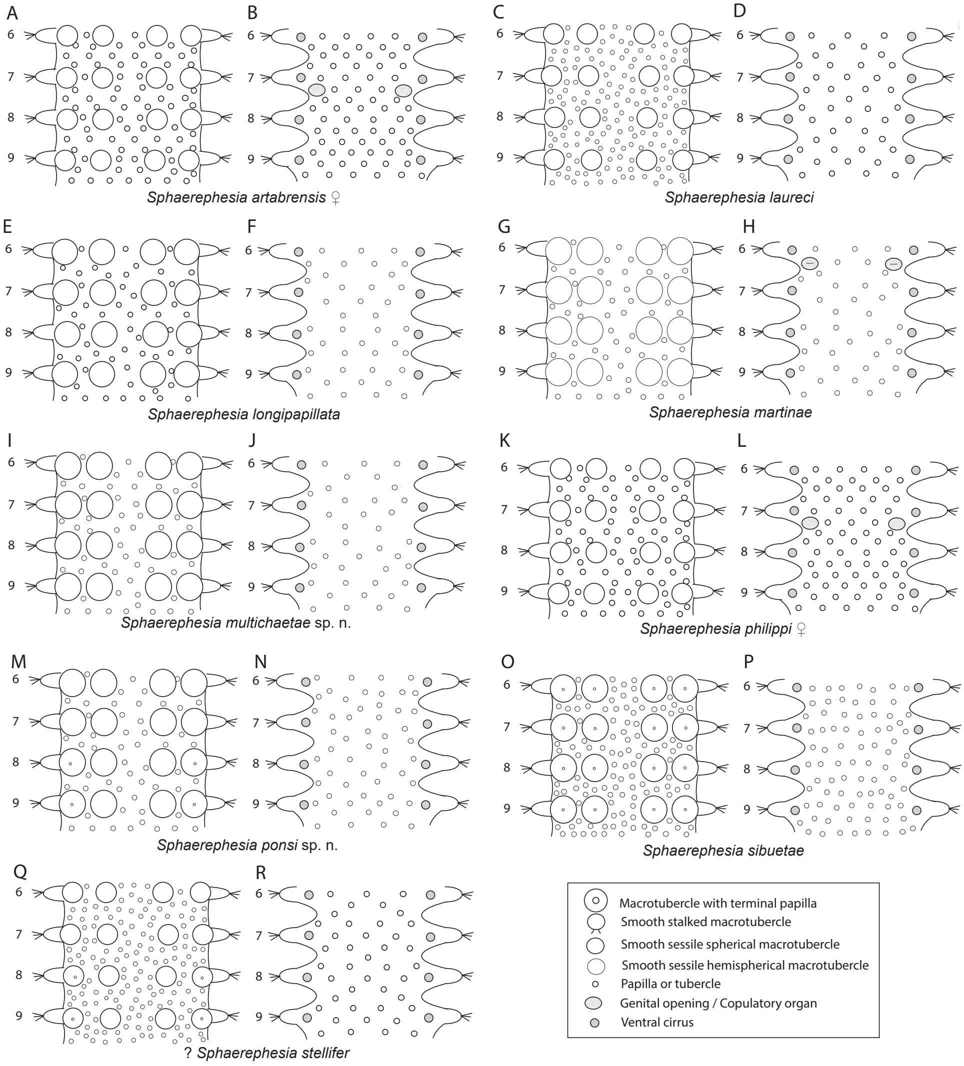

Figure 15. Stylized drawings of selected dorsal and ventral segments of species of *Sphaerephesia*, showing number and arrangement of epithelial tubercles and papillae. Epithelial papillae in Fig. 15E and F may not be accurate and the dorsal and ventral surfaces are covered by a thin layer of sediment.

cal, with 3–4 sub-equal papillae (1–2 ventral, one anterior, one dorsal). Acicular lobe from chaetiger 2. Ventral cirri digitiform as long as acicular lobe tip, or shorter. Compound chaetae with long blades (8–20 times as long as wide), unidentate and with serrated edge. Some live and fixed specimens have pigmented orange to brown macrotubercles. Some females with oocytes, without visible nucleus; genital pores observed between chaetiger 7 and 8.

Remarks. *Sphaerodoropsis artabrensis* was described based on the unique combination of the following morphological features: spherical to pear-shaped macrotubercles arranged in four longitudinal rows, 3–4 sub-equal parapodial papillae, chaetae with long blades (8–20 times as long as wide), showing gradation within each fascicle. The original description of this species is complete and re-examination of Iberian material, even under the SEM, did not provide additional information about morphological features, but allowed to verify some of the attributes. Palps and antennae are smooth, lacking spurs or basal papillae (Fig. 14B, C); median antenna shortest (Fig. 14B). Antenniform papillae present (Fig. 14B). Small spherical papillae over dorsum forming four irregular transverse rows with about 20 papillae per segment in addition to the four macrotubercles (Fig. 15A), similar number and arrangement on ventrum (Fig. 15B). Parapodia conical, with 3–4 sub-equal papillae (1–2 ventral, one anterior, one dorsal) (Figs 5I, 14E, F, H). Acicular lobe from chaetiger 1–2. Ventral cirri digitiform as long as acicular lobe tip, or shorter (Fig. 14F). Compound chaetae with long blades (8–20 times as long as wide), unidentate and with serrated edge (Fig. 14F, H–J). It is the first time that genital pores are reported in the species. These have only been observed in females, as a flat, porous area, between parapodia of chaetiger 7 and 8 (Fig. 14G).

This species is herein transferred to the genus *Sphaerephesia* due to the number and arrangement of dorsal macrotubercles in four longitudinal rows.

Specimens of *S. artabrensis* comb. n., resemble those assigned herein as *Sphaerephesia philippi* comb. n. from Nordic waters but they present subtle but consistent differences. Northern specimens are generally larger (Iberian specimens are up to 1.75 mm long and northern ones almost double in size), and bear a few more papillae in the prostomium, dorsum and parapodia (6–7 instead of the 3–4 in Iberian specimens). Specimens from northern localities present an acicular lobe from segment 1, instead of segment 2. Ventral cirri do not surpass the acicular lobe. It would be most interesting to confirm that these differences can be attributed to different lineages and not to the intraspecific range of variation of a species with a broad distribution from Spain to the Kara Sea. However, we have been unable to find specimens collected all along the coasts, and instead only in NW Spain and then from Skagerrak to the North. Moreover, extraction and amplification of DNA in specimens collected in the NW of Spain was unsuccessful and were therefore not included in analyses.

Distribution. NW Iberian Peninsula (Moreira and Parapar 2007, Moreira et al. 2011).

Habitat. Continental slope, in sandy-muddy sediments, 200–2200 m (Moreira and Parapar 2007, Moreira et al. 2011).

Sphaerephesia laureci **(Desbruyères, 1980), comb. n.**

Figs 5J, K, 15C, D, 16

Sphaerodoropsis laureci Desbruyères, 1980: 219, pl. 5A–C.

Type locality. Meriadzek, Terrace, Bay of Biscay, 47°31'N, 9°35'W, 2325 m.

Material examined. Holotype: MNHN TYPE 1286, Meriadzek, Terrace, Bay of Biscay, 47°31'N, 9°35'W, 2325 m.

Additional material. (2 specs) **Barents Sea:** NTNU-VM 73789, (2 specs, one on SEM stub), Hopenbanken, 75°21.940'N, 26°37.120'E, 191 m, 29 Apr 2008.

Diagnosis. Body cylindrical, with blunt anterior end, up to 4 mm long. Head appendages smooth, without spurs, median antenna shorter than other appendages. Antenniform papillae present. Dorsum with four longitudinal rows of macrotubercles in a single transverse row per segment, from segment 2. Macrotubercles sessile, spherical in anterior and pear-shaped in posterior segments. Additional small hemispherical papillae on dorsum, in four irregular transverse rows per segment, each segment with ca. 30 papillae. Ventrum with four slightly irregularly arranged transverse rows of papillae per segment, each segment with ca. 30–40 papillae. Parapodia digitiform from chaetiger 3, with ca. 12–14 rounded sub-equal papillae. Acicular lobe from segment 2. Ventral cirri digitiform surpassing acicular lobe tip. Compound chaetae with medium length blades (6–8 times as long as wide), showing slight gradation within fascicles.

Variation. For this species only the holotype is known. However, some specimens from Norway are herein considered as potentially belonging to the same species. There are, however, some differences between the holotype and the Norwegian specimens. Norwegian specimens lack antenniform papillae (Fig. 16A, B). Dorsal papillae (additional to the macrotubercles) are arranged in four transverse rows per segment, each with 14–18 papillae on mid-body segments (near half of those in the original description, Fig. 15C). Ventral papillae also about half as many as in the holotype (Figs 15D, 16C). Interestingly, the parapodia bear ca. 16–18 rounded sub-equal papillae (Figs 5J, 16D, E) instead of the 14 reported in the original description. The acicular lobe is present from segment 1 (instead of 2). Ventral cirri are digitiform and do not surpass the acicular lobe tip (Fig. 16D, E). Otherwise, the general aspect, number and relative length of prostomial appendages and chaetal morphology, is similar between specimens examined.

Remarks. Re-examination of the holotype resulted in a different interpretation of some morphological attributes with respect of the original description. We now state the prostomial appendages to be small and simple, instead of the bifurcated median antenna described originally. The dorsal macrotubercles are not invaginated and neither dorsoventrally flattened anymore in the preserved specimen. The number and arrangement of papillae is not clear from the original description. Approximately 12–14 spherical papillae randomly distributed over parapodial surface have been counted after re-examination (Fig. 5J).

Sphaerephesia laureci comb. n. is distinguished from other species in the genus by a unique combination of features: head appendages smooth, without papillae or spurs, dorsal macrotubercles spherical to pear-shaped, ca. 30 additional papillae, arranged in four irregular transverse rows both in dorsum and ventrum, 12–14 parapodial papillae and compound chaetae with blades up to eight times as long as wide.

Distribution. Bay of Biscay and the western Barents Sea (Desbruyères, 1980, present study).

Habitat. No details were provided in the original description.

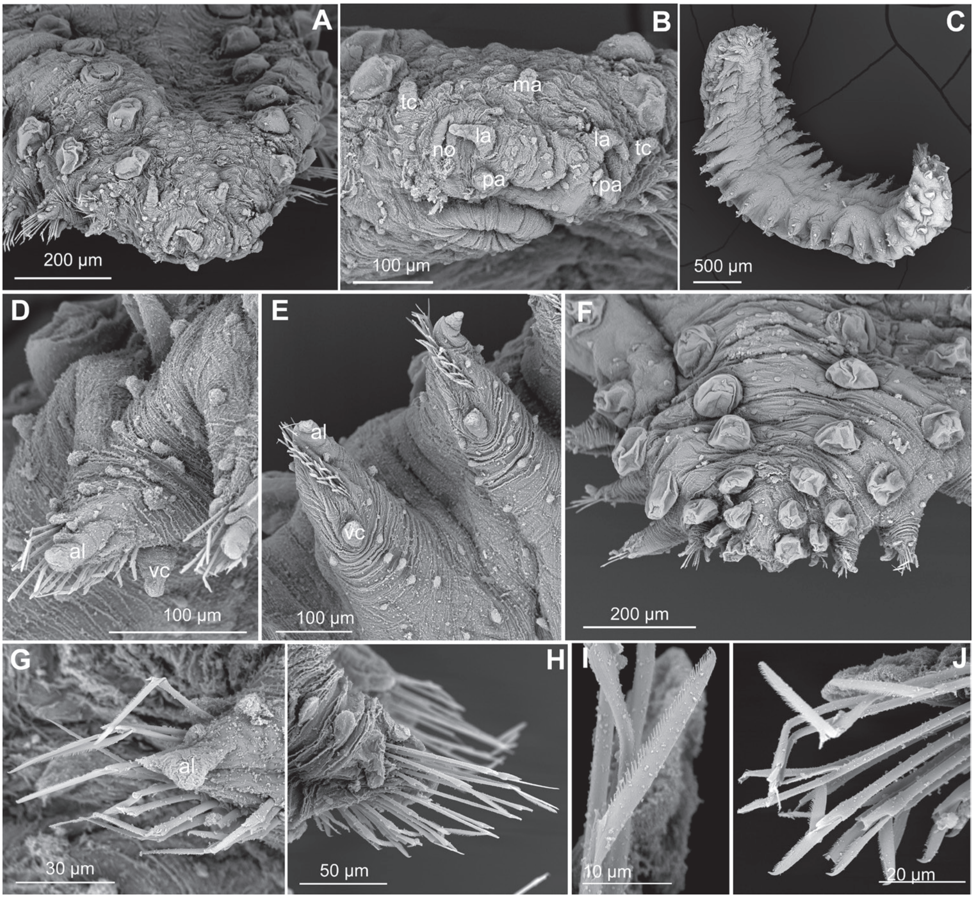

Figure 16. *Sphaerephesia* cf. *laureci* comb. n., scanning electron micrographs (NTNU-VM 73789). **A** Anterior end, frontal view **B** detail of head, frontal view **C** complete specimen, ventral view **D** anterior parapodium, anterior view **E** midbody parapodia ventral view **F** posterior end, dorsal view **G** chaetal bundle, first chaetiger **H** chaetae, midbody chaetiger **I** detail of chaeta **J** chaetae posterior chaetiger.

Sphaerephesia longipapillata (Desbruyères, 1980), comb. n.

Figs 5L, 15E, F

Type locality. Bay of Biscay, 47°31'N, 9°35'W, 4150 m.

Material examined. Holotype: MNHN TYPE 1283, Bay of Biscay, 47°31'N, 9°35'W, 4150 m.

Diagnosis. Body elongated, almost rounded in cross section, with blunt anterior end. Head appendages smooth, without spurs, median antenna shorter than other appendages. Antenniform papillae not conspicuous. Dorsum with four longitudinal rows macrotubercles in a single transverse row per segment, from segment 2. Macrotubercles large, sessile, spherical. Additional small spherical papillae on dorsum with unclear arrangement due to sediment covering epithelium. Ventrum with small hemispherical papillae. Parapodia digitiform from chaetiger 3, with 7–8 elongated papillae, larger papilla in dorso-distal position. Acicular lobe from segment 2. Ventral cirri digitiform surpassing acicular lobe tip. Approximately 20–25 compound chaetae with long blades (ca. 8–12 times as long as wide), showing slight gradation within fascicles.

Remarks. The holotype has large, turgid, and almost spherical dorsal macrotubercles, but it is covered by a thin layer of sediment that makes the assessment of the number and arrangement of the small epithelial papillae over the dorsal and ventral body surface difficult (therefore Fig. 15E and F not necessarily accurate). A feature not highlighted in the original description is the number of chaetae, that can reach up to 30 in some mid-body fascicles, all with relatively long blades, measuring 8–12 times as long as wide. *Sphaerephesia longipapillata* comb. n. is distinguished from other congeners in the combination of three features: elongated and almost cylindrical body, presence of large (occupying most of the dorsum surface) and spherical macrotubercles, not pear-shaped (Fig. 15E) and chaetae with medium-long blades (ca.ten times longer than wide). The parapodia and parapodial papillae in the holotype are stretched, but it could be due to muscular relaxation of this particular specimen. The sigmoid acicula could not be verified in the opaque specimen. Two other NE Atlantic *Sphaerephesia* species with similar body shape and chaetae are *S. philippi* comb. n. and *S. artabrensis* comb. n., but both present pear-shaped macrotubercles in at least posterior chaetigers. Moreover, *S. artabrensis* comb. n. has less parapodial papillae (3–4 on each parapodium). *Sphaerephesia longipapillata* comb. n. was also characterised by the length of a dorso-distal parapodial papilla, a feature that could vary after fixation (Helm and Capa 2015). However, the dorso-distal papilla is longer than the others in the material examined, and could be a distinct diagnostic feature together with the high number of chaetae per fascicle.

Distribution. Only known from type locality.

Habitat. No details were provided in the original description.

Sphaerephesia martinae (Desbruyères, 1980), comb. n.

Figs 5M, 15G, H, 17

Type locality. Banc Le Danois, Bay of Biscay, 44°05.2'N, 4°19.4'W, 1913 m.

Material examined. Holotype: Banc Le Danois, Bay of Biscay, 44°05.2'N, 4°19.4'W, 1913 m.

Additional material. (18 specs) **Argentinian Basin**: SMF DZMB HH 21466 (2 specs, 1 spec. used for DNA sequencing, SPH021), 036°00.61'S 049°01.54'W, 4607 m, 16 Jul 2009; **Iceland**: SMF 25283 (1 spec.), South Iceland, Iceland Basin, 60°02.73'N, 021°28.06'W, 2749 m, 28 Aug 2011; SMF 25286 (8 specs, 2 on SEM stub), South Iceland, 60°02.73'N, 4 021°28.06'W, 2749 m, 28 Aug 2011; SMF 23911 (1 spec., DNA SPH063.), South Iceland, 60°02.73'N, 021°28.06'W, 2749 m, 28 Aug 2011; SMF 23910 (1 spec. used for DNA sequencing, SPH048), Iceland, 036°00.61'S 049°01.54'W, 2749 m, 7 Sep 2011; SMF DZMB HH 31236 (1 spec. on SEM stub), South Iceland, Iceland Basin, 60°21.48'N, 018°08.24'W, 2567 m, 30 Aug 2011; SMF 25285 (2 specs) South Iceland, Iceland Basin, 62°33.10'N, 020°23.71'W, 1384 m, 2 Sep 2011. **Barents Sea**: NTNU-VM 68189 (1 spec. used for DNA sequencing, SPH 293), Finnmark, 72°18.588'N, 32°20.478'E, 313 m, 4 Aug 2013.

Diagnosis. Body ellipsoid, with convex dorsum and slightly flattened dorsoventrally, up to 3 mm long. Head appendages smooth, without spurs, median antenna slightly shorter than other appendages. Antenniform papillae shorter than lateral antennae. Dorsum with four longitudinal rows of large, hemispherical sessile macrotubercles in a single transverse row per segment, from segment 2. Additional papillae on dorsum arranged in four irregular transverse rows. Ventrum with three transverse rows of papillae similar in shape and size to dorsal. Parapodia short and conical, with 2–3 small, rounded papillae: one on each anterior and posterior surfaces, one in the ventrum of some parapodia. Acicular lobe from segment 1. Ventral cirri digitiform reaching acicular lobe tip. Approx. 7–10 compound chaetae with medium length blades (ca. 5–6 times as long as wide); unidentate and with fine spinulation along its margin. Several paratypes were described as possessing orange macrotubercles (Desbruyères, 1980). One pair of genital structures between the base of parapodia 6 and 7.

Re-description of holotype. *Measurements and general morphology.* Holotype 15 chaetigers, 2.9 mm long, 0.5 mm maximum width. Body almost cylindrical, slightly more rounded anteriorly and tapering posteriorly (Fig. 17A). Segmentation not distinct, pigmentation absent in preserved material examined.

Head. Prostomium fused to peristomium (Fig. 17B). Palps and lateral antennae digitiform, slightly wider at base, similar in shape and size. Median antenna digitiform, shorter than other appendages. Antenniform papillae present, slightly larger than other head papillae. Head with more than ten hemispherical papillae. Tentacular cirri digitiform, half of the length of lateral antennae (Fig. 17B).

Tubercles. Dorsal macrotubercles, hemispherical, wide and low, sessile and smooth, arranged in four rows, occupying most of dorsum; one transverse row per segment, except for the first segment where only two are present (Figs 15G, 17A). Dorsal papillae low and rounded, distributed in four transverse rows approximately, more numerous and conspicuous in anterior segments (Fig. 17C). Ventral papillae similar in shape and size to dorsal, arranged in three transverse rows per segment (Figs 15H, 17D).

Parapodia. Parapodia short and wrinkled, twice as long as wide, conical in shape. Ventral cirri conical, shorter than the width of parapodia. Acicular lobe, shorter than ventral cirri, present from first chaetiger (Fig. 17A). Two or three small, rounded papillae: one on each anterior and posterior surfaces, one in the ventrum of some parapodia (Figs 5M, 17E–G).

Chaetae. Seven to ten chaetae per parapodia. All chaetae compound medium in length (5–6 times as long as wide), similar within and between parapodia, unidentate and with fine serrated edge (Fig. 17E, G, I, J).

Pygidium. Two globular cirri, similar to dorsal macrotubercles and two ventral small cirri (perhaps the ventral cirri of last segment). Median papilla not observed.

Internal features. Pigmented nuchal organs or eyes not seen. Pharynx not observed.

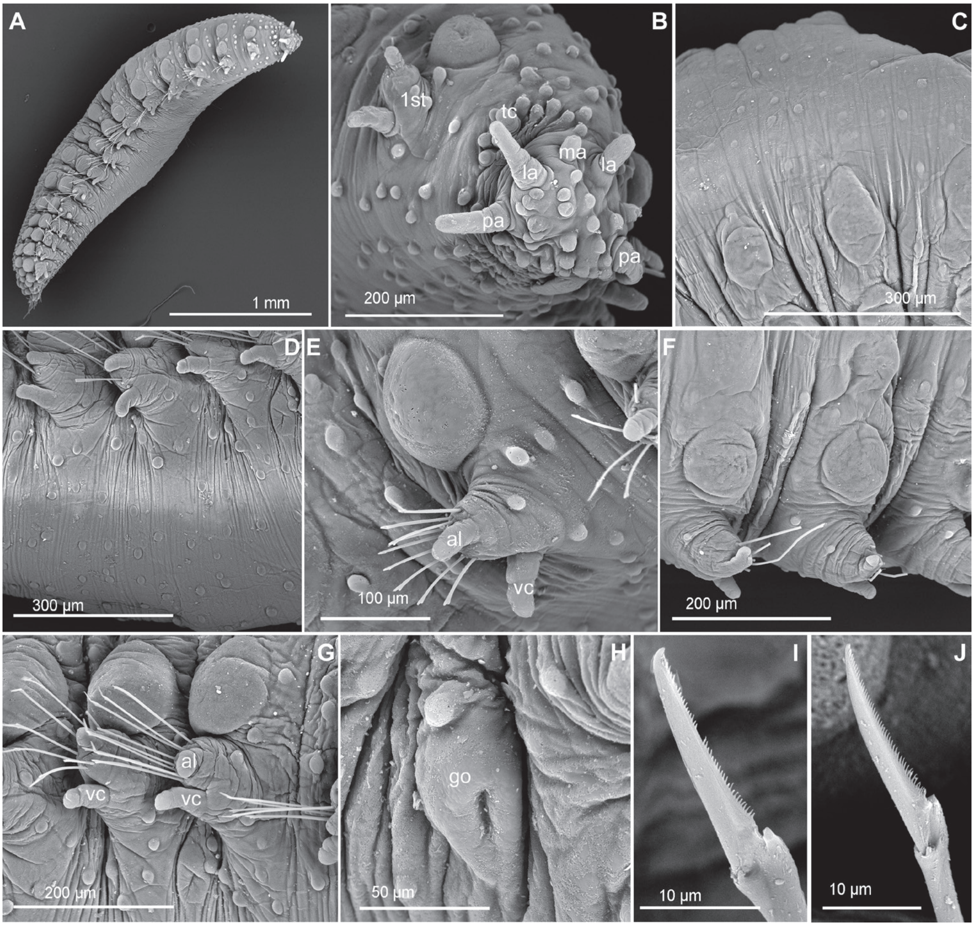

Figure 17. *Sphaerephesia martinae* comb. n., scanning electron micrographs (SMF DZMB HH 31236 and SMF 25286). **A** Complete specimen, lateral view **B** head, frontal view **C** dorsal epithelial tubercles, mid-chaetigers **D** mid-body chaetigers, ventral view **E** parapodium and macrotubercle third chaetiger, anterior view **F** chaetiger mid-body segment, dorsal view **G** chaetiger mid-body segment, ventral view **H** genital opening **I, J** chaetae mid-body segments.

Reproductive features. Sexual structures, genital openings or gametes not observed in holotype, paratypes or additional material.

Variation. Studied specimens measured 2–3 mm long. In all specimens macrotubercles are hemispherical. Some variation regarding the number of parapodial papillae has been observed. Most specimens present one hemispherical papilla on the anterior surface and a similar one on the posterior side, but a smaller ventral papilla may be also present. One pair of genital openings between the base of parapodia 6 and 7 in one specimen (SMF DZMB HH 31236, Fig. 17H).

Remarks. The shape of macrotubercles is remarkable: hemispherical, low and wide, with a rounded and smooth surface and no papillae. This feature, together with the presence of almost inconspicuous additional epithelial papillae is one of its main diagnostic features (Desbruyères, 1980), that distinguishes this species from other congeners.

The invaginations described behind the lateral antennae in the original description, are here considered as the openings of the nuchal organs. The parapodial papillae were not described in the original description, and at least one hemispherical papilla was observed in the anterior parapodial surface, from chaetiger 6 in the holotype, and additional material present up to three parapodial papillae. Holotype is full of gametes but sexual structures or genital openings were not detected. Sexual structures are described in this species for the first time in additional material from Iceland.

Distribution. The species is here newly reported for Iceland and the Barents Sea. It had previously been reported in Bay of Biscay (Desbruyères, 1980).

Habitat. Sediments from 30 to 2750 m (Desbruyères, 1980, present study).

Sphaerephesia multichaeta **Capa, Moreira & Parapar, sp. n.**

http://zoobank.org/416D3A0B-25AE-48CC-B68B-0A2B917142F4
Figs 5N, 15I, J, 18, 19

Type locality. Borgenfjorden, Trondheimsfjord, 25 m.

Material examined. Holotype: NTNU VM 24856, Norway, Trondheimsfjord, Borgenfjorden, 63°53'N, 11°20'E, 25 m, 14 July 1970. **Paratypes** (10 specs): **Norwegian Sea**, Trondheimsfjord, Borgenfjorden NTNU-VM 24809, 63°53'N11°20'E, 10 m, 04 May 1971 (1 spec. on SEM stub); NTNU-VM 24810 (2 specs, 1 on SEM stub), 10 m, 11 Aug 1970; NTNU-VM 24852 (1 spec.), 10 m, 02 Jun 1971; NTNU-VM 24854 (1 spec.), 20 m, 11 Aug 1970; NTNU-VM 24851 (1 spec.), 10 m, 13 May 1970; NTNU-VM 24853 (1 spec.), 15 m, 06 Oct 1970; NTNU-VM 24855 (1 spec.), 20 m, 06 Oct 1970; NTNU-VM 24857 (1 spec.), 25 m, 16 Jun 1970; NTNU-VM 24858 (1 spec.), 25 m, 09 Feb 1971; NTNU-VM 24859 (1 spec.), 25 m, 02 June1971.

Additional material. (1 spec.) **Skagerrak** ZMH P13351, 58°07'N, 10°34'E, 196m, (1 spec. on SEM stub).

Diagnosis. Body ellipsoid, with convex dorsum and slightly flattened dorsoventrally, up to 1 mm long. Palps and antennae smooth, lacking spurs. Four longitudinal rows of dorsal macrotubercles, in a single transverse row per segment. Macrotubercles sessile, spherical to pear-shaped. Additional minute spherical papillae scattered on dorsum (approx. seven transverse rows with ca. 100 low papillae per segment), often inconspicuous. Ventrum with even smaller papillae in four transverse rows per segment, often inconspicuous. Parapodia with 20–40 spherical papillae. Acicular lobe from segment 1, small and rounded. Compound chaetae, numerous (up to 40 per fascicle), with blades slightly decreasing in length dorso-ventrally (3–8 times their width), unidentate, with finely serrated edge.

Description. *Measurements and general morphology.* Holotype with ellipsoid body, 0.7 mm long, 0.1 mm wide and with 27 segments; with blunt ends, with a convex dorsum and flattened ventrum. Segmentation not conspicuous. Pale, with brownish granules in some macrotubercles, in fixed material.

Head. Head fused to first chaetiger (Fig. 18A–C). Palps and lateral antennae conical, 2–3 times longer than wide, wrinkled, and lacking spurs or basal papilla (Fig. 18A–C). Median antenna conical, slightly shorter than lateral antennae (Fig. 18A–C). Antenniform papillae absent (Fig. 18A–C). Head papillae rounded, apparently randomly arranged. Tentacular cirri conical, similar to lateral antenna (Fig. 18A–C).

Tubercles. Medium-sized dorsal macrotubercles arranged in four longitudinal rows, one transverse row per segment, with exception of first chaetiger with only two macrotubercles (Fig. 18A–C). Macrotubercles sessile, spherical and smooth in anterior segments, and pear-shaped in posterior segments (Fig. 18A–E). Distance between dorsalmost rows is larger than these to lateralmost longitudinal rows. Additional dorsal papillae, low, rounded, arranged in approximately seven irregular transverse rows per segment along dorsal surface (Figs 15I, 18D), and in four transverse rows per segment in ventrum (Figs 15J, 18F). Papillae are not conspicuous in all segments; consequently epithelium seems smooth in some parts of the body.

Parapodia. Parapodia subtriangular, with wide dorso-ventral base as long as wide at mid-body segments (Figs 18D–H, 19A). Ventral cirri conical, small, not protruding from parapodia (Fig. 18H). Acicular lobe from chaetiger 1. Numerous (ca. 20 in mid-chaetigers) small and spherical papillae distributed randomly over parapodial surfaces (Fig. 5N).

Chaetae. All chaetae compound, with unidentate and finely serrated blades. First chaetiger with blades 7–9 times longer than wide. Midbody chaetigers with blades ranging 3–6 times longer than wide within each parapodia. Number of chaetae from 11–13 in first segment to 25–30 in mid-body segments (Figs 18G–H, 19B–D). One straight acicula per parapodia.

Pygidium. A pair of piriform anal cirri, similar to posterior macrotubercles and digitiform medio-ventral anal papilla (Fig. 18D, E).

Internal features. Pharynx slightly protruded though mouth in some specimens. Pharynx and internal organs not discernible.

Reproductive features. Sexual structures or genital openings not observed. Preserved specimens opaque and gametes not detected.

Variation. Size range of material examined: 0.6–0.9 mm long, 0.08–0.15 mm wide, with 21–30 chaetigers. The holotype is somehow more inflated and elongated than the paratypes. These are more flattened dorso-ventrally and bodies seem to be more ellipsoid. This could be due to body collapse or perhaps the holotype is inflated from preservation. Head appendages are small and conical in all specimens examined; antenniform papillae not observed. Paratypes are homogenous in the general shape of the body, presence of large parapodia, small ventral cirri and presence of numerous, medium length blade falcigers. They differ in the number of epithelial papillae observed, in part probably due to the different conditions of the epithelium. We suspect the body and parapodia bear numerous small spherical papillae but these are only conspicuous in well-preserved specimens, otherwise they look almost smooth. Nuchal organs pits observed in several specimens (e.g., Fig. 18C). Sexual structures not seen.

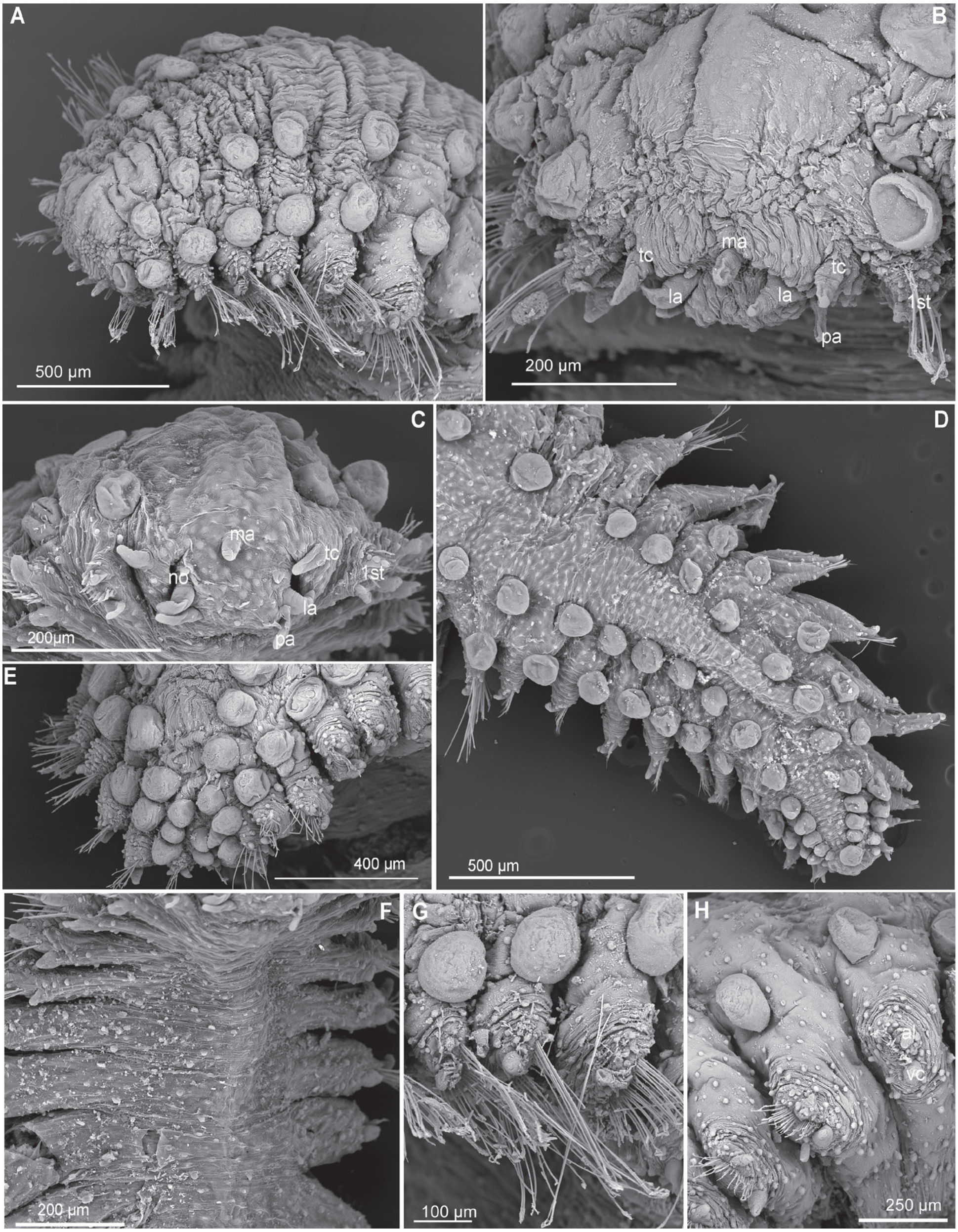

Figure 18. *Sphaerephesia multichaeta* sp. n. (NTNU-VM24809, ZMH P13351), scanning electron micrographs. **A** Anterior end, side view (NTNU-VM 24809) **B** head, frontal view (NTNU-VM 24809) **C** head, antero-ventral view (ZMH P13351) **D** posterior end, dorsal view (ZMH P13351) **E** posterior end, dorsal view (NTNU-VM 24809) **F** ventrum, showing arrangement of ventral papillae (ZMH P13351) **G** Chaetigers 4–6, antero-dorsal view (NTNU-VM 24809) **H** mid-body parapodia, lateral view (NTNU-VM 24809).

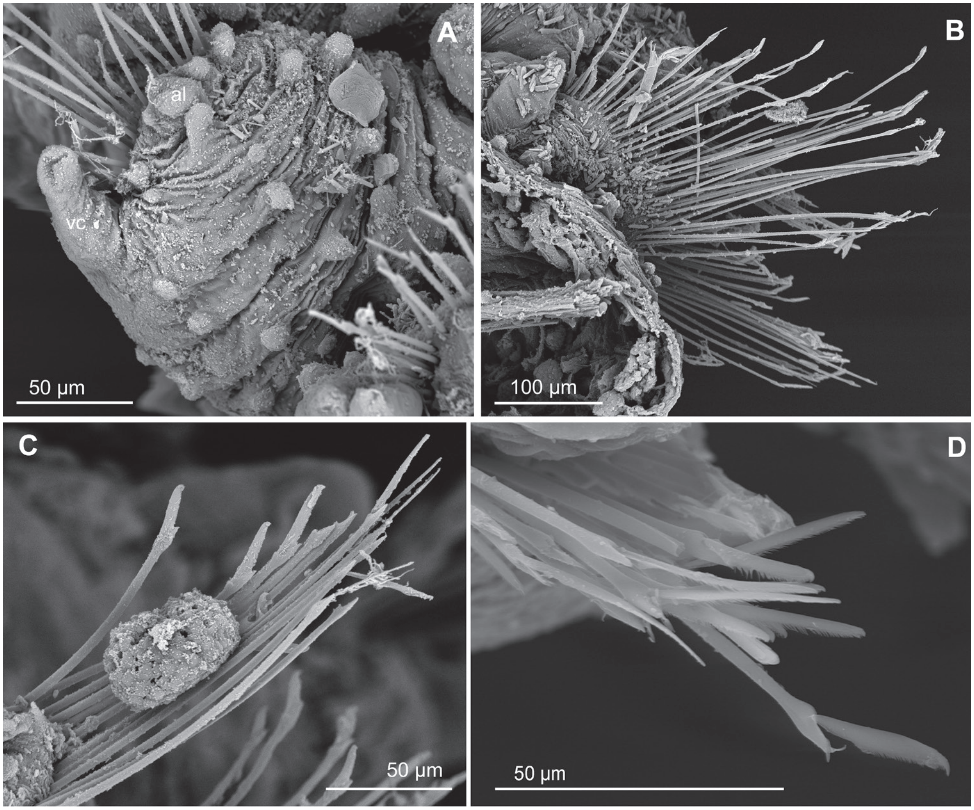

Figure 19. *Sphaerephesia multichaeta* sp. n. (NTNU-VM 24809, NTNU-VM 24810), scanning electron micrographs. **A** posterior parapodia, anterior view (VM 24809) **B** complete chaetal fascicle, mid-body chaetiger (VM 24809) **C** chaetiger 1, anterior view (NTNU-VM 24809) **D** chaetae, mid-body chaetiger (NTNU-VM 24810).

Etymology. The specific epithet, *multichaeta* (masculine), refers to the extraordinary number (*multi*) of bristles (*chaetae*, Greek origin) present in the fascicles of, at least, some specimens.

Remarks. *Sphaerephesia multichaeta* sp. n. belongs to the group of spherodororids with four longitudinal rows of dorsal and macrotubercles (i.e., *Sphaerephesia* after the present study). It is characterised by a unique combination of features: macrotubercles at least in posterior segments are pear-shaped, parapodia bear a great number of papillae (20–40) and chaetae (20–40). Only *Sphaerephesia sibuetae* and *S. similisetis* have been reported with 20–25 chaetae per fascicle (Fauchald 1972, Desbruyères 1980, Moreira et al. 2011). Likewise, also these two species have been reported with 20–30 parapodial papillae (Fauchald 1972, Desbruyères 1980, Moreira et al. 2011), but these numbers do not reach those accounted in the new species. *Sphaerephesia multichaeta* sp. n. is distinguished from these two congeners in the chaetal morphology (with blades up to eight times as long as wide) while *S. sibuetae* and *S. similisetis* have longer blades (7–13 and 20–25 times as long as wide, respectively).

Distribution. Most specimens were collected in the Trondheimsfjord, but also from Skagerrak.

Habitat. Habitat soft bottom with mud, 10–25 m deep.

Sphaerephesia philippi (Fauvel, 1911), comb. n.

Figs 5O, 8D, 15K, L, 20

Sphaerodorum philippi Fauvel, 1911: 19–21, fig. 16–20 (not *S. philippi* Hartmann-Schröder, 1971).

Type locality. Kara Sea, Russia, 71°32'N, 57°10'E, 220–0 m.

Material examined. (ca 1480 specs) **Greenland Sea**: ZMBN 127275 (~25 spec.), 68°53.5'N, 14°14.3'W, 1588 m, 15 Mar 1984; ZMBN 127287 (15 spec.), Jan Mayen, 70°48.6'N, 09°43.7'W, 886 m, 27 Jul 1986; ZMBN 127295 (4 spec.), 69°57.3'N, 18°08.9'W, 1618 m, 12 Jun 1987; NTNU-VM 32347 (2 spec.), Jan Mayen, 70°36.19'N, 9°20.72'W, 31 m, 17 Sep 1999; NTNU-VM 32348 (15 spec.), Jan Mayen, 71°06.41'N, 9°35.26'W, 514 m, 15 Sep 1999; NTNU-VM 32349 (35 spec.), Jan Mayen, 70°45.07'N, 7°57.74'W, 771 m, 16 Sep 1999; NTNU-VM 32350 (496 spec., 1 on SEM), Jan Mayen, 70°38.87'N, 9°22.33'W, 599 m, 17 Sep 1999; SMF 24843 (1 spec. for DNA sequencing, SPH052), East Greenland, Denmark Strait, 67°12.81'N, 026°14.50'W, 696.9 m, 14 Sep 2011; SMF 25287 (7 specs), East Greenland, Denmark strait, 67°50.79'N, 023°41.76'W, 1248 m, 15 Sep 2011; SMF 25288DZMB-HH 30452 (3 specs), East Greenland, Denmark Strait, 67°50.79'N, 023°41.76'W, 1248 m, 15 Sep 2011; SMF 25289 (4 specs), East Greenland, Denmark Strait, 67°50.790'N 23°41.760'W, 1248 m, 15 Sep 2011; SMF 25290 (1 spec.), East Greenland, Denmark Strait 67°38.77'N, 026°44.78'W, 320 m, 14 Sep 2011; **Iceland**: SMF 25291 (6 specs), East Iceland, Norwegian Sea, 66°18.06'N, 012°22.38'W, 730,8m¸ 22 Sep 2011; SMF 25292 (1 specs), East Iceland, 66°18.06'N, 012°22.38'W, 730,8m¸ 22 Sep 2011; SMF 23903 (1 for DNA sequencing), North East Iceland, 69°6.66'N, 9°55.02'W, 2202 m , 17 Sep 2011; SMF 25293 (3 specs), North East Iceland, 69°6.66'N, 9°55.02'W, 2202 m , 17 Sep 2011; SMF 23903 (1 spec. For DNA sequencing, SPH061), North East Iceland, 69°6.66'N, 9°55.02'W, 2202 m , 17 Sep 2011; SMF 25294; (2 specs), South Iceland, Iceland Basin, 62°33.50'N, 020°21.18'W, 1392m, 2 Sep 2011; **Barents Sea**: ZMBN 127298 (5 spec.), Finnmark, 71°16.53'N, 27°0.94'E, 276 m, 16 Apr 2011; ZMBN 127305 (6 spec.), Finnmark, 71°11.415'N, 32°14.991'E, 226 m, 10 Aug 2013; ZMBN 127323 (10 spec.), Finnmark, 70°17.79'N, 31°18.83'E, 217 m, 18 Aug 2013; **Norwegian Sea**: ZMBN 127299 (10 spec.), Nordland, 67°48.276'N, 9°41.126'E, 823 m, 22 Sep 2011; ZMBN 127302 (18 spec.), Nordland, 67°57.337'N, 9°35.556'E, 1315 m, 6 May 2012; ZMBN 127301 (18 spec.), Nordland, 68°3.937'N, 9°28.129'E, 1712 m, 6 May 2012; ZMBN 127304 (24 spec.), Nordland, 67°17.06'N, 8°7.982'E, 1117 m, 8 May 2012; ZMBN 129496 (1 spec. on SEM stub), 67°17.0604'N 8°7.9824'E, 1117 m, 8 May 2012; ZMBN 127264 (~30 spec.) 67°47.0'N, 07°43.9'E, 2025 m, 03

Jun 1981; ZMBN 127265 (~40 spec.), 65°39.5'N, 02°38.0'E, 2019 m, 07Jun 1981; ZMBN 127267 (~50 spec.), 63°35.6'N, 00°23.0'E, 2090 m, 15 Aug 1981; ZMBN 127266 (2 spec.), 64°16.9'N, 00°11.7'W, 2630 m, 14 Aug 1981; ZMBN 127268 (3 spec.), 62°29.5'N, 01°43.3'E, 604 m, 21 Jan 1982; ZMBN 127269 (10 spec.), 63°12.8'N, 03°07.3'E, 1003 m, 23 Aug 1982; ZMBN 127270 (6 spec.) 62°59.1'N, 03°13.1'E, 804 m, 27 Nov 1982; ZMBN 127272 (1 spec.), 64°26.1'N, 11°10.2'W, 400 m, 07 Jun 1983; ZMBN 127274 (2 spec.), 68°42.4'N, 10°29.5'W 2168 m, 13 Mar 1984; ZMBN 127276 (~100 spec.), 67°39.5'N, 11°36.7'W, 1811 m, 16 Mar 1984; ZMBN 127277 (~50 spec.), 62°35.1'N, 1°47.6'E, 656 m, 23 May 1984; ZMBN 127278 (1 spec.), 62°35.4'N, 01°47.7'E, 650 m, 23 May 1984; ZMBN 127279 (~25 spec.), 62°33.2'N, 01°49.2'E, 625 m, 21 Nov 1984; ZMBN 127280 (~50 spec.), 62°31.5'N, 01°26.6'E, 701 m, 08 Jan 1985; ZMBN 127281 (2 spec.), 63°45.2'N, 00°08.0'W, 2304 m, 11 Jan 1985 ; ZMBN 127282 (~20 spec.), 63°24.4'N, 00°20.3'E, 1880 m, 12 Jan 1985; ZMBN 127283 (~50 spec.), 63°02.9'N, 00°47.8'E, 1293 m, 12 Jan 1985; ZMBN 127284 (1 spec.), Faroes, 62°44.7'N, 06°46.9'W, 2538 m, 24 Jul 1986; ZMBN 127285 (~100 spec.), 69°01.4'N, 08°24.6'W, 879 m, 25 Jul 1986; ZMBN 129497 (1 spec. on SEM stub), 1243m, 70°40.68'N 7°37.86'W, 27. Jul 1986, ZMBN 127286 (1 spec.), 69°36.4'N, 09°54.6'W, 2212 m, 26 Jul 1986; ZMBN 127289 (2 spec.), 70°26.2'N, 06°31.8'W, 2525 m, 28 Jul 1986; ZMBN 127290 (~20 spec.), 62°36.6'N, 01°34.4'E, 654 m, 15 Aug 1986; ZMBN 127292 (~25 spec.), 63°42.7'N, 00°09.7'W, 2259 m, 17 Aug 1986; ZMBN 127293 (~25 spec.), 63°35.1'N, 00°06.0'W, 2150 m, 17 Aug 1986; ZMBN 127294 (~50 spec.), 62°41.5'N, 01°45.4'E, 750 m, 17 Aug 1986; ZMBN 127291 (7 spec.), 63°28.8'N, 00°14.5'E, 1957 m, 16 Aug 1986; ZMBN 127306 (3 spec.) Aktivneset, 62°44.89'N, 3°1.98'E, 569 m, 24.09.2013; ZMBN 127314 (~20 spec.), 63°2.23'N, 4°41.34'E, 760 m, 30 Sep 2013.

Diagnosis. Body ellipsoid, flattened dorsoventrally, up to 3 mm long. Body unpigmented; orange macrotubercles in live specimens, or brownish in fixed material. Head appendages smooth and digitiform. Tentacular cirri smaller than prostomial appendages. Dorsum with four longitudinal rows of large, spherical or pear-shaped sessile macrotubercles in a single transverse row per segment, from segment 2. Additional papillae on dorsum. First parapodia short and digitiform, with two rounded papillae on dorsal surface. Acicular lobe from segment 1. Eight to ten parapodial papillae. Ventral cirri digitiform shorter than acicular lobe tip. About eight compound chaetae with medium length blades (ca. ten times as long as wide); unidentate.

Description of specimens from the Nordic Seas. *Measurements and general morphology.* Ellipsoid body, flattened dorsoventrally, up to 2.8 mm long, mm 0.6 wide and with up to 20 chaetigers. Segmentation not conspicuous. Live specimen with some orange granules in macrotubercles (Fig. 8D, E), brownish in fixed material.

Head. Head fused to first chaetiger (Figs 8D, 20A). Palps and lateral antennae conical, near five times longer than wide, lacking spurs or basal papilla (Fig. 20A–C). Median antenna conical, shorter than lateral antennae (Fig. 20A–C). Antenniform papillae present (Fig. 20B). Approximately 8–10 papillae confined by prostomial appendages. Tentacular cirri digitiform, similar to lateral antenna (Fig. 20B).

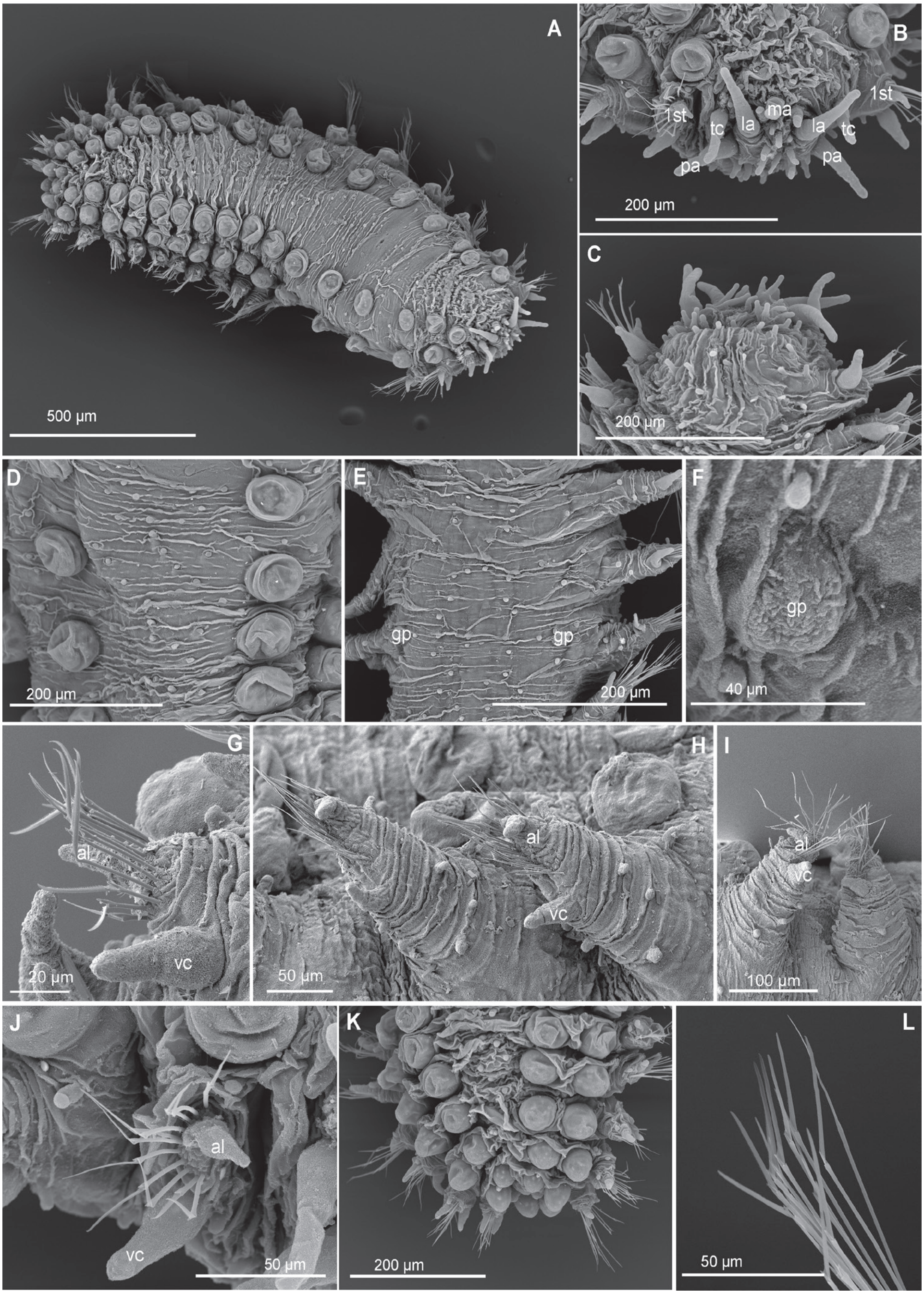

Figure 20. *Sphaerephesia philippi* (ZMBN 129496; **G–I** ZMBN 129497), scanning electron micrographs. **A** Complete specimen, dorsal view **B** head, frontal view **C** head, antero-ventral view **D** mid-body chaetigers, dorsal view **E** mid-body chaetigers, ventral view **F** genital pores, between parapodia of chaetiger 7 and 8 **G** parapodium, chaetiger 1, posterior view **H** mid-body parapodia, anterior view **I** mid-body parapodia, lateral view **J** chaetal fascicle, chaetiger 1 **K** posterior end, dorsal view **L** chaetae, mid-body chaetiger, detail.

Tubercles. Medium-sized dorsal macrotubercles arranged in four longitudinal rows, one transverse row per segment, with exception of first chaetiger with only two macrotubercles (Figs 8D, E, 20A, B). Macrotubercles sessile, spherical and smooth in anterior segments, and pear-shaped in posterior segments (Figs 8D, 20A). Distance between dorsalmost rows is larger than these to lateralmost longitudinal rows (Figs 8D, 20A). Additional dorsal papillae, spherical, arranged in about four irregular transverse rows per segment along dorsal surface, with ca. 20 papillae per segment, and in four transverse rows per segment in ventrum (Fig. 15K, L, 20D, E).

Parapodia. Parapodia conical, with acicular lobe from chaetiger 1 (Fig. 20G). Ventral cirri conical, not protruding from parapodia. Six or seven spherical parapodial papillae (two in anterior surface, two in ventral side, two in posterior side and one or two dorsally; Fig. 5O)

Chaetae. All chaetae compound, with unidentate and finely serrated blades 8–20 times longer than wide. Up to 18–20 chaetae per fascicle (Fig. 20G, J, L). One straight acicula per parapodium.

Pygidium. A pair of piriform anal cirri, similar to posterior macrotubercles and digitiform medio-ventral anal papilla.

Internal features. Eyes not seen. Muscular pharynx not evident in live and fixed material (e.g., Fig. 8D).

Reproductive features. The holotype seems to be a female with some eggs inside the coelom (Fauvel 1911). Some females with oocytes (Fig. 8D); genital openings observed in females, between chaetigers 7 and 8 (Fig. 20 E, F).

Remarks. The single type specimen of this species (in the Museum natural d'Histoire naturelle in Paris) is apparently lost, and the original description and drawings (Fauvel 1911) are simple and inadequate to describe all characters. The median antenna is not mentioned by Fauvel (1911), indicating it is probably small and similar to other prostomial papillae. The shape and number of dorsal and epithelial papillae are not cited either. The number of parapodial papillae is not explicitly mentioned and has been interpreted differently in the literature (e.g., Fauchald 1974, Aguado and Rouse 2006, Shimabukuro et al. 2017). There is indication of *S. philippi* comb. n. bearing 10–11 parapodial papillae (Fauchald 1974), or 20–22 parapodial papillae (e.g., Aguado and Rouse 2006, Shimabukuro et al. 2017). The first chaetigers bear at least two spherical dorsal papillae. According to original drawings, mid-body segments bear four dorsal parapodial papillae, and four are visible from the ventral side (Fauvel 1911, Figs 18, 19). Ventral cirri do not protrude from the acicular lobe, although both are well developed.

Several of the specimens found and re-examined from museum collections had previously been identified as belonging to this species. However, they were misidentified in several cases, as there are other similar species in the North East Atlantic (as reported herein) and, as mentioned, different interpretation of the parapodial papillae and chaetal morphology according to previous records. The description and drawings by Hartmann-Schröder (1971) do not correspond to this species since the original drawings of *S. philippi* comb. n. indicate that blades of chaetae are long (Fauvel 1911: Fig. 16) and these other records described, refer to or have illustrated short-blade chaetae.

The numerous specimens found from different localities in northern latitudes (and herein assigned to *S. philippi* comb. n.) resemble *Sphaerephesia artabrensis* comb. n. in the overall appearance, the shape and distribution of dorsal macrotubercles and dorsal and ventral papillae, the chaetal morphology, the presence and arrangement of sexual structures/genital pores (Moreira and Parapar 2007). However, there are some consistent minor differences between the specimens examined from southern and northern localities. Specimens of *S. artabrensis* comb. n. are generally smaller (Iberian specimens are up to 1.75 mm long and Nordic specimens almost double in size), and bear a few more papillae in the prostomium, dorsum and parapodia (6–7 in specimens assigned to *S. philippi* comb. n., and 3–4 in *S. artabrensis* comb. n.). Specimens identified as *S. philippi* bear a well-developed acicular lobe from segment 1, instead of segment 2 as in members of *S. artabrensis* comb. n. (Moreira and Parapar 2007).

It would therefore be most interesting to study in detail more material from intermediate localities (not found so far), as well as the genetic structures of these populations to test if they actually belong to a single lineage with a range of morphological features, or if the northern and southern forms (herein *S. artabrensis* comb. n. and *S. philippi* comb. n.) truly belong to separate species. Given that the types of *S. philippi* comb. n. from the Kara Sea are lost, and that the description of the species is not very detailed, it is not guaranteed that the broadly distributed lineage found in Nordic waters (e.g., Fig. 1) belongs to this species. However, based in the presence of acicular lobe from first segment (bifurcated in original description), approximate number of parapodial papillae, and chaetal morphology (Fauvel 1911), we have opted for this possibility.

Distribution. Arctic and Nordic Seas (Fauvel 1911, present study).

Habitat. Sediments, at shelf to slope depths (Fauvel 1911, present study).

Sphaerephesia ponsi **Capa, Parapar & Moreira, sp. n.**

http://zoobank.org/40F740FF-6DFF-4083-8135-1A907657426E

Figs 5P, 15M, N, 21

Type locality. Irminger Basin, SW of Iceland, North Atlantic Ocean, 63° 0.46'N, 28° 4'W, 1593 m.

Examined material. Holotype: SMF 25295, Irminger Basin, SW of Iceland, 63°00.46'N, 28°04.09'W, 1593 m, 8 Sep 2011. **Paratypes** SMF 24841 (1 spec. used for DNA sequencing and SEM, SPH047), Irminger Basin, SW of Iceland, 63°00.46'N, 28°04.09'W, 1593 m, 8 Sep 2011; SMF 25296 (1 spec., on SEM stub), Irminger Basin, SW of Iceland, 63°00.46'N, 28°04.09'W, 1593 m, 8 Sep 2011.

Diagnosis. Body ellipsoid, flattened dorsoventrally. Body unpigmented (fixed specimen). Head appendages smooth and digitiform. Tentacular cirri smaller than prostomial appendages. Dorsum with four longitudinal rows of large, sessile and pear-shaped macrotubercles in a single transverse row per segment, from segment 2. Additional papillae on dorsum and ventrum. Acicular lobe from segment 1. Parapodia with four papillae. Ventral cirri digitiform reaching tip of acicular lobe. Approximately eight compound chaetae with medium length blades (7–9 times as long as wide); unidentate.

Description. *Measurements and general morphology*. Holotype 1.8 mm long, 0.5 mm wide; with 12 chaetigers (Fig. 21A). Body ellipsoid. Segmentation not conspicuous.

Head. Head fused to first segment (Fig. 21A–C). Head appendages digitiform (Fig. 21C). Palps and lateral antennae three times longer than wide, smooth, and lacking spurs or basal papillae (Fig. 21C). Median antenna two-thirds the length of lateral antennae, slightly wider (Fig. 21C). Antenniform papillae absent (Fig. 21C). Head papillae elliptical, ca. 20 papillae enclosed by prostomial appendages. Tentacular cirri digitiform, similar in shape and size to lateral antennae (Fig. 21C).

Tubercles. Four longitudinal rows of dorsal macrotubercles, in one transverse row per segment, from segment 2 (Fig. 21A–E). Macrotubercles, sessile, large, pear-shaped or with a terminal papilla (Fig. 21A–E). Distance between mid-dorsal rows larger than between these and lateral longitudinal rows of macrotubercles. Additional papillae, rounded, arranged in three or four irregular transverse rows along dorsal and ventral surfaces (Figs 15M, N, 21A). Ventrum with few papillae in holotype.

Parapodia. Parapodial conical, as long as wide (Fig. 21F–J). Ventral cirri conical, as long as maximum wide of parapodia, reaching the tip of the acicular lobe, or shorter (Fig. 21G, H, K). Acicular lobe from chaetiger 1. Anterior segments with two parapodial papillae, one ventral, near the base of parapodium and one posterior (Fig. 21F–H). Three or four parapodial papillae in mid-body segments, sub-equal, rounded (one dorsal, one or two anterior, one ventral near base of parapodium) (Figs 5P, 21G, J).

Chaetae. All chaetae compound, ca. eight in mid-body parapodia, with medium size blades (7–9 times as long as wide), unidentate, with finely serrated edge (Fig. 21L, M). One straight acicula per parapodia.

Pygidium. A pair globular anal cirri, similar to dorsal macrotubercles but smaller and digitiform medio-ventral anal papilla similar in length to lateral cirri (Fig. 21I).

Internal features. Holotype with everted proboscis, as long as 5–6 segments. Eyes not observed.

Reproductive features. No gametes, sexual structures, or genital pores observed.

Variation. Paratypes 1–2 mm long, 0.3 mm wide, 15–17 segments. Epithelial parapodial papillae are more evident in paratypes, and ventral papillae include of ca. 20 rounded and sub-equal papillae, arranged in four irregular transverse rows per segment (Fig. 15N). Acicular lobe and ventral cirri are almost spherical in holotype while in the paratypes show longer and digitiform parapodial appendages. The rest of features are consistent among specimens studied.

Remarks. *Sphaerephesia ponsi* sp. n. is distinguished from other congeners by the unique combination of following features: head appendages smooth and without spurs or basal papillae, antenniform papillae absent, macrotubercles in four longitudinal rows, pear-shaped and with terminal papillae, parapodial papillae with four spherical papillae, chaetae with blades up to nine times as long as wide. Other *Sphaerephesia* with ca. four parapodial papillae are *S. artabrensis* comb. n., *S. mamalaensis*, *S. longisetis* comb. n., and *S. amphorata*. *Sphaerephesia amphorata* is clearly distinguished from *S. ponsi* sp. n.

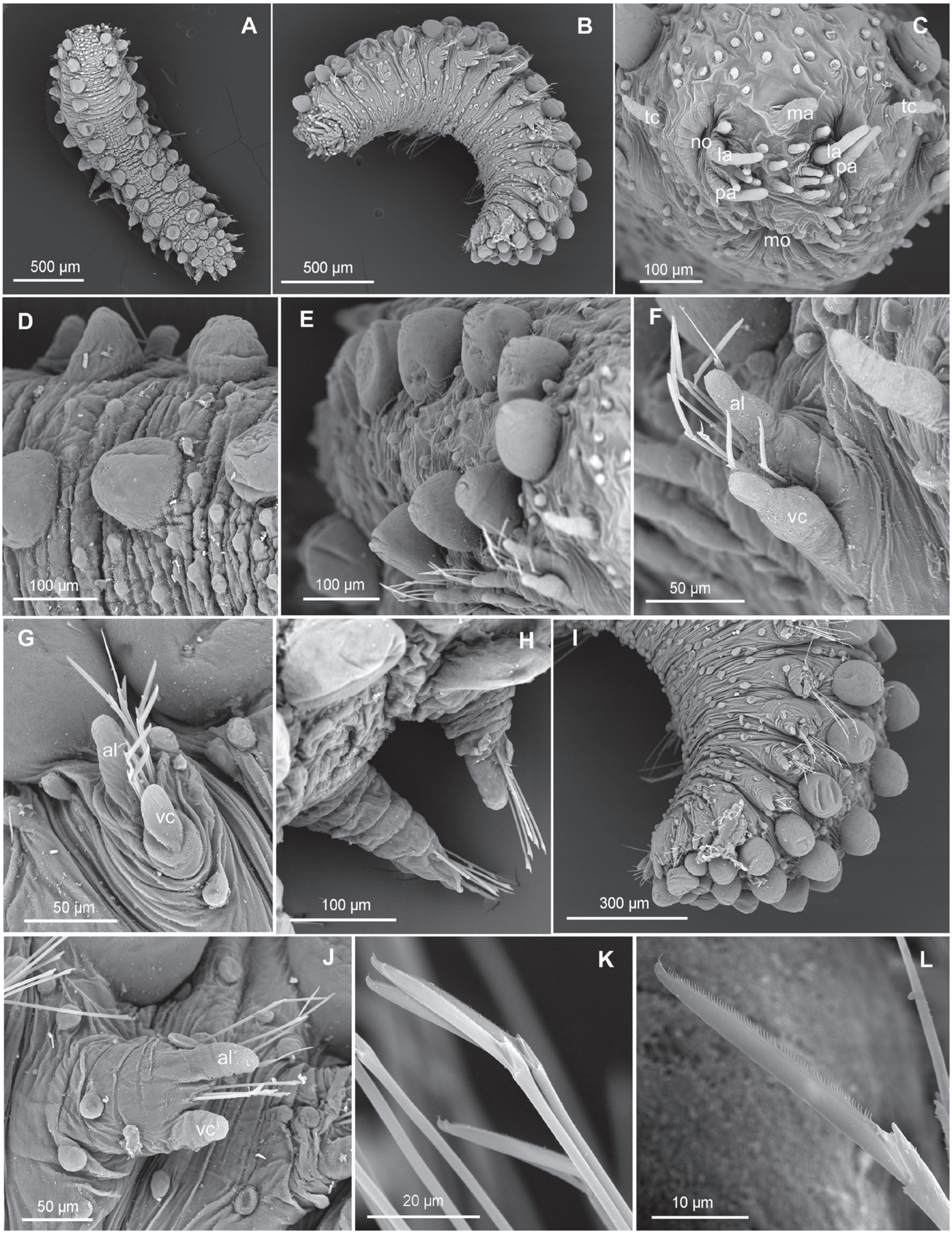

Figure 21. *Sphaerephesia ponsi* sp. n., scanning electron micrographs (Paratype, SMF 24841, SPH047). **A** Complete specimen, dorsal view **B** same, lateral view **C** head, anterior view **D** mid-body macrotubercles, frontal view **E** anterior chaetigers, frontal view **F** parapodium, chaetiger 1, anterior view **G** parapodium, chaetiger 2, side view **H** posterior parapodia, dorsal view **I** posterior chaetigers, lateral view **J** parapodium, chaetiger 7, anterior view **K** chaetae, mid-body chaetigers **L** chaetae, anterior chaetiger, detail.

in the shape of the macrotubercles, with a long terminal papilla. *Sphaerephesia ponsi* sp. n. is distinguished from *S. artabrensis* comb. n. and *S. longisetis* in the length of chaetal blades, over ten times as long as wide in the former two species and shorter in the new species; and shorter in *S. mamalaensis* (up to six times as long as wide).

Etymology. This new species is dedicated to Joan Pons, a researcher from the Mediterranean Institute of Advanced Studies (IMEDEA), Balearic Islands, colleague, and friend.

Distribution. Only known from type locality, the Irminger Basin in the North East Atlantic.

Habitat. Sediments at ca. 1600 m.

Sphaerephesia sibuetae (Desbruyères, 1980), comb. n.

Figs 5Q, 15O, P, 22

Sphaerodoropsis sibuetae Desbruyères, 1980: 226–229, Figs 9–10; Moreira et al. 2011: 26–28, Fig. 1.

Type locality. Banc le Danois, Bay of Biscay, 44°5.2'N, 05°19.4'W, 1913 m.

Examined material. Holotype: MNHN TYPE1284, Banc Le Danois, Bay of Biscay, 44°05.2'N, 5°19.4'W, 1913 m. **Paratypes**: same sample (6 specs, 2 on SEM stub).

Additional material. (28 specs) **Iceland**, SMF 25297, (16 specs), Irminger Basin, 63°00.46'N, 028°04.09'W, 1593m, 8 Sep 2011; SMF 23906 (1 spec. used for DNA sequencing, SPH273), Irminger Basin, 63°00.46'N, 028°04.09'W, 1593m, 8 Sep 2011; SMF 23906 (1 spec. used for DNA sequencing, SPH 044), Irminger Basin, 63°00.46'N, 028°04.09'W, 1593m, 8 Sep 2011; SMF25298 (22 specs), Irminger Basin, 63°00.46'N, 028°04.09'W, 1593 m, 8 Sep 2011; SMF24855 (1 spec. used for DNA sequencing, SPH273), Irminger Basin, 63°00.46'N, 028°04.09'W, 1593 m, 8 Sep 2011; ZMBN 127325 (8 specs) South Iceland, 61°38.2'N, 16°27.7'W, 2355 m, 5 Jun 1983. **NW Iberian Peninsula**, MNCN 16.01/13268 (1 spec.), 42°31.66'N, 09°40.06'W, 1974–2034 m, 29 Sep 2008.

Diagnosis. Body ellipsoid, flattened dorsoventrally, up to 5 mm long. Head appendages smooth, lacking spurs or basal papillae. Antenniform papillae present. Four longitudinal rows of macrotubercles, in a single transverse row per segment, from segment two. Macrotubercles sessile, pear-shaped or with terminal papilla. Small spherical papillae scattered on dorsal (four irregular transverse rows with ca. 30 papillae per segment) and on ventral surfaces (four irregular transverse rows per segment). Parapodia with acicular lobe from segment 1, with 16–19 rounded sub-equal papillae, apparently randomly arranged. Approximately 20–25 compound chaetae with long blades (9–13 times as long as wide).

Re-description of holotype. *Measurements and general morphology*. Holotype 2.82 mm long, 0.5 mm wide and with 19 segments. Body with rounded anterior end, tapering from segment 6 to pygidium, circular in transverse section. Segmentation not conspicuous and pigmentation absent (Fig. 22A).

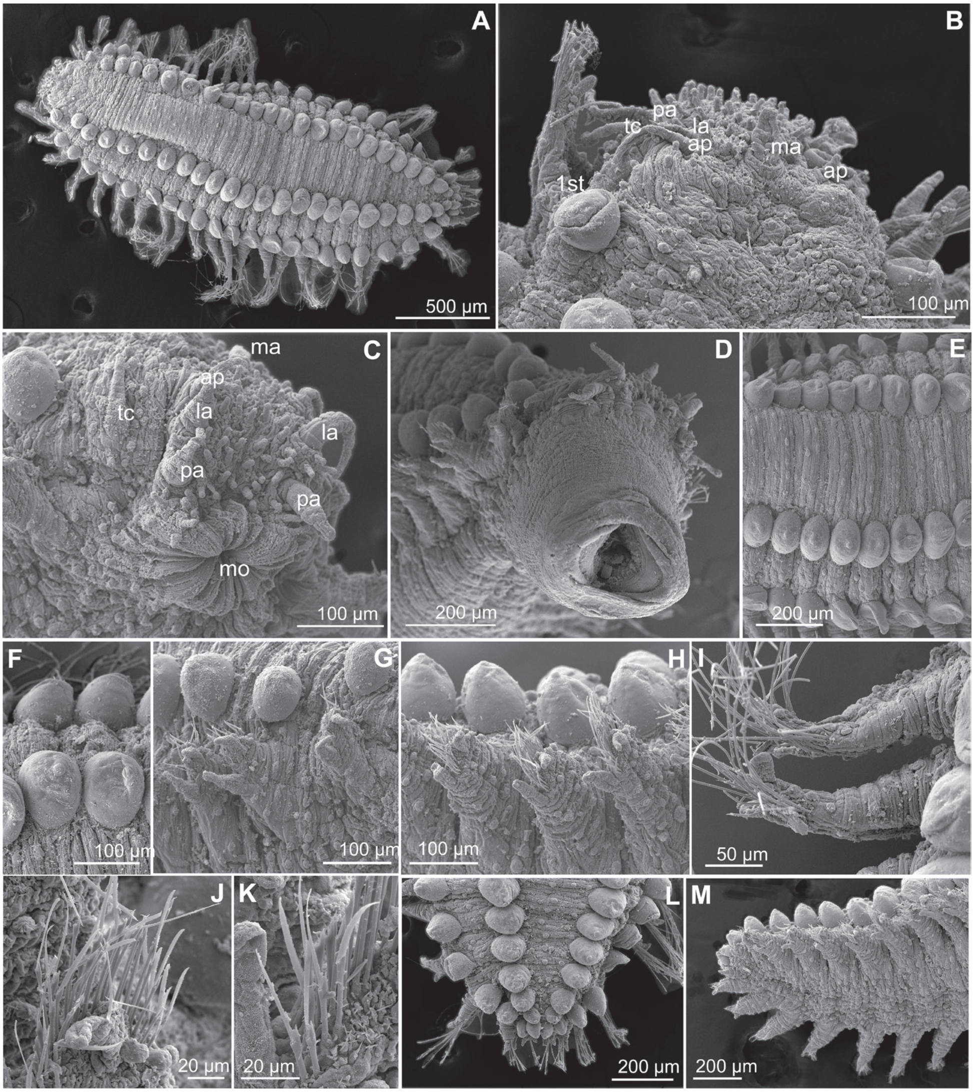

Figure 22. *Sphaerephesia sibuetae* (Paratypes, MNHN TYPE1284), scanning electron micrographs. **A** Complete specimen, dorsal view **B** head, dorsal view **C** head, ventral view **D** anterior end with everted proboscis, ventral view **E** mid-body chaetigers, dorsal view **F** dorsal macrotubercles, detail **G** parapodia, chaetigers 1–3, anterior view **H** mid-body parapodia, anterior view **I** mid-body parapodia, dorsal view **J** chaetal fascicle, mid-body chaetiger **K** chaetae, posterior chaetiger **L** posterior chaetigers, dorsal view **M** posterior chaetigers, ventral view.

Head. Head fused to first segment (Fig. 22A, B). Prostomial appendages, palps, lateral antennae, and median antenna conical (Fig. 22B–D). Palps and lateral antennae three times longer than wide, smooth, and lacking spurs or basal papillae (Fig. 22B–D). Median antenna almost one third of the length of lateral antennae, digitiform (Fig. 22B, C). Antenniform papillae present (Fig. 22C). Head papillae rounded, numerous and randomly arranged (over 20 papillae enclosed by prostomial appendages). Tentacular cirri digitiform, shorter than lateral antennae and longer than median antenna (Fig. 22B, C).

Tubercles. Four longitudinal rows of dorsal macrotubercles, in one transverse row per segment, from segment 2 (Figs 15O, 22A). Macrotubercles, sessile, large pear-shaped or with a terminal papilla (Fig. 22A, E–H, L). Additional papillae, rounded, arranged in three or four irregular transverse rows along dorsal and ventral surfaces (Figs 15O, P, 22E, M).

Parapodia. Parapodial conical or cylindrical, three or four times longer than wide at mid-body (Fig. 22G–I). Ventral cirri digitiform, as long as maximum wide of parapodia, reaching the tip of the acicular lobe (Fig. 22H, I). Acicular lobe from chaetiger 1. Parapodial papillae (16–19) rounded, hemispherical and randomly distributed over their surface, being one, dorsal to acicular lobe, slightly larger than the rest. Three papillae on dorsal surface, 6–7 anterior, 3–4 ventral and 4–5 posterior (Figs 5Q, 22G–I).

Chaetae. All chaetae compound, ca. 15–25 in mid-body chaetigers, with long, unidentate compound chaetae with long blades (ca. 9–13 times their width showing some variation within parapodia) and with finely serrated edge (Fig 22J, K). One straight acicula per parapodia.

Pygidium. A pair of globular anal cirri, similar to dorsal macrotubercles but smaller and digitiform medio-ventral anal papilla similar in length to lateral cirri (Fig. 22L, M).

Internal features. Muscular pharynx present through segments 1–4. Nuchal organs openings behind lateral antennae.

Reproductive features. Sexual structures or genital pores not observed in holotype.

Variation. Size range of material examined: 2–5 mm long; 0.8–1.5 mm wide; with 17–31 chaetigers. Sexual dimorphism or reproductive features not observed in paratypes or additional material examined. Everted pharynx bare (Fig. 22D).

Remarks. The species was originally considered as belonging to *Sphaerodoropsis* (Desbruyères 1980) even though the original description and iconography revealed that specimens have pear-shaped macrotubercles or with distal papilla; this was corroborated with the new scanning electron micrographs of paratypes provided herein (e.g., Fig. 22A).

Sphaerephesia sibuetae comb. n. differs from other species reported as presenting dorsal pear-shaped macrotubercles or with terminal papilla in the following combination of features: ellipsoid in shape, flattened dorsoventrally; head appendages smooth, without spurs or basal papillae; four irregular transverse rows of rounded papillae in both dorsum and ventrum, with ca. 30 papillae per segment; parapodia with ca. 16–19 papilllae and 15–25 compound chaetae with blades up to 13 times longer than wide in mid chaetigers. Other NEA similar congeners include *Sphaerephesia multichaeta* sp. n., distinguished from *S. sibuetae* in the chaetal morphology (with shorter blades, up to seven times longer than wide) while *S. sibuetae* have longer blades (7–13 times as long as wide).

Distribution. Newly recorded in southern Iceland (present study). Previously reported in Bay of Biscay and NW Iberian Peninsula (Moreira et al. 2011).

Habitat. Sediments at 1400–2000 m (Desbruyères 1980, Moreira et al. 2011, present study).

***Sphaerephesia stellifer* (Aguirrezabalaga & Ceberio, 2005), comb. n.**
Fig. 5R, 15Q, R

Sphaerodoropsis stellifer Aguirrezabalaga & Ceberio, 2005: 13–16, Figs 3– 4.

Type locality. Capbreton Canyon, Bay of Biscay, 43°42.01'N, 2°18.52'W, 990 m.

Material examined. Holotype: MNCN 16.01/9051, Bay of Biscay, Capbreton Canyon, 43°42.01'N, 2°18.52'W, 990 m; **Paratype**: MNHN, apparently lost.

Diagnosis. Body ellipsoid, flattened dorsoventrally, up to 3.2 mm long. Head appendages digitiform, lacking spurs. Median antenna shorter than palps and lateral antennae. Antenniform papillae present. Dorsum with four longitudinal rows of macrotubercles, in a single transverse row per segment, from segment 2. Macrotubercles sessile pear-shaped. Additional small spherical papillae on dorsum, arranged in 3–4 transverse rows per segment, each with ca. ten papillae. Ventrum with papillae, in 3–4 transverse rows per segment. Parapodia conical, with 7–10 sub-equal papillae uniformly distributed. Ventral cirri digitiform not surpassing acicular lobe tip. Approximately 6–12 compound chaetae with medium length blades (near six times their width), showing small gradation within fascicles; unidentate and subtle spinulation along its cutting margin.

Variation. According to the original description, the range of variation of material examined is 18–20 chaetigers, 1.7–3.1 mm long and 0.6–0.8 mm wide.

Remarks. *Sphaerephesia stellifer* comb. n. was described as a new species due to the star-shaped epithelial papillae, instead of spherical, oval of hemispherical, typical from other sphaerodorids. Revision of the holotype did not ensure this particular condition any longer, and instead it has the characteristic pear-shaped dorsal macrotubercles, resembling other *Sphaerephesia* species. The original drawings even include a close up of a macrotubercle with a small terminal papilla. Therefore, we suspect the shape described by Aguirrezabalaga and Ceberio (2005) as '*macrotubercles with funnel-like distal invaginations*' can be attributable to temporary collapse of the tubercles and it has now reverted to the typical pear-shaped tubercles. Collapsed epithelial tubercles has been observed in specimens of different species, indicating it may be related to particular fixation procedures and making it a not reliable diagnostic feature.

A combination of features may allow distinguishing *S. stellifer* comb. n. from other NEA *Sphaerephesia*. These include the ellipsoid body shape, presence of pear-shaped macrotubercles, 3–4 transverse rows of additional papillae over dorsum and ventrum, conical parapodia with ca. ten papillae, and 6–12 chaetae, near six times as long as wide. Nevertheless, *Sphaerephesia laureci* comb. n. is a similar species with a more elongated body and also longer parapodia (Desbruyères, 1980); further studies should conclude if these features are enough to separate representatives of these species, or if *S. stellifer* comb. n. is in fact a junior synonym of *S. laureci* comb. n.

Distribution. Capbreton Canyon, Bay of Biscay (Aguirrezabalaga and Ceberio 2005).

Habitat. Soft bottoms at depths of between 990–1040 m.

Sphaerephesia sp. 1

Fig. 8E

Diagnosis. Body ellipsoid, flattened dorsoventrally, up to 3 mm long. Body unpigmented; macrotubercles in live specimens orange, or brownish in fixed material. Head appendages smooth, digitiform. Tentacular cirri smaller than prostomial appendages. Dorsum with four longitudinal rows of large, spherical, or pear-shaped sessile macrotubercles in a single transverse row per segment, from segment 2. Additional papillae on dorsum. First parapodia short and digitiform, with two rounded papillae on dorsal surface. Acicular lobe from segment 1. Eight to ten parapodial papillae. Ventral cirri digitiform shorter than acicular lobe tip. Approximately eight compound chaetae with medium length blades (ca. ten times as long as wide); unidentate.

Examined material. (5 specs) **Iceland Sea**, SMF 23908 and 23907 (2 spec, used for DNA sequencing, SPH056 and SPH057, respectively), NE Iceland, 66°32.63'N, 12°52.48'W, 317.2 m, 22 Sep 2011; **Svalbard**, ZMBN 127327 (1 spec. used for DNA sequencing, SPH 296), Svalbard, 81°0.066'N, 19°17.802'E, 168 m, 01 Sep 2009; **Barents Sea**, ZMBN 127326 (1 spec. used for DNA sequencing, SPH292); Finnmark, 72°18.59'N, 32°20.48'E, 312 m, 04 Aug 2013; **Skagerrak**, ZMBN 125432 (1 spec. used for DNA sequencing SPH 297 photographed alive Fig. 8D), 58°40.806'N, 10°23.982'E, 238 m, 16 May 2009; ZMBN 127328 (1 spec. used for DNA sequencing, SPH 298.) 58°40.806'N, 10°23.982'E, 237 m, 16 May 2009.

Remarks. These specimens were initially identified as *Sphaerephesia philippi* comb. n., as there seems to be no noticeable morphological differences between them. However, analyses of molecular data recovered some of the specimens forming a different lineage, sister group to a clade containing *S. discolis* and *S. sibuetae* (Fig. 1). We would like to corroborate this information with further data before describing it as a new species.

Distribution. Iceland Sea, Svalbard, Barents Sea, and Skagerrak.

Habitat. Continental shelf sediments (100–350 m).

Sphaerodoridium Lützen, 1961

Sphaerodoridium Lützen, 1961; Fauchald 1974: 270 (in part).

Sphaerodoropsis Hartman & Fauchald, 1971: 69 (in part); Fauchald 1974: 261 (in part); Borowski 1994: 23 (in part); Moreira 2012: 30 (in part); Capa et al. 2014: 17 (in part).

Type species. *Sphaerodorum claparedii* Greeff, 1866.

Diagnosis. Body short and ovoid, some forms slender. Prostomial appendages short, spherical or digitiform; median antenna shorter or as long as lateral antennae;

antenniform papillae absent or present. Macrotubercles sessile or stalked; smooth, without terminal papilla, arranged in more or less clear longitudinal rows, one transverse row per segment, with at least seven macrotubercles each. Microtubercles absent. Additional papillae over body surface and parapodia. Parapodia with compound chaetae; stout hooks in anterior chaetigers absent.

Remarks. In the present study, a clade was recovered containing species previously assembled under *Sphaerodoropsis* Group 2 (Borowski 1994) (that is with sessile dorsal macrotubercles arranged in six or more longitudinal rows, and only one transverse row per segment), nested among other previously considered as *Sphaerodoridium* (that is with stalked macrotubercles) with more than seven longitudinal rows of macrotubercles (Fig. 1). This provides evidence that the macrotubercle morphology (i.e., sessile or stalked dorsal macrotubercles) is not a valid character separating reciprocally monophyletic groups. Instead, members of this clade should be considered as one genus containing sphaerodorids with more than six longitudinal rows of macrotubercles, arranged in a single transverse row per segment. Note that Borowski (1994) included one species bearing six macrotubercles in the first chaetiger under the artificial Group 2, like others in this group, but otherwise more than six. It is therefore here interpreted as belonging to the newly interpreted *Sphaerodoridium*: that is with more than six longitudinal rows of macrotubercles.

The type species of the genus *Sphaerodoridium*, *S. claparedii,* and the type species of *Sphaerodoropsis*, *Sphaerodoropsis sphaerulifer* share this feature. However, *Sphaerodoridium* was erected previous (Lützen 1961) to *Sphaerodoropsis* (Hartman and Fauchald 1971). Therefore, we consider this clade should bear the genus name *Sphaerodoridium.*

The diagnosis of the genus *Sphaerodoridium* differs from the original concept. In order to accommodate these, several systematic (all and only sphaerodorid species presenting seven or more longitudinal rows of macrotubercles, arranged in one transverse row per segment) are consider belonging to this group and nomenclatural changes are required.

Species currently considered within *Sphaerodoridium* are:

Sphaerodoridium aestuarum (Averincev, 1990), comb. n.
  Type locality: Laptev Sea, 3–6.5 m.
Sphaerodoridium amoureuxi Aguirrezabalaga & Cebeiro, 2005
  Type locality: Capbreton Canyon, Bay of Biscay, 984–1029 m.
Sphaerodoridium andamanense (Bakken, 2002), comb. n.
  Type locality: Off Phi Phi Island, Andaman Sea, Thailand, 29 m.
Sphaerodoridium auranticum (Capa & Rouse, 2015), comb. n.
  Type locality: Yonge Reef, Great Barrier Reef, Australia, 4–12 m.
Sphaerodoridium balticum (Reimers, 1933), comb. n.
  Type locality: Kiel, Baltic Sea, 6–8 m.
Sphaerodoridium bengalorum (Fauchald, 1974), comb. n.
  Type locality: Porto Novo, Madras, India, 1.5 m.
Sphaerodoridium benguellarum (Day, 1963), comb. n.

Type locality: Off eastern coast of South Africa, 172 m.
Sphaerodoridium campanulata Borowski, 1994.
Type locality: Peru Basin, Pacific Ocean, 4163 m.
Sphaerodoridium claparedii Greeff, 1866
Type locality: Dieppe, English Channel, France.
Sphaerodoridium evgenovi Gagaev, 2015
Type locality: Barents Sea, 226 m.
Sphaerodoridium gudmunduri (Moreira & Parapar, 2012), comb. n.
Type locality: North of Iceland, 97 m.
Sphaerodoridium guerritai Moreira & Parapar, 2015
Type locality: North of Iceland, 600 m.
Sphaerodoridium katchemakensis (Kudenov, 1987), comb. n.
Type locality: Alaska, USA, 10 m.
Sphaerodoridium kolchaki Gagaev, 2015
Type locality: Barents Sea, 290 m.
Sphaerodoridium kupetskii Gagaev, 2015
Type locality: Canada Basin, 1004 m.
Sphaerodoridium japonicum Ozolin'sh, 1987
Type locality: Sea of Japan, 33–62 m.
Sphaerodoridium lutzeni Kudenov, 1987
Type locality: E Florida, Gulf of Mexico, 34 m.
Sphaerodoridium minutum (Webster & Benedict, 1887)
Type locality: Off New England, USA, shelf depths.
Sphaerodoridium octopapillatum (Hartmann-Schröder, 1965), comb. n.
Type locality: Off Galera, Chile, 260 m.
Sphaerodoridium polypapillatum (Hartmann-Schroder & Rosenfeldt,1988), comb. n.
Type locality: King George Island, Antarctica, 263 m.
Sphaerodoridium sphaerulipher (Moore, 1909), comb. n.
Type locality: Monterey Bay, California, USA.
Sphaerodoridium uzintunensis (Kudenov, 1987), comb. n.
Type locality: Alaska, USA, 3 m.

***Sphaerodoridium amoureuxi* (Aguirrezabalaga & Ceberio, 2005), comb. n.**

Figs 5S, 23A, B

Sphaerodoropsis amoureuxi Aguirrezabalaga & Ceberio, 2005: 10–13, figs 1, 2; Moreira et al. 2011: 28–29, fig. 2; Moreira 2012, 36–39, fig. 11.

Type locality. Capbreton Canyon, Bay of Biscay, 984–1029 m.

Material examined. Holotype: MNCN 16.01/8925, Capbreton Canyon, Bay of Biscay, 984–1029 m. **Paratype**: not found in MNHN, seems to be missing.

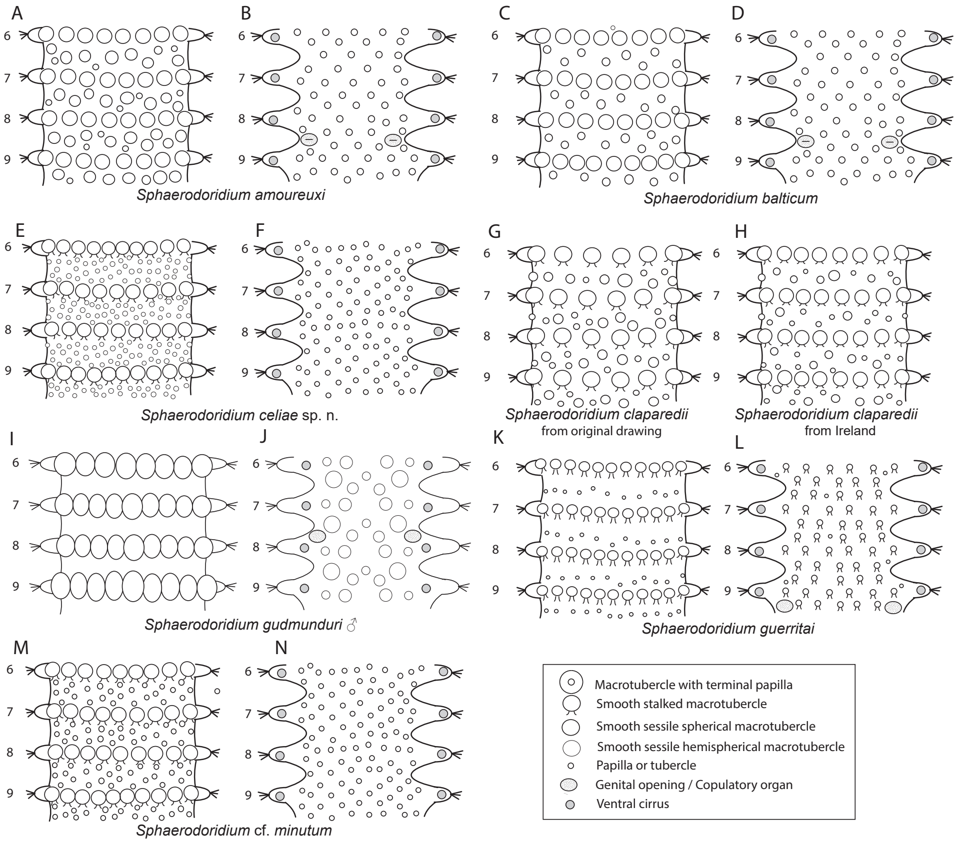

Figure 23. Stylized drawings of selected dorsal and ventral segments of species of *Sphaerodoridium*, showing number and arrangement of epithelial tubercles and papillae.

Additional material. (1 spec) **NW Iberian Peninsula**: MNCN 16.01/13269 (1 spec.), 43°36.22'N, 08°52.84'W, 200 m, 26 Sep 2004.

Diagnosis. Body short and cylindrical, less than 3.5 mm long. Palps, lateral antennae, and tentacular cirri, with spurs or basal papillae (lateral antennae 6–8). Median antenna smooth, shorter than other head appendages. Antenniform papillae present. Dorsal macrotubercles sessile, almost spherical, arranged in eight longitudinal rows in a single transverse row per segment, from segment 3. Dorsum with additional large spherical papillae, arranged between macrotubercles in more or less clear transverse rows, 25–30 papilla per segment. Ventrum with ca. 20 small spherical papillae per segment in midbody, arranged in 3–4 transverse rows per segment. Parapodia with three papillae; two sub-equal spherical papillae on ventral and anterior surfaces, and one postchaetal terminal papilla. Acicular lobe from segment 3. Approximately 6–8 compound chaetae with medium blades (up to seven times as long as wide), showing slight intra-fascicle variation in size.

Remarks. This species has been described in detail (Aguirrezabalaga and Ceberio 2005) and some additional intraspecific variation has been reported (Moreira et al. 2011) and incorporated in the diagnosis. The antenniform papillae can be contracted and not evident in some specimens; variation regarding the number of parapodial papillae with three instead of 2–4. The postchaetal lobes mentioned in the original description and by Moreira et al. (2011) are herein considered a distal postchaetal papilla. Some macrotubercles seem to have a short stalk (or at least they are almost spherical) in the types re-examined. *Sphaerodoropsis amoureuxi* comb. n. belongs to the clade of sphaerodorids with over six longitudinal rows of macrotubercles arranged in a single segmental transverse row. Females with visible eggs, sexual or sexual structures not observed.

Sphaerodoridium amoureuxi comb. n. differs from other congeners in the number of macrotubercles (up to eight, Fig. 23A), presence of spurs and basal papillae in paired head appendages, and shape, number of papillae per segment (spherical, 24–30, Fig. 5S) and chaetal morphology, with blades up to seven times as long as wide. The description of this species was justified based in the number of head appendages (Aguirrezabalaga and Ceberio 2005), a feature that seems to show some variability (Moreira et al. 2011), and the number of parapodial lobes (Aguirrezabalaga and Ceberio 2005), but these could have a different misinterpretation and be considered as parapodial papillae (Moreira et al. 2011 and herein).

Distribution. Capbreton Canyon, Bay of Biscay (Aguirrezabalaga and Ceberio 2005); NW Iberian Peninsula (Moreira et al. 2011).

Habitat. Soft bottoms between 100–1030 m (Moreira 2012).

Sphaerodoridium balticum (Reimers, 1933), comb. n.

Figs 5T, 23C, D, 24

Sphaerodorum balticum Reimers, 1933: 41–110, 45 figs

Type locality. Kiel, Baltic Sea, 6–8 m.

Material examined. (16 specs) **Barents Sea**: ZMBN 127332 (1 spec. used for DNA sequencing, SPH 280), 70°17.79'N, 31°18.83'E, 217 m, 18 Aug 2013; **Norwegian Sea**: ZMBN 127331 (11 spec.), Mørebanken, 62°45.5'N, 5°31.56'E, 91 m, 04 Oct 2012; ZMBN 127329 (1 spec. used for DNA sequencing, SPH281), Mørebanken, 62°45.5'N, 5°31.56'E, 91 m, 04 Oct 2012; ZMBN 127330 (1 spec. used for DNA sequencing SPH282), Mørebanken, 62°45.5'N, 5°31.56'E, 91 m, 04 Oct 2012; ZMBN 129499 (1 spec. on SEM stub), Mørebanken, 62°45.5'N, 5°31.56'E, 91 m, 04 Oct 2012. **Kattegat**: NHMD 302862 (1 spec.), Kattegat, Samsø, NW of Bosserne, 23–26 m, 18 Jul 1969; NHMD 302861 (1 spec.), Kattegat, Samsø, NW Møgelskår, Nordby, 14 Jul 1979.

Diagnosis. Body short and ellipsoid. Prostomial appendages digitiform, smooth, longer than wide. Palps and lateral antennae with basal spurs or basal papillae, the later with 3–4 spurs. Median antenna as long as or slightly shorter than other head appendages. Antenniform papillae absent. Eight to nine longitudinal rows of spherical and sessile macrotubercles in one transverse row per segment. Additional spherical papillae arranged in three transverse rows per segment, in dorsum and ventrum. Parapodia with acicular lobe from chaetiger 3, digitiform; ventral cirri digitiform, projecting well beyond acicular lobe; four spherical parapodial papillae. Compound chaetae with medium length blades (6–7 times as long as wide), showing little dorso-ventral gradation; unidentate, finely serrated.

Re-description of NEA material. *Measurements and general morphology.* Body ellipsoid, with rounded anterior and posterior ends, with convex dorsal surface and slightly flat ventrum; cross section almost circular (Fig. 24A). Segmentation inconspicuous and pigmentation absent. Measuring 1.3–2.2 mm in length and near 0.5 mm wide; with 10–18 chaetigers.

Head. Prostomium fused to first segment. Prostomial appendages including palps and lateral antennae digitiform, similar in shape and size (Fig. 24B). Palps and lateral antennae with 3–4 basal papillae or spurs (Fig. 24C, D). Median antenna shorter than lateral appendages, or similar to other rounded prostomial papillae, without spurs. Tentacular cirri, similar in size and shape to median antenna (Fig. 24C).

Tubercles. Dorsal macrotubercles, sessile, spherical, smooth. Arranged in 8–9 longitudinal rows from second chaetiger to posterior segments, and one transverse dorsal row per segment (Fig. 24A). All macrotubercles similar in size. Additional spherical dorsal papillae arranged in two or three irregular transverse rows, ca. 20 papillae in mid-body segments (Figs 23C, 24A). Ventral papillae, similar to dorsal in shape and size, arranged in three transverse rows per segment (Figs 23D, 24A).

Parapodia. Parapodia conical, as long as wide. Ventral cirri digitiform. Acicular lobe similar or slightly shorter, similar in shape and size to parapodial papillae. Four parapodial papillae, two dorsal and two posterior, one behind the chaetal fascicle and another one closer to the base (Figs 5T, 24F–I).

Chaetae. Five to seven compound chaetae on each parapodium, with fine and medium size blades (ca. 5–8 times as long as wide), unidentate, finely serrated (Fig. 24F–H, K, L). A single straight acicula per parapodium.

Pygidium. Pygidium with paired anal cirri resembling macrotubercles and medioventral digitiform anal papilla.

Internal features. Two dark eyes visible dorsally inside the head. Pharynx extending over two chaetigers.

Reproductive features. Sexual structures between parapodia of chaetigers 8 and 9. They resemble a large ventral cirrus or a hemispherical knob (Fig. 24A, H, J).

Remarks. This species has been widely recorded across the North and Baltic seas (Hartmann-Schröder 1996) but giving the similarity with other species also present in the area these records require revisions. Other similar species reported from European waters are *Sphaerodoridium* cf. *minutum* (Webster & Benedict, 1887) (see below) that bears 10–14 stalked macrotubercles per segment. One of the diagnostic features of this species is the presence of spurs in palps and lateral antennae. These are only clearly

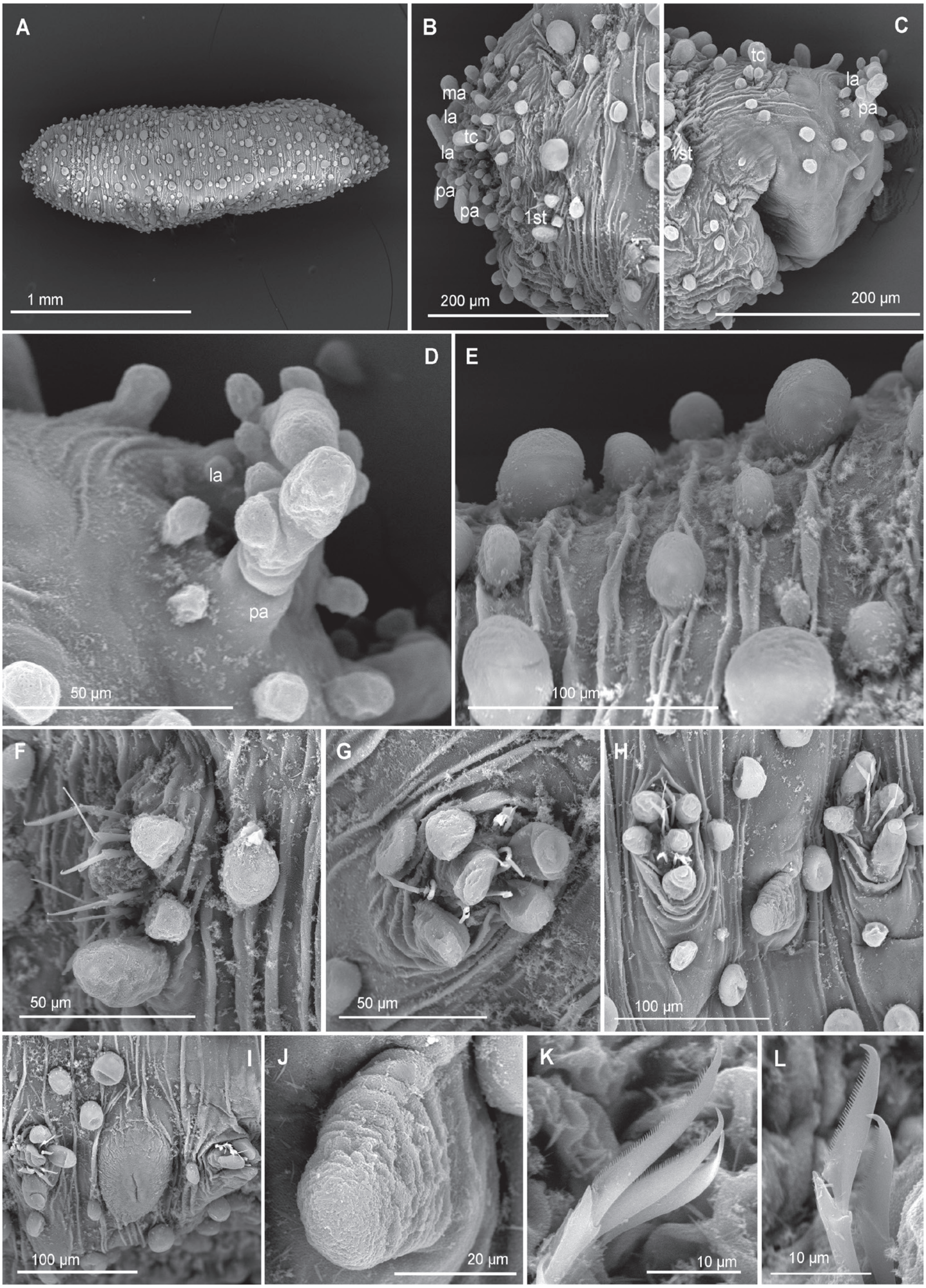

Figure 24. *Sphaerodoridium balticum,* from Norwegian Sea (ZMBN 129499 , SPH281), scanning electron micrographs. **A** Complete specimen, dorsal view **B** head, lateral view **C** palps with spurs and lateral antennae (behind), detail **D** epithelial tubercles over dorsum **E** parapodium, chaetiger 1 **F** parapodium, chaetiger 4 **G** parapodia, chaetigers 7 and 8, with a sexual structure in between (male) **H** genital pores between parapodia chaetiger 7 and 8 (female) **I** male genital organ, detail **J** chaetae, chaetiger 1 **K, L** chaetae, mid-body parapodia.

recognised in specimens with a relaxed head and appendages (e.g., Fig. 24C, D) but are not obvious on specimens with contracted anterior end (e.g., Fig. 24B)

Distribution. New records for the Barents Sea, Norwegian Sea, and Kattegat. Reported in the North and Baltic seas (Hartmann-Schröder 1996).

Habitat. Sandy and muddy sediments, 6–200 m (Hartmann-Schröder 1996, present study).

Sphaerodoridium celiae Moreira, Capa & Parapar, sp. n.

http://zoobank.org/DDFF262D-F131-4DC3-8A3B-68362EF256ED

Figs 5U, 23E, F, 25, 26, 27A

Type locality. NW Iceland, 67°30.76'N, 24°10.03'W, 1012 m.

Material examined. Type series: **Holotype**: IINH 38817, Iceland, 67°30.72'N, 24°10.03'W, 1012 m, 25 Aug 1999. Paratypes (535 specs).: IINH 38795 (6 specs on SEM stub), 63°08.60'N, 22°14.80'W, 248 m, 30 June 1996; IINH 38796 (1 spec.), 67°0.25'N, 17°25.01'W, 248 m, 10 July 1994; IINH 38797 (1 spec.), 67°55.91'N, 15°21.29'W, 1098 m, 13 July 1994; IINH 38798 (3 specs), 66°50.20'N, 16°15.74'W, 227 m, 15 July 1994; IINH 38799 (2 specs), 66°43.92'N, 16°50.54'W, 150 m, 15 July 1994; IINH 38800 (1 spec.), 68°01.13'N, 20°39.28'W, 970 m, 31 July 1995; IINH 38801 (34 specs), 63°15.00'N, 17°59.40'W, 175 m, 24 Aug 1995; IINH 38802 (26 specs), 63°30.12'N, 17°42.07'W, 120 m, 25 Aug 1995; IINH 38803 (20 specs), 63°25.06'N, 16°50.40'W, 272 m, 25 Aug 1995; IINH 38804 (22 specs), 62°20.17'N, 16°59.40'W, 2074 m, 28 Aug 1995; IINH 38805 (6 specs), 65°21.22'N, 27°25.43'W, 513 m, 24 Aug 1996; IINH 38806 (19 specs), 65°31.14'N, 26°13.11'W, 157 m, 28 Aug 1996; IINH 38807 (25 specs), 65°39.90'N, 26°11.33'W, 166 m, 28 Aug 1996; IINH 38808 (5 specs), 65°42.18'N, 25°16.99'W, 160 m, 29 Aug 1996; IINH 38809 (31 specs), 65°08.01'N, 23°36.17'W, 120 m, 30 Aug 1996; IINH 38810 (207 specs), 63°45.60'N, 14°50.60'W, 216 m, 5 July 1997; IINH 38811 (33 specs), 67°11.02'N, 21°45.68'W, 230 m, 21 Aug 1999; IINH 38812 (42 specs); IINH 38813 (9 specs), 66°10.23'N, 12°00.94'W, 243 m, 14 July 2001; IINH 38814 (11 specs), 65°50.34'N, 12°01.27'W, 192 m, 14 July 2001; IINH 38815 (1 spec.), 68°00.92'N, 009°14.78'W, 1727 m, 16 July 2004; IINH 38816 (30 specs), 66°31.42'N, 20°56.69'W, 200 m, 27 July 2004.

Additional material. (17 specs) **Barents Sea**: ZMBN 127338 (1 spec.), Finnmark 71°16.53'N, 27°0.94'E, 278 m, 16 Apr 2011; ZMBN 127336, (1 spec. used for DNA sequencing, SPH 279), Finnmark, 71°20.262'N, 25°13.17'E, 297 m, 23 Apr 2011. ZMBN 127337 (1 spec. used for DNA sequencing, SPH013), Finnmark 71°16.53'N, 27°0.94'E, 278 m, 16 Apr 2011; **Skagerrak**: ZMBN 127335 (4 spec.), 58°35.254'N, 10°19.395'E, 274 m, 14 May 2009; ZMBN 127334 (3 spec.), 58°33.795'N, 10°23.725'E, 254 m, 14 May 2009; ZMBN 103136 (1 spec. used for DNA sequencing, SPH008), 58°35.254'N, 10°19.395'E, 274 m, 14 May 2009; ZMBN 127333 (1 spec. used for DNA sequencing, SPH014.), Skagerrak 58°33.795'N, 10°23.725'E, 254 m, 14 May 2009; ZMBN 125434 (1 spec. used for DNA sequencing, SPH316 photographed alive, Fig. 27A), 58°30.733'N, 10°25.109'E, 275 m, 14 May 2009; ZMBN 127339 (1 spec. used for DNA sequencing, SPH317), 58°30.733'N, 10°25.109'E, 275 m, 14 May 2009; ZMBN 127340 (1 spec. used for DNA sequencing, SPH318), 58°30.733'N, 10°25.109'E, 275 m, 14 May 2009; ZMBN 127341 (1 spec. used for DNA sequencing, SPH319), 58°30.733'N, 10°25.109'E, 275 m, 14 May 2009.

Diagnosis. Body ellipsoid with strongly convex dorsum and flat ventrum, up to 6 mm long. Median antenna and head appendages digitiform, elongated. Median antenna smooth, shorter than other head appendages. Lateral antennae and palps similar, with 4–10 papillae (spurs) on proximal half. Antenniform papillae absent. Tentacular cirri digitiform, with 2–3 elongated papillae on proximal third. Dorsal macrotubercles stalked, without terminal papilla, arranged in 10–12 longitudinal rows in mid-body chaetigers; stalk half as long as tubercle, with 0–1 small papilla on proximal half. Dorsum with up to additional 50–60 spherical-oval papillae with short stalk, in front of each row of macrotubercles, somewhat arranged in 3–4 irregular transverse rows roughly following a zig-zag pattern. Ventrum with ca. 20 papillae per segment in mid-body, arranged in at least four more or less defined transverse rows in a zig-zag pattern. Parapodia with digitiform acicular lobe from chaetiger 3; large ventral cirri, not surpassing the length of acicular lobe; mid-body parapodia with 7–8 papillae. Chaetae blades showing slight gradation in length between chaetigers, slightly shorter in posterior chaetigers; ca. 8–9 times longer than maximum width.

Description. *Measurements and general morphology.* Holotype 5.5 mm long, 0.8 mm wide; with 29 segments (Figs 25A, 27A). Body ellipsoid with strongly convex dorsum and flat ventrum. Segmentation not distinct. Pigmentation absent (Fig. 27A).

Head. Prostomium with five digitiform elongated appendages, including a pair of palps and lateral antennae, similar in size and shape, and a shorter median antenna (Fig. 25C, D). Lateral antennae and palps with ca. 8–10 papillae (spurs) on proximal half. Tentacular cirri shorter than lateral antennae and palps, with three papillae on proximal third. Many rounded to digitiform small papillae scattered around head appendages (Fig. 25C, D).

Tubercles. First chaetiger with 12 dorsal macrotubercles (Fig. 25A); following chaetigers each with one transverse row of 12 (sometimes 11 or 13) dorsal macrotubercles, last chaetiger with ten macrotubercles. Macrotubercles spherical to club-shaped with a stalk near half-length of macrotubercle; first six chaetigers with smooth stalk, from chaetiger 7 backwards stalk provided with small basal papilla (Figs 25B, 26B); all macrotubercles mostly similar in shape and size (Fig. 23E). Additional spherical-oval papillae in different sizes over dorsum, with short stalk, somewhat arranged in 3–4 irregular transverse rows per chaetiger roughly following a zig-zag pattern; ranging from 40 to 60 papillae on each mid-body chaetiger (Fig. 23E). Ventral surface with spherical papillae with short stalk, arranged in four transverse rows in a zig-zag pattern, with ca. 20 papillae per segment in mid-body; numbers decreasing towards posterior end (Figs 23F, 26C).

Parapodia. Parapodia sub-conical, increasing in size towards chaetiger 3–4 (Fig. 25E–G), ca. 2–2.5 times longer than wide, some with wrinkled appearance (Figs 25E, 26D–G). Acicular lobe anterior to chaetae, digitiform, longer than parapodial papillae and projecting distally (Figs 25G–J, 26G). Ventral cirri digitiform projecting 1/2 to

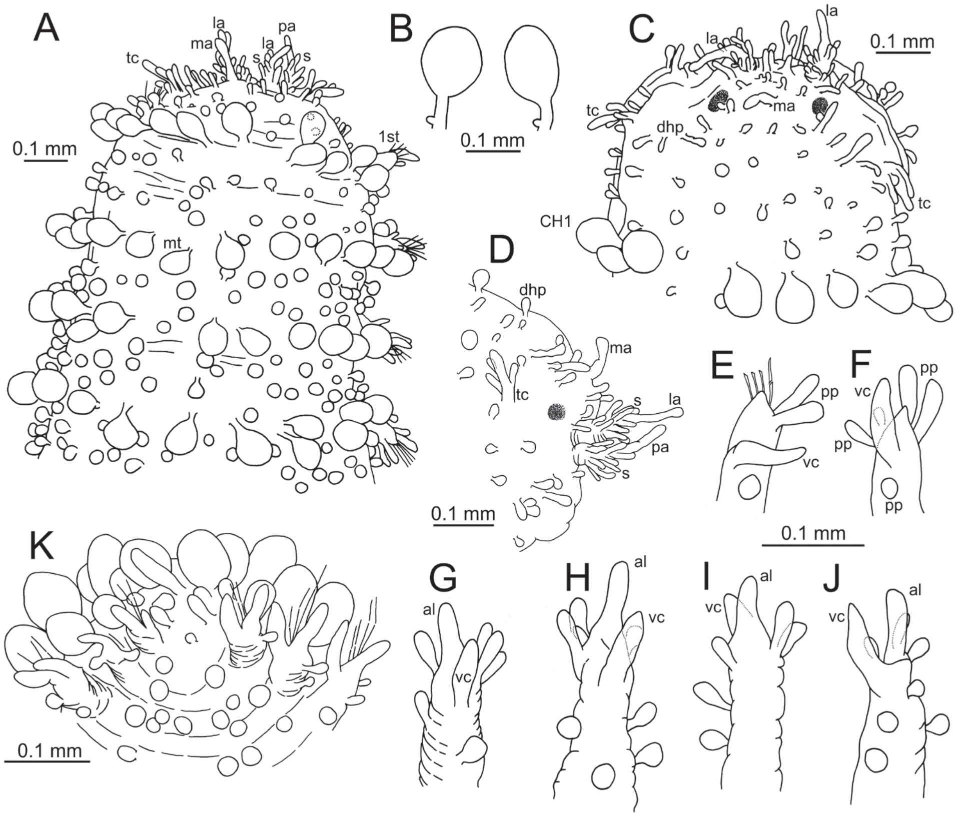

Figure 25. *Sphaerodoridium celiae* sp. n., line drawings (holotype, IINH 38817,: **A, B, E–K**; paratype, IINH 38812: **C, D**). **A** Anterior end, dorsal view **B** macrotubercles, chaetigers 7 and 19 **C, D** anterior end, dorsal and lateral view, respectively **E–J** parapodia **E** chaetiger 1, left side, ventral view **F** chaetiger 2, left side, ventral view **G** chaetiger 4, left side, ventral view **H** chaetiger 9, right side, ventral view **I** chaetiger 11, right side, dorsal view **J** chaetiger 23, right side, ventral view **K** posterior end, ventral view.

2/3 as long as acicular lobe on anterior mid-body segments, almost as long as in posterior segments (Figs 25I, J, 26D–G). First three chaetigers with parapodia provided with 3–5 spherical to clavate papillae: one on antero-dorsal surface, one on antero-lateral surface, one on medio-ventral surface, and two on posterior surface opposite to acicular lobe (Fig. 25E, F); following chaetigers through mid-body with up to three additional papillae: one on posterior surface opposite to acicular lobe, one on antero-lateral/lateral surface and one on ventro-basal position (Fig. 5U); last 3–4 chaetigers lacking some of aforementioned papillae.

Chaetae. All parapodia with 8–10 compound chaetae, arranged in a curved transverse row around acicular lobe (Figs 5U, 26G, H). Shaft distal end with thin spinulation (Fig. 26I). Serrated, long blades, 8–9 times longer than maximum width, with a curved tip (Fig. 26H, J), blades slightly shorter in posterior chaetigers.

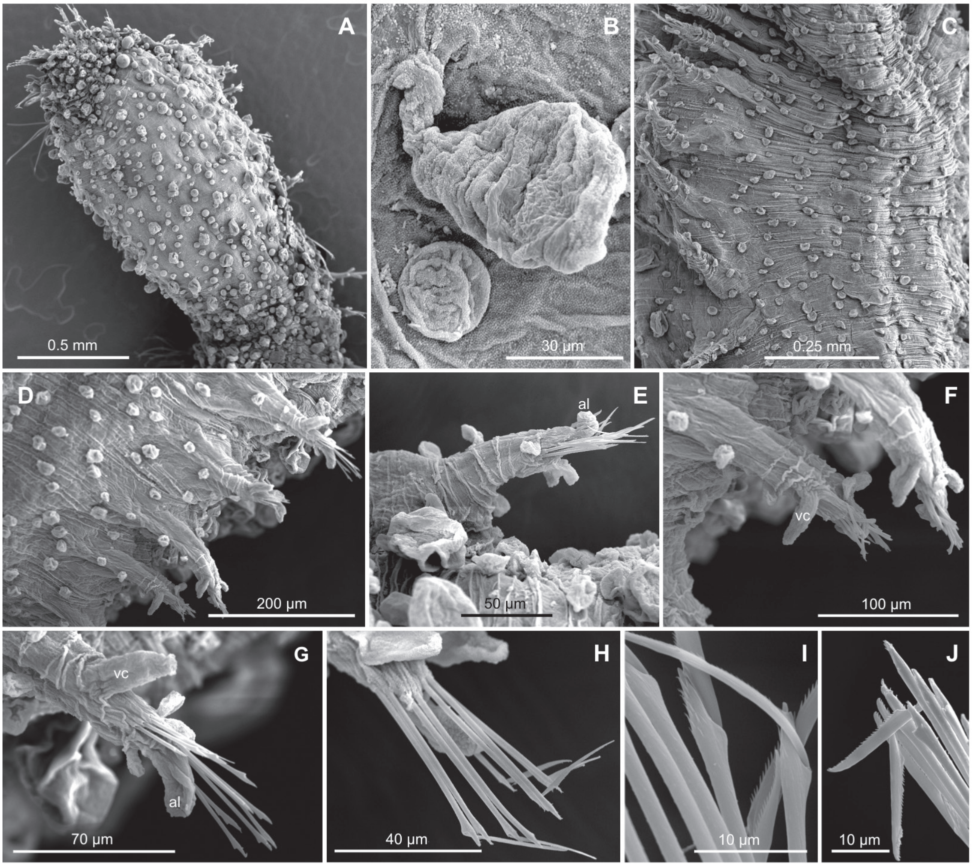

Figure 26. *Sphaerodoridium celiae* sp. n. (IINH 38795), scanning electron micrographs. **A** Anterior end, dorsal view **B** macrotubercle and stalk, detail **C** mid-body chaetigers, ventral view **D** parapodia, mid-body chaetigers, ventral view **E** parapodium, mid-body chaetiger, dorsal view **F** parapodia, mid-body chaetigers, ventro-lateral view **G** parapodium, mid-body chaetigers, detail of ventral cirrus and chaetae disposition **H** chaetal fascicle, mid-body chaetiger **I** chaetae, detail of shaft **J** chaetae, detail of blades.

Pygidium. Pygidium terminal, with one mid-ventral digitiform anal cirrus projecting beyond last parapodia, flanked by four spherical papillae (2+2) and one pair of clavate anal cirri at base (Fig. 25K).

Internal features. Eyes not discernible in holotype. Pharynx extending over three chaetigers.

Reproductive features. Sexual structures or genital pores not observed in holotype. Several oblong eggs visible by transparency ca. 170 µm in length.

Variation. Paratypes measuring 1.1–6.0 mm long, 0.4–0.9 mm wide, with 16–30 chaetigers. Most specimens measuring ca. 2–4 mm in length, 0.4–0.7 mm in width with 20–25 chaetigers. Two dark dorsal eyes behind lateral antennae observed in many paratypes. Some variation occurring in number of papillae and spurs on head appendages: lateral antennae and palps with at least four spurs and tentacular cirri with two

Figure 27. Photographs of live specimens, dorsal view. **A** *Sphaerodoridium celiae* sp. n., from Skagerrak (ZMBN 125434, SPH 316) **B, C** *Sphaerodoridium* cf. *minutum* from the UK (ZMBN 127346 SPH 320, ZMBN 127347 SPH 321, respectively).

short papillae near base. Macrotubercles numbering 7–11 on first chaetiger and usually 10–12 in mid-body. Small papilla at base of macrotubercle stalk not distinguished in all specimens, not related to size or degree of contraction of stalks or body. Short stalk of body papillae (dorsum and ventrum) not always distinguished. Variation in number and distribution of body, ventrum, and parapodial papillae similar to holotype. Pharynx extending over 3–4 chaetigers. Sexual dimorphism not observed in paratypes or additional material examined; several females with oocytes observed.

Remarks. *Sphaerodoridium celiae* sp. n. is characterized by the unique combination of following features: head appendages with up to ten spurs or basal papillae, 10–12 stalked macrotubercles per mid-body chaetiger, many body papillae among rows of macrotubercles (up to 50 per chaetiger), ventrum of each mid-body chaetiger with at least 20 papillae, and chaetae with blades up to 8–9 times as long as wide.

Sphaerodoridium cf. *minutum,* from European waters (see below), also presents a similar range of variation in the number of macrotubercles, many dorsal additional papillae between consecutive rows of macrotubercles and ca. 20 papillae per chaetiger on ventrum. However, *Sphaerodoridium celiae* sp. n. bears more dorsal papillae per chaetiger showing a more "crowded" appearance (up to 50–60) and parapodial papillae are more numerous (7–8 vs. 3). *Sphaerodoridium guerritai* is also similar to *Sphaerodoridium* celiae sp. n. in general body appearance and size but dorsal body papillae are less numerous being dorsal side of chaetigers more "smooth"; stalk of macrotubercles are usually provided with at least a small papilla (sometimes up to three) while in *Sphaerodoridium celiae* sp. n. the presence of the only papilla is more variable across specimens or at least harder to distinguish. The number of parapodial papillae is similar between both species but they differ in their distribution, mostly in the presence in *S. guerritai* of one papilla on the anterior lateral surface that is lacking in *Sphaerodoridium celiae* sp. n.; the former presents, in turn, one anterior papilla that is present instead on the dorsal surface (cf. Fig. 5U).

The three species recently described from Arctic waters (*S. evgenovi* Gagaev, 2015; *S. kolchaki* Gagaev, 2015; *S. kupetskii* Gagaev, 2015) also present up to 10–14 macrotubercles per chaetiger and dorsal body papillae. However, the original description does not mention explicitly how many papillae are between two consecutive rows of macrotubercles. Furthermore, the drawings of the stalk of the macrotubercles of the three species show a small basal papilla that is not mentioned in the description, and is similar to that present in *S. guerritai* and *Sphaerodorodium celiae* sp. n. The aforementioned species differ, however, from *Sphaerodoridium celiae* sp. n. in the number and distribution of parapodial papillae (only 2–3). On the other hand, Gagaev (2015) characterizes *S. evgenovi*, *S. kolchaki* and *S. kupetskii* according to the relative length of anal cirri, macrotubercle stalk and body length but these characters may show variation according to the state of contraction of specimens. Otherwise, they are morphologically close to *S. guerritai* and a comparative review of the four species would be desirable (Capa et al. 2016b).

Etymology. This new species is dedicated to Celia Moreira, in regard of her support and friendship to her brother, JM.

Distribution. Around Iceland and coastal Norwegian waters from the Skagerrak in the south to Finnmark in the north.

Habitat. Soft bottoms, from gravelly sand to silt, at depths of 120–2074 m.

Sphaerodoridium claparedii (Greeff, 1866)

Fig. 5V, 23G, H, 28

Sphaerodorum claparedii Greeff, 1866: 338–350, Taf 6. figs 1–14. Southern 1914: 89–90; Fauvel 1923: 379–380; Amoureux et al. 1978: 88.

Sphaerodoridium claparedii Lützen, 1961: 415; Fauchald 1974: 270. ? Campoy 1982: 464–465; ? Moreira 2012: 26–28, Fig. 5; ? Wehe and Fiege 2002: 138.

Type locality. Dieppe, France, English Channel.

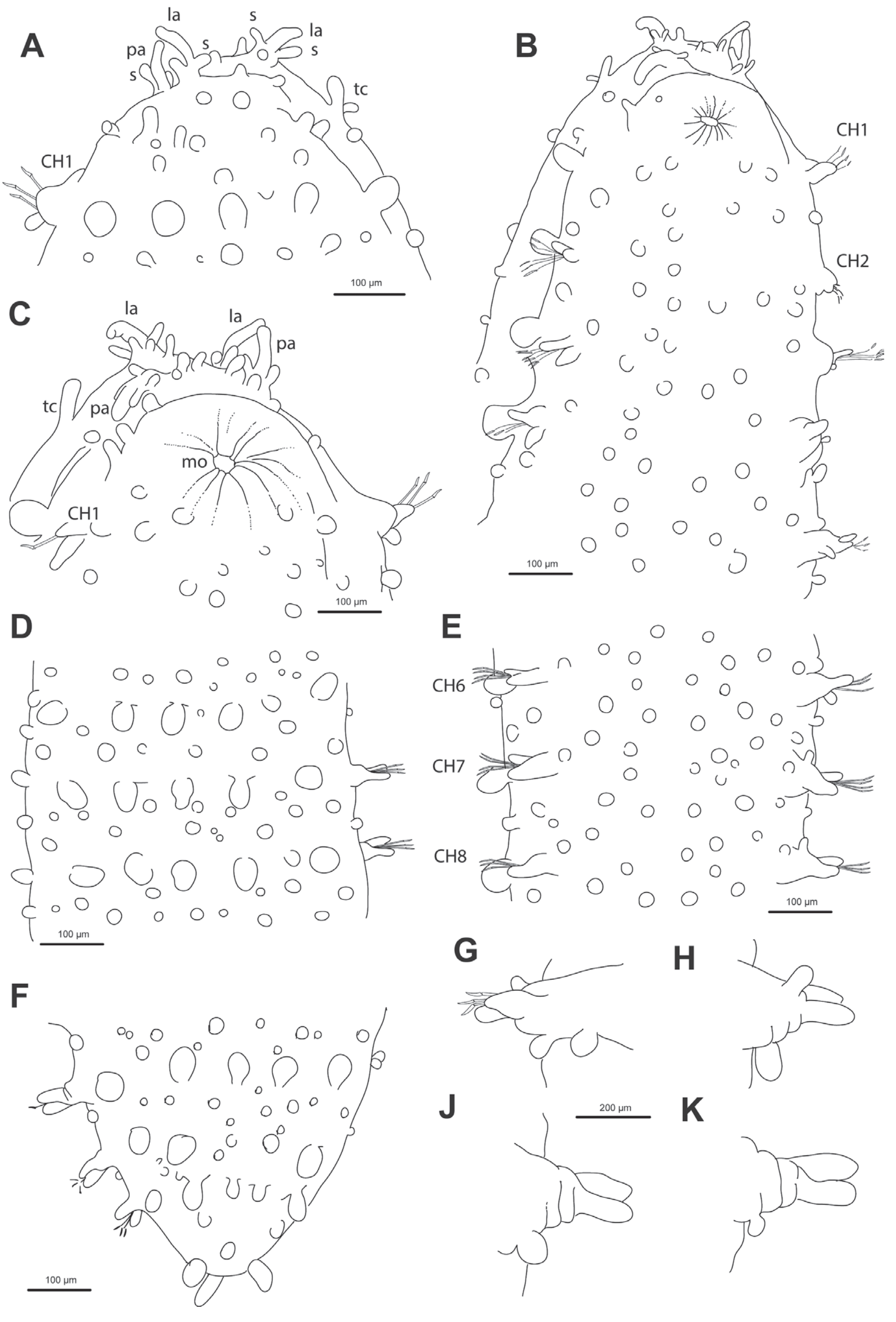

Figure 28. *Sphaerodoridium claparedii*, line drawings (MNINH 1908.77.31). **A** Anterior end, dorsal view **B** anterior end, ventral view, detail **C** detail of anterior end, ventral view **D** mid-body chaetigers, dorsal view **E** same, ventral view **F** posterior end, dorsal view **G** chaetiger 5, left side, dorsal view **H** chaetiger 5, right side, ventral view **I** chaetiger 6, left side, dorsal view **K** chaetiger 8, left side, dorsal view

Material examined. (3 specs). **Ireland**: NMINH: 1908.77 (1 spec.), St. Ballynakill xxviii, 0.2 m, 10 Apr 1899; NMINH:1914.313 (1 spec.), St. W236, Blacksod Bay, Co. Mayo, 1.8 m, on 25 Sept 1911; NMINH:1914.313, (1 spec.) Station W181, Blacksod Bay, Co. Mayo, 5.5 m, on 15 Mar 1911.

Diagnosis. Body ellipsoid. Prostomial appendages digitiform, elongated. Median antenna smooth, shorter than lateral antennae. Lateral antennae similar in length to palps, with 3–4 basal papillae (spurs). Tentacular cirri digitiform, smooth, slightly shorter than lateral appendages. Dorsal macrotubercles stalked, smooth, arranged in eight longitudinal rows in mid-body chaetigers; stalk as long as or shorter than tubercle. Dorsum with additional 10–12 rounded papillae between transverse rows of macrotubercles somewhat arranged in a zig-zag pattern. Ventrum with 3–4 transverse rows of papillae per segment. Parapodia with digitiform, large ventral cirri, and acicular lobe; parapodia without papillae, or with a spherical papilla in anterior surface. Approximately six chaetae per parapodium, with short blades (ca. four times as long as wide).

Description of Irish material. *Measurements and general morphology.* Body ellipsoid, with rounded anterior and posterior ends, with convex dorsal surface and flat ventrum. Segmentation inconspicuous and pigmentation absent (Fig. 28A, B).

Head. Prostomium fused to first segment (Fig. 28A, B). Prostomial appendages including palps and lateral antennae similar in shape and size, digitiform and longer than wide, except for median antenna that is shorter and similar to other rounded prostomial papillae. Lateral antennae with 3–4 basal papillae or spurs (Fig. 28C). Tentacular cirri, similar in size and shape to prostomial appendages (Fig. 28B).

Tubercles. Dorsal macrotubercles, spherical, smooth, and with a short stalk, arranged in eight longitudinal rows from second chaetiger (six in first chaetiger), and one transverse dorsal row per chaetiger (Figs 23H, 28A, C, D). All macrotubercles similar in size. Approximately 10–12 spherical papillae per segment over dorsum (less in anterior and posterior segments), arranged in three irregular transverse rows (Fig. 28A, D). Ventral papillae hemispherical, arranged in four longitudinal rows (Fig. 28B).

Parapodia. Parapodia conical, slightly longer than wide (Fig. 28G–J). Ventral cirri digitiform, similar on shape and size to the acicular lobe (Fig. 28G–J). Parapodial papillae absent or in some parapodia, one spherical papilla in anterior surface, close to the base of parapodium (Figs 5V, 28G–J).

Chaetae. Four to six compound chaetae on each parapodium, with short and wide blades (ca. four times as long as wide), unidentate, finely serrated; all similar in size and shape. A single straight acicula per parapodium.

Pygidium. Pygidium with paired anal cirri resembling macrotubercles and medioventral digitiform anal papilla.

Internal features. Two dark eyes visible dorsally inside the head of holotype. Pharynx extending over two chaetigers.

Reproductive features. Not described. Sexual structures not observed in Irish material.

Variation. The species was described as bearing six rows of longitudinal and stalked macrotubercles (Fig. 23G). The number of longitudinal rows of macrotubercles counted in the Irish material is eight (Fig. 23H), but two of the lateralmost rows were difficult to assess given the strongly convex dorsum of specimens, that hide them below the animal, in specimens flattened by the microscopy slides (Fig. 28A, C). This could also be the case in the holotype. Some features were not addressed in the original description but found in the Irish specimens (Southern 1914). These are the presence of a short median antenna, and a pygidial median papilla. These attributes seem to be the norm in other sphaerodorids and therefore considered as present in *S. claparedii* comb. n. Irish specimens were smaller than the holotype, all (including mature adults) with less than 18 chaetigers and measuring up to 1.8 mm long. An important note on the variation observed among the studies reported in the literature concerns the number of ventral papillae. While the species was described with four transverse rows of papillae in the ventrum (Greeff 1866), the material collected in Claire Island has small papillae scattered in the ventrum, resembling the dorsal papillae (Southern 1914). Parapodia were described without papillae but in the Irish specimens, a spherical papilla is present in the anterior side of some parapodia.

Remarks. This species has only been reported twice, from Dieppe, France (Greeff 1866, original description), and Claire Island, Ireland (Southern 1914, complementary morphological features). There are reports of this species across European coasts (Atlantic and Mediterranean) and the Red Sea but no description was provided (e.g., Saldanha 1974, Amoureux et al. 1978, Méndez and Cardell 1996). For instance, Mòllica (1995) considers the presence of this species in Italy as doubtful.

Sphaerodoridium claparedii is distinguished from other congeners by the presence of only eight rows of stalked macrotubercles, a feature that is shared by *S. amoureuxi* comb. n. (if macrotubercles are considered with a short stalk), *S. campanulata* comb. n. and *S. guerritai*. *Sphaerodoridium guerritai* is clearly distinguished from *S. claparedii* in the presence of stalked macrotubercles with papillae prostomial appendages also with spurs, and 5–6 parapodial papillae. *Sphaerodoridium campanulata* comb. n. was described as bearing different sized bell-shaped macrotubercles, not arranged in clear longitudinal or transverse rows (Borowski 1994), unlike the turgid and in line dorsal tubercles of *S. claparedii*.

Distribution. English Channel and western coast UK. ? Atlantic coast of Iberian Peninsula, ? Mediterranean, ? Red Sea (Campoy 1982, Wehe and Fiege 2002).

Habitat. Among algae and shallow sediments (1–5 m). Also collected in planktonic samples (Southern, 1914).

Sphaerodoridium gudmunduri **(Moreira & Parapar, 2012), comb. n.**

Figs 5W, 23I, J, 29

Sphaerodoropsis gudmunduri Moreira & Parapar, 2012: 585–588, figs 1A, 2–3, 6A–C.

Type locality. Northwest Iceland, 66°33.95'N, 20°00.71'W, 97 m.

Material examined. (11 specs) **South Greenland:** ZMBN 127350 (5 spec.), 63°07'N, 52°17'W, 162.5 m, 06 Nov 2002; NTNU-VM 74199 (2 specs on SEM

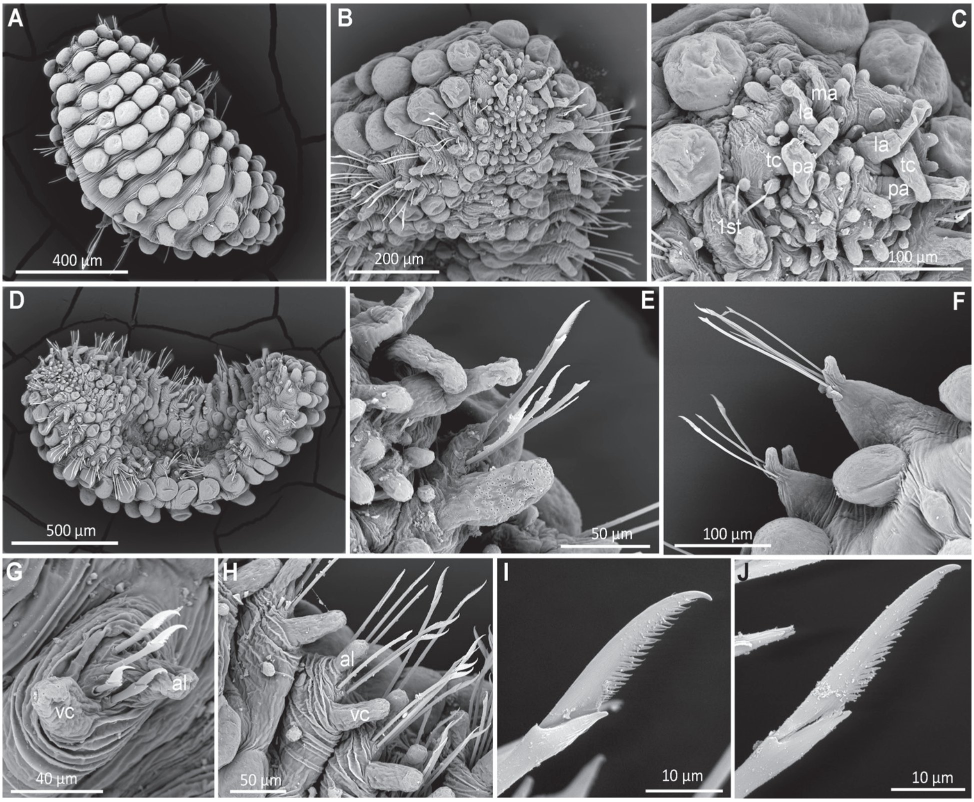

Figure 29. *Sphaerodoridium gudmunduri* (NTNU-VM 74199), scanning electron micrographs. **A** Complete specimen, dorsal view **B** anterior end, frontal view **C** detail of head, frontal view **D** complete specimen, ventral view **E** parapodium, chaetiger 1, anterior view **F** parapodium, anterior chaetiger, dorsal view **G** parapodium, mid-body chaetiger, side view **H** parapodia, mid-body chaetigers, anterior view **I, J** detail of chaetae, mid-body chaetigers.

stub), 63°07'N, 52°17'W, 162.5 m, 06 Nov 2002. **Norwegian Sea:** ZMBN 127349 (6 spec.) 64°26.1'N, 11°10.2'W, 400 m, 07 Jun 1983.

Diagnosis. Body short and ellipsoid, less than 2 mm long. Prostomial appendages smooth, lacking spurs. Median antenna as long or slightly shorter than other prostomial appendages. Lateral antennae, palps, and tentacular cirri of similar shape and length. Antenniform papillae absent. 8–12 longitudinal rows of large spherical and sessile macrotubercles in one transverse row per mid-body segment. Dorsum without papillae; ventrum with seven (♂) or 9 (♀) spherical papillae per segment. Parapodia with 1–4 papillae. Acicular lobe from chaetigers 3–4, digitiform. Ventral cirri digitiform, projecting well beyond acicular lobe. Compound chaetae with short blades (less than five times its maximum width), showing little dorso-ventral gradation; unidentate and fine spinulation along its cutting margin.

Remarks. This is the first report of this species from southern Greenland. Specimens show some minor variations to original description. The species was described with 20–25 chaetigers but specimens with less segments have been found (16–19, Fig. 29A), measuring 1.5–2 mm long, 0.5–0.8 mm wide, and with maximum number of macrotubercles in mid-dorsal segments of eight (Fig. 29A) instead of the 10–12 previously described (Moreira and Parapar 2012). This variation could be size related, since the specimens examined for this study are smaller and have less segments than those from original description. Females with small oocytes visible through epidermis. Males observed with a pair of digitiform and distally opened sexual structures between parapodia or segments 7–8 (Fig. 23J), as in original description (Moreira and Parapar 2012). Other diagnostic features are shared by the North East and South Greenland specimens.

Differences between this species and other congeners are the large, sessile, and spherical macrotubercles, arranged in one single transversal row of up to 12 per segment, and absence of any other dorsal papillae (Fig. 29A). Other members of *Sphaerodoridium* with sessile macrotubercles bear also additional papillae between transverse rows. In addition, *S. gudmunduri* comb. n. presents large papillae in ventrum, especially close to the lateral edges, nearby the parapodia (Fig. 29D). All other *Sphaerodoridium* bear smaller ventral papillae.

Distribution. From East Iceland to South Greenland, Norwegian Sea (Moreira and Parapar 2012, present study).

Habitat. Silty sand, at depths of 88–400 m (Moreira and Parapar 2012, this study).

Sphaerodoridium guerritai Moreira & Parapar, 2015

Figs 5X, 23K, L

Sphaerodoridium guerritai Moreira & Parapar, 2015: 93–103, figs 1–6.

Type locality. Northern Iceland, 67°16.86'N, 16°37.77'W, 600 m.

Material examined. (51 specs) **Iceland**, SMF 25299 (8 specs), North-East Iceland, Norwegian Sea, 66°32.63'N, 012°52.48'W, 317,2 m; SMF 23900 (1 spec. used for DNA sequencing SPH 058), North-East Iceland, Norwegian Sea, 66°32.63'N, 12°52.48'W, 317,2 m; SMF 24845 (1 spec. used for DNA sequencing, SPH 059), North-East Iceland, Norwegian Sea, 66°32.63'N, 12°52.48'W , 317,2 m; **Svalbard**, NTNU-VM 73794 (2 specs), Svalbard, Hinlopen, 79°43.1'N, 18°19.9'E, 433 m, 17 Aug 2003; NTNU-VM 73795 (1 spec.), Svalbard, Hinlopen trench, 80°23.8'N, 16°11.9'E, 420 m, 29 Aug 2003; ZMBN 127357 (3 specs), 80°9.144'N, 16°56.124'E, 340 m, 28 Aug 2009; ZMBN 127356 (1 spec. SPH278), 80°9.144'N, 16°56.124'E, 340 m, 28 Aug 2009; ZMBN 127358 (1 spec. used for DNA sequencing, SPH 327), 80°9.144'N, 16°56.124'E, 340 m, 01 Sep 2009; **Norwegian Sea**: ZMBN 127351 (9 specs), 62°29.5'N, 01°43.3'E, 604 m, 21 Jan 1982; ZMBN 127352 (2 specs), 62°35.1'N, 1°47.6'E, 656 m, 23 May 1984; ZMBN 127353 (9 specs), 63°02.9'N, 00°47.8'E, 1293 m, 12 Jan 1985; ZMBN 127354 (1 spec.), 62°50.6'N, 1°25.9'E, 951 m, 15 Aug 1986; ZMBN, 127355 (>10 specs), 63°2.23'N, 4°41.34'E, 760 m, 30 Sep 2013; SMF 25300 (1 spec.), East Iceland, 66°18.060'N 012°22.380'W, 730,8 m, 22 Sep 2011.

Diagnosis. Body ellipsoid, up to 8 mm long. Median antenna and prostomial appendages digitiform, elongated. Median antenna smooth, near half of length of lateral antennae. Lateral antennae longer than palps, with 6–10 basal papillae (spurs). Antenniform papillae absent. Tentacular cirri digitiform, with two elongated papillae on proximal third. Dorsal macrotubercles stalked, without terminal papilla, arranged in 11–12 longitudinal rows in mid-body chaetigers; stalk as long as or slightly longer than tubercle, with 1–3 small papillae along proximal half. Dorsum with additional 10–16 hemispherical spherical papillae in front of each row of macrotubercles, somewhat arranged in two irregular transverse rows following a zig-zag pattern. Ventrum with 10–18 papillae per chaetiger, arranged in three more or less defined transverse rows. Parapodia with digitiform acicular lobe from chaetiger 3; large ventral cirri, not surpassing the length of acicular lobe; midbody parapodia with 5–6 papillae. Chaetae blades showing gradation in length within and between chaetigers, slightly shorter in mid-body to posterior chaetigers; ca. six times longer than maximum width.

Remarks. The description of this species is complete and no amendments or comments are needed.

Distribution. First record of the species in Svalbard and Norwegian Waters. Already reported around Iceland (Moreira and Parapar 2015).

Habitat. Mostly in muddy sediments (sandy silt and silt), 49–1253 m depth (Moreira and Parapar 2015, present study).

***Sphaerodoridium* cf. *minutum* (Webster & Benedict, 1887)**

Figs 5Y, 23M, N, 27B, C, 30

Ephesia minuta Webster & Benedict, 1887: 728–729, pl. IV, figs 64–66.
Sphaerodoropsis minuta.– Imajima 1969: 153–154, fig. 2; Hartmann-Schröder 1996: 237; Moreira 2012: 39–41, fig. 13.
Sphaerodorum minutum.– Berkeley and Berkeley 1948: 27–28, fig. 34.
Sphaerodoridium minutum.– Lützen 1961: 415; Capa et al. 2016b: 19–23, fig. 7.

Type locality. Off Maine, United States, North Atlantic Ocean, shelf depths.

Material examined. Lectotype: USNM 393, Eastport, Maine, United States, North Atlantic Ocean, coll. Webster, H. E; **Paralectotypes**: USNM 1407984 (11 specs and 4 slides), Eastport, Maine, United States, North Atlantic Ocean, coll. Webster, H. E. Paratypes: USNM 22873 (29 specs, 3 for SEM) Eastport, Maine, United States, North Atlantic Ocean, coll. Webster, H. E.

Additional material. (13 specs) **South Greenland**, ZMBN 127345 (1 spec.), 63°21'N, 52°35'W, 105,5 m, 07 Nov 2002; **Svalbard**, ZMBN 127344 (1 spec. for DNA sequencing SPH277), 79°43.434'N, 11°5.55'E, 216 m, 27 Aug 2009; **Barents Sea**, ZMBN 129500 (1 spec. in SEM stub), Finnmark, 71°20.262'N, 25°13.17'E, 297 m, 23 Apr 2011. **Great Britain**: ZMBN 127346 (1 spec. for DNA sequencing SPH 320), Plymoouth, Mount Sant Michelle, 50°7.148'N, 5°28.419'W, 15 m, 16 Mar

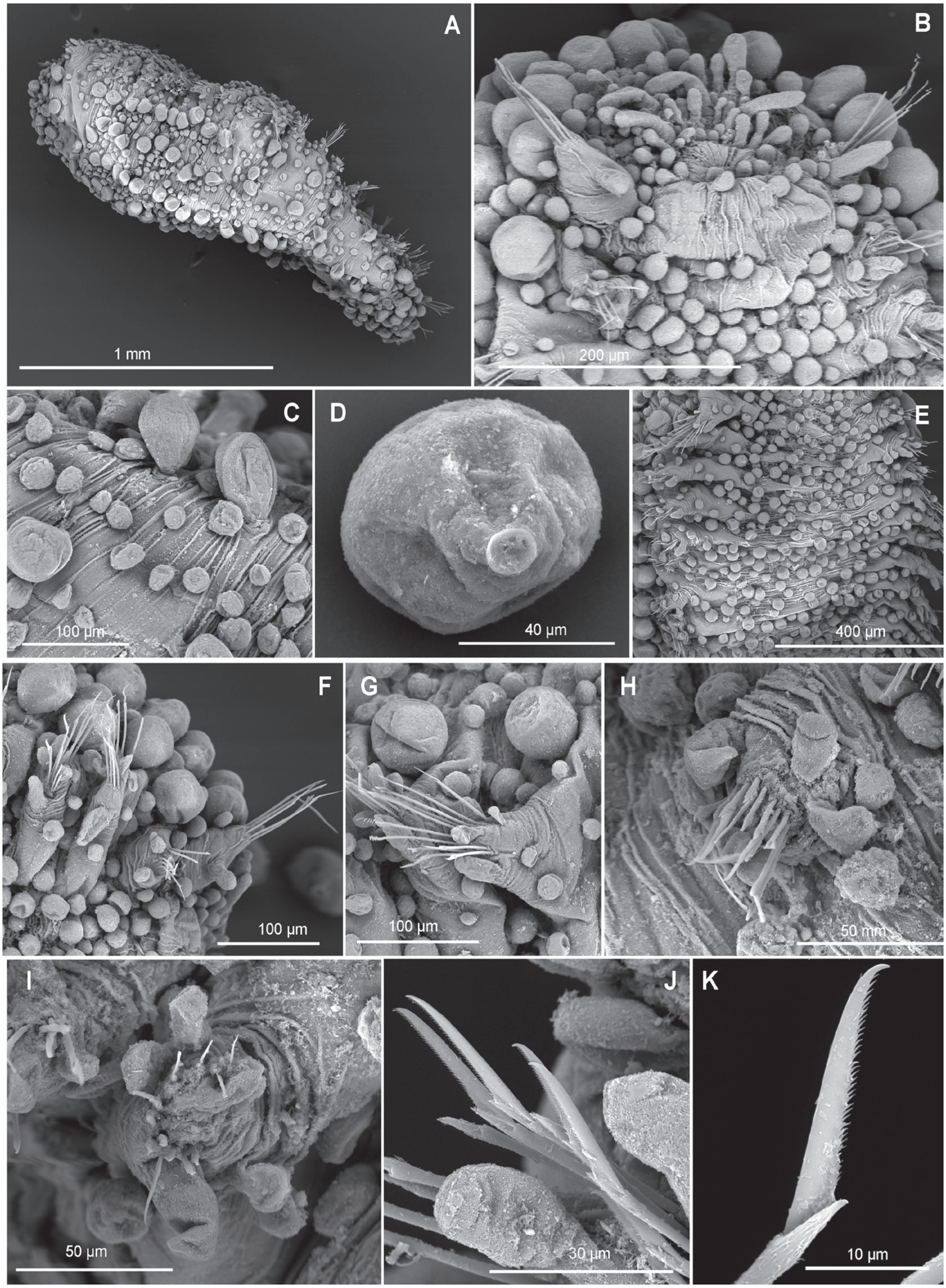

Figure 30. *Sphaerodoridium* cf. *minutum*, from Barents Sea (ZMBN 129500), scanning electron micrographs. **A** Complete specimen, dorsal view **B** anterior chaetigers, ventral view **C** dorsal macrotubercles (slightly stalked) and epithelial papillae, mid-body chaetigers **D** detached macrotubercle, showing short peduncle **E** ventral papillae, mid-body chaetigers **F** parapodia, chaetigers 1–4, side view **G** parapodium, chaetiger 5, anterior view **H** parapodium, chaetiger 3, posterior view **I** parapodium, chaetiger 5 **J** chaetal fascicle, mid-body chaetiger **K** chaetae, detail.

2011; ZMBN 127347 (1 spec. for DNA sequencing SPH 321), The Sound, Plymoouth, 50°21.5'N, 4°8.9'W, 15 m, 16 Mar 2011; ZMBN 127348 (1 spec. for DNA sequencing SPH 322), The Sound, Plymoouth, 50°21.5'N, 4°8.9'W, 15 m, 16 Mar 2011.

Diagnosis. Body short and ellipsoid. Prostomial appendages digitiform, smooth, lacking spurs; median antenna as long as or slightly shorter than other head appendages. Antenniform papillae absent. Ten to twelve longitudinal rows of spherical and stalked macrotubercles in one transverse row per segment, in mid-body segments. Additional spherical papillae arranged in three transverse rows per segment, in dorsum and ventrum. Parapodia with acicular lobe from chaetiger 3, digitiform; ventral cirri digitiform, projecting well beyond acicular lobe; four spherical parapodial papillae. Compound chaetae with medium length blades (6–7 times as long as wide), showing little dorso-ventral gradation.

Description of NEA material. *Measurements and general morphology.* Body with oval contour strongly convex dorsum and flat ventrum. Size range of material examined 20–27 chaetigers; 2–5 mm long; 0.8–0.9 mm wide. Segmentation not distinct. Pigmentation absent in live or fixed material (Figs 27B, C, 30A).

Head. Prostomium with five short and digitiform appendages, including a pair of palps and lateral antennae, similar in size and shape, and a shorter median antenna (Fig. 30B). Tentacular cirri shorter than lateral antennae and palps. A few rounded small papillae scattered around head appendages (Fig. 30B).

Tubercles. First chaetiger with eight dorsal macrotubercles; following chaetigers each with one transverse row of dorsal macrotubercles increasing to 10–12 tubercles per segment from chaetiger 5 (Fig. 23M). Macrotubercles spherical to club-shaped with a short and smooth stalk (Fig. 30C, D); all macrotubercles similar in shape and size. Additional spherical and sessile papillae in different sizes over dorsum, arranged in 2–3 irregular transverse rows per chaetiger; 20–30 papillae on each mid-body chaetiger (Fig. 30A, C). Ventral surface with spherical papillae in different sizes, arranged in 2–3 transverse rows in a zig-zag pattern, with ca. 20 per segment in mid-body (Fig. 23N); numbers decreasing towards posterior end (Fig. 30E, F).

Parapodia. Parapodia sub-conical, increasing in size towards chaetiger 3, ca. 2 times longer than wide (Fig. 30F, G). Acicular lobe anterior to chaetae, digitiform to clavate, longer than parapodial papillae and projecting distally (Fig. 30G, H). Ventral cirri digitiform projecting 1/2 to 2/3 as long as acicular lobe on anterior and mid-body segments, almost as long as in posterior segments (Fig. 30 F–I). Parapodia with three spherical to clavate papillae: one on antero-dorsal surface, one on antero-basal position, and one on the posterior surface (Fig. 30 F–I).

Chaetae. All parapodia with 4–7 compound chaetae, arranged in a curved transverse row around acicular lobe (Fig. 30G–I). Serrated, long blades, 4–5 times longer than maximum width, with a curved tip (Fig. 30J, K), similar throughout.

Pygidium. Pygidium terminal, with one mid-ventral digitiform anal cirrus projecting beyond parapodia, and one pair of clavate anal cirri, at base on median cirrus.

Internal features. Specimens are all opaque after fixation and preservation and internal features not observable.

Reproductive features. Sexual structures or eggs not seen in type specimens.

Remarks. *Sphaerodoridium minutum* (as re-described by Capa et al. 2016b) is characterized by having up to 10–12 macrotubercles in mid-body, a parapodium that bears three (sometimes four) parapodial papillae and compound chaetae with blades 4–5 times as long as maximum width on mid-body chaetigers. Furthermore, the macrotubercles have a short stalk that was overlooked until Capa et al. 2016b reported their morphology. This species was originally described from NW Atlantic coasts (Webster and Benedict 1887) and since then has been reported worldwide (see Capa et al. 2016b for a comparison with related species). However, it is likely that many records from other oceans might refer to other similar, yet undescribed species. Specimens examined from NE Atlantic reported here differ from those of NW Atlantic in having chaetae with slightly longer blades (6–7 times as long as wide) and four parapodial papillae. They might represent a new species but to truly assess this possibility more material from other European localities (both Atlantic and Mediterranean) should be examined. Anyway, NE Atlantic specimens could be distinguished from *S. celiae* sp. n. and *S. guerritai* because the latter bear prostomial appendages with spurs, the stalk of the macrotubercles are longer and parapodia are provided with more papillae (6–7 and 7–8 respectively).

Distribution. Reported as a common species in the North Atlantic and Arctic. However, some records should be reviewed as they could be misidentifications (e.g., Moreira 2012).

Habitat. Shelf or slope depths (Moreira 2012, Capa et al. 2016b).

Identification key to genera and NEA sphaerodorid species

1 Body elongate, with somewhat parallel sides (except for blunt anterior and tapering posterior ends). Two longitudinal rows of dorsal macrotubercles (large tubercles) with terminal papilla (one pair per segment) **2**

– Body ellipsoid (sometimes elongate). Dorsal tubercles different **3**

2 Parapodia with only simple chaetae .... ***Sphaerodorum***

– Parapodia with only compound chaetae (except of, sometimes chaetiger 1) .... ***Ephesiella***

– Parapodia with both compound and simple chaetae .... ***Ephesiopsis***[*]

3 Dorsum with four longitudinal rows of sessile macrotubercles, in a single transverse row per segment **4**

– Dorsum with more than four longitudinal rows of tubercles **5**

4 All chaetae simple, unidentate, enlarged subdistally. Macrotubercles and dorsal papillae small, most of dorsal surface smooth .... ***Commensodorum commensalis***

– All chaetae compound. Large macrotubercles, covering most of dorsal surface. Additional papillae often present… *Sphaerephesia* **12**

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[*] Not reported in NEA waters

5 Dorsal macrotubercles stalked, without terminal papilla, arranged in up to six longitudinal rows, one transverse row per segment…. *Clavodorum* **6**

– Dorsal macrotubercles (sometimes not clearly larger than other dorsal papillae) stalked or sessile, arranged in more than six longitudinal rows or in more than one transverse row per segment..7

6 Dorsum with additional 10–12 papillae per segment, in two irregular transverse rows, following a zig-zag pattern. One or two parapodial papillae .... ***Clavodorum fauchaldi***

– Dorsum with additional epithelial papillae other than the six longitudinal rows of macrotubercles absent. Three parapodial papillae............................. ....***Clavodorum kristiani*** **comb. n., nom. n.**

7 Dorsal tubercles small and of similar size (difference in size between them less than twice), in several transverse rows per segment. All chaetae simple unidentate, enlarged subdistally… *Euritmia*...**8**

– Dorsal tubercles include macrotubercles and papillae (less than half of the size of macrotubercles) **9**

8 Dorsal tubercles in four irregular transverse rows per segment. Parapodia with a large dorsal papilla...***Euritmia hamulisetosa***

– Dorsal tubercles in three irregular transverse rows per segment. Parapodia without papilla..***Euritmia nordica*** **sp. n.**

9 Tubercles sessile, arranged in two transverse rows per segment *Geminofilum* gen. n.. **10**

– Tubercles sessile or stalked, arranged in one single transverse row per segment *Sphaerodoridium* **19**

10 Dorsal macrotubercles sessile, hemispherical, arranged in two transverse rows per segment, with five and six macrotubercles each, from segment 2.........**11**

– Dorsal macrotubercles sessile, almost spherical, arranged in two transverse rows per segment, with six and seven macrotubercles each, from segment 3............ .... ***Geminofilum halldori*** **comb. n.**

11 Dorsum with 4–6 additional papillae per segment in mid-body. Parapodia without papillae.................................... ***Geminofilum distichum*** **comb. n.**

– Dorsum with additional five papillae per segment in mid-body. Parapodia with one papilla on anterior surface .... ***Geminofilum garciaalvarezi*** **comb. n.**

12 Dorsal macrotubercles hemispherical, clearly wider than high...................... .... ***Sphaerephesia martinae*** **comb. n.**

– Dorsal macrotubercles spherical, pear-shaped or with a terminal papilla........**13**

13 ?Dorsal papillae star-shaped...***Sphaerephesia stellifer*** **comb. n., nomen dubium**

– Dorsal papillae rounded (spherical, hemispherical, ellipsoid) **14**

14 Parapodia with more than 10 papillae..**15**

– Parapodia with less than 10 papillae..**16**

15 Parapodia with ca. 12–14 papillae. Compound chaetae, 10–15, with medium length blades (ca. 6–8 times as long as wide).....***Sphaerephesia laureci*** **comb. n.**

– Parapodia with 20–40 spherical papillae. Compound chaetae, up to 40, with medium length blades (3–8 times as long as wide) .... ***Sphaerephesia multichaeta* sp. n.**

– Parapodia with ca. 16–19 papillae. Chaetae, 20–25, with long blades (9–13 times as long as wide) .... ***Sphaerephesia sibuetae* comb. n.**

16 Parapodia with more than five papillae **17**

– Parapodia with less than five papillae **18**

17 Parapodia with 7–8 papillae, larger papilla in dorso-distal position. Approximately 20–25 compound chaetae with long blades (ca. 8–12 times as long as wide) .... ***Sphaerephesia longipapillata* comb. n.**

– Eight to ten parapodial papillae. Approximately eight compound chaetae with medium length blades (ca. ten times as long as wide) .... ***Sphaerephesia philippi* comb. n. (inc. *Sphaerephesia* sp. 1)**

18 Parapodia with 3–4 sub-equal papillae. Compound chaetae with long blades (8–20 times as long as wide) .... ***Sphaerephesia artabrensis* comb. n.**

– Parapodia with four papillae. Ventral cirri digitiform reaching tip of acicular lobe. About eight compound chaetae with medium length blades (ca. 7–9 times as long as wide); unidentate .... ***Sphaerephesia ponsi* sp. n.**

19 Dorsal macrotubercles sessile **20**

– Dorsal macrotubercles stalked **22**

20 Dorsum with additional papillae between transverse rows of macrotubercles **21**

– No additional papillae covering dorsum .... ***Sphaerodoridium gudmunduri* comb. n.**

21 Lateral antennae with 6–8 spurs..... ***Sphaerodoridium amoureuxi* comb. n.**

– Lateral antennae with 3–4 spurs......... ***Sphaerodoridium balticum* comb. n.**

22 Eight macrotubercles in mid-body segments .... ***Sphaerodoridium claparedii* comb. n.**

– Ten to 12 macrotubercles in mid-body segments **23**

23 Lateral antennae and palps with spurs. Dorsal macrotubercles with stalk about half as long as tubercle, with 0–1 small papilla on proximal half. Parapodia with 7–8 papillae. Chaetae with blades about 8–9 times longer than wide .... ***Sphaerodoridium celiae* sp. n.**

– Lateral antennae and palps with spurs. Dorsal macrotubercles with stalk as long as or slightly longer than tubercle, with 1–3 small papillae along proximal half. Parapodia with 5–6 papillae. Chaetae with blades ca. six times longer than wide .... ***Sphaerodoridium guerritai***

– Prostomial appendages lacking spurs. Dorsal macrotubercles with stalked shorther than tubercle, without basal papillae. Parapodia with four spherical parapodial papillae. Chaetae with blades 6–7 times as long as wide .... ***Sphaerodoridium* cf. *minutum***

Summary and discussion

The North East Atlantic holds a large diversity of species belonging to the family Sphaerodoridae compared with other worldwide regions (26 before this study, 22 of which are regarded as short-bodied forms). This is probably due to historic and economic reasons: European taxonomists have been thoroughly working along the coastline and in deeper waters for more than two centuries. Seven of these species were described after 2000 (Moreira et al. 2004, Aguirrezabalaga and Ceberio 2005, Moreira and Parapar 2007, 2012, 2015). This is related to the number of contemporary expeditions in this geographic area, focusing on continental shelf and slope environments, where sphaerodorids seem to be most abundant (Fauchald 1974, Borowski 1994, Capa et al. 2014). However, there was still material waiting to be studied in museum collections and other institutions that has nurtured the present project.

The present integrative taxonomic study, including morphological examination and DNA analyses of specimens, has allowed us to assess the presence of 25 species of short-bodied sphaerodorids including four new species: *Euritmia nordica* Capa & Bakken, sp. n., *Sphaerephesiamultichaeta* Capa, Moreira & Parapar, sp. n., *Sphaerephesia ponsi* Capa, Parapar & Moreira, sp. n., and *Sphaerodoridium celiae* Moreira, Capa & Parapar, sp. n. In addition, the synonymisation of *S. chardyi* is herein proposed and the presence of *S. parva* in the area (Desbruyères 1980) has not been confirmed.

Some of the most revealing outcomes of the present study are the results obtained after analyses of the DNA sequences of selected specimens. After some recent papers, the family Sphaerodoridae was regarded to contain six genera (Capa et al. 2016b), although there was indication that some of them (at least *Sphaerodoridium* and *Sphaerodoropsis*) were not monophyletic (Capa et al. 2016a). The analyses carried out herein are far from being a comprehensive revision of the family, but they allow confirming paraphyly of most of the groups equivalent to genus level in current classification (Read and Fauchald 2018) and involve nomenclatural changes to accommodate these results.

The phylogenetic hypothesis presented herein, is congruent with that presented by Capa et al. (2016), with *Sphaerodoropsis* and *Sphaerodoridium* (*sensu* Read & Fauchald, 2018) being paraphyletic, but since it increases the number of taxa considered, offers more details regarding the relationships and content of some groups. The results also impulses the erection of a new genus to accommodate the species previously considered as *Sphaerodoropsis* with two transverse rows of dorsal macrotubercles per segment herein named as *Geminofilum* gen. nov. Nevertheless, further analyses considering type species of traditional genera are required in order to confirm the diagnosis and delimitation of these groups. Incorporation of members of *Euritmia* and *Sphaerodoropsis* Group 4 (according to Borowski 1994) will also allow to test their position in the sphaerodorid radiation and if they are closely related, as suggested by Capa et al. (2016b).

The newly proposed classification suggests that the main feature characterising genera is the number of longitudinal and transverse rows of dorsal macrotubercles, and not so much the shape of these macrotubercles (as per Fauchald 1974).

Acknowledgements

This study would have been unfeasible without the access to the material hosted by different institutions and the colleagues who collected, processed, and curated those samples. In this regards, we would like to thank collection managers and curators from NTNU University Museum, Norwegian University of Science and Technology, Trondheim, Natural History Collections, University of Bergen; Akvaplan-Niva, Tromsø; Museo Nacional de Ciencias Naturales, Madrid; Museo de Historia Natural, Universidade de Santiago de Compostela; Museum National d'Histoire Naturelle, Paris; Zoological Museum Hamburg, Hamburg; Deutsches Zentrum für Marine Biodiversitätsforschung (DZMB), Hamburg; Senckenberg Museum and Research Institute (SMF), Frankfurt; National Museum of Ireland; Icelandic Institute of Natural History, Reykjavik; and Natural History Museum of Denmark, University of Copenhagen. Scanning electron micrographs were taken at Museo Nacional de Ciencias Naturales de Madrid, Servizos de Apoio á Investigación-SAI (Universidade da Coruña, Spain) and at Cellular & Molecular Imaging Core Facility (NTNU). We would like to thank Jerry Kudenov and Greg Rouse for suggested improvements and enthusiastic feedback about the manuscript. Financial support was provided to MC by ForBio Research School, funded by the Research Council of Norway (project no. 248799) and the Norwegian Taxonomy Initiative (project no. 70184215) and by the Ramón y Cajal program (RYC-2016-20799) funded by the Spanish Ministerio de Economía, Industria y Competitividad, Agencia Estatal de Investigación, Comunidad Autónoma de las Islas Baleares and the European Social Fund. The Norwegian Taxonomy Initiative provided financial support to AN (knr 49-13, pnr 70184228), to TB (knr 53-09, pnr 70184216, knr 55-12, pnr 70184227); and by the Swedish Taxonomy Initiative [https://www.artdatabanken.se/en/the-swedish-taxonomy-initiative/] (dnr 140/07 1.4 and 166/08 1.4), to AN. Collections at MNCN and MNHN were visited by MC thanks to the European Commission Taxonomic Initiative SYNTHESYS (ES-TAF-2839, ES-TAF-7033, and FR-TAF-2644), SEM work was partially funded by Fauna Ibérica: Polychaeta VI (CGL2014-53332-C5-3-P). Publication fees were covered by NTNU Publishing Fund to MC.

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ZooKeys 845: 99–117 (2019)
doi: 10.3897/zookeys.845.33566
http://zookeys.pensoft.net

RESEARCH ARTICLE

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Two new species of the genus *Symphylella* (Symphyla, Scolopendrellidae) from Tibet, China

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Academic editor: *Pavel Stoev* | Received 1 February 2019 | Accepted 21 March 2019 | Published 15 May 2019

http://zoobank.org/2C4523C4-4097-4904-8797-D03F55DD47D9

Citation: Jin Y-L, Bu Y, Jiang Y (2019) Two new species of the genus *Symphylella* (Symphyla, Scolopendrellidae) from Tibet, China. ZooKeys 845: 99–117. https://doi.org/10.3897/zookeys.845.33566

Abstract

The Symphyla of Tibet are studied for the first time. *Symphylella macropora* **sp. n.** and *Symphylella zhongi* **sp. n.** from southeastern Tibet are described and illustrated. *Symphylella macropora* **sp. n.** is characterized by large, elongated oval openings of the Tömösváry organ with its inner margins covered by minute irregular teeth, rudimentary spined sensory organs present on the dorsal side of most antennal segments, and cerci with numerous long and slightly curved setae. *Symphylella zhongi* **sp. n.** is characterized by a globular Tömösváry organ with a small and roundish opening, mushroom-shaped sensory organs present on apical antennal segments, and by having tergal processes longer than their basal width with ovoid swollen ends. The newly described species are compared to the morphologically closest congeners: *S. javanensis*, *S. asiatica*, *S. multisetosa*, and *S. simplex*. A key for 43 species of the genus is also provided.

Keywords

Chaetotaxy, key, Myriapoda, sensory organ, taxonomy, Tömösváry organ

Introduction

Knowledge of the myriapod class Symphyla from China is poor. Only two species have been recorded until now: *Hanseniella caldaria* (Hansen, 1903) from Zhejiang province and *Scolopendrellopsis glabrus* Jin & Bu, 2018 from Zhejiang and Hainan provinces

(Zhang and Wang 1992; Bu and Jin 2018; Jin and Bu 2018). There are no records of Symphyla from Tibet so far.

During an investigation of soil arthropods in southeast Tibet in November 2015, plenty of specimens of the family Scolopendrellidae were obtained. Among them, two new species of the genus *Symphylella* Silvestri, 1902 were identified and are described here.

Materials and methods

Specimens were collected by Berlese-Tullgren funnels and preserved in 80% ethanol. They were mounted under slides using Hoyer's solution and dried in an oven at 60 °C. Observations were performed under a phase-contrast microscope (Leica DM 2500). Photographs were taken by a digital camera installed on the microscope (Leica DMC 4500). Line drawings were done using a drawing tube. All specimens are deposited in the collections of Shanghai Natural History Museum (SNHM), Shanghai, China.

Abbreviations used in this paper: ***al***-anterolateral seta, ***as***-apical seta, ***bo***-bladder-shaped organ, ***co***-cavity-shaped organ, ***cs***-central seta, ***ibs***-inner basal seta, **is**-inserted seta, ***lms***-lateromarginal seta, ***mo***-mushroom-shaped organ, ***rso***-rudimentary spined sensory organ, ***so***-spined sensory organ.

Results

Taxonomy
Family Scolopendrellidae Bagnall, 1913

Genus *Symphylella* Silvestri, 1902

Type species: *Symphylella isabella* (Grassi, 1886)

Diagnosis. Central rod on head broken and distinct in both anterior and posterior portions. Antennae with 14–22 segments. Trunk with 17 tergites or fewer, with the first tergite vestigial. Triangular processes present on posterior margins of 13 tergites. Belts of longitudinal striae between processes absent. First pair of legs vestigial, as small protuberances with a few setae. Styli rudimentary. Coxal plates with sacs only present on 3rd–9th legs. Cerci relatively long, terminal area with transverse stripes, ending in a single long seta (Bagnall 1913; Szucsich and Scheller 2011).

Distribution. The genus *Symphylella* currently includes 47 extant subcosmopolitan species (Szucsich and Scheller 2011; Jin and Bu 2018). It has previously been recorded from China, but the species have never been identified (Zhang and Wang 1992).

Symphylella macropora **Jin & Bu, sp. n.**

http://zoobank.org/7AAA91E2-37AF-45CE-B14F-9433EBD3FF75
Figures 1, 2, Tables 1–3

Diagnosis. *Symphylella macropora* sp. n. is characterized by large, elongated oval openings of the Tömösváry organs, with their inner margins of these openings covered by minute irregular teeth, as well as by having rudimentary spined sensory organs on the dorsal side of most antennal segments, and cerci with numerous long and slightly curved setae.

Material examined. Holotype, female (slide no. XZ-SY2015030) (SNHM), China, Tibet, Motuo county, Dexing town, extracted from soil samples from broadleaf forest, alt. 1100 m, 29°40'N, 95°26'E, 3-XI-2015, coll. Y. Bu & G. Yang. Paratypes, 6 females (slides nos. XZ-SY2015023–XZ-SY2015026, XZ-SY2015029, XZ-SY2015032) (SNHM), 3 males (slides nos. XZ-SY2015027, XZ-SY2015028, XZ-SY2015031) (SNHM), same date as holotype; 1 female (slide no. XZ-SY2015034) (SNHM), China, Tibet, Motuo county, Beibeng town, extracted from soil samples from broadleaf forest, alt. 1500 m, 29°30'N, 95°38'E, 5-XI-2015, coll. Y. Bu & G. Yang. Other materials (SNHM): 1 juvenile with 9 pairs of legs (slide no. XZ-SY2015033) (SNHM), China, Tibet, Motuo county, Beibeng town, extracted from soil samples from broadleaf forest, alt.1500 m, 29°30'N, 95°38'E, 5-XI-2015, coll. Y. Bu & G. Yang; 2 juveniles with 9–10 pairs of legs (slides nos. XZ-SY2015035–XZ-SY2015036) (SNHM), same date as holotype; 10 juveniles with 8–10 pairs of legs (slides nos. XZ-SY2015037–XZ-SY2015046) (SNHM), China, Tibet, Motuo county, Dexing town, Naerdong village, extracted from soil samples from broadleaf forest, alt. 1800 m, 29°30'N, 95°23'E, 4-XI-2015, coll. Y. Bu.

Description. Adult body 1.90 mm long in average (1.55–2.71 mm, n=11), holotype 1.89 mm (Fig. 1A).

Head length 210–270 μm, width 225–300 μm, with widest part somewhat behind the middle on a level with the points of articulation of mandibles. Central rod distinct in both anterior (50–70 μm) and posterior (58–75 μm) portions, with a middle knot. Anterior branches well developed, median branches vestigial. Head dorsally moderately covered with setae of different length, longest setae (25–35 μm) located most anteriorly, at least 3.0 times as long as central ones (8–12 μm). Cuticle at anterolateral part of head with rather coarse granulation. Tömösváry organ surrounded by fine granulation, other areas with fine dense granulation (Fig. 1D).

Tömösváry organ oval, length 19–32 μm, width 10–22 μm, at least half of greatest diameter of 3rd antennal segment (35–50 μm), openings large and elongated oval (length 13–26 μm, width 5–10 μm), with their inner margins covered by minute irregular teeth (Figs 1C, 1D).

Mouthparts Mandible with two fused lamellae and 11 teeth in total (Fig. 2A). First maxilla with two lobes, inner lobe with four hook-shaped teeth, palp bud-like with 1 distal point close to outer lobe (Fig. 2B). Anterior part of second maxilla with many

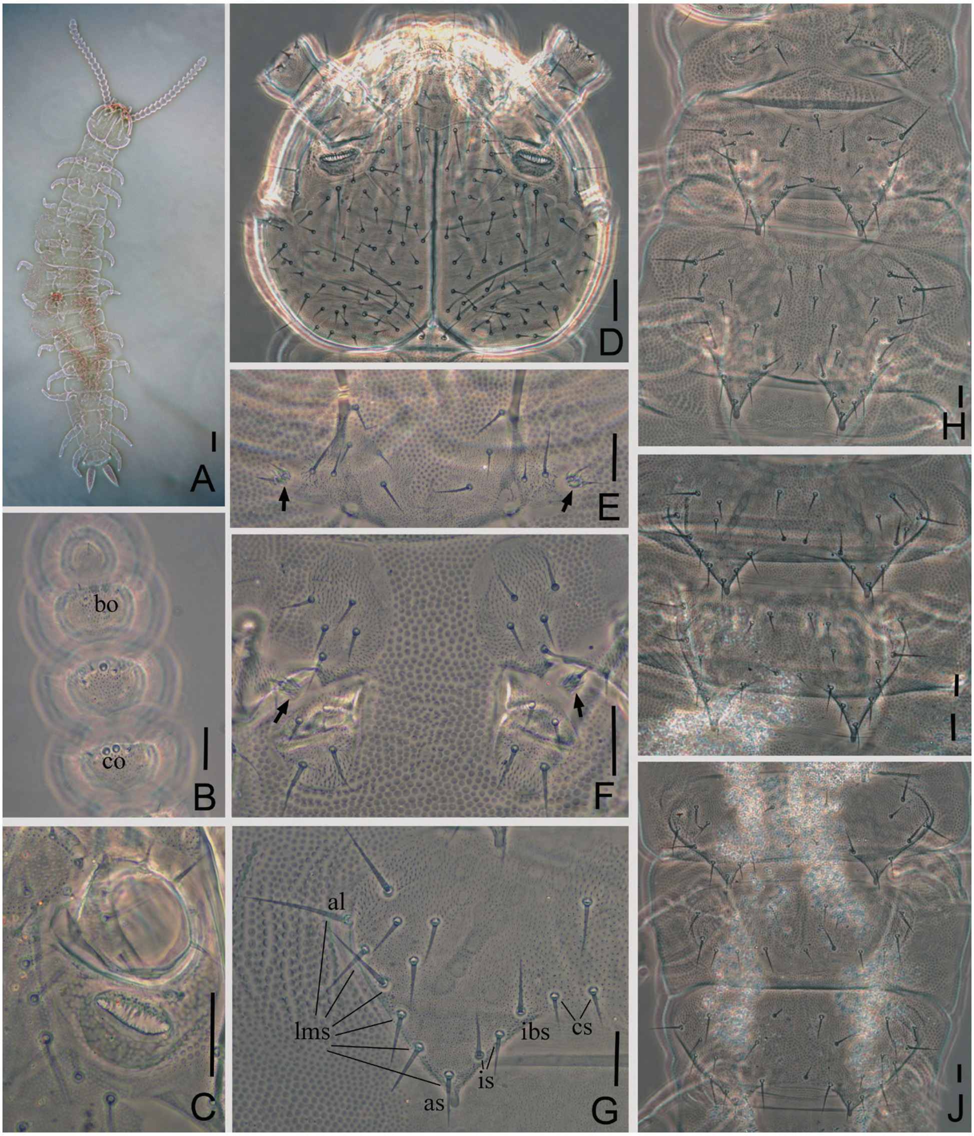

Figure 1. *Symphylella macropora* sp. n. **A** habitus **B** left antenna, 15th–18th segment, dorsal view (*bo*-bladder-shaped organ, *co*-cavity-shaped organ) **C** right Tömösváry organ **D** head, dorsal view **E** first pair of legs (arrows indicate the legs) **F** stylus and coxal sacs of leg 3 (arrows indicate styli) **G** 4th tergite, left side (*al*-anterolateral seta, *as*-apical seta, *cs*-central seta, *ibs*-inner basal seta, *is*-inserted seta, *lms*-lateromarginal seta) **H** 1st–3rd tergites **I** 4th–5th tergites **J** 13th–15th tergites. Scale bars: 100 μm (**A**); 20 μm (**B–J**).

small protuberances which carry one seta each, distal setae thickened; posterior part with sparse setae. Cuticle of maxilla and labium covered with pubescence.

Antennae with 16–23 segments (18 in holotype), length 570–680 μm (620 μm in holotype), about 0.3 of body length. 1st segment cylindrical, much shorter than follow-

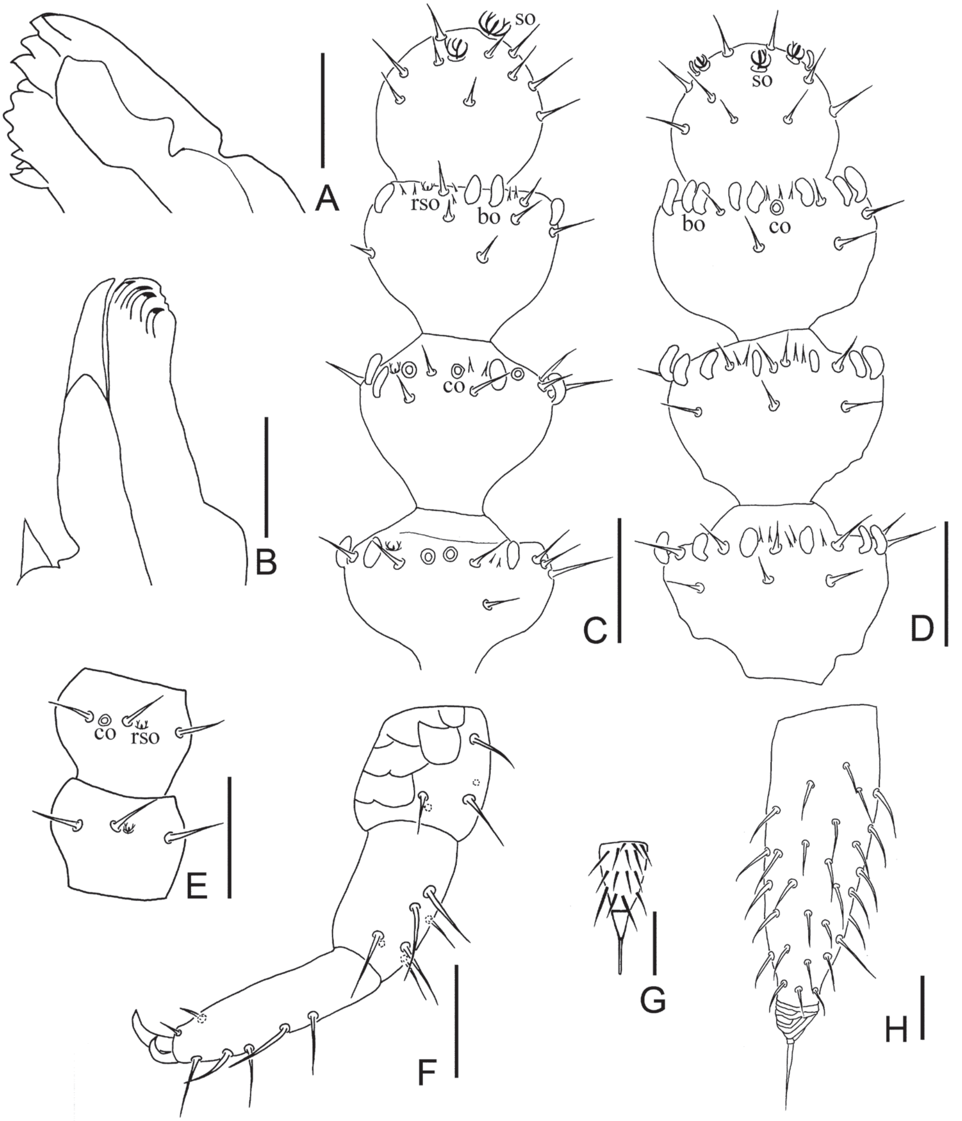

Figure 2. *Symphylella macropora* sp. n. **A** mandible **B** first maxilla **C–D** 15th–18th segments of left antenna **C** dorsal view (*bo*-bladder-shaped organ, *co*-cavity-shaped organ, *rso*-rudimentary spined sensory organ, *so*-spined sensory organ) **D** ventral view **E** 4th–5th segments of right antenna, dorsal view **F** 12th leg **G** stylus on base of 4th leg **H** right cercus, dorsal view. Scale bars: 20 µm (**A–F, H**); 5 µm (**G**).

ing ones, greatest diameter wider than long (37–45 µm, 13–33 µm), with 2–3 microsetae and 6–9 long mesosetae in one whorl, longest seta (20–24 µm) inserted at inner side and distinctly longer than outer ones (15–18 µm). 2nd segment wider (35–44 µm) than long (28–35 µm), with eight or nine setae evenly inserted around antennal wall,

Table 1. Numbers of setae and sensory organs of antennae (holotype).

Segments	Nos. of primary whorl setae	Nos. of secondary whorl setae	Rudimentary spined sensory organs (rso)	Cavity-shaped organs (co)	Bladder-shaped organs (bo)	
				Dorsal	Dorsal	Ventral
1st	6		1			
2nd	8		1			
3rd	8		1			
4th	9		1			
5th	10		1			
6th	10		1			
7th	11		1			
8th	11		1			
9th	11		1			
10th	11		1			
11th	11	3	1			
12th	12	4	1			
13th	12	4	1	2	2	
14th	12	4	1	3	3	
15th	12	4	1	9	3	6
16th	12	4	1	11	4	7
17th	12	5	1		4	8

interior setae (23–26 µm) slightly longer than exterior ones (16–19 µm). Chaetotaxy of 3rd segment like preceding ones. Setae on basal segments slender and on distal segments shorter. Basal segments of antennae with only primary whorl of setae, in middle and subapical segments with several minute setae in secondary whorl. Three kinds of sensory organs on most antenna segments: *rso* on dorsal side of most segments (Figs 2C, 2E); *co* on dorsal side of 3rd–21th segments; *bo* on subapical 5–9 segments (Figs 1B, 2C, 2D). Apical segment subspherical, somewhat wider than long (width 28–32 µm, length 24–26 µm), with 13–15 setae on distal half and 2 baculiform organs on apex, 4–7 *so* consisting of 3–4 curved spines around a central pillar in depressions in distal surface (Figs 2C, 2D). All segments covered with short pubescence. Chaetotaxy and sensory organs of antennae are given in table 1.

Trunk with 17 tergites. Most tergites overlap, with intertergal zones present between adjacent tergites, except for borders between 14th and 15th, as well as 16th and 17th tergite. Tergites 2–13, and 15 each with one pair of triangular processes. Basal distance between processes of 4th–13thand 15th tergites longer than their length from base to tip, and the latter shorter than its basal wide (Table 2). Anterolateral setae of 2nd, 3rd, 4th, 6th, 7th, 9th and10th tergites distinctly longer than other lateromarginal setae, that of 5th, 8th, 11th–13th and 15th subequal or slightly longer than other lateromarginal setae. Triangular processes without ovoid swollen ends (Fig. 1G). One to three inserted setae (setae between inner basal seta and apical seta). All tergites pubescent.

Tergites 1st tergite reduced and build up of two short plates separated in the median axis of the body, with 6–9 short setae in a row. 2nd tergite complete, with two posterior

Table 2. Chaetotaxy of tergites (holotype in brackets).

No. of tergites	Lateromarginal setae	Inserted seta	Central setae	Other setae
1st				
2nd	5–8 (5)	1–2 (1)	1–4 (1)	6–13 (8)
3rd	6–10 (6–8)	1–3 (1)	1–4 (1)	14–25 (14)
4th	5–7 (5)	1–3 (1)	2–5 (2)	7–15 (7)
5th	5–8 (5)	1–4 (1)	2–5 (2)	9–15 (9)
6th	8–11 (8)	1–3 (1)	2–6 (2)	16–36 (16)
7th	4–8 (4)	1–3 (1)	4–7 (4)	9–15 (9)
8th	5–9 (5–6)	1–3 (1)	3–5 (3)	8–17 (8)
9th	8–12 (8)	1–3 (1)	3–6 (3)	14–32 (14)
10th	5–7 (6)	1–2 (1)	3–6 (3)	7–15 (7)
11th	5–8 (5)	1–3 (1)	2–6 (2)	7–16 (7)
12th	6–10 (6–7)	1–3 (1)	2–6 (2)	16–31 (16)
13th	4–7 (4)	0–2 (0–1)	2–5 (2)	6–13 (6)
14th	11–17 (11)*			3–11 (3)
15th	5–9 (5–6)	0–2 (0–1)	1–3 (1)	11–24 (11)
16th	6–14 (6)*			2–7 (2)
17th				20–31(20)

Note: * – marginal setae.

processes, 5–8 lateromarginal setae, 1–2 inserted setae, 1–4 central setae, with anterolateral setae distinctly longer than other lateromarginal setae, processes approximately 0.9 times as long as broad, basal distance between processes approximately 0.7 times as long as their length. 3rd tergite entire, broader and longer than preceding one with ratios mentioned nearly the same as for the 2nd tergite, 6–10 lateromarginal setae (Fig. 1H). 4th tergite broader than 3rd tergite, with ratios approximately 0.7 and 1.4 respectively, 5–7 lateromarginal setae (Fig. 1I). Shape and chaetotaxy of 5th–7th, 8th–10th, and 11th–13th tergite similar as 2nd–4th tergite. 15th tergite shorter with smaller processes than remaining long tergites (3rd, 6th, 9th and 12th tergites). 14th and 16th tergites without processes, with 11–17 and 6–14 marginal setae respectively (Fig. 1J). 17th tergite with 20–31 setae. Chaetotaxy and measurements of tergites are given in Table 2, 3.

Legs 1st pair of legs reduced to two small hairy cupules, each with two long setae (Fig. 1E). Basal areas of legs 2–12 each with 4–6 setae (Fig. 1F). Leg 12 about 0.1 time as long as body, subequal length with head. Trochanter longer than wide (52–76 μm, 40–56 μm) with 6–8 subequal setae. Femur as long as wide (32–42 μm, 30–41 μm), with 4–6 setae and one of them (17–28 μm) distinctly longer than others (10–20 μm); pubescent dorsally, ventrally with cuticular thickenings in pattern of large scales. Tibia nearly 2 times longer than wide (40–60 μm, 23–30 μm), with 5–7 dorsal setae and the longest one slightly shorter than greatest diameter of tibia (19–28 μm).Tarsus subcylindrical, at least 3 times as long as wide (50–70 μm, 15–20 μm), with 6–9 setae: 3 straight and protruding, 2 curved and depressed; longest setae (20–27 μm) about same length of greatest width of podomere, and 2 ventral setae inserted near claw distinctly shorter than dorsal ones. Claws rather curved, anterior one distinctly longer and

Table 3. Measurements of tergites and processes (mean ± se, n = 11) (in µm).

No. of tergites	Length	Width	Length of processes	Basal width of processes	Basal distance between processes
1st	35.6±3.1	148±9.9			
2nd	62.9±4.6	146.7±4.7	39.5±1.9	45.4±2.8	27.6±1.4
3rd	107.5±6.2	179.3±4.9	42±1.7	50.8±2.7	30.8±1.6
4th	71.2±7.6	193.8±10.2	37±1.5	55±2.9	53.1±1.5
5th	80±6.8	189±5.9	42±0.8	52.6±2.5	53.7±2.9
6th	122.9±9.3	229.3±8.4	45.7±1.3	54.3±2	58.9±2.4
7th	78.6±8	237.3±8.1	38.6±0.8	60.5±3.6	71.3±2.2
8th	90.1±8	209.5±6.8	40.9±1.5	51.7±2.4	65.7±3.7
9th	138.1±9.5	245.3±8.6	45.7±1.7	56.6±2.6	64.7±3.7
10th	76.4±9	252.6±9.7	37.6±1.3	58.7±3.2	80.5±3.1
11th	85.7±6.9	204.7±10.5	42.6±1.6	55.8±2.8	71.4±2.5
12th	121.7±7.7	258.7±7.6	41.5±2.1	60±4.1	70.3±3.2
13th	75±6	242.9±8.9	32.5±1.9	57.9±3.4	75.9±3.6
14th	73.1±5.4	202.7±5.8			
15th	88.7±7.1	210.2±13.7	32±1.9	49.3±3.3	56.4±3.9
16th	62.2±2.7	170.7±11.6			
17th	104.8±2.7	143.8±10.3			

broader than posterior one, the latter more curved than the former (Fig. 2F). All legs covered with dense pubescence except areas with cuticular thickenings.

Coxal sacs present at bases of 3rd–9th pairs of legs, fully developed, each with 4 setae on its surface (Fig. 1F).

Styli present at base of 3rd–12th pairs of legs, subconical (length 6–9 µm, width 4–6 µm), basal part with straight hairs; distal one fourth hairless and blunt (3–6 µm) (Figs 1F, 2G).

Sense calicles with smooth margin to pit, length about the same as outer diameter (18–39 µm, 20–35 µm). Sensory seta inserted in cup center, extremely long, length 130–165 µm, at least 5.5 times longer than other two lateral setae (20–35 µm, 14–22 µm respectively) that inserted at the edge of cup.

Cerci subuliform, short, about 0.6 of head length and leg 12, length at least three times as long as its greatest width (126–172 µm, 40–53 µm), moderately covered with subequal length and slightly curved setae, with longest (20–40 µm) at least half of the greatest width of the cerci, terminal area (23–32 µm) short, circled by 6–8 layers of curved ridges. Terminal setae length 18–28 µm (Fig. 2H).

Etymology. The species name *macropora* is referring to the large opening of the Tömösváry organ.

Distribution. Known only from the type locality.

Remarks. *Symphylella macropora* sp. n. is most similar to *S. javanensis* Scheller, 1988 from Java in the shape of tergites and processes, leg 12 and sensory organs on antennae. However, it can be readily distinguished from the latter by the shape of Tömösváry organ (oval, openings large and elongated with inner margins covered by minute irregular teeth vs subspherical, diameter of opening about half of the organ in *S. javanensis*), central rod (both anterior and posterior portions distinct in *S. macropora* sp. n. vs anterior half and anterior branches very thin with traces in *S. javanensis*), and the stylus (with blunt apex in *S. macropora* sp. n. vs with truncate apex in *S. javanensis*). It is also closely related to *S. asiatica* Scheller, 1971 from Indiaand Sri Lanka in the shape and chaetotaxy of tergites 1–3, leg 12 and the sensory organs on antenna, but easily distinguished by characters of Tömösváry organ (openings very small in *S. asiatica*), and the cerci (most setae subequal length and slightly curved in *S. macropora* sp. n. vs long and erect setae on dorsal, ventral and outer sides arranged in one or two rows in *S. asiatica*).

***Symphylella zhongi* Jin & Bu, sp. n.**

http://zoobank.org/159AD15C-EB70-409D-8E5F-3A1E25B62C22
Figures 3, 4, Tables 4–7

Diagnosis. *Symphylella zhongi* sp. n. is characterized by a globular Tömösváry organ with small and roundish opening, processes on tergites mostly longer than their basal width, ovoid swollen ends of processes, and mushroom-shaped sensory organs present on apical antennal segments.

Material Examined. Holotype, female (slide no. XZ-SY2015049) (SNHM), China, Tibet, Linzhi City, Bomi county, Songzong town, extracted from soil samples from broadleaf forest, alt. 3000 m, 29°76'N, 95°96'E, 7-XI-2015, coll. Y. Bu & G. Yang. Paratypes, 2 females (slides nos. XZ-SY2015047–XZ-SY2015048) (SNHM), same date as holotype. Other materials: 3 juvenile with 8 or 9 pairs of legs (slides nos. XZ-SY2015050–XZ-SY2015052) (SNHM), same date as holotype.

Description. Adult body 2.48 mm long on average (2.22–2.93 mm, *n* = 3), holotype 2.93 mm (Fig. 3A).

Head length 250–262 µm, width 262–287 µm, with widest part somewhat behind the middle on a level with the points of articulation of mandibles. Central rod distinct in both anterior (65–70 µm) and posterior (75–90 µm) portions, with a middle knot. Anterior branches well developed, median branches vestigial. Dorsal side of head moderately covered with setae of different length, longest setae (27–35 µm) located most anterior on head, at least 3.0 times as long as central ones (8–11 µm). Cuticle at anterolateral part of head with rather coarse granulation. Tömösváry organ surrounded by fine granulation, other area with faint dense granulation (Fig. 3D).

Tömösváry organ globular, length19–24 µm, width 16–22 µm, about half of greatest diameter of 3rd antennal segments (40–42 µm), opening small and roundish (length 8 µm, width 3–6 µm) (Figs 3C, D).

Mouthparts. Mandible with two fused lamellae and 11 teeth in total (Fig. 4A). First maxilla has two lobes, inner lobe with four hook-shaped teeth, palp bud-like with one distal point close to outer lobe (Fig. 4B). Anterior part of second maxilla with many small protuberances which carry one seta each, distal setae more thick and hard; posterior part with sparse setae. Cuticle of maxilla and labium covered with pubescence.

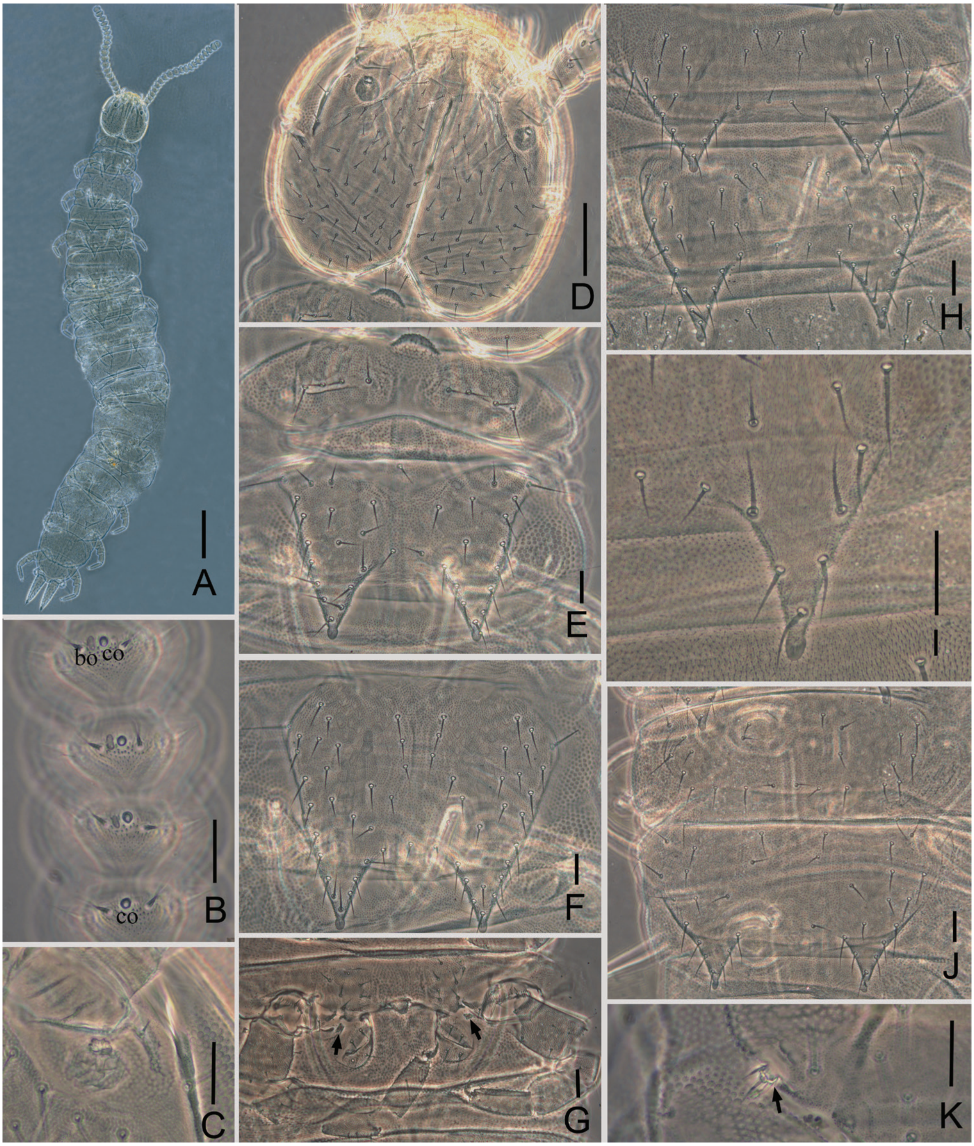

Figure 3. *Symphylella zhongi* sp. n. **A** habitus **B** right antenna, 8th–11th segments, dorsal view (*bo*-bladder-shaped organ, *co*-cavity-shaped organ) **C** right Tömösváry organ **D** head, dorsal view **E** 1st–2nd tergites **F** 3rd tergite **G** female gonopore, styli, and coxal sacs on base of leg 4 (arrows indicate styli) **H** 4th–5th tergite **I** 8th tergite, right side **J** 14th–15th tergites **K** leg 1 (arrow indicates the leg). Scale bars: 200 µm (**A**); 20 µm (**B–K**).

Antennae with 18–23 segments (left antenna with 19, right antenna with 21 in holotype), length 513–663 µm (663 µm in holotype), about one fourth of body length. 1st segment cylindrical, greatest diameter somewhat wider than long (40–42 µm, 23–40 µm), with 1 or 2 microsetae and 6 or 7 mesosetae in one whorl, longest

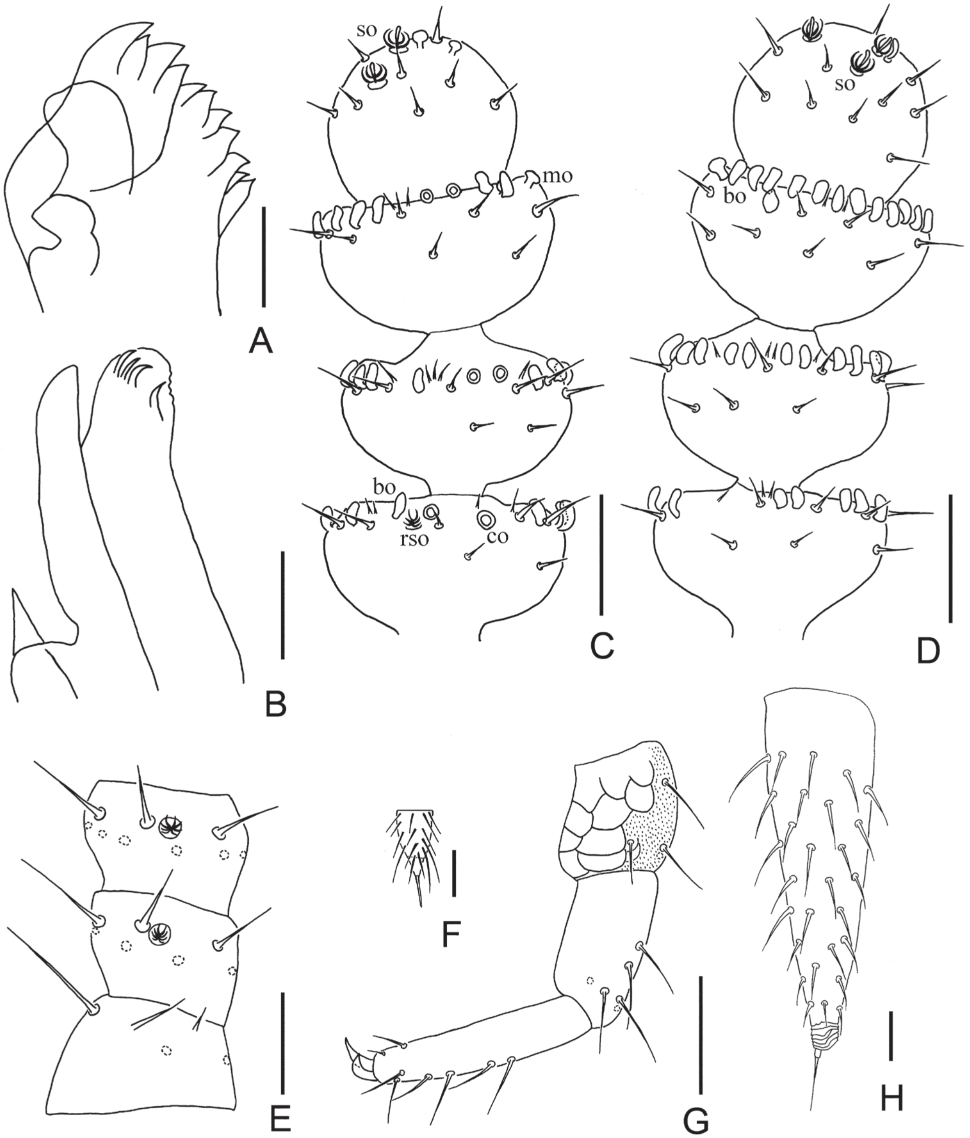

Figure 4. *Symphylella zhongi* sp. n. **A** mandible **B** first maxilla **C–D** 18th–21th segments of right antenna **C** dorsal view (*bo*-bladder-shaped organ, *co*-cavity-shaped organ, *mo*-mushroom-shaped organ, *rso*-rudimentary spined sensory organ, *so*-spined sensory organ) **D** ventral view **E** 1st–3rd segments of right antenna, dorsal view **F** stylus on base of 5th leg **G** 12th leg **H** right cercus, dorsal view. Scale bars: 20 μm (**A–E, G, H**); 5 μm (**F**).

seta (20–22 μm) inserted at inner side and distinctly longer than outer ones (14–15 μm). 2nd segment wider (25–28 μm) than long (40 μm), with 7 or 8 setae evenly inserted around the antennal wall with interior setae (20–21 μm) slightly longer than exterior ones (14–15 μm). Chaetotaxy of 3rd segment similar to preceding ones. Setae

Table 4. Numbers of setae and sensory organs of antennae (holotype).

Segments	No. of primary whorl setae	No. of secondary whorl setae	Rudimentary spined sensory organs (rso)	Cavity-shaped organs on dorsal side (co)	Bladder-shaped organs (bo)		Mushroom-shaped organs (mo)
					Dorsal	Ventral	
1st	7						
2nd	8		1				
3rd	8		1				
4th	9		1				
5th	9		1				
6th	11		1				
7th	11		1	1			
8th	11			1			
9th	11	1		1	1		
10th	11	1	1	1	1		
11th	12	4	1	1	2	1	
12th	12	4	1	1	2	2	
13th	10	5	1	1	2	1	
14th	10	5	1	1	3	2	
15th	10	5	1	1	3	3	
16th	10	5	1	1	5	5	
17th	12	5	1	2	5	12	
18th	12	5		2	9	14	
19th	12			2	7	14	2
20th	12						2

on basal segments longer and on distal segments shorter. Basal antennae segments with only primary whorl of setae, in middle and subapical segments several setae in secondary whorl. Four kinds of sensory organs on antenna: *rso* on dorsal side of most segments (Figs 4C, E); *co* on 7th–19th segments; *bo* on 9–11 segments next to apical one increasing in number on subdistal segments to a maximum of 21 (Figs 3B, 4C); *mo* on distal 2 segments (Fig. 4C). Apical segment subspherical, somewhat longer than wide (width 24–27 μm, length 32–35 μm), with 15–18 setae on distal half; 3–5 spined sensory organs consisting of 3 or 4 curved spines around a central pillar in depressions in distal surface; 2 baculiform organs on apex of segment (Figs 4C, D). All segment covered with short pubescence. Chaetotaxy and sensory organs of antennae are given in Table 4.

Trunk with 17 dorsal tergites. Most tergites overlap, with intertergal zones present between adjacent tergites, except for borders between 14th and 15th, as well as 16th and 17th tergite. Tergites 2–13 and 15 each with one pair of triangular processes. Length from base to tip of processes somewhat longer than its basal width except for the 4th, 7th, 10th and 13th tergites, where processes are broader than long; basal distance between processes of 4th–13th and 15th tergite longer than their length from base to tip (Table 5). Triangular processes with ovoid swollen ends (Fig. 3I). Anterolateral setae of 2nd, 3rd, 4th, 6th, 7th, 9th and10th tergite dis-

Table 5. Measurements of tergites and processes (in µm, $n = 3$) (holotype in brackets).

No. of tergites	Length	Width	Length of processes	Basal width of processes	Basal distance between processes
1st	35–50 (50)	160–175 (160)			
2nd	75–80 (75)	160–180 (180)	43–50 (50)	38–45 (45)	38–40 (40)
3rd	75–145 (145)	190–230 (206)	53–58 (55)	43–50 (50)	40–50 (50)
4th	75–96 (96)	220–236 (236)	45–50 (50)	48–58 (58)	70–75 (75)
5th	76–95 (95)	200–232 (232)	50–60 (60)	45–53 (53)	60–78 (78)
6th	125–156 (156)	283–310 (310)	60–60 (60)	53–58 (58)	55–88 (88)
7th	75–90 (90)	270–300 (300)	50–53 (53)	53–60 (60)	73–100 (100)
8th	90–100 (95)	246–264 (264)	53–60 (55)	53–55 (53)	73–105 (105)
9th	158–160 (158)	310–370 (370)	60–63 (63)	50–58 (58)	88–100 (100)
10th	97–114 (114)	300–350 (350)	48–58 (58)	55–63 (63)	100–110 (110)
11th	88–100 (100)	246–272 (272)	53–63 (63)	48–60 (60)	88–110 (110)
12th	150–190 (190)	312–334 (312)	53–60 (58)	50–55 (50)	83–110 (110)
13th	85–150 (150)	280–330 (330)	48–50 (50)	53–63 (63)	88–113 (113)
14th	101–142 (142)	220–276 (276)			
15th	110–190 (190)	260–328 (328)	45–60 (45)	45–58 (45)	73–95 (95)
16th	78–135 (135)	220–280 (280)			
17th	140–170 (170)	180–195 (195)			

tinctly longer than other lateromarginal setae, that of 5th, 8th, 11th–13th and 15th subequal or slightly longer than other lateromarginal. One to two inserted setae. All tergites pubescent.

Tergites. 1st tergite reduced and build up of two short plates separated in the median axis of the body, with 8 short setae in a row. 2nd tergite complete, with two slender posterior processes, 6–8 lateromarginal setae, 1 or 2 inserted setae, 2 central setae, with anterolateral setae distinctly longer than other lateromarginal ones, processes approximately 1.1 times as long as broad, basal distance between processes approximately 0.8 times as long as their length (Fig. 3E). 3rd tergite complete, broader and longer than preceding one with ratios of 1.1 and 0.9 respectively, 8 or 9 lateromarginal setae (Fig. 3F). 4th tergite broader than 3rd tergite, with ratios approximately 0.8 and 1.5 respectively, 6 or 7 lateromarginal setae (Fig. 3H). Chaetotaxy of 5th–7th, 8th–10th, and 11th–13th tergites similar to 2nd–4th tergites. Pattern of alternating tergite lengths of two short tergites followed by a long tergite only disrupted at the caudal end (Table 5). Within short tergites (1, 2, 4, 5, 7, 8, 10, 11, 13, 14, 16) the length augments toward caudal. Same is generally true for long tergites (3, 6, 9, 12, 15, 17), but for the 15th tergite being shorter than the others, with likewise smaller processes. 14th and 16th tergite without processes with 13–18 and 10–15 marginal setae respectively (Fig. 3J). 17th tergite with 32–44 setae. Chaetotaxy and measurements of tergites are given in Tables 5 and 6.

Legs. 1st pair of legs reduced to two small hairy cupules, each with two long setae (Fig. 3G). Basal areas of legs 2–12 each with 5–7 setae. Leg 12 about 0.1 times the length of the body, about same length like head. Trochanter distinctly longer than wide (70–83 µm, 40–50 µm), with 7 or 8 subequal setae. Femur as long as wide (38–43 µm,

Table 6. Chaetotaxy of tergites (holotype in brackets).

No. of tergites	lateromarginal	Inserted seta	Central setae	Other setae
1st				
2nd	7–8 (8)	1–2 (2)	2 (2)	9–12 (9)
3rd	8–9 (9)	2 (2)	2–3 (3)	17–28 (17)
4th	6–7 (7)	1 (1)	3–4 (4)	11–16 (16)
5th	6–7 (7)	1–2 (2)	4–7 (7)	15–17 (17)
6th	8–11 (11)	2 (2)	3–5 (5)	26–36 (36)
7th	6–7 (6–7)	1–2 (2)	3–5 (5)	15–18 (18)
8th	6–8 (8)	1–2 (2)	4–5 (5)	13–15 (15)
9th	9–12 (11–12)	1–2 (2)	4 (4)	28–36 (36)
10th	6–7 (7)	1–2 (1–2)	4–5 (5)	14–17 (17)
11th	6–7 (7)	2 (2)	4 (4)	13–15 (15)
12th	8–10 (10)	1–2 (2)	4 (4)	22–33 (33)
13th	6–7 (6)	1–2 (2)	3–6 (6)	12–14 (14)
14th	13–18 (18)*			7–15 (15)
15th	7–9 (8–9)	1–2 (1)	2–4 (4)	18–26 (26)
16th	10–15 (15)*			6–8 (8)
17th				32–44 (44)

Note: * – marginal setae.

35–40 μm), with 5 setae and one of them (22 μm) distinctly longer than others (12–18 μm); trochanter and femur pubescent dorsally, ventrally with cuticular thickenings in pattern of large scales. Tibia nearly 2 times longer than wide (50–60 μm, 27–30 μm), with 6 dorsal setae and longest one nearly the same length as greatest diameter of tibia (21–30 μm). Tarsus subcylindrical, about 3.5 times as long as wide (68–75 μm, 20 μm) with 5 dorsal setae: 3 straight and protruding, 2 curved and depressed; longest setae (20–22 μm) about same length of greatest width of podomere; 2 ventral setae inserted near claw distinctly shorter than dorsal ones. Claws curved, anterior one somewhat longer and broader than posterior one, the latter more curved than the former (Fig. 4G). All legs covered with dense pubescences except areas with cuticular thickenings.

Coxal sacs present at bases of 3rd–9th pairs of legs, fully developed, each with 4 setae on surface (Fig. 3G).

Styli present at base of 3rd–12th pairs of legs, subconical (length 5–8 μm, width 3–4 μm), basal part with straight hairs; distal quarter hairless and blunt (3–4 μm) (Figs 3G, 4F).

Sense calicles with smooth margin to pit, about same length as outer diameter (28–30 μm, 26–30 μm). Sensory seta inserted in cup center, extremely long, length 170–180 μm, at least 5.5 times longer than other two lateral setae (20–24 μm, 13–20 μm respectively) inserted at edge of cup.

Cerci subuliform, about 0.7 of head length and leg 12, length at least three times as long as its greatest width (150–188 μm, 45–58 μm), moderately covered with subequal length and slightly curved setae, with longest (25–28 μm) at least half of greatest width of cerci, terminal area (24–28 μm) short, circled by 6–8 layers of curved ridges. Terminal setae length 25 μm (Fig. 4H).

Table 7. Comparison of *S. macropora* sp. n., *S. zhongi* sp. n. and the similar species.

Characters	*S. macropora* sp. n.	*S. javanens*is	*S. asiatica*	*S. zhongi* sp. n.	*S. multisetosa*	*S. simplex*
Tömösváry organ	Oval, with large and elongated oval openings	Subspherical, openings middle size and flat	Openings small	Globular, openings small and roundish	Opening small	Opening moderate size
Central rod	Both anterior and posterior portions distinct	Anterior half and anterior branches very thin with traces	Both anterior and posterior portions distinct	Both anterior and posterior portions distinct	Both anterior and posterior portions distinct	Both anterior and posterior portions distinct
Processes on tergites 2–4	Broad	Broad	Broad	Slender	Slender	Slender
Stylus	Apex blunt	Apex truncate	Short	Apex blunt	Slender	?
Mushroom-shaped organs on antenna	Absent	?	?	Present	?	?
End of processes	Without swollen ends	With small glabrous triangular or ovoid swollen ends	with small swollen ends	With ovoid swollen ends	Without swollen ends	With small swollen ends
Setae of cerci	Subequal length and slightly curved	Mainly short, thin, slightly curved	Long and erect setae on dorsal, ventral and outer sides arranged in 1 or 2 rows	Subequal length and slightly curved	Long, straight , erect setae on dorsal, ventral and outer sides arranged in 1 or2 rows	8–10 longish setae protruding, others short and depressed

Etymology. We dedicate this new species in honor of the late Professor Zhong Yang (1964–2017) who was an eminent botanist from Fudan University, for his great contribution to the knowledge of flora and biodiversity of Tibet.

Distribution. Known only from the type locality.

Remarks. *Symphylella zhongi* sp. n. is most similar to *S. multisetosa* Scheller, 1971 in the shape of the Tömösváry organ, as well as the shape and chaetotaxy of the tergites 1–4, 1st leg, but it deviates distinctly in the shape of the ends of the processes (with ovoid swollen ends in *S. zhongi* sp. n. vs without ovoid swollen ends in *S. multisetosa*), chaetotaxy of the cerci (most setae subequal length and slightly curved in *S. zhongi* sp. n. vs long, straight, erect setae on dorsal, ventral, and outer sides of cerci arranged in one or two rows in *S. multisetosa*). It is also similar to *S. simplex* (Hansen, 1903) in the shape and chaetotaxy of first two tergites, sensory organs of antennal segments and 1st leg, but differs in the shape of 1st antennal segment (moderate in *S. zhongi* sp. n. vs very short in *S. simplex*), chaetatoxy of 3rd tergite (8 or 9 lateromarginal setae in *S. zhongi* sp. n. vs 11 or 12 in *S. simplex*) and 4th tergite (6 or 7 lateromarginal setae in *S. zhongi* sp. n. vs 8 in *S. simplex*), chaetotaxy of cerci (8–10 longish setae protruding, others short and depressed in *S. simplex*).

The new species is compared with similar species in Table 7.

The 43 species of the genus *Symphylella* can be distinguished by the following key, but six species (*Symphylella natala* Hilton, 1938, *Symphylella vaca* Hilton, 1938, *Symphylella elongata* Scheller, 1952, *Symphylella foucquei* Jupeau, 1954, *Symphylella maorica* Adam & Burtel, 1956, and *Symphylella* sp. Rochaix, 1956), which have very brief original descriptions, are not included.

Key to the species of the genus *Symphylella*

1 Without seta between inner basal setae and apical setae **2**
– At least with one seta between inner basal setae and apical setae **3**
2 Setae on antennae plumose .... ***S. plumosa* Scheller, 1971**
– Setae on antennae glabrous **4**
3 Processes of anterior tergites blunt or broad **10**
– Processes of anterior tergites slender or prominent **27**
4 Lateral margins of tergites slightly concave as in the genus *Scolopendrellopsis* .... ***S. tenuis* Scheller, 1961**
– Lateral margins of tergites not concave **5**
5 Cerci at least 3 times longer than wide **6**
– Length of cerci less than 3 times of width **7**
6 Central rod with only hind part visible .... ***S. cylindrica* Scheller, 1961**
– Central rod distinct **8**
7 Anterior branch of central rod well developed, cerci with dense setae .... ***S. bornemisszai* Scheller, 1961**
– Anterior branch of central rod indistinct, cerci with sparse setae **9**
8 Cerci with strongly bulging outer sides .... ***S. abbreviata* Scheller, 1971**
– Cerci without strongly bulging outer sides .... ***S. hintoni* Edwards, 1958**
9 Central rod interrupted in the middle .... ***S. australiensis* Scheller, 1961**
– Central rod complete .... ***S. oligosetosa* Scheller, 1971**
10 Several setae on antennae with fine hairs .... ***S. antennata* (Hansen, 1903)**
– All setae on antennae normal **11**
11 Long lateral setae present between tergites 2–3, 3–4, 6–7 .... ***S. santa* Hilton, 1931**
– Long lateral setae absent between tergites 2–3, 3–4, 6–7 .... **12**
12 Central rod with three branches caudally .... ***S. cubae* Hilton, 1931**
– Central rod not branched caudally **13**
13 Anterior branch of central rod faint, indistinct, or only trace visible **14**
– Anterior branch of central rod distinct or well developed **18**
14 Cerci with dense setae, setae between inner basal setae and apical setae as long as anterior lateral setae .... ***S. erecta* Domínguez Camacho, 2012**
– Cerci with moderate setae, setae between inner basal setae and apical setae distinctly shorter than anterior lateral setae **15**
15 Processes without swollen ends; inner margins of openings on Tömösváry organs covered by minute irregular teeth .... ***S. macropora* sp. n.**
– Processes with swollen ends, inner margins of openings on Tömösváry organs without teeth **16**
16 First tergite with 5 setae .... ***S. lubumbashi* Domínguez Camacho, 2012**
– First tergite with at least 6 setae **17**
17 Apex of styli spatulate .... ***S. javanensis* Scheller, 1988**
– Apex of styli pointed .... ***S. asiatica* Scheller, 1971**
18 Length of cerci less than 3 times of greatest width **19**
– Cerci at least 3 times longer than greatest width **21**

19 Central rod interrupted medially, anterior lines extending laterally to near insertion of antennae, lines also extending laterally from the mid-point interruption of the central rod and then diagonally to near insertion of antennae .... ***S. delawarensis* Allen & Walther, 1993**

– Central rod interrupted medially, without any lateral line through it **20**

20 Cerci with dense setae, slightly curved and depressed on all sides, one erect and longer seta on ventral side .... ***S. fuko* Domínguez Camacho, 2012**

– Cerci with moderate setae, outer side with one protruding setae in the distal part, ventral with five setae arranged in a longitudinal row .... ***S. tanganyika* Domínguez Camacho, 2012**

21 Cerci 4 times longer than greatest width, with densely setae **22**

– Length of cerci less than 4 times of greatest width, with moderate or sparse setae **23**

22 Anterior lateral setae short, less than 0.5 of processes ... ***S. texana* (Hansen, 1903)**

– Anterior lateral setae long, at least 0.5 of processes .... ***S. isabellae* (Grassi, 1886)**

23 Cerci with all setae slightly curved and depressed, central rod distinct posteriorly only .... ***S. malagassa* Domínguez Camacho, 2012**

– Cerci with two kinds of setae, slightly curved setae and erect long setae **24**

24 Processes without swollen ends .... ***S. tenella* Scheller, 1961**

– Processes with swollen ends **25**

25 Cerci with sparse setae .... ***S. kalundu* Domínguez Camacho, 2012**

– Cerci with moderate setae **26**

26 With 1–2 setae between inner basal setae and apical setae .... ***S. vulgaris* (Hansen, 1903)**

– With at least 2 setae between inner basal setae and apical setae .... ***S. neotropica* (Hansen, 1903)**

27 Setae on tergites very long .... ***S. longiseta* Michelbacher, 1941**

– Setae on tergites in moderate length **28**

28 Fine sutures or lines that apparently passes through the interruption and continues on either side perpendicularly to the central rod for some distance and then turns obliquely forward ending at the side of the Tömösváry organs .... ***S. sierra* Michelbacher, 1939**

– Without any sutures or lines connected with the central rod **29**

29 Central rod not or hardly divided in the middle **30**

– Central rod divided distinctly in the middle **31**

30 Tergite 2 with only 5 lateral setae .... ***S. capicola* Michelbacher, 1942**

– Tergite 2 with 7-8 lateral setae .... ***S. rossi* Michelbacher, 1942**

31 Each tergites at least has 2 setae between inner basal setae and apical setae **32**

– 1-3 setae between inner basal setae and apical setae **33**

32 Anterior lateral setae much shorter than processes .... ***S. subterranean* Michelbacher, 1939**

– Anterior lateral setae at least 2/3 length of processes .... ***S. oviceps* Michelbacher, 1939**

33 Lateral margin of cerci nearly straight .... ***S. major* Scheller, 1961**

– Lateral margin of cerci slightly curved **34**

34 Anterior branch of central rod vestigial **35**
– Anterior branch of central rod well developed **36**
35 Posterior part of central rod very thick, dorsal side of head with sparse setae .... ***S. tentabundna* Scheller, 1971**
– Posterior part of central rod normal, dorsal side of head with dense setae .... ***S. multisetosa* Scheller, 1971**
36 Anterior branch of central rod faint **41**
– Anterior branch of central rod distinct **37**
37 Tergite 4 with 5 lateral setae **38**
– Tergite 4 with at least 6 lateral setae **42**
38 Cerci with sparse setae .... ***S. geum* Michelbacher, 1941**
– Cerci with moderate or dense setae **39**
39 Anterior part of central rod slender .... ***S. brevipes* (Hansen, 1903)**
– Anterior part of central rod normal **40**
40 Length of cerci more than 3.5 times of greatest width ... ***S. pusilla* (Hansen, 1903)**
– Length of cerci less than 3.5 times of greatest width .... ***S. brincki* Scheller, 1971**
41 Body length 4–4.8 mm; antennae setae on inner side of basal segments about 1.5 times as long as those on outer side .... ***S. essigi* Michelbacher, 1939**
– Body length 3 mm; antennae setae on inner side of basal segments slightly longer than those on outer side. .... ***S.capitata* Michelbacher, 1939**
42 Anterior branch of central rod thin, cerci at least 4 times longer than greatest of width .... ***S. simplex* (Hansen, 1903)**
– Anterior branch of central rod well developed, cerci less than 4 times of greatest width .... ***S. zhongi* sp. n.**

Acknowledgements

We give our cordial gratitude to Dr Tian-Meng Liu, who was a doctoral student of Professor Zhong Yang, for his well organization of expedition to Tibet in November 2015. We appreciate Professor José G. Palacios-Vargas (Mexico) for his linguistic corrections of the manuscript as well as his valuable advice. We also thank Dr Gang Yang and Mr Zheng-Wei Wang for their generous help during the collection. Special thank are given to Dr Nikolaus Szucsich (Austria) and Dr Miguel Domínguez Camacho (Spain) for their valuable comments in review of the manuscript. This research was supported by the National Natural Science Foundation of China (no: 31772509), the Natural Science Foundation of Shanghai (no: 17ZR1418700), and the Basic Research Foundation of Shanghai Science and Technology Museum.

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ZooKeys 845: 119–137 (2019)
doi: 10.3897/zookeys.845.30095
http://zookeys.pensoft.net

RESEARCH ARTICLE

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Type material comparison of possible cryptic species of the genus *Electrogena* (Ephemeroptera, Heptageniidae) in Central Europe

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Academic editor: *L. Pereira-da-Conceicoa* | Received 26 September 2018 | Accepted 19 March 2019 | Published 15 May 2019

http://zoobank.org/EA8F0F6D-DDD7-4DC8-AEE5-B09FA798B1EA

Citation: Polášek M, Šupina J, Godunko RJ (2019) Type material comparison of possible cryptic species of the genus *Electrogena* (Ephemeroptera, Heptageniidae) in Central Europe. ZooKeys 845: 119–137. https://doi.org/10.3897/zookeys.845.30095

Abstract

The genus *Electrogena* Zurwerra & Tomka, 1985 is a diverse mayfly group in the Western Palaearctic with a partially unclear taxonomy, even in well-examined areas such as Central Europe. Recently, one of the species belonging to this genus, *Electrogena Újhelyii* (Sowa, 1981), was identified as a complex of genetically and geographically separated species. Two other species, *Electrogena samalorum* (Landa, 1982) and *Electrogena rivuscellana* Sartori & Landolt, 1991 were formerly stated as junior synonyms of the earlier species. The fact that the synonymy of *E. samalorum* and *E. Újhelyii* was stated without comparison of any larval or adult material and both species reportedly have different altitude preferences makes the taxonomical position of *E. samalorum* (and possibly *E. rivuscellana*) questionable. Among others, a comparison of type series is one of the first methods that should be used to clarify the taxonomical position of closely related taxa.

The present study aims to comparatively examine the type material and topotypes of *E. Újhelyii* and its presumed junior synonym *E. samalorum* for the first time in detail. Additionally, some notes on the status of the geographically extralimital *E. rivuscellana* are discussed briefly. We noted a significant similarity of all studied material from both the larval and imaginal stages, and suggest considering both junior synonyms (*E. samalorum* and *E. rivuscellana*) as *species inquirendae*.

Keywords

Electrogena samalorum, *Electrogena Újhelyii*, *Electrogena rivuscellana*, species inquirenda, synonymy, type series

Introduction

Despite a long history of research on European mayfly taxonomy and ecology, there are still several groups of taxa with unresolved and unclear taxonomy. One of those groups is the genus *Electrogena* Zurwerra & Tomka, 1985. The first described species of this genus was *Electrogena lateralis* (Curtis, 1834), and the last described European species of this genus thus far is *Electrogena brulini* Wagner, 2017. The latter species was delimited from the closely related species *Electrogena gridellii* (Grandi, 1953) using mitochondrial gene sequence analyses. This illustrates the possible existence of closely related undistinguished species within this genus even in a well-examined area. In Central Europe, we identified a similar situation with two species recently considered to be synonyms, *Electrogena Újhelyii* (Sowa, 1981) and *Electrogena samalorum* (Landa, 1982) as a junior synonym of the former species (Zurwerra and Tomka 1986).

The species *Electrogena Újhelyii* was reported for the first time as "*Ecdyonurus subalpinus* Klp." by Sándor Újhelyi based on larval material collected in August 1957 and 1958 (Újhelyi 1966: 205) from Aszófö, a small tributary stream that empties into Lake Balaton. Later (in August 1975 and 1976), S. Újhelyi collected additional larval and imaginal material, which was passed to Ryszard Sowa (Kraków, Poland) for a study. The species *E. Újhelyii* was described based on that material and was originally attributed by Sowa (1981: 375) to the *lateralis* species group of the genus *Ecdyonurus* Eaton, 1868.

Landa (1969: 193) indicated *E. samalorum* for the first time in Czechoslovakia in a monograph as *Electrogena lateralis* (Curtis, 1834) [orig. *Heptagenia lateralis*]. Vladimír Landa collected larvae in 1963 in the Poprad River in the town Podolínec, Slovakia. Later, V. Landa and Tomáš Soldán collected other material for *E. samalorum* in the Czech Republic and Slovakia (including type material from Podhorodský Stream in the village of Podhoroď, Slovakia). Finally, based on the material listed above *E. samalorum* was described as a new species for former Czechoslovakia (Landa and Soldán 1982).

A few years later, Zurwerra and Tomka (1986) established the synonymy of *E. Újhelyii* and *E. samalorum* with reference to personal communications with Dietrich Braasch (Potsdam, Germany) without any other details or comments. During our personal contact (RJG, October 2008) with D. Braasch, he reported that the conclusion on the synonymy of *E. Újhelyii* and *E. samalorum* was made by him based on an analysis of his own larval collection of *E. Újhelyii* from Germany in 1982 (the territory of the former German Democratic Republic), which in his opinion, corresponded to the description of both species at once (see also Braasch and Jacob 1984: 81–82). Later, Kluge (2004) and Bauernfeind and Soldán (2012) supported the synonymy. However, this was also determined without any details or argument. Nevertheless, in several other works (e.g. Landa and Soldán 1989; Deván 1989; Kłonowska-Olejnik 2003), *E. samalorum* has been indicated as a separate species, although its larvae (e.g. in Deván 1993) were compared with larvae of the species *E. lateralis*, but not of *E. Újhelyii.* In addition to the absence of a detailed material comparison, there is another detail that brings into question the synonymy of both species. Landa and Soldán (1982) stated that *E. samalorum* lives only in highlands, while Sowa (1981) reported lowland occurrences of *E. Újhelyii* (in the vicinity of Lake Balaton, approx. 150 m a.s.l.).

In addition to the synonymy of the two species discussed above, Belfiore and Desio (1995) proposed a synonymy between *E. Újhelyii* and *E. rivuscellana* Sartori & Landolt, 1991 based on a comparison of larval material from Austria, Italy (*E. Újhelyii*) and Switzerland (one paratype of *E. rivuscellana*). After analysing the set of 16 numerical characters, the authors noticed a considerable overlap of the main diagnostic qualitative and quantitative characters in mouthparts, gills, legs and femoral setation, most of which were not considered in the original description of *E. rivuscellana* (Landolt et al., 1991).

Most recent results on the genetic diversity of Central European representatives of the genus *Electrogena* show that specimens identified as *E. Újhelyii* belong to a complex of two morphologically indistinguishable but geographically separated species (Polášek et al. 2018). Moreover, the distribution areas of both cryptic species indicate that one of those indistinguishable species might belong to the former *E. samalorum*, while the other species can be assigned to *E. Újhelyii* sensu stricto due to the availability of collected topotypic material. The material from the type locality of *E. samalorum* (Podhoroď, Slovakia) was unfortunately not available, the only species found in the adjacent region belong to *E. lateralis*.

In this work, a revision and comparison of type material for both problematic Central European species was conducted for the first time, and we discuss possible larval and adult characters to distinguish between the species. Furthermore, some notes on the status of the extralimital *E. rivuscellana* are discussed briefly.

Materials and methods

Type material

Type series of *Electrogena Újhelyii* (Sowa, 1981)

The original description of the species *E. Újhelyii* is based on a male imago (holotype), four other male imagines, eight female imagines and seven mature larvae (all paratypes). All of the type material originated from the environs of the village of Tihany (Hungary) on the Aszófö stream and was first kept at the Department of Hydrobiology (Jagiellonian University, Poland) (Sowa 1981). In 1997, R. Sowa's collection was transferred to the Musée Cantonal de Zoologie Lausanne (Switzerland). Finally, this material was provided at our disposal on a long-term loan in April 2012, and is provisionally housed at Masaryk University, Brno, Czech Republic.

At present, the available type material on *E. Újhelyii* includes only five specimens preserved in alcohol.

(i) Holotype (Figs 1A–C, 2A, B), male imago, labelled as: "Ecdyonurus Újhelyii Sowa Holotype ♂ im. stream near Aszófö, Balaton Bassin, Hungary, 1.07.1976"; well preserved specimen in a separate tube, missing the left foreleg and the right hindleg; S Újhelyi leg.
(ii) Paratype I (Fig. 2C, D), male imago, labelled as: "E. Újhelyii Sowa Aszófö, stream in Balaton Bassin 1.vii.76"; "Aszófö 76.VII.1 leg. Ujh." (Fig. 2E(1), E(2)); well preserved specimen, missing the right foreleg and the left hindleg; in a tube together with paratype II and paratype III (see below); S. Újhelyi leg.
(iii) Paratype II, male imago, label is the same as for paratype I; the specimen was preserved during the moult, with subimaginal skin; S Újhelyi leg.
(iv) Paratype III, female imago with preserved eggs, label is the same as for paratype I; incomplete specimen, missing legs.
(v) Paratype IV (Fig. 4A, B), mature male larva, labelled as: "Hungary: Aszófö 10.8.1958 leg. Újhelyi".

Holotype label was prepared by Małgorzata Kłonowska-Olejnik (Kraków, Poland) in the 1990s; labels of paratypes were written by R Sowa and S Újhelyi. Hitherto, any slides of other specimens of the type series or their parts were not preserved.

Besides the original type material collected by S. Újhelyi, we collected and analysed topotypic material from the Aszófőii-séd brook near Aszófő (GPS loc.: 46°56.0648'N, 17°49.8379'E) sampled on July 12, 2012. Altogether, we used seven mature larvae for subsequent analyses and comparisons.

Type series of *Electrogena samalorum* (Landa, 1982)

The description of the species *E. samalorum* is based on imaginal and larval material, which was collected in the basins of the Elbe and Vistula Rivers. With the exception of the holotype (male imago reared from larva), female imago and two larvae, which have their localities, date of collection, and the name of collector clearly labelled, the collection data and other details for the other 13 larvae and three male imagines are indicated but not specified, which would be helpful for identification of the type material. Hence, when analysing the present volume of the type series of *E. samalorum*, we used the information from publications, original labels and the personal comments of T. Soldán. The type specimens, designated as *E. samalorum,* are preserved in alcohol and partly mounted on slides. Among the materials indicated as types of *E. samalorum*, we found two male imagines without genitalia in alcohol, labelled as "Brook–Valeč–Doupov North Bohemia–12.7.1956". Marked locality and collection data correspond to that belonging to the paratype of female imago *E. samalorum* (see Landa and Soldán 1982: 34).

The identification of two males listed above has shown that one of them undoubtedly belongs to the type series *E. samalorum* based on the colouration of body, the colour pattern of lateral sides of abdominal terga II–VIII as described by Landa and Soldán (1982) and the structure of genitalia mounted on slide (see below). Another male imago probably belongs to the subgenus *Helvetoraeticus* of the genus *Ecdyonurus* according to the presence of the characteristic *L*-shape markings on the lateral sides of abdominal terga II–VIII, which is poorly visible due to the long-term preservation. It is possible that in this case we deal with the species *Ecdyonurus subalpinus* (Klapálek, 1907), mentioned by Landa (1969: 220) from Valeč village.

Together with the material in alcohol in the collection of the Institute of Entomology (Biology Centre of the Czech Academy of Sciences), the slide with genitalia of two *E. samalorum* males, was found and mounted as a single slide and labelled by M Kłonowska-Olejnik during her stay at the Institute of Entomology, Biology Centre of the Czech Academy of Science in 2002. One of two genitalia belongs to the paratype of the male imago, discussed above, and is labelled as: "Electrogena samalorum, Valeč brook, West Bohemia, 12.07.1956, ♂ im paratype, leg. V. Landa (preparat zewnętrzny) [external slide]" (Fig. 3A–C). The second male genitalia belong to the specimen of *E. samalorum*, and is labelled as: "E. samalorum Výrovka, Kostomlaty, 29.07.1961, ♂ im leg. V. Landa (preparat wewnętrzny) [internal slide]" (Fig. 3D, E). A complete specimen of this male has not been found and is probably lost; this specimen was not a part of type series.

Alcohol material:

(i) Paratype I (Fig. 3A, B), male imago, labelled as: "Brook–Valeč–Doupov North Bohemia–12.7.1956"; damaged specimen without forelegs, middle right leg, and hind left leg; genitalia mounted on slide; V Landa leg.

(ii) Paratype II, mature male larva; in same tube subimaginal skin also (probably belongs to the holotype male imago reared from larva); both labelled as: "Podhorod – paratypes"; significantly damaged larva; complete subimaginal skin; T Soldán leg.

(iii) Paratype III and paratype IV, male and female larvae, labelled as: "pot. u Lendak 25.7.61"; significantly damaged specimens; V Landa leg.

(iv) Paratype V and paratype VI, mature male larva and male larva, labelled as: "Heptagenia sp 1", "Poprad / Podolince 24.6.1963"; significantly damaged larvae; V Landa leg.

(v) Paratype VII, mature female larva, labelled as: "Javorinka – Podspády / 26.8.63"; damaged larva; V Landa leg.

(vi) Paratype VIII, mature male larva, labelled as: "Potok u Maková / 18.6.63"; well preserved larva; V Landa leg.

(vii) Paratype IX, mature male larva, labelled as: "Pot. Lopušna / 18.6.63"; damaged larva; V Landa leg.

(viii) Paratype X, female larva, labelled as: "Pot. nad Brusnicou 27.7.61"; well preserved larva; V Landa leg.

(ix) Paratype XI and paratype XII, mature male and female larvae, labelled as: "Potok u Kastánie / 18.6.63"; damaged larvae; V Landa leg.

Slides (mounted based on paratypes XII and XIII):

(x) Paratype XII [mounted using paratype XII] (Figs 4C, F, 5A, B, D, F) and paratype XIII (Fig. 4E, G), female larvae, labelled as: "Electrogena samalorum Podhorod, Podhorský brook, 16.07.1975, L ♀ paratype A [another slide labelled as "L ♀ paratype B"], leg. T Soldán"; slides mounted with Liquide de Faure and labelled by M Kłonowska-Olejnik.
(xi) Paratype XIII (Figs 4D, 5C, E), female larva, labelled as: "Electrogena samalorum, Lopušna brook, 18.06.1963, L ♀ leg. V Landa"; idem.
(xii) male genitalia [paratype I (Fig. 3A, B); for details see above]; male genitalia [imago, not of type (Fig. 3D, E); for details see above]; idem.

In addition to the *E. samalorum* holotype and 19 paratypes indicated in the original description, hitherto, 13 paratypes have been preserved, of which three larval paratypes originated from the type locality. The holotype of the species has not been found, and is probably lost.

Material processing

The line drawings of the morphological structures of the specimens belonging to the type series of Central European species were made using a Zeiss Axoiplan and Olympus BX41 microscopes, both equipped with a drawing attachment (camera lucida). The material was observed with a Leica M205 C binocular stereomicroscope; the eggs structure was investigated using phase-contrast microscope Di-Li 2026-P with 16 MP digital camera. Photographs of types were taken using a Leica Z16 APO microscope and processed with the Leica Application Suite™ Version 3.1.8 to obtain combined photographs with a suitable depth of field at the Staatliches Museum für Naturkunde Stuttgart. Photographs were subsequently enhanced with Adobe Photoshop™ CS3.

The numerical morphological characters defined by Carlo Belfiore for *Electrogena* species identification (Belfiore 1996, 1997) have been measured and minimum, maximum and mean value of each character was used for both species comparison. The preservation of available material did not allow to measure all defined characters; the characters based on number of fine setae or fragile body parts were thus omitted. The following characters were measured:

N_CBS	number of comb-shaped bristles on fore margin of galea-lacinia;
N_CLW	number of teeth on pretarsal claws;
N_BVF	number of bristles on ventral side of femora near hind margin;
R_LBR	total width of labrum divided by mean width of lateral lobes of labrum;

R_GLA	relative distance between glossae (outer distance divided by inner distance between glossae);
R_GLB	relative width of glossae (outer distance divided by width of glossae);
R_1GI	relative width of 1st gill plate;
R_4GI	relative width of 4th gill plate;
R_7GI	relative width of 7th gill plate.

For detailed description of the characters see Belfiore (1996, 1997) and Polášek et al. (2018).

Results

Male imagines

Figs 1–3

Body colouration. The natural colour pattern is poorly preserved, especially in the paratype of the male imago of *E. samalorum*. Most changes were caused by long-term storage in alcohols of different concentrations and qualities. In the holotype and paratypes of *E. Újhelyii,* the general colour of the body is pale, dirty yellow, yellowish-brown to brown. The body colour of the preserved paratype of *E. samalorum* is distinctly darker than in all of the *E. Újhelyii* adult type specimens, with a brown to dark brown head and thorax and brown abdominal segments. Such a difference in coloration may be the result of inter-population variability. Besides, the lack of new topotype material on adult specimens of both species at our disposal makes it impossible to define the limit between inter- and intraspecific variability in colour pattern.

Head. In *E. Újhelyii* the head is light brown without conspicuous maculation; compound eyes widely separated, the sclerite joining the compound eyes weakly rounded, forming a wide U (Fig. 1B) (the same for *E. samalorum* based on the study of type material); compound eyes bluish-grey to whitish-grey apically, and blackish towards the base, without distinct rings laterally (Fig. 1A, C) (in *E. samalorum*: bicoloured laterally, with light dirty brown upper 2/3, and blackish grey lower 1/3 of eyes height [*eyes whitish gray, dorsal surface darker without rings*: original description of *E. samalorum*]).

Thorax. In *E. Újhelyii* the thorax is slightly darker than other body parts, with distinct contrast maculation dorsally and laterally (Fig. 1A–C) ["*with slight violet pigmentation*": original description of *E. Újhelyii*]: pronotum with a pair of triangular light brown spots laterally; mesonotum with brown median longitudinal, mesonotal and lateroparapsidal sutures; anterior part of the anteronotal protuberance of the mesonotum, area between the antelateroparapsidal suture and the sublateroscutum, and scutoscutellar impression (area between posterior scutal protuberances) with brown markings; metanotum uniformly light dirty brown (all terminology based on Kluge 2004). Lateral and ventral sides of thorax light dirty brown, with brown anterior paracoxal suture. In *E. samalorum* the orientation of markings is the same as in *E. Újhelyii*

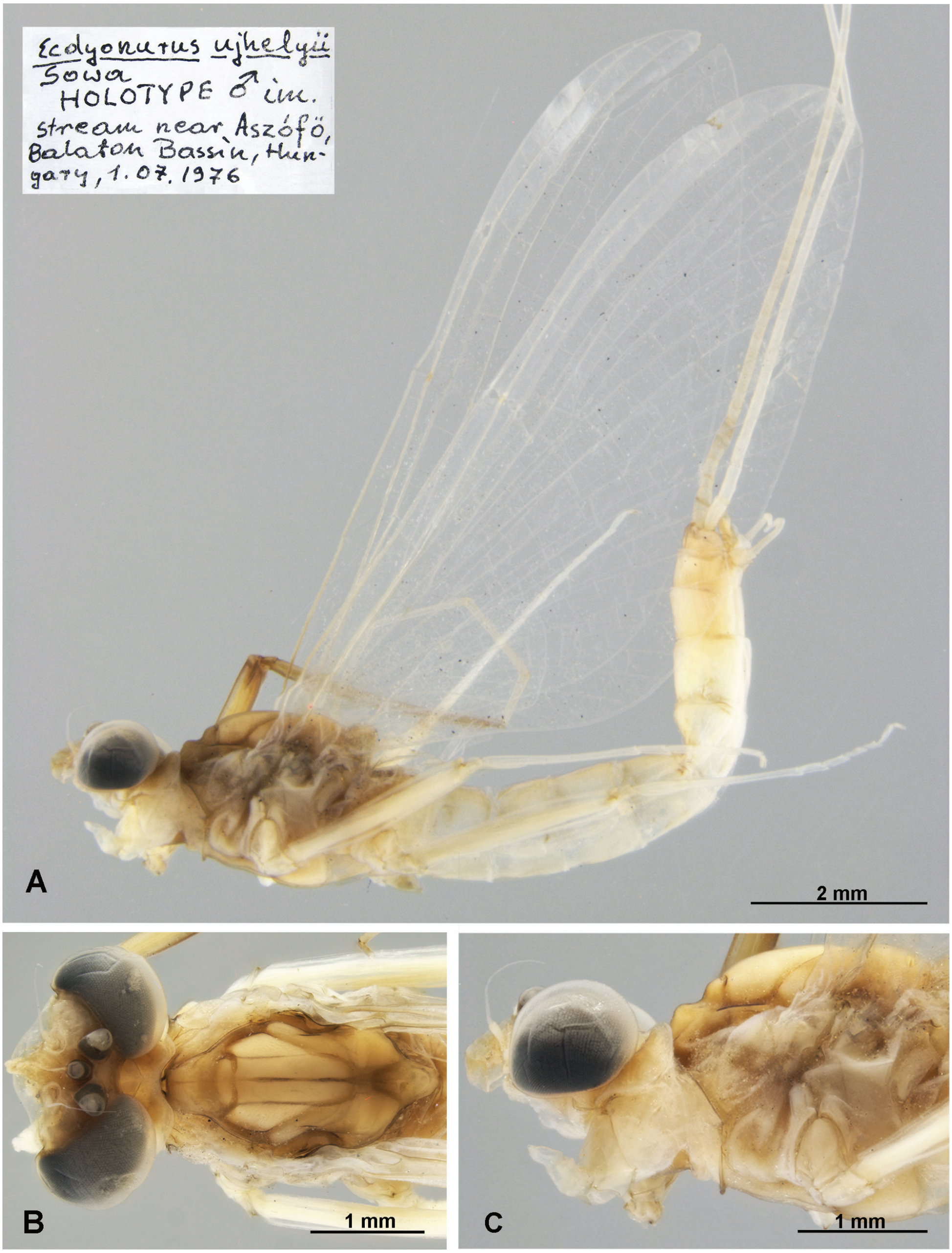
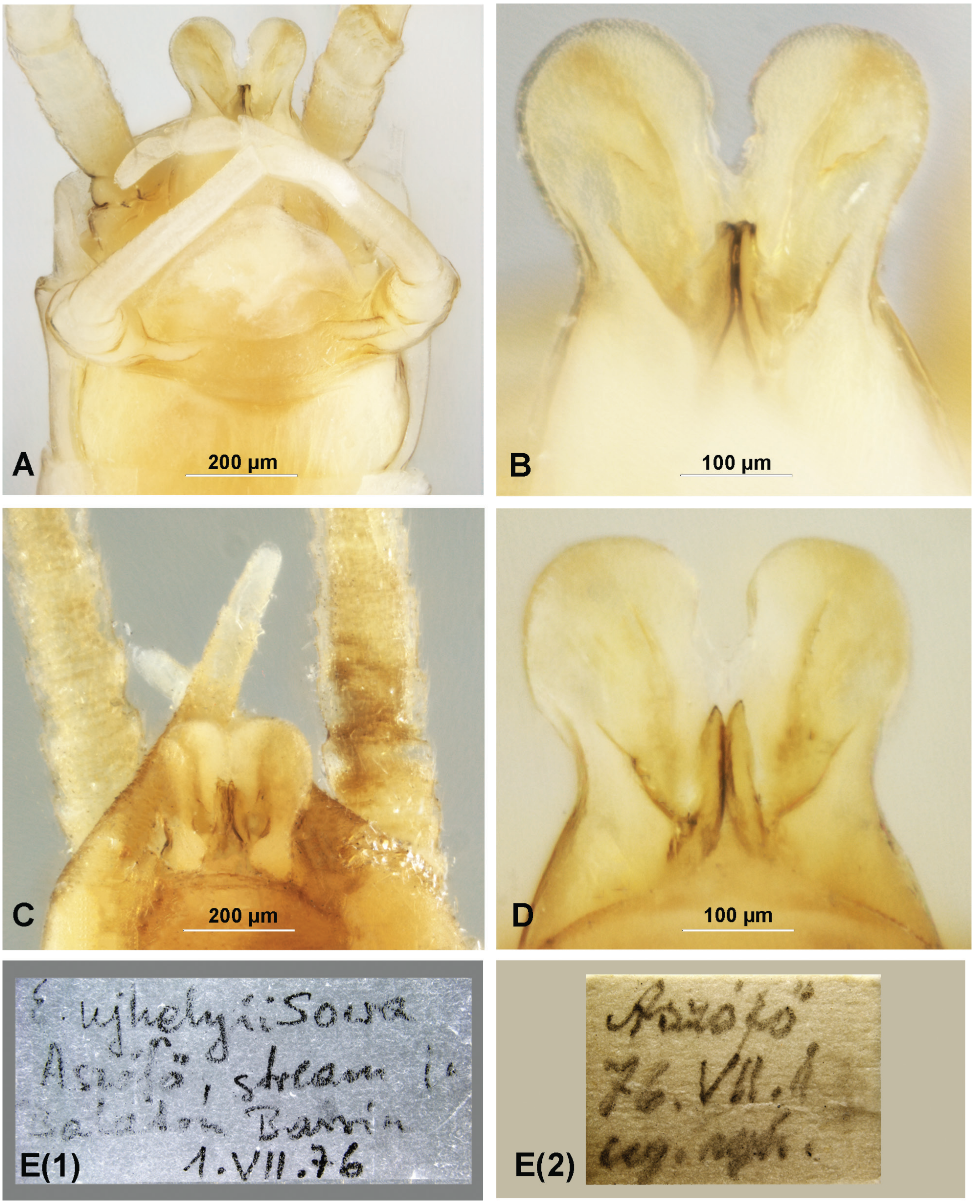


Figure 1. *Electrogena Újhelyii* (Sowa, 1981), male imago, holotype: **A** body, left lateral view **B** head and thorax, dorsal view **C** head and thorax, left lateral view.

holotype and paratypes, but the general coloration of thoracic structures is distinctly darker, with marked brown sutures and respective maculation [“*thorax dark brown*”: Landa and Soldán (1982)].



E. ujhelyii Sowa
Aszófő, stream in
Balaton Basin
1.VII.76

Aszófő
76.VII.1
leg. [illegible]

Figure 2. *Electrogena Újhelyii* (Sowa, 1981), male imagines, holotype (**A, B**); paratype I (**C, D**): **A, C** male terminalia, ventral view **B, D** penis lobes, ventral view **E(1), E(2)** original labels of paratype I.

Legs. The forelegs of *E. Újhelyii* distinctly darker than the middle and hind legs (Fig. 1A); forefemur and foretibia intensely brown, markedly dark brown apically (the same in original description of *E. samalorum*); middle and hind legs uniformly whitish-yellow, transversal band on middle and hind femora not preserved (diffuse unclear macula in paratype of *E. samalorum*; the same in original description of *E. Újhelyii*).

Wings of *E. Újhelyii* translucent, pterostigmatic area dirty milky or yellowish coloured; longitudinal and transversal veins yellowish (the same in male paratype of *E. samalorum*). The characters of the veins' colouration are different in both the original descriptions and preserved types, probably due to long-term storage in alcohol.

Abdominal segments. E. Újhelyii: light yellow to dirty yellowish-brown, segments (I) II–VI translucent or not transparent; traces of preserved dirty violet maculation relatively visible on abdominal terga II–VIII (poorly visible in holotype, more distinct in both paratypes); the pattern of abdominal terga similar to those described and figured by Sowa (1981: 376–377, fig. 1) and Bauernfeind and Soldán (2012: 299), but differs from the colour pattern figured by Haybach (2005: 42–43, fig. 5), with a dirty violet spot basolaterally near the anterior and posterior margins of the segments (the spot near the posterior margin of segments poorly visible). The sterna are uniformly yellowish brown; the ganglionic chain is not visible.

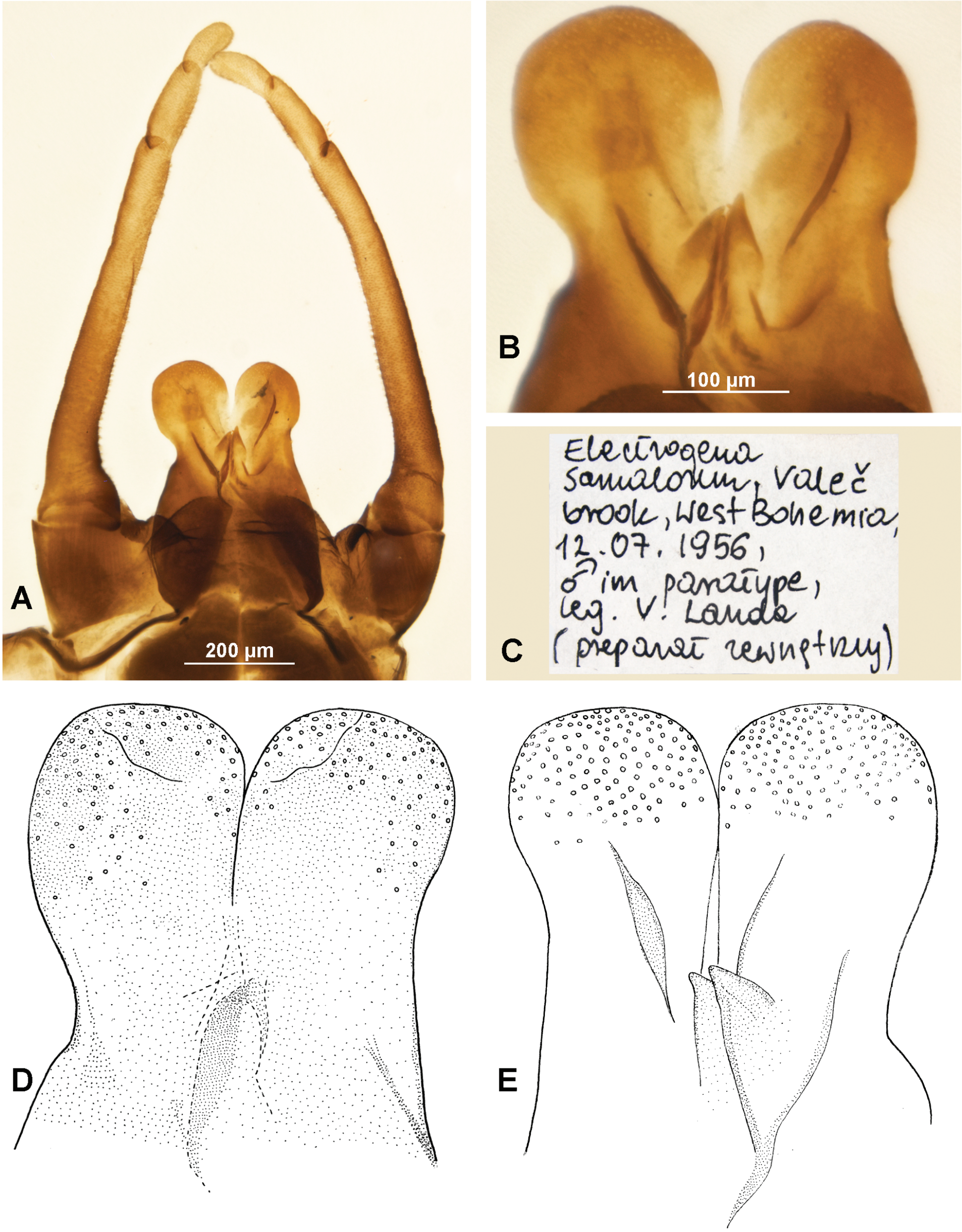
In the male paratype of *E. samalorum* the pattern of the abdominal terga poorly visible, but nevertheless corresponds with the original description (Landa and Soldán 1982: 32): a pair of elongated brown strokes (occasionally fused together on terga II, IV, and VI) near anterolateral margin of segments.

Genitalia. *E. Újhelyii* (Fig. 2A–D): The base of the forceps with small asymmetrical apically rounded projections laterally, broadly convex in the middle; the forceps yellowish-brown to brown, and paler distally (Fig. 2A, C); the penis lobes stout and divergent apically with relatively wide interspace, U or V shaped; the lobes widely rounded apically or slightly truncate along the outer margin [the similar shape of lobes is depicted by Sowa 1981: 376, fig. 2; Bauernfeind and Soldán 2012: 594, fig. 188], the lobes moderately expanded laterally; both ventral folds of the lobes well developed (Fig. 2B, D); a few small pointed setae occur basodorsally (the same as in the original description of *E. Újhelyii*). The titillators relatively broad, slightly asymmetrical, bluntly pointed at the tip, straight basally and strongly bent apically (ventral edge sinuous).

The structure of forceps base and penis lobes of the male paratype of *E. samalorum* completely corresponds with the original description (Fig. 3A, B, D, E; see also figs 2–4 in Landa and Soldán 1982: 33). The male genitalia of the specimen collected 29.vii.1961 generally with similar structure of penis lobes. However the lobes are closely touching, without deep interspace (Fig. 2D, E; the same shape of penis lobes is depicted for *E. Újhelyii* by Landolt et al. 1991: 467, fig. 8).

Female imago

Only a single specimen of the female paratype of *E. Újhelyii* has been preserved hitherto. The preserved colour of the body is similar to those in male specimens. Com-



Electrogena samalorum, Valeč brook, West Bohemia, 12.07.1956, ♂ im paratype, leg. V. Landa (preparat zewnetrzy)

Figure 3. *Electrogena samalorum* (Landa, 1982), male imago, paratype I (**A–C**), 12.vii.1956; male imago, not type (**D, E**), 29.vii.1961: **A** male terminalia, dorsal view **B** penis lobes, ventral view **C** label on microslide **D** penis lobes, dorsal view **E** penis lobes, ventral view.

pound eyes uniformly black, with thin brownish edging. The shape of subgenital and subanal plates corresponds to those described and figured by Sowa (1981: 377, fig. 3) and Haybach (2005: 42–43, fig. 2a, b). A single female paratype of *E. samalorum* has most probably been lost.

Eggs

The structure of eggs is described and figured in details for *E. Újhelyii* by Sowa (1981: 377), Haybach (2005: 42–43, fig. 8) and Bauernfeind and Soldán (2012: 300, 631, fig. 188), and for *E. samalorum* by Landa and Soldán (1982: 32, 37, pl. 1, figs 1–4). We have studied egg chorion structure in the species *E. Újhelyii*, based on the material prepared from a single preserved female paratype. The result of our observations completely corresponds with the information published previously for both species.

Mature larva

Figs 4, 5

Body colouration. Like in adult specimens of the type series of *E. Újhelyii* and *E. samalorum*, the cuticular colouration of the studied paratypes of the larvae was also poorly preserved. Nevertheless, some aspects of colour pattern, which are important for identification and comparison of the taxa, are visible enough. The general colouration of the body in larvae of *E. Újhelyii* and *E. samalorum* is yellowish-brown to brown; a variable colour pattern is more or less preserved on the thorax, legs and abdomen.

Head of *E. Újhelyii* (paratype and topotypes) with broadly rounded anterior margin, the broadest part near to anterior end of eyes (Figs. 4A, B); in *E. samalorum* the head capsule of similar shape, or the posterior margin occasionally truncated (Fig. 4C). The head colour of *E. Újhelyii* uniformly light brown to brown, without visible spots (the same in Landa and Soldán 1982; Bauernfeind and Soldán 2012), occasionally two small yellowish spots between the eyes and the lateral ocelli. In larval paratypes of *E. samalorum* the same head colour is observed; occasionally additional yellow spot between the base of the antennae and two smaller spots on both sides of the central ocellus. The labrum in *E. Újhelyii* and *E. samalorum* are shaped differently, slightly bent backwards or rather straight (Fig. 4D, E; Sowa 1981, fig. 4; Landa and Soldán 1982, fig. 8); a row of a relatively stout bluntly pointed setae available on the ventral side of the labrum (Fig. 4G).

Thoracic colour pattern is variable in both species, but generally corresponds to those in the original descriptions. Generally, the pronotum with two elongated transversal whitish spots near the anterior margin; the lateral sides of the pronotum regularly rounded, slightly stretched laterally with two yellowish strokes along the outer margin

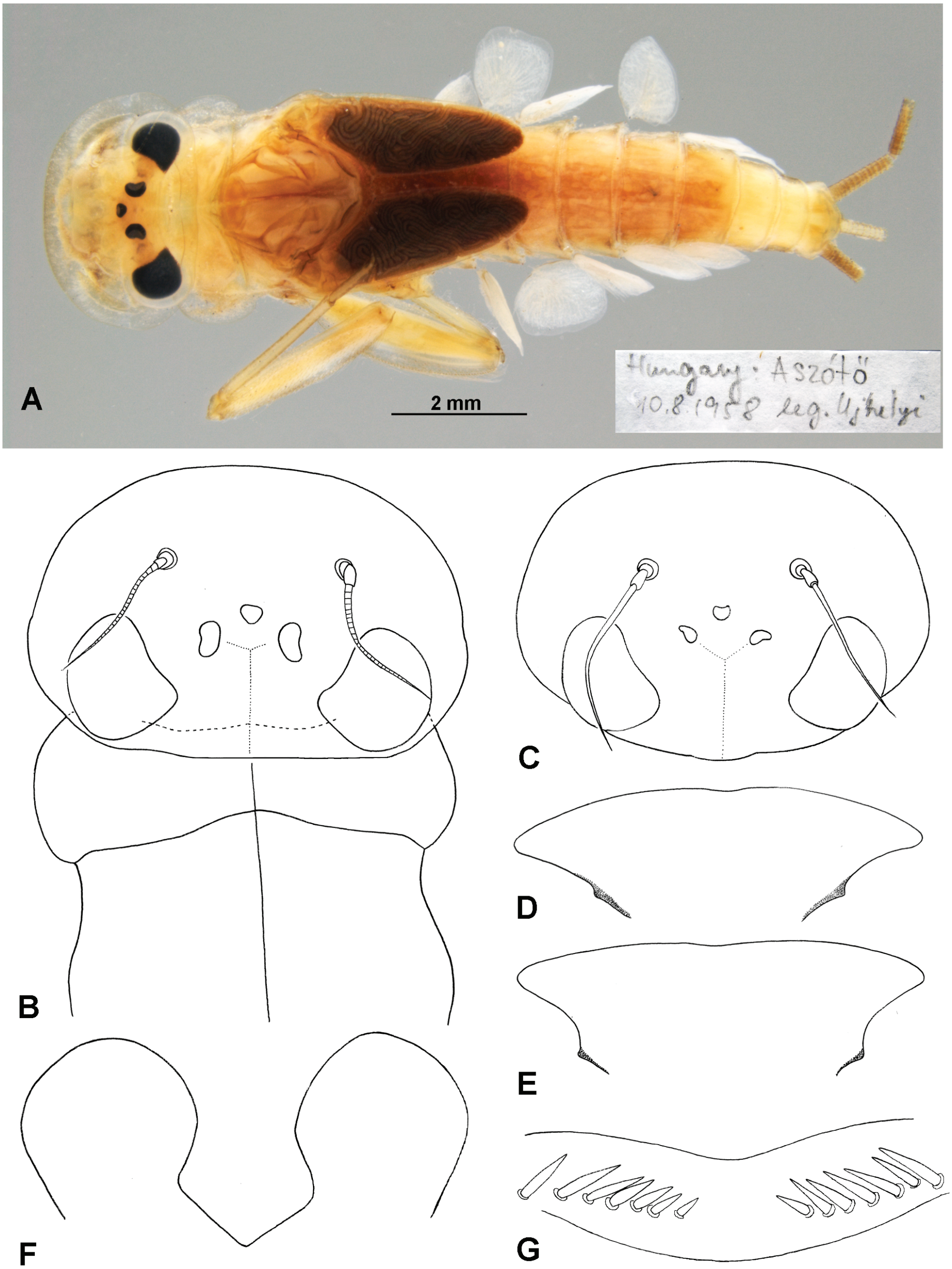


Figure 4. *Electrogena Újhelyii* (Sowa, 1981), mature male larva, paratype IV (**A, B**); *Electrogena samalorum* (Landa, 1982), mature female (**C, E, G**) and mature male (**D, F**) larvae, paratypes XII and XIII: **A** body, dorsal view, 10.viii.1958 **B** head and pronotum, dorsal view, 10.viii.1958 **C** head, dorsal view, 16.vii.1975 **D** labrum, ventral view, 18.vi.1963 **E, G** labrum, ventral view, 16.vii.1975 **F** glossae, ventral view, 18.vi.1963.

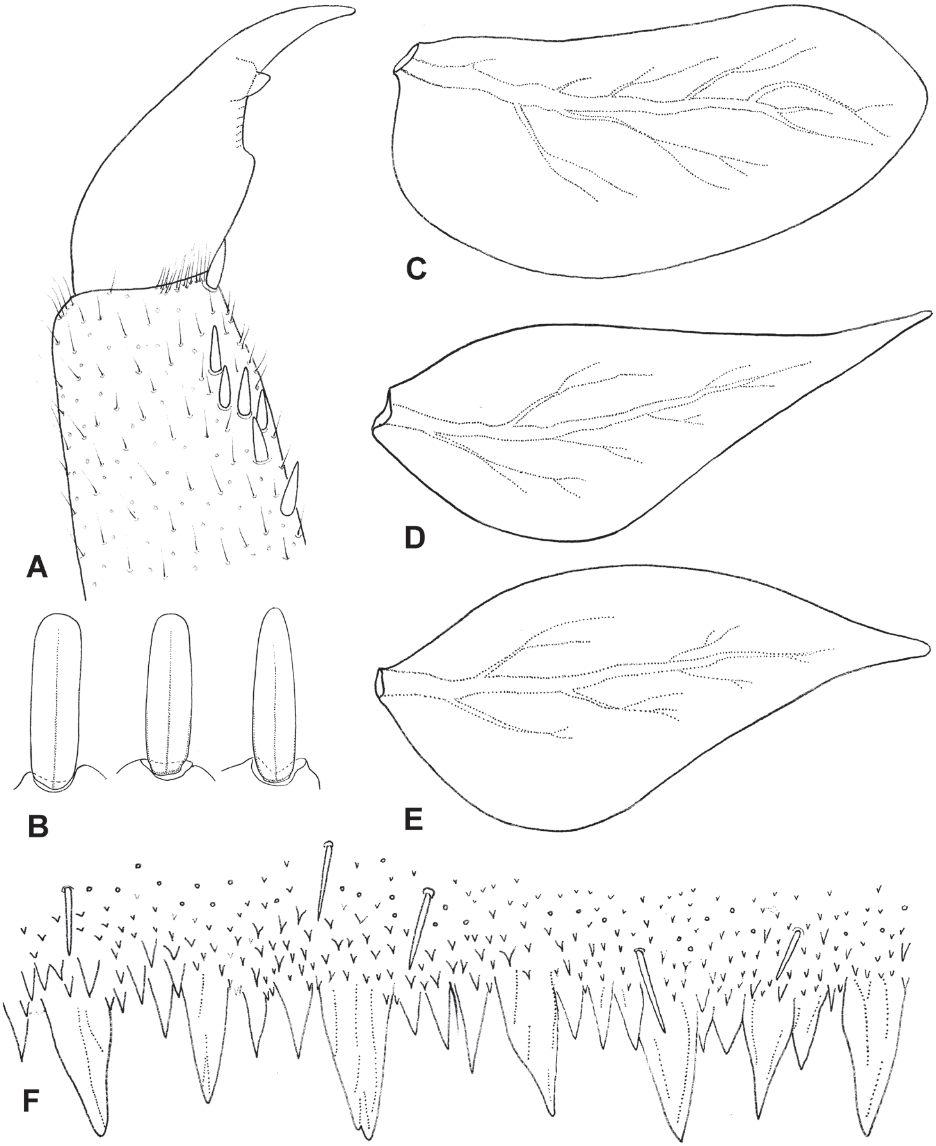


Figure 5. *Electrogena samalorum* (Landa, 1982), mature male (**A, C, E**) and mature female (**D**) larvae, paratypes XII and XIII: **A** pretarsal claw, 18.vi.1963 **B** femoral setae, dorsal surface of hind femur (based on two mentioned paratypes) **C** gill I, 18.vi.1963 **D** gill 7, 16.vii.1975 **E** gill 7, 18.vi.1963 **F** tergite IV, posterior margin.

(Fig. 4B). The mesonotum with several elongated whitish-yellow markings of variable shape, and two diffuse spots near the wing pad bases in *E. Újhelyii* and *E. samalorum*.

Legs. The coxae of both species with distinct brown marking around the segment; the femora yellowish-brown with a pair of transversal zigzag-like light brown spots proximally and distally; the tip of the femora light brown; tibiae contrasted, with ¾ of the distal part light brown and ¼ of the proximal part yellow; tarsi light brown and

Table 1. Minimum, mean and maximum values of some numerical characters for *E. Újhelyii* and *E. samalorum,* based on the larval type and topotype material.

Numerical characters	*E. samalorum*			*E. Újhelyii*		
	min	mean	max	min	mean	max
N_CBS	13	15.14	17	13	15.50	20
N_CLW	2	2,43	3	2	2,83	4
N_BVF	19	23.6	27	13	32,61	49
R_LBR	4.31	4.95	5.27	5.31	5.82	5.86
R_GLA	3.33	3.46	3.50	3.16	4.21	4.26
R_GLB	2.78	2.79	2.86	2.00	2.93	3.11
R_1Gl	2.18	2.29	2.33	1.97	2.21	2.47
R_4Gl	1.09	1.17	1.30	1.18	1.26	1.39
R_7Gl	2.23	2.48	2.76	2.15	2.35	2.54

slightly darker at the tip; pretarsal claw brown with 2–4 teeth (occasionally with one strong tooth, Fig. 5A). The characters of leg setation (including dorsal femoral setation) correspond with those in contributions published by Sowa (1981), Landa and Soldán (1982), Haybach and Belfiore (2003) and Bauernfeind and Soldán (2012).

Abdominal segments of both species with two pairs of diffuse yellow to light brown spots on a brown background on terga (I) II–VII (a pair of smaller spots close to the anterior margin of the segment centrally; a second pair of spots near the posterior margin of the segment laterally); tergite VIII occasionally with a large diffuse light spot centrally; tergite IX with a diffuse U-shaped light spot centrally; tergum X with elongated yellow spots centrally and smaller spots laterally (generally the same colour pattern was described for *E. samalorum* by Landa and Soldán 1982). Some differences occur between the observed shapes of the 1st and 7th gill plates in paratypes and topotypes of *E. Újhelyii* and *E. samalorum*, and drawings in the original descriptions are noted (see Fig. 5C, D, E). Nevertheless, in all materials studied, the 7th gill abruptly tapers in its distal third. Additionally, Landa and Soldán (1982: fig. 12) depicted a row of broad nearly triangular or rectangular jagged teeth apically along the posterior margin of the abdominal terga. All observed specimens can be characterised by the presence of a mainly regular row of stout triangular teeth, alternating with a group of 1–3 smaller teeth (Fig. 5F).

Numerical characters

The comparison of minimum, mean and maximum of selected numerical characters is presented in Tab. 1. We did not find any reliable character for delimitation of both studied species using the defined set of numerical characters. The range of all characters strongly overlapped, usually with values of those for *E. samalorum* within the range of *E. Újhelyii*. The only character with apparent difference between both species was R_LBR (total width of labrum divided by mean width of lateral lobes of labrum). Nevertheless the preservation of type material (namely of *E. samalorum*) and thus the number of measurements of this character did not allow the statistical evaluation.

Discussion

In our comparison of the *E. Újhelyii* and *E. samalorum* type material and our attempt to reliably decide the taxonomical position of both species we encountered many obstacles. In contrast to the well-preserved type material and available topotypic material of *E. Újhelyii*, there are only sparse specimens of type material of *E. samalorum*. Notably, the holotype of *E. samalorum* is missing and part of remaining material is heavily damaged. In addition, we were unsuccessful at collecting topotypic material in eastern Slovakia. Using a unified set of numerical larval characters suggested by Belfiore (1996, 1997) has turned out to be impractical for the separation of these taxa. The preservation and number of type materials did not allow us to compare both taxa with sufficient credibility. The only character which differed between both species was R_LBR. However, this character is highly variable, the value of this character for *E. Újhelyii* varies from 3.7 to 5.9 (see Supplement in Polášek et al. 2018). For this reason, we considered this difference as a random result of insufficient number of measurements.

Thus, we have failed to find any substantial differences between the type material of *E. Újhelyii* and *E. samalorum* for all stages investigated. Only a few peculiarities in body coloration of *E. samalorum* in comparison with *E. Újhelyii* have been noted. In males (**i**) the body is markedly darker; (**ii**) the compound eyes have a relatively distinct border between the paler top and the darker base; (**iii**) the abdominal terga have brown strokes near the anterolateral margin of the segments only. In larva (**iv**) the head occasionally has two additional pairs of small spots on frons and vertex. However, we can assume that some of these differences may be related to the material storage mode during the past 35 years. As a consequence, the additional information for the delimitation of *E. Újhelyii* and *E. samalorum* based on the characters of colour pattern, which was recently discussed and successfully used by Wagner et al. (2017), was inaccessible to us. Moreover, these small differences between *E. Újhelyii* and *E. samalorum* might be a result of intraspecific variability of *E. Újhelyii*, as was mentioned by Sowa (1981) in the original description. On the other hand, recent research on the genetic diversity of Central European *Electrogena* species indicates that specimens identified as *E. Újhelyii* actually belong to two geographically distinct species (Polášek et al. 2018).

The status of *E. rivuscellana,* described for the first time from Switzerland (Landolt et al. 1991) can also be considered as problematic. The synonymy was stated by Belfiore and Desio (1995) by examination of only one larval skin, probably the paratype using Carlo Belfiores' system of numerical characters. However, limited usability of this system for closely related species delimitation has been proven in Polášek et al. (2018). Moreover, there are some differences in published larval and adult morphological characters which could make the recent synonymy questionable. In contrast to the types of *E. Újhelyii* and *E. samalorum*, the genitalia of *E. rivuscellana* is described as follows: (**i**) the penis lobes are visibly stretched laterally, with a relatively obtuse outer margin and posterolaterally the constriction of lobes is marked by a notch (giving the impression of small hump under the lobes); (**ii**) the forceps base has lateral protuberances which rise above the central convexity; and (**iii**) the titillators are comma-shaped, short and broadly rounded from both sides (see Landolt et al. 1991: figs 4, 5, 18–20, 22; Malzacher 1996: 84, figs 2, 5a, c, d). The larvae differ in the following details: different shape of the first gill plate (widest in the distal part in *E. rivuscellana* and in the proximal part in *E. Újhelyii*, see Landolt et al. 1991: fig 14; Sowa 1981: fig 7), different shape of the 4th gill plate (more quadrancular in *E. rivuscellana*, see Landolt et al. 1991: fig 15; Sowa 1981: fig 8) and slightly different body coloration in *E. Újhelyii* (violet spots on abdominal segments, violet ganglia, Sowa 1981). Despite two recent studies on genetic diversity of *Electrogena* species including *E. Újhelyii* (Wagner et al. 2017; Yanai et al. 2017), no data about Swiss populations of *E. Újhelyii* (and therefore possibly *E. rivuscellana*) have been published thus far except one analysed specimen of *E. Újhelyii* s. str. in Polášek et al. 2018, and could therefore be a possible case of cryptic diversity too.

Conclusions

We noted a remarkable similarity of all studied material from both larval and imaginal stages of *E. Újhelyii* and *E. samalorum*. However, due to the considerable damage of studied material and some noted differences between *E. Újhelyii* and *E. samalorum* type material, we cannot presently confirm their synonymy which was previously established without comparison of any material. Moreover, the recently revealed cryptic intrageneric diversity and existence of (at least) two morphologically nearly identical species with geographical distribution overlapping with type localities of *E. Újhelyii* and *E. samalorum* makes their synonymy even more doubtful. For similar reasons, the taxonomical position (suggested synonymy) of *E. rivuscellana* can be also considered as problematic. We found some significant differences in *E. Újhelyii* and *E. rivuscellana* larval and adult morphology based partially on comparison of drawings and descriptions in available literature. Additionally, the synonymy has been established using Carlo Belfiores' system of numerical characters which using must be considered carefully due to the limitations revealed in our last publication (Polášek et al. 2018). Given these uncertainties, it would be imprudent to assume synonymy of these species and we suggest that both species (*E. samalorum* and *E. rivuscellana*) be considered not as junior synonyms, but as *species inquirendae*.

Acknowledgements

This research would not have been possible without the invaluable help, consultation, and material of the recently deceased Tomáš Soldán (Czech Academy of Sciences). The authors are grateful to Michel Sartori (Museum of Zoology, Lausanne, Switzerland) for material of the species of the genus *Electrogena*. We are indebted to Milan Pallmann (SMNS, Stuttgart) for macrophotos of adults and larvae. Graphic material was prepared during the fellowship stay of RJG in SMNS within the Georg Forster Research Fellowship (Alexander von Humboldt Foundation, Bonn, Germany). This research was conducted with institutional support RVO: 60077344 for RJG and MUNI/A/0816/2017 for MP and JS.

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ZooKeys 845: 139–152 (2019)
doi: 10.3897/zookeys.845.32893
http://zookeys.pensoft.net

RESEARCH ARTICLE

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Two new and one little-known damsel bug of the subfamily Prostemmatinae Reuter (Hemiptera, Heteroptera, Nabidae) from China

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Academic editor: *F. Konstantinov* | Received 8 January 2019 | Accepted 29 March 2019 | Published 15 May 2019

http://zoobank.org/7EEE79D3-4EAD-410C-B636-7FEF8738CC61

Citation: Zhao P, Mao R, Cao L (2019) Two new and one little-known damsel bug of the subfamily Prostemmatinae Reuter (Hemiptera, Heteroptera, Nabidae) from China. ZooKeys 845: 139–152. https://doi.org/10.3897/zookeys.845.32893

Abstract

Two damsel bugs belonging to two genera of the subfamily Prostemmatinae from China are reported as new to science: *Alloeorhynchus* (*Alloeorhynchus*) *yunnanensis* **sp. n.** and *Rhamphocoris guizhouensis* **sp. n.** The little-known species *Alloeorhynchus* (*Alloeorhynchus*) *reinhardi* Kerzhner & Günther, 1999 is redescribed. All species are illustrated in detail. Keys to the Chinese species of *Rhamphocoris* and *Alloeorhynchus* are provided aid in identification.

Keywords

China, Nabidae, new species, Prostemmatinae

Introduction

Prostemmatinae is a small subfamily in the family Nabidae with five genera and approximately 150 species worldwide (Schuh and Štys 1991; Kerzhner and Konstantinov 2008; Cassis 2016; Brailovsky and Barrera 2017); four genera and 27 species are found in the Palaearctic Region (Kerzhner 1996). However, only 17 species and four genera of the subfamily were reported in China prior to this study, mainly from Yunnan Province and adjacent southern provinces (Hsiao and Ren 1981; Ren 1998; Li et al. 2012; Kerzhner and Günther 1999). During fieldwork to Guizhou and Yunnan provinces, we collected several rare specimens of Prostemmatinae. Herein two new species are described, illustrated, and keyed. *Alloeorhynchus* (*Alloeorhynchus*) *reinhardi* Kerzhner & Günther, 1999 was described based on two short-winged females from Sichuan Province of China. We found a third macropterous female from Guizhou Province of China, which is redecribed herein.

Species of Prostemmatinae are considered primarily ground-inhabiting predators (Kerzhner 1996; Kerzhner and Konstantinov 2008). However, we found several specimens of *Rhamphocoris guizhouensis* under the bark of dead broadleaved evergreen trees along with an unknown species of Aradidae (Figs 19, 20), but nothing else is known about the biology of these three species.

Materials and methods

The material examined in this study is now deposited in Guangdong Institute of Applied Biological Resources, Guangzhou, China. The external structures were examined using a binocular dissecting microscope. Male genitalia were soaked in hot 90% lactic acid for approximately ten minutes to remove soft tissue, then in hot distilled water, and dissected under a microscope. The dissected parts of the genital structures were placed in a plastic microvial with lactic acid under the corresponding specimen. All drawings were traced with the aid of a camera lucida. Measurements were obtained using a calibrated micrometer. Body length was measured from the apex of head to the tip of the hemelytra in resting position. Maximum width of the pronotum was measured across humeral angles. All measurements are given in millimeters. Classification system and morphological terminology mainly follow those of Ren (1998) and Kerzhner (1992). The tribal, generic, and specific names in the text are arranged alphabetically.

Taxonomy

Subfamily Prostemmatinae Reuter, 1890
Tribe Phorticini Kerzhner, 1971

Genus *Rhamphocoris* Kirkaldy, 1901

Rhamphocoris Kirkaldy, 1901: 221; Ren 1998: 47; Cassis 2016: 172. Type species: *Rhamphocoris dorothea* Kirkaldy, 1901, by monotypy.

Aristonabis Reuter & Poppius, 1909: 48 (syn. by Kerzhner 1970: 280). Type species: *Aristonabis pulcher* Reuter & Poppius, 1909, by original designation.

Harrisiella China & Miller, 1953: 115 (syn. by Kerzhner 1970: 280). Type species: *Harrisiella humeralis* China & Miller, 1953, by original designation.

Diagnostic characters. Body elongate-oblong, flattened dorso-ventrally; body shiny, black or red with yellow markings (Figs 1, 19). Head slightly declined anteriorly (Fig. 2); rostrum 4-segmented, first segment short and thickened, second segment longest, third approximately half length of second, fourth segment shortest (Fig. 2); first and second antennal segments distinctly thickened and thicker than third or fourth segments (Fig. 1). Pronotum constricted slightly between collar and anterior pronotal lobe and distinctly between anterior lobe and posterior lobe (Figs 1, 2); posterior pronotal lobe distinctly wider than anterior lobe; anterior lobe with middle longitudinal sulcus, sides slightly anteriorly bulged; posterior lobe laterally roundly produced, posterior margin straight; scutellum subtriangular, sub-basally with two small round depressions, apical part strongly acute. Hemelytra oval, membrane with three elongate cells (Fig. 1); fore femur beneath with a large acute angular process medially and with two lines of small dentate tubercles from median angular process to apex of femur; fore tibiae slightly curved, apex dilated, without spongy fossula; ostiolar peritreme gradually posteriorly widened, elongated, somewhat curved (Fig. 4).

Remarks. *Rhamphocoris* is a small genus of the subfamily Prostemmatinae with ten known species worldwide. Five species (including the new species described herein) have been recorded in China, *R. borneensis* (Schumacher, 1914) [China (Yunnan, Hainan); Malaysia, Vietnam], *R. elegantulus* (Schumacher, 1914) [China (Taiwan)], *R. hasegawai* (Ishihara, 1943) [China (Yunnan, Taiwan)], *R. tibialis* Hsiao, 1981 [China (Yunnan)], and *R. guizhouensis* sp. n. [China (Guizhou)] (Hsiao and Ren 1981; Ren 1998).

Key to the Chinese Species of *Rhamphocoris* Kirkaldy

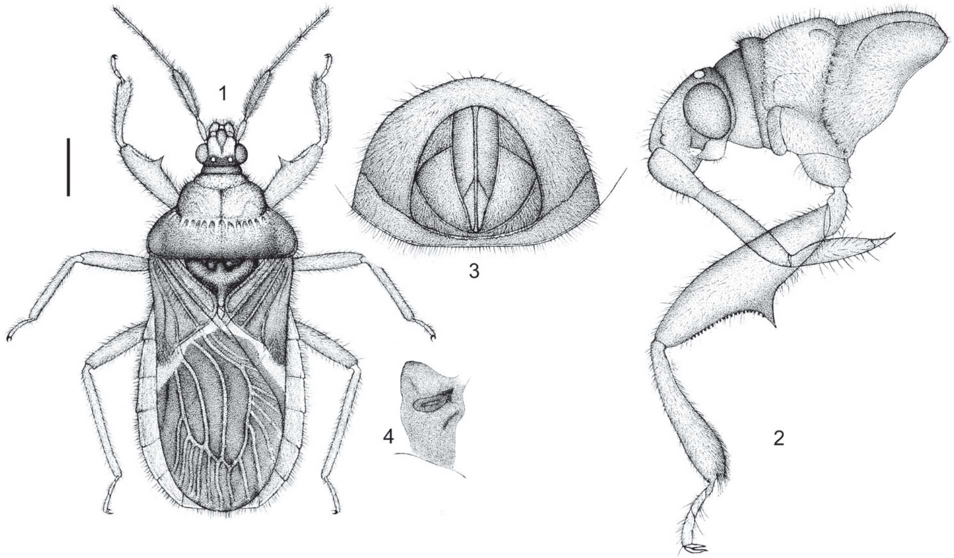
1 Pronotum bicolored, black with anterior pronotal lobe and basal part of posterior lobe red .... ***R. guizhouensis* sp. n.**
– Pronotum unicolorous, uniformly red or black **2**
2 Pronotum black .... ***R. hasegawai* (Ishihara, 1943)**
– Pronotum red **3**
3 Tibiae blackish brown .... ***R. tibialis* Hsiao, 1981**
– Tibiae red **4**
4 Scutellum red .... ***R. borneensis* (Schumacher, 1914)**
– Scutellum black .... ***R. elegantulus* (Schumacher, 1914)**

***Rhamphocoris guizhouensis* sp. n.**

http://zoobank.org/CC9D5DE7-61D7-420C-91F4-D30A3E158A6D
Figs 1–4, 19, 20

Type material. Holotype: female, China, Guizhou, Liping, Taiping Mountain, 28-VII-2009, 26°14'19.54"N, 109°18'38.59"E, Zhao Ping leg.

Diagnosis. Body length 5.48 mm. Body color red with black markings, shiny; head and pronotum bicolored, mostly red, but vertex of head, dorsal surface of neck,



Figures 1–4. *Rhamphocoris guizhouensis* sp. n., female holotype. **1** habitus, dorsal view **2** head and pronotum, antennae removed, lateral view **3** apical part of abdomen, ventral view **4** ostiolar peritreme of metathoracic scent gland. Scale bars: 0.87 mm (**1**); 0.48 mm (**2**); 0.40 mm (**3, 4**).

anteocular area of head, collar, most of posterior pronotal lobe blackish brown to black; scutellum black.

Description. Color. Body red, shiny. First antennal segment pale yellow, second antennal segments blackish brown, third to fourth antennal segments pale brown; vertex of head, dorsal surface of neck, anteocular area, eyes, anterior margin of collar of pronotum, propleural epimeron, pleuron and sternum of meso- and metathorax, fore wing (except strip or markings on basal part of membrane and basal part of clavus yellowish white) dark brown to blackish brown (Figs 1, 19); posterior pronotal lobe (except basal part), anterior margin of each abdominal segment pale brown to brown; scutellum, small spines of underside of fore femur blackish brown to black; abdomen ventrally pale yellowish brown and laterally blackish brown; strip of basal part of membrane yellowish white (Figs 1, 19), basal part of clavus pale yellowish brown.

Structure. Body clothed with golden yellow setae. Body flattened dorsoventrally. Head with rounded processes ventrally (Fig. 2); pronotum distinctly transversely constricted between collar and anterior lobe and between anterior and posterior lobe; anterior pronotal lobe bulged, arcuately laterally shallowly sulcate, medially longitudinally sulcate; scutellum sub-basally concave and with two small rounded depressions, apical part produced; fore femur somewhat thickened, and beneath with acute angular process. Abdomen oblong, not covered completely by fore wing; posterior margin of abdomen in female straight; fore wing reaches to abdominal tip. Ostiolar peritreme of metathoracic scent gland shown in Fig. 4.

Measurements Female, n = 1. Body length 5.48; maximal width of abdomen 3.33. Length of head 0.71; width of head 0.71; length of anteocular part 0.31; length of postocular part 0.05; length of neck 0.16; length of synthlipsis 0.38; interocellar space 0.19; length of antennal segments I–IV= 0.33, 0.76, 0.67, 0.55; length of rostral segments I–IV=0.31, 0.71, 0.48, 0.19; length of collar 0.19; length of anterior lobe of pronotum 0.48; length of posterior lobe of pronotum 0.67; maximal width of thorax 2.19; length of scutellum 0.67; length of hemelytron 3.76.

Male. Unknown.

Distribution. China (Guizhou).

Etymology. The specific name is derived from the type locality of the species.

Remarks. The new species resemble to *R. hasegawai* in body shape and color, but in the latter the head and pronotum are totally black. The new species is similar to *R. elegantulus* but easily distinguished by the body color: the head (except the vertex) is black; the collar and most of the posterior lobe of pronotum black, the anterior lobe and basal part of posterior lobe red (Fig. 19) (vs. the head and pronotum totally red in *R. elegantulus*) (Ren 1998). The five Chinese species in the genus *Rhamphocoris*, including the new one described herein, can be distinguished in the above key. The new species is flattened and the single specimen was collected together with the flat bug *Aradus* sp. (Aradidae) under the bark, and possibly feeds on flat bugs. The fifth-instar nymph is red except for the brown to yellow antennae and the blackish brown wing pads (Fig. 20).

Tribe Prostemmatini Reuter, 1890

Genus *Alloeorhynchus* Fieber, 1860

Alloeorhynchus Fieber, 1860: 43; 1861: 159; Ren 1998: 51; Distant 1904. Type species: *Pirates flavipes* Fieber, 1836, by subsequent monotypy (Fieber 1861: 159).

Falda Gross, 1954: 139 (syn. by Kerzhner 1970: 282). Type species: *Falda queenslandica* Gross, 1954, by original designation.

Diagnostic characters. Body elongate oblong. Anterior part of head strongly declined, or somewhat declined; anteocular area of head short, nearly conical; posterior margin of eyes adjacent to anterior margin of pronotum; ocelli present; antennae clothed with long setae, first antennal segment short, extending beyond apex of head; rostrum slender, extending to metasternum, first segment short and thick, second and third segments longest, fourth segment short; pronotum distinctly constricted transversally behind middle, posterior margin straight; scutellum long, subequal to width at base. Fore and mid femora moderately thickened, underneath with two to three rows of small spines; fore tibia slightly shorter than femur, apical part widened, with spongy fossula.

Remarks. The genus includes two subgenera, *Alloeorhynchus* and *Psilistus,* and 49 species in the world (Ren 1998; Brailovsky and Barrera 2017). Eight species have been recorded in China, including one new and one little-known species described in the present study: *A.* (*A.*) *notatus* Distant, 1919 [China (Yunnan); India, Nepal], *A.* (*A.*) *sinicus* Ren, 1998 [China (Zhejiang)], *A.* (*A.*) *vinulus* Stål, 1864 [China (Hainan, Taiwan); Japan, Vietnam, Java, Philippines, Burma], *A.* (*A.*) *yunnanensis* sp. n. [China (Yunnan)], *A.* (*A.*) *reinhardi* Kerzhner & Günther, 1999, and *A.* (*P.*) *corallinus* (Stål, 1873) [China (Yunnan); Burma, Sikkim, India, Malaysia], *Alloeorhynchus* (*P.*) *bakeri* Harris 1930 [China (Yunnan)] (Hsiao et al. 1981; Ren 1998; Kerzhner and Günther 1999; Gapon and Konstantinov 2008; Li et al. 2012).

Key to the Chinese Species of *Alloeorhynchus* Fieber

1 Middle of fore and mid femora ventrally not dentate or without horn-like extensions **2**
– Middle of fore and mid femora ventrally dentate or with horn-like extensions **3**
2 Body red, transverse constriction on pronotum distinct, apex of scutellum with two small tubercles .... ***Alloeorhynchus* (*P.*) *corallinus* (Stål, 1873)**
– Body black, transverse constriction on pronotum indistinct, apex of scutellum round, without tubercles .... ***Alloeorhynchus* (*P.*) *bakeri* Harris, 1930**
3 Head blackish brown to black **4**
– Head yellow **6**
4 Anterior pronotal lobe yellow or pale yellowish brown .... ***A.* (*A.*) *vinulus* Stål, 1864**
– Anterior pronotal lobe blackish brown **5**
5 Posterior pronotal lobe blackish brown, middle part paler; fore wing brown, middle part paler .... ***A.* (*A.*) *sinicus* Ren, 1998**
– Posterior pronotal lobe blackish brown to black; fore wing blackish brown, basal part paler .... ***A.* (*A.*) *reinhardi* Kerzhner & Günther, 1999**
6 Basal part of corium distinctly yellow; fore femur beneath with three distinct tubercles .... ***A.* (*A.*) *notatus* Distant, 1919**
– Basal, middle and apical part of corium with obscure yellow markings; fore femur beneath with four distinct tubercles .... ***A.* (*A.*) *yunnanensis* sp. n.**

***Alloeorhynchus* (*Alloeorhynchus*) *reinhardi* Kerzhner & Günther, 1999**
Figs 5–9, 21

Alloeorhynchus (*Alloeorhynchus*) *reinhardi* Kerzhner & Günther, 1999, 33: 221; Gapon and Konstantinov 2008: 24.

Material examined. 1 female, China, Guizhou, Kaili, 3-III-2011, 26°34'15.93"N, 107°58'34.53"E, Zhao Ping leg.

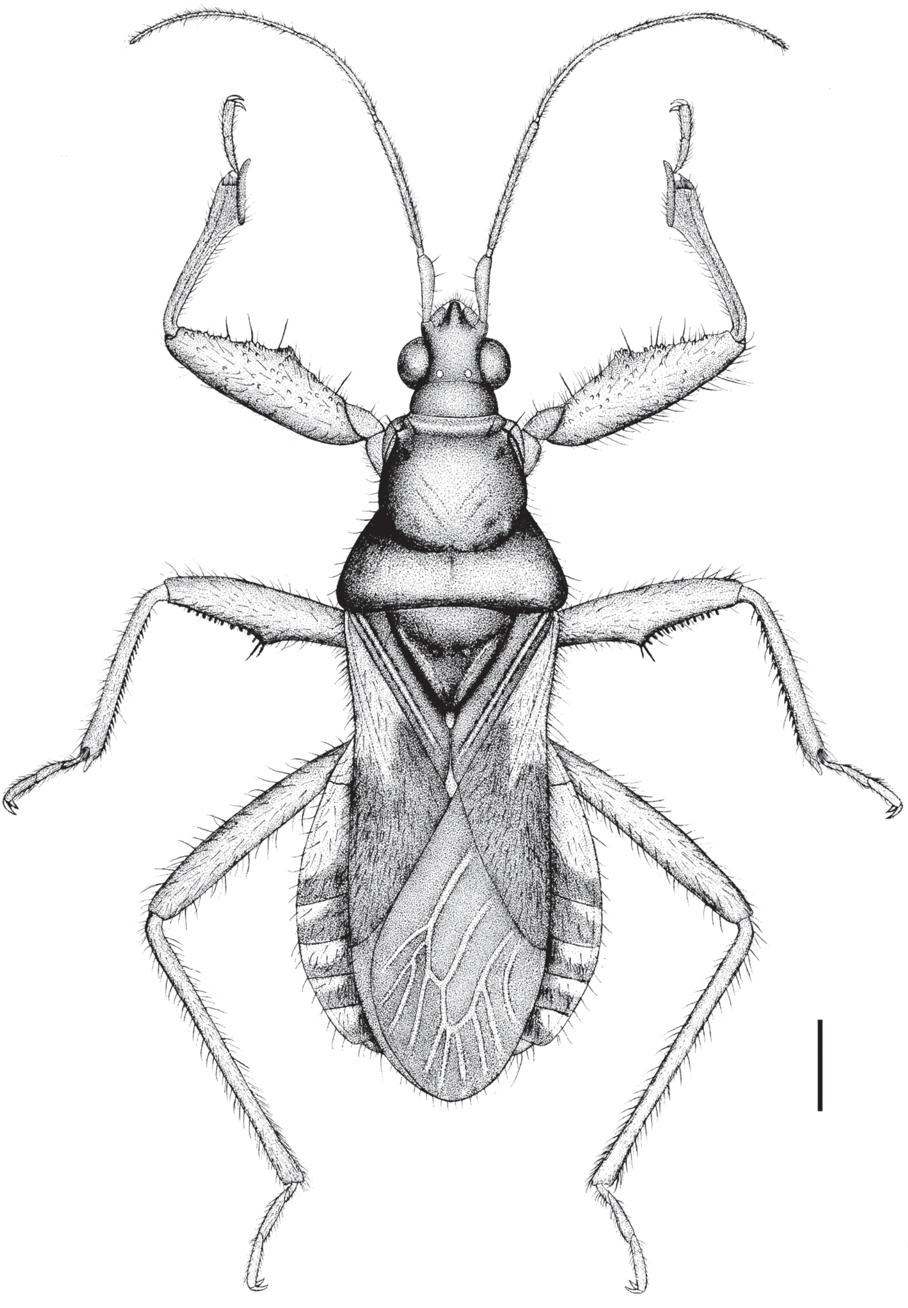
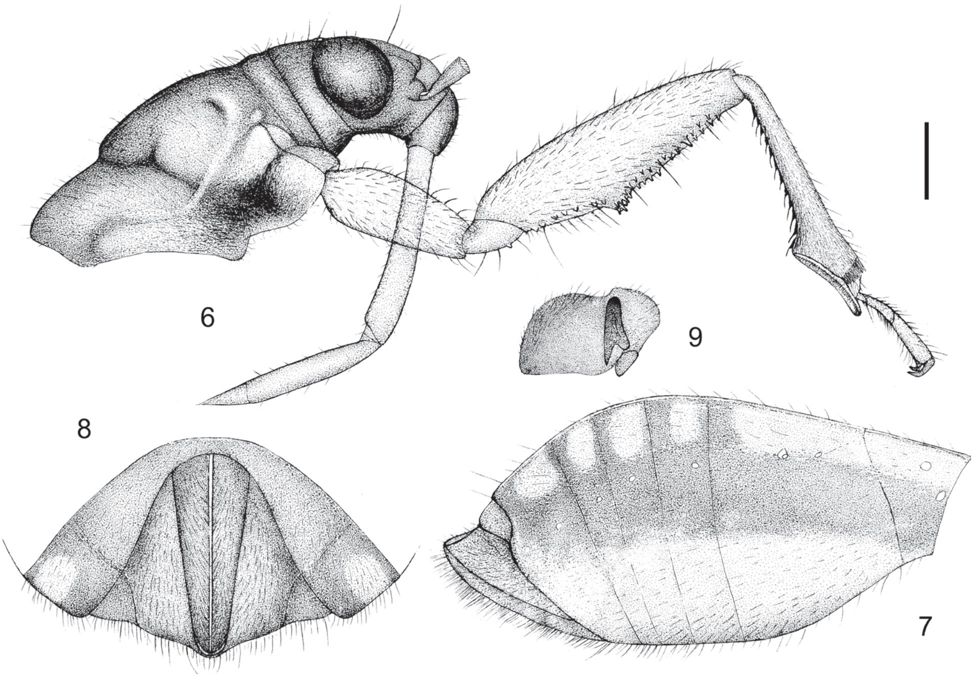


Figure 5. *Alloeorhynchus* (*Alloeorhynchus*) *reinhardi* Kerzhner & Günther, 1999, female, habitus, dorsal view. Scale bar: 0.67 mm.

Diagnosis. Body blackish brown with pale yellowish-brown markings; head, thorax, scutellum, fore wing (except basal part of corium), and lateral sides of abdominal sterna blackish brown to black; antennae, rostrum, and legs yellow.



Figures 6–9. *Alloeorhynchus* (*Alloeorhynchus*) *reinhardi* Kerzhner & Günther, 1999, female. **6** head and pronotum, antennae removed, lateral view **7** abdomen, lateral view **8** apical part of abdomen, ventral view **9** Ostiolar peritreme of metathoracic scent gland. Scale bar: 0.32 mm (**6**); 0.8 mm (**7**); 0.4 mm (**8**); 0.32 mm (**9**).

Redescription. Color. Body blackish brown to black (Figs 5, 21). Head, first rostral segment, thorax, scutellum, corium (except basal part), clavus, membrane, spines beneath femora and tibia, apical part and sides of abdominal sterna (Fig. 7), apical part of third to seventh connexival segments, eighth connexival segment blackish brown to black (Figs 5, 7, 21); second to fourth antennal segments, apical part of femora, apical and basal parts of tibiae, tarsi pale yellowish brown; first antennal segment, second to fourth rostral segments, coxae, trochanters, femora (except apical part), tibiae (except basal and apical parts), basal part of corium, middle part of abdominal sternum (third to sixth segments), second connexival segment, basal part of third to seventh connexival segments yellow.

Structure and vestiture. Macropterous. Body elongate oblong, posteriorly gradually widened (Fig. 5). Head, pronotum, ventral surface of abdomen, legs and antennae smooth and shiny (Fig. 21). Body sparsely clothed with white long setae; first antennal segment sparsely clothed with oblique setae, second to fourth segments densely clothed with oblique setae; tibiae and corium of fore wing clothed densely with setae (Fig. 5). Subapical part of first antennal segment curved outward. Anterior pronotal lobe somewhat bulged and twice as long as posterior pronotal lobe; scutellum sub-angular, apical part with small protuberance. Fore coxa strong, subequal to 2/5 of femur in length; fore and mid femora distinctly thickened, ventrally sub-basal 2/5 dilated in a protrusion, and apical half beneath with two lines of black dentate spines; fore tibia apically dilated with spongy fossula and underneath with two lines of black spines; mid tibia beneath with a line of distinct spines and a line of indistinct spines (Fig. 6). Abdomen in female widened posteriorly; fore wing extending to tip of abdomen (Figs 5, 7). Ostiolar peritreme of metathoracic scent gland shown in Fig. 9. Apical part of abdomen in female shown in Figs 7, 8.

Measurements. Female, n = 1. Body length 5.70; maximal width of abdomen 2.30. Length of head 0.93; length of anteocular part 0.83; length of postocular part 0.50; length of synthlipsis 0.40; interocellar space 0.15; length of antennal segments I–IV= 0.60, 1.07, 0.97, 1.40; length of rostral segments I–IV=0.33, 1.07, 0.76, 0.27; length of collar 0.20; length of anterior lobe of pronotum 0.90; length of posterior lobe of pronotum 0.50; maximal width of thorax 1.73; length of scutellum 0.87; length of hemelytron 3.93.

Distribution. China (Guizhou, Sichuan).

Remarks. Kerzhner and Günther (1999) described the species *A.* (*A.*) *reinhardi* in German based on two short-winged females collected from Sichuan Province in Southern China. We found a macropterous female in Guizhou Province, which is redescribed here in English to facilitate identification. We identified this species by comparing it with the description and the color illustration in the paper published by Kerzhner and Günther (1999) with the help of Dr Steffen Roth (University Museum of Bergen), but we were unable to examine the type specimens.

Alloeorhynchus (*Alloeorhynchus*) *yunnanensis* sp. n.

http://zoobank.org/D668063A-B4A4-4AEF-AA89-F18CD5BD3834
Figs 10–18

Type material. Holotype, male, China, Yunnan, Xishuangbannan, Mengla, Mengman Town, Nanping Village, 23-IV-2013, 21°17'18.86"N, 101°17'48.86"E, Wan Renjing and Zhao Ping leg.

Diagnosis. Corium reddish brown, and its basal, middle and apical part with obscure yellow markings; fore femur beneath with four distinct tubercles; head greyish yellow, anterior pronotal lobe greyish brown with median longitudinal part yellow.

Description. Color. Body greyish brown dorsally and pale yellowish ventrally. Basal, middle, and apical markings of corium, apical part of femur, basal part of tibia, two sides of abdomen ventrally tinged with red (Figs 10, 12). Antennae, neck dorsally, thorax (except metapleuron somber black), scutellum, corium (except markings), clavus (except basal part), subapical part of femur, hind tibia (except basal part), hind tarsus, basal part of fourth to seventh connexival segments brown (Figs 10, 12); spines beneath femur, tibiae of fore and mid legs, membrane black (Figs 10–12); head (except neck dorsally), rostrum, coxae, trochanters, femora (except apical part), fore and mid tibiae, markings of corium, middle part of abdominal

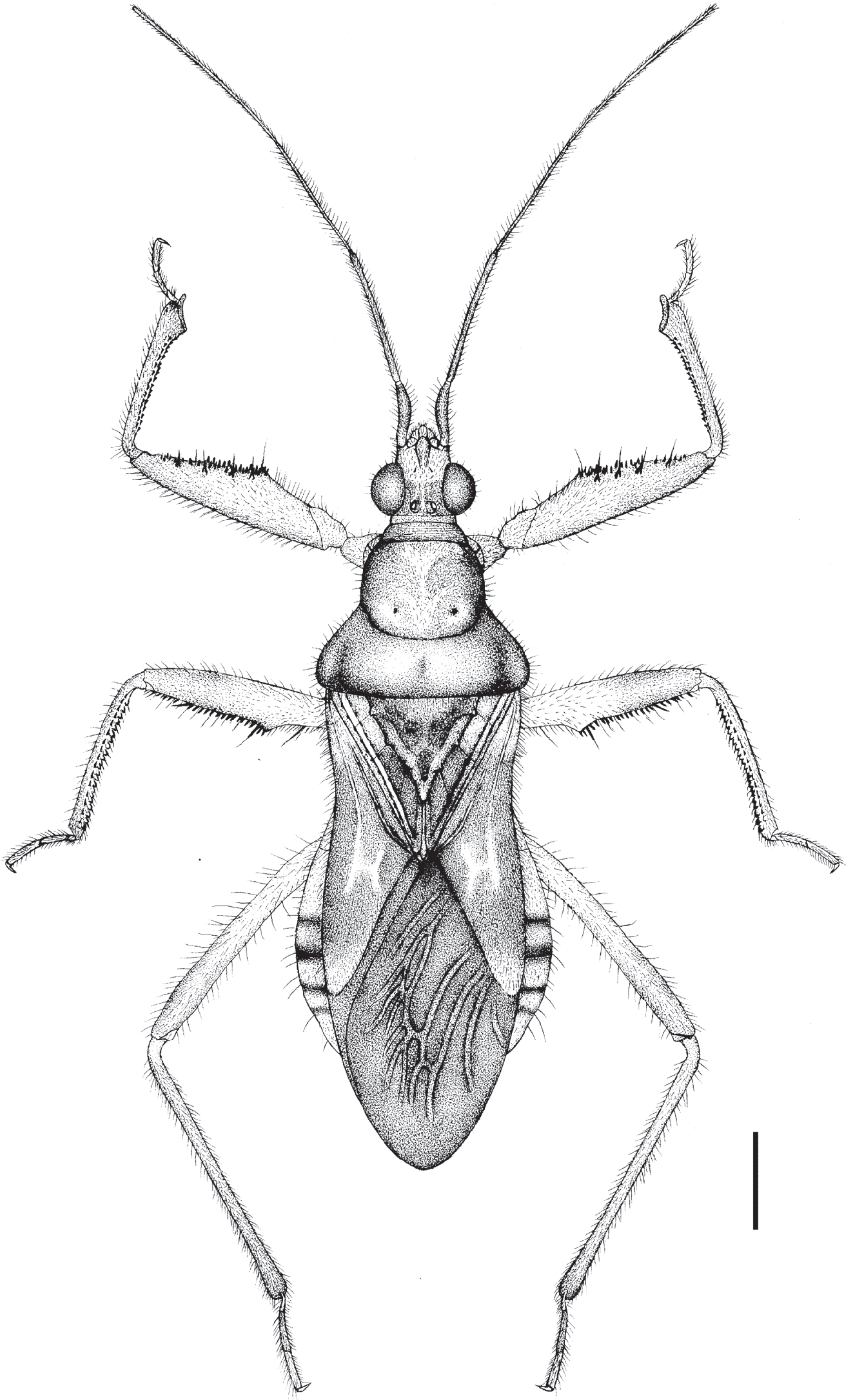


Figure 10. *Alloeorhynchus* (*Alloeorhynchus*) *yunnanensis* sp. n., male holotype, habitus, dorsal view. Scale bar: 0.8 mm.

sternum, second connexival segment, apical part of third to seventh connexival segments yellow.

Structure and vestiture. Body elongate oblong (Fig. 10). Body clothed with yellowish to white setae; first antennal segment sparsely clothed with oblique setae, second to fourth segments densely clothed with oblique setae; scutellum and corium of fore wing clothed with blackish setae (Figs 10–12). Subapical part of first antennal segment somewhat curving outward. Pronotum smooth and shiny, anterior pronotal lobe somewhat bulged; scutellum sub-angular, apical part somewhat produced posteriorly. Fore coxa strong, subequal to 1/2 of femur in length; fore and mid femora thickened and ventrally sub-basal 2/5 dilated in a protrusion, and fore femur beneath inside with four small short spines and outside with numerous black denticles from the protrusion to apical part of femur; fore tibiae apically dilated with spongy fossula and beneath with two lines of black spines; mid tibiae beneath with a line of distinct spines and a line of indistinct spines (Figs 10, 11); fore wing extending beyond tip of abdomen. Pygophore round, median pygophore process broad and produced acutely laterally (Fig. 13); paramere triangulate, apical part dilated (Figs 17, 18); basal plate of phallobase short and thick, pedicel short (Figs 14, 17). Phallosome elliptic, shown in Figs 17, 18.

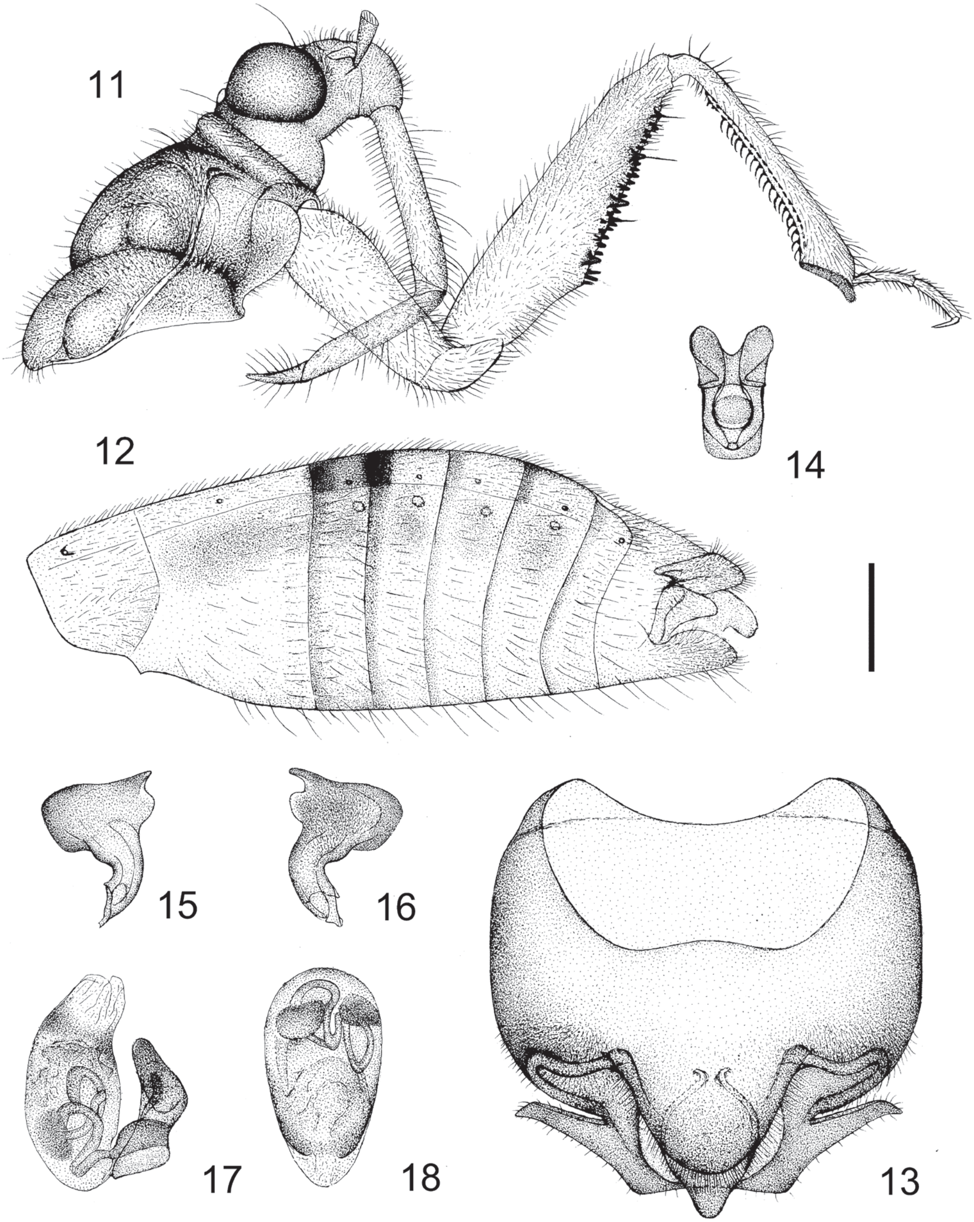
Measurements. Male, n = 1. Body length 5.86; maximal width of abdomen 2.00. Length of head 0.80; length of anteocular part 0.27; length of postocular part 0.20; length of synthlipsis 0.33; interocellar space 0.07; length of antennal segments I–IV= 0.53, 1.20, 1.13, 1.71; length of rostral segments I–IV=0.33, 0.97, 0.73, 0.27; length of anterior lobe of pronotum 0.93; length of posterior lobe of pronotum 0.53; maximal width of thorax 1.73; length of scutellum 1.00; length of hemelytron 4.00.

Female. Unknown.

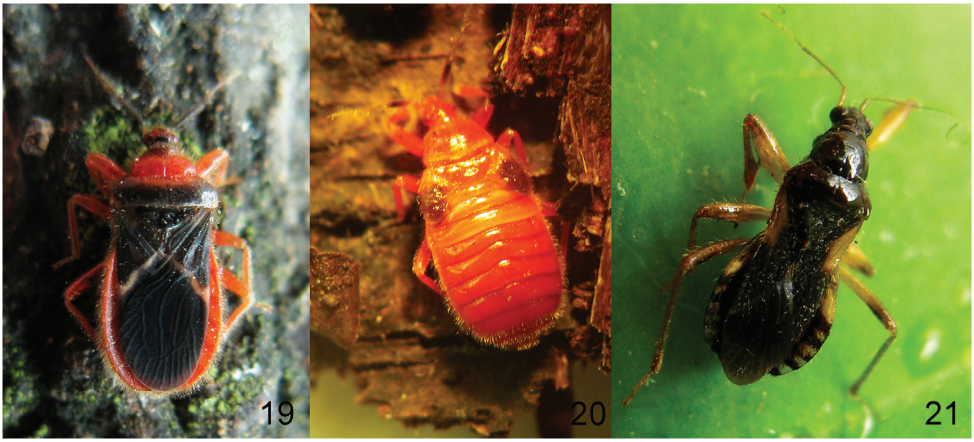
Distribution. China (Yunnan).

Etymology. The specific name refers to the type locality of the new species.

Remark. The general body shape and the structure of fore leg resemble those of *Alloeorhynchus* (*Alloeorhynchus*) *maculosus* Kerzhner, 1992 (India, Sumatra). In the new species the neck of the head is greyish, the anterior pronotal lobe is greyish brown with pale markings, the markings on the corium of fore wing is obscure, and the fourth to seventh connexival segments are yellow basally with brown markings (vs. the anterior pronotal lobe yellowish and its anterior margin darker, the head is yellow, the markings on the corium of fore wing are distinct, and the fourth to fifth connexival segments have brown markings in *A.* (*A.*) *maculosus*). The species is also similar to *Alloeorhynchus* (*Alloeorhynchus*) *fuscescens* Kerzhner, 1992 (Nepal, Vietnam) and *Alloeorhynchus* (*Alloeorhynchus*) *himalayensis* Kerzhner, 1992 (northern India) in the body coloration and the body size, but the paramere in the new species is triangular with an apical protuberance (Figs 15, 16) [vs. the paramere clavate without an apical protuberance in *A.* (*A.*) *fuscescens* and *A.* (*A.*) *himalayensis*]. The fore femur of the new species is with many small spines and four distinct larger spines [vs. the fore femur beneath with many small spines but without four distinct larger spines in *A.* (*A.*) *distanti* Harris, 1940 (Northern India and Nepal)] (Kerzhner 1992).



Figures 11–18. *Alloeorhynchus* (*Alloeorhynchus*) *yunnanensis* sp. n., male holotype. **11** head and pronotum, antennae removed, lateral view **12** abdomen, lateral view **13** pygophore, ventral view **14** phallobase **15, 16** paramere **17** phallus, lateral view **18** phallus, ventral view. Scale bar: 0.50 mm (**11**); 0.40 mm (**12**); 0.26 mm (**13–18**).



Figures 19–21. **19**, **20**, *Rhamphocoris guizhouensis* sp. n., female holotype; **21** *Alloeorhynchus* (*Alloeorhynchus*) *reinhardi* Kerzhner & Günther, 1999, female **19, 21** adult **20** fifth-instar nymph.

Acknowledgments

We sincerely thank Professor Ren Shuzhi (College of Life Science, Nankai University) and Dr Steffen Roth (University Museum of Bergen) for their helpful suggestions and constructive comments on the manuscript. This research is supported by grants from the National Natural Science Foundation of China (No. 31760634), GDAS Special Project of Science and Technology Development (2019GDASYL-0302007, 2018GDASCX-0107, 2017GDASCX-0107), Science and Technology Foundation of Guizhou Province [2015] 2008.

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ZooKeys 845: 153–180 (2019)
doi: 10.3897/zookeys.845.31155
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RESEARCH ARTICLE

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Montiphylax, (Trichoptera, Limnephilidae), a new genus to accommodate the western North American species: *Stenophylax antennatus* Banks, 1900, *Philocasca thor* Nimmo, 1971, and *Philocasca alba* Nimmo, 1977

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Academic editor: *Simon Vitecek* | Received 4 November 2018 | Accepted 13 April 2019 | Published 15 May 2019

http://zoobank.org/26489D4D-B0C3-4350-A253-F0D0039F64D7

Citation: Ruiter DE, Mutch RA (2019) *Montiphylax*, (Trichoptera, Limnephilidae), a new genus to accommodate the western North American species: *Stenophylax antennatus* Banks, 1900, *Philocasca thor* Nimmo, 1971, and *Philocasca alba* Nimmo, 1977. ZooKeys 845: 153–180. https://doi.org/10.3897/zookeys.845.31155

Abstract

Montiphylax, a new genus within the Limnephilidae, is proposed to include *Philocasca alba*, *P. antennata,* and *P. thor*. Characters for the adults and larvae are presented to separate *Montiphylax* from *Philocasca*. A summary of the distribution and life history of the *Montiphylax* species is provided. A key to ease separation of the known North American caddisfly larvae with gill clusters of single filaments is given.

Keywords

Association, Cascade Mountains, diagnostic key, distribution, female, larvae, Rocky Mountains, systematics

Introduction

The generic placement for the seven *Philocasca* taxa [*P. alba* Nimmo, 1977, *P. antennata* (Banks, 1900) as *Stenophylax* Kolenati, 1848, *P. banksi* (Denning, 1941) as *Anisogamus* McLachlan, 1874, *P. demita* Ross, 1941, *P. oron* Ross, 1949, *P. rivularis* Wiggins & Anderson, 1968, *P. thor* Nimmo, 1971] has been confused since Schmid (1955) placed *Stenophylax antennatus* within *Philocasca*. Wiggins and Anderson (1968) examined the known *Philocasca* taxa at that time and accepted Schmid's placement of *S. antennatus* in *Philocasca*. Two additional taxa (*P. thor* Nimmo, 1971, *P. alba* Nimmo, 1977) were subsequently described. Mutch (1981) pointed out the polyphyletic nature of *Philocasca*. Vshivkova et al. (2007) elevated *Philocasca* to the subfamily Philocascinae based only on the characters of *P. rivularis*. In order to clarify the status of *Stenophylax antennatus*, a new genus, *Montiphylax* (Limnephilidae, Limnephilinae) is proposed to accept *P. antennata*, *P. thor,* and *P. alba*.

Wiggins and Anderson (1968) presented, in detail, the prior problems associated with description and relationships within the *Philocasca* and its placement within the Limnephilidae. These problems were the result of only five male specimens spread across the four known species. No females, or larvae, had been associated at the time. And, at the time, only Banks and Ross seem to have examined those same specimens, and they disagreed on their generic placement. Wiggins and Anderson (1968), with still only the type of *S. antennatus* male available, did not acknowledge the significant generic dissimilarities pointed out by Banks and added no further information to support their placement of *S. antennatus* within *Philocasca*. In the discussion below we present the detailed history of the confusion, and rationale for the creation of a new genus, *Montiphylax*, to resolve the confusion. The information is based, in part, on now available female and larval associations.

Also, since Wiggins and Anderson (1968), *Philocasca* has been removed from the Limnephilinae and placed within the Philocascinae (Vshivkova et al. 2007). *Philocasca* can be distinguished by many non-Limnephilinae characters: wings very broad, rounded throughout, without obvious color patterns/spotting, etc.; mesonotal warts absent; female without mesal lobe of vulvar scale; larvae with strongly rounded anterior portion of pronotum without transverse groove, and with unique, long, flattened, scale-like setae on head and pronotum. The arrangement and shape of these larval setae are diagnostic for the *Philocasca* species.

While the spotted wings, female three-part vulvar scale, and pronotal transverse groove of the larva currently place *Montiphylax* within the Limnephilinae sensu Vshivkova et al. (2007) its further placement is unclear. This has resulted in the need to clarify the larval characters currently used in North American larval keys (Wiggins 1996, Morse and Holzenthal 2008) to separate the genera. We have provided a key to more consistently separate these subfamilies and genera.

Materials and methods

Abdomens were removed, cleared in 10% potassium hydroxide, mounted in glycerin and examined/imaged with the use of Leica stereo and Olympus compound microscopes, Canon DSLR cameras and EOS image capture software. Subsequent images were processed with Zerene image stacking software and Photoshop Elements image editing software. All collected material is preserved in 70% ethyl alcohol. Barcoding was successful for *M. antennatus* and Barcode of Life Datasystems, Ratnasingham and Hebert (2007), has *M. thor* barcodes available. Morphological terminology follows that of Wiggins (1996), Wiggins and Currie (2008) and Schmid (1998).

Taxonomic accounts

Diagnosis of the new genus *Montiphylax*

The *Montiphylax* male genitalia superficially resemble *Philocasca*; however, examination of head, setal warts, venation, and 9th and 10th segments shows no sister relationship. Vshivkova et al. (2007) completely separated *Philocasca* from the Limnephilinae based on characters of *P. rivularis*. *Philocasca* adults are readily separated from *Montiphylax* adults by the lack of irrorate forewings and metanotal setal warts in *Philocasca*. *Montiphylax* females have a mesal lobe on the vulvar scale that *Philocasca* females lack. *Montiphylax* larvae lack head and thoracic scale setae that are present on *Philocasca* larvae. *Montiphylax* larvae are distinguished from other North American Limnephilidae larvae by the combination of: pronotum not convex in lateral view, with a distinct indentation present between the anterior third to half of pronotum; all gill clusters consist of single filaments; sclerites of metanotal setal area 2 broadly separated; lateral line gills absent, and forked lamellae absent.

Limnephilidae, Limnephilinae

Montiphylax gen. n.

http://zoobank.org/BB66211A-F24F-46F8-B205-1ACEB1488D00
Figures 1–10

New combinations. *Stenophylax antennatus* Banks, 1900, new combination (type species); *Philocasca antennata* (Banks, 1900), new combination; *Philocasca alba* Nimmo, 1977, new combination; *Philocasca thor* Nimmo, 1971, new combination

Description. Adult (Fig. 1). Head to wingtip length: *Montiphylax antennatus* male - 19–21 mm (n = 5); *antennatus* female - 19–21 mm (n = 5). *Montiphylax albus* male - 18–19 mm (n = 8); *albus* female - 18–20 mm (n = 3). *Montiphylax thor* male - 18–21mm (n = 3). Eyes large with numerous fine setae located between ommatidia. Head rectangular in dorsal view; ocelli large, posterior ocelli set midlength. Several small setae scattered on head surface, primarily between and behind posterior ocelli. Two pair of warts evenly spread between anterior and posterior ocelli. Posterior warts small, linear with acute apices. Malar projection as long as length of 1st labial palp segment. Antennae shorter than wing length, stout, basal segment shorter than eye width.

Pronotal warts oval, wide, nearly touching mesally. Mesonotal macrosetae in linear row, basal warts located midlength, slightly merged but not fused into a single smooth oval wart; mesocutellar macro setae scattered linearly, less fused than mesonotal wart; most dorsal head and thoracic setae pale.

Forewings (in alcohol) reddish brown, finely irrorate; third radial vein and discoidal cell with a fairly long common boundary approximately equal to length of the first transverse vein; discoidal cell longer than its pedicel; all apical cells without pedicels. Anterior and posterior anastomosis nearly perpendicular to wing length, clearly located distad from posterior anastomosis. Hindwings brown, without irrorations; discoidal cell longer than its pedicel; all apical cells without pedicels. Anterior anastomosis perpendicular to wing length, clearly located distad from posterior anastomosis. Posterior anastomosis strongly oblique to wing margin. Most setae on wing membrane recumbent.

Legs long and thin, tarsi long with basal segment more than 0.5 length of mesotibia, Apical tarsal segments without ventral spines. Spines on legs black, spurs golden, spur count 1-2-4.

Male genitalia (Figs 6, 8, 9). Eighth segment without adornment, slightly swollen on dorsal apical margin. In lateral view 9th segment annular, narrowed dorsally and broadest at base of short, tall inferior appendages; deeply invaginated dorsally in caudal view. Tenth segment cupped anteriorly, appearing as two, slightly fused hemispheres extending broadly anteriad within the 9th. Superior appendages of 10th fused to intermediate appendages; in lateral view, variously broad and projecting, diagnostic by species. In dorsal view intermediate appendages of 10th extended mesally as two long, tapered, downward directed, thin parallel projections. Inferior appendages of 10th short, broad ventrally; nearly fused mesally. Phallus with heavily sclerotized, dorsomesal, conical projection at base of dorsolateral parameres. Parameres heavily sclerotized, projecting fingerlike, parallel to body of phallus; shape diagnostic by species. Apical portion of phallus membranous, extensile, with ejaculatory duct ending in an apical, upward directed, sclerotized cup.

Female genitalia (Figs 7, 10), female of *M. thor* unknown. Ninth tergite and sternite fused laterally; 10th segment fused to 9th, broadly projecting distad to blunt, rounded apex in lateral view. In dorsal view 10th apex cleft to approximately midlength mesally. In ventral view, 9th sternal lateral projections fused to mesal supragenital plate. Vulvar scale stout, broadly merged to 8th segment laterally, with wide, smoothly conical, medial lobe slightly shorter than lateral lobes.

Larva (Figs 2–4), (n = 3 *antennatus* and 4 *albus*; larva of *M. thor* unknown). Head nearly circular in dorsal view, widest mid-length, rugulose, specimens in alcohol rust colored. Muscle scars indistinct. Typical limnephiloid setation, without accessory setae. Anterior ventral apotome small, equal, or shorter than ventral ecdysial suture. Submental sclerites distinctly separated from stipes and mesally separated.

Prothorax rust colored (in alcohol) like head; setae scattered, without distinct setal areas; in lateral view, slight transverse indentation approximately midlength; posterior margin thick and dark, with deep, preceding furrow; ventrally with a single, wide, short, prosternite between legs. Mesothorax paler than prothorax; setal areas nearly merged; posterior black margin extending along lateral margin nearly to anterior margin; ventral area with a linear row of small, dark, mesosclerites along each side of posterior margin. Dorsal metanotal setal areas on distinct sclerites, without additional setae on metonotal membrane. Ventrally, mesosternite with very pale linear row of small sclerites along each side of posterior margin, may be difficult to see, appearing as a row of indentations. Legs typical limnephiloid form with short, stout proleg and hind leg the longest. Meso and metafemur with two, long, dark setae ventrally and a row of very small, fine spinelike setae along entire ventral setal margin. Anterior face of meso and metafemur with numerous accessory setae; posterior face usually with one or two accessory setae.

First abdominal segment with numerous long setae anterior of dorsal spacing hump; lateral spacing hump with several small sclerites on dorsal margin and one larger sclerite along posterior margin; ventrally with numerous long setae and a pair of posterior setal warts on mature larvae. Chloride epithelia present ventromesally, much wider than long (*albus* 2–7 [n = 3]; *antennatus* 3–7 [n = 4]). Lateral fringe on segments 2–8 (*antennatus*), 3–8 (*albus*); segment 2 portion is very short. Forked lamellae absent. Gill clusters consist of single filaments dorsally on segment 2 through 5 or 6, ventrally on 2 through 5, lateral line gills absent.

Ninth tergite with 3–4 pairs of long setae and several additional shorter setae. Lateral sclerite of anal proleg without short, stout, pale setae. Anal claw with single dorsal accessory hook.

Pupal case of final instar slightly curved, non-tapered, wood and mineral, or all mineral construction. The limited larval material available indicates the earlier instars may build vegetation cases.

Pupa (Fig. 5), (n = 4 *albus*). Labral setae long, with apices spirally twisted, not hooked. Mandibles triangular with apical half strongly tapered and flattened into an acute blade; mesal edge of blade slightly serrate. Antennal scape with a ventrolateral setal tuft and a single seta at the dorsal margin. Second antennal segment with a dorsal tuft. Antennae shorter than abdominal apex. Spined ridge of 1st abdominal tergite weak, linear with small scattered spines. Anterior hook plates present on abdominal tergites 3–7, with strong hooks directed posteriad. Small, oval posterior hook plates present on tergum 5. Abdominal lateral fringe present on segments 5–8. Anal processes elongate, slender, tubular, with patch of minute, dorsal spines at apex. Four long setae on each anal process; one located basally, and three apically.

Etymology. *Montiphylax* from the Latin *montis* (mountain) and the Greek *phylax* (guard), referring to the mountainous habitat of this genus.

Differential diagnosis of the Montiphylax species. The male of *M. antennatus* is distinguished from *M. albus* and *M. thor* by the long, narrow superior appendages in lateral view and the blunt paramere apex. The *M. thor* superior appendage has a wide base, appearing more triangular in lateral view. The superior appendage of *M. albus* is shorter than either *M. antennatus* or *M. thor* although wide at the base like *M. thor*. In lateral view, the paramere apex of *M. albus* and *M. thor* is acute; in *M. albus* the paramere apex is downturned while it is upturned in *M. antennatus* and *M. thor*.

The female of *M. antennatus* is separated from *M. albus* by the round anterior margin of the vaginal apparatus that is more quadrate in *M. albus* in ventral view. The female of *M. thor* is unknown. The pupa of only *M. albus* is known.

The lateral setal fringe of *M. antennatus* larvae originates on the posterior margin of the 2rd abdominal segment while the lateral fringe of *M. albus* starts at the anterior margin of the 3rd segment. The larva of *M. thor* is unknown.

***Montiphylax antennatus* (Banks, 1900)**

Figures 1, 4C, D, 6, 7

Stenophylax antennatus Banks, 1900: 254–255 (male description) Washington.

Anisogamus antennatus Milne, 1935: 29; Banks, 1943: 350, fig. 41 and 50 (describes 2nd specimen from Wallace, Idaho. This Idaho specimen is *M. thor*, see discussion below.).

Stenophylax antennatus Ross, 1944: 299.

Philocasca antennata Schmid, 1955: 201; Flint, 1966: 379, fig. 2m, n; Wiggins & Anderson, 1968: 74; Wiggins, 1977: 274; Mutch, 1981: 223; Wiggins, 1996: 338; Schmid, 1998: 121; Ruiter et al., 2005: 162; Blinn & Ruiter, 2013: 292.

Description. Head to wingtip length: male 19–21 mm (n = 5); female 19–21 mm (n = 5).

Male genitalia (Fig. 6): 8th tergite without dorsal modified spines or projections. Ninth segment annular with tergite narrow and strap-like, directed distad dorsally resulting in slightly sigmoid anterior margin of 9th in lateral view; remainder of 9th broad in lateral view, directed downward at approximately a 45 degree angle from the narrow tergite; inferior appendages appearing separated from 9th. In caudal view, inferior appendages slightly cupped around phallic apparatus and slightly separated mesally. Tenth segment cupped anteriorly, appearing as two, slightly fused hemispheres extending broadly anteriad within the 9th. Superior appendage nearly twice as long as tall in lateral view. Intermediate appendages arise ventrally, strongly sclerotized and extending as two long, tapered, parallel projections, curving downward at apex. In caudal view, below the intermediate appendages are paired, curved, narrow projections nearly surrounding the anus. Phallus large, with strongly sclerotized phallicata; membranous endophallus with dorsal, strongly sclerotized band, projected upward and distad apically; strong, thick parameres originate at the base of the dorsal band, extend distally; tapering to blunt, rounded apex in lateral view and slight curved upward throughout. Parameres originate dorsolaterally and extend posteriorly over 3 times as long as wide; thick throughout, ending in blunt, rounded apex in dorsal view. The aedeagus apex a sclerotized tube within an extensile sheath; ending in the bottom of a posteriorly directed sclerotized cup.

Allotype female genitalia (Fig. 7): 9th segment fused laterally and incomplete ventrally, separated ventrally by broad supragenital plate. Ninth fused with 10th; 9th tergite ca. half as long as 10th in lateral view; in lateral view 10th with dorsal and ventral margins slightly tapered throughout to rounded apex. In dorsal view, 10th cleft less than half the distance to base. In lateral view, ventrolateral corners of 9th extend distally beyond remainder of 9th; acute at apex and directed inward in ventral view. The medial lobe of the vulval scale short, shorter than lateral lobes, longer than wide. The vaginal apparatus, in lateral view, rectangular, ca. twice as long as tall; in ventral view, egg-shaped with smoothly rounded anterior margin.

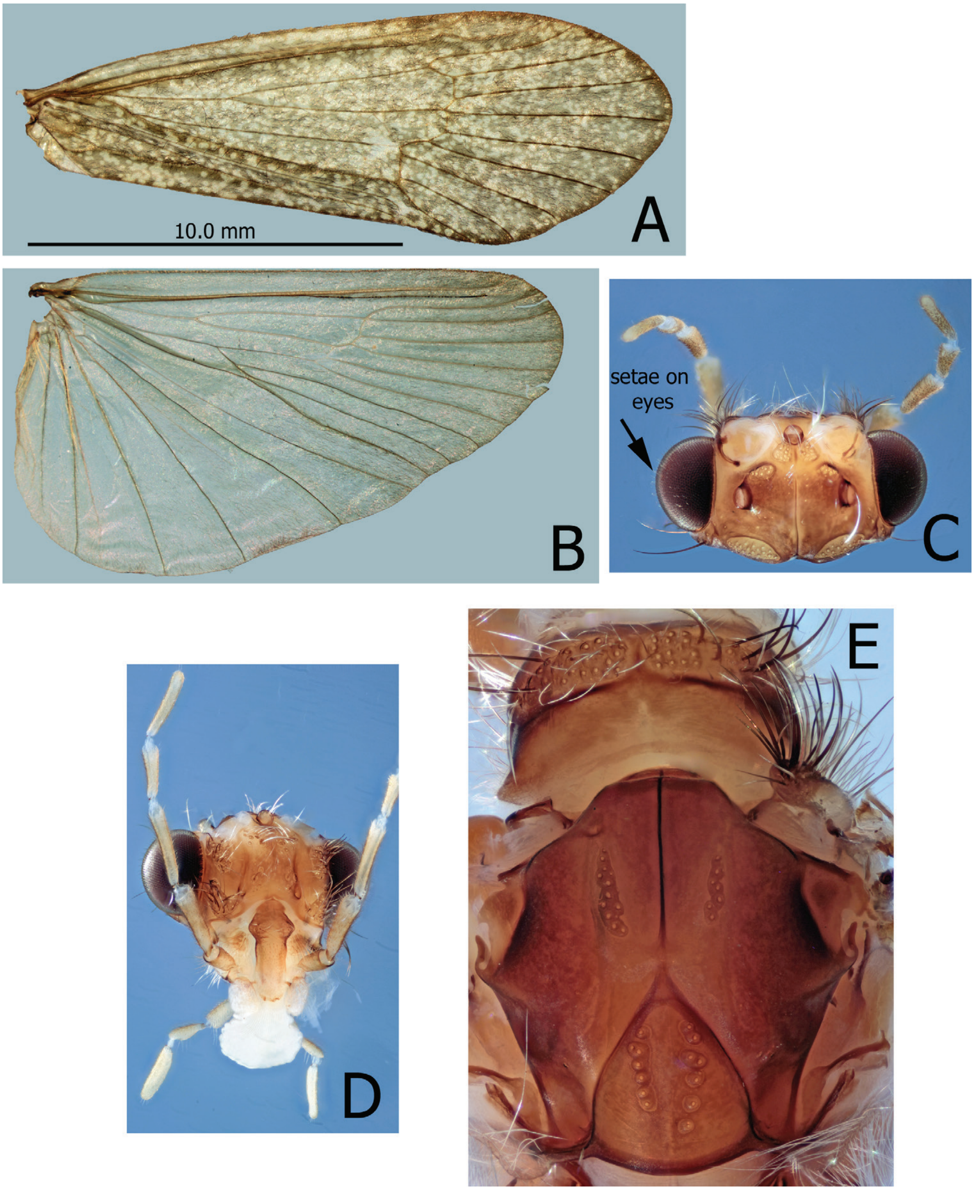

Figure 1. *Montiphylax antennatus.* Male (**A–E**) **A** right side forewing, dorsal **B** right side hindwing, dorsal **C** head, dorsal **D** head, anterior **E** prothorax and mesothorax, dorsal.

Material examined. WA: Whatcom County, stream near Heather Meadow Information Center on Artist Point Road, D.W. Blinn, 28 July 2009, blacklight trap, 2M; stream on Fire and Ice Trail, near top of Mt. Baker Highway, 48.85586 –121.68795,

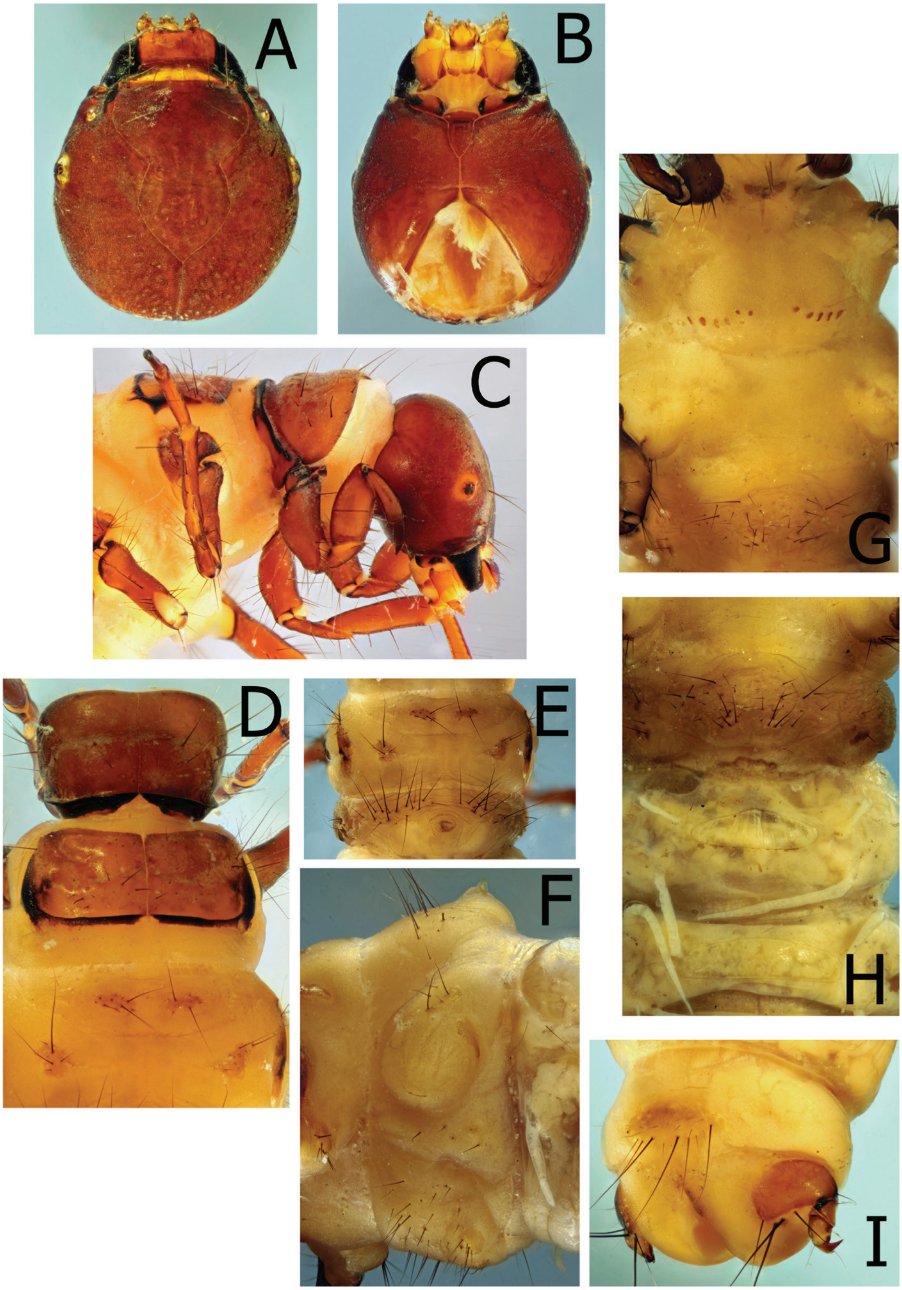

Figure 2. *Montiphylax albus*. Larva (**A–I**) **A** head, dorsal **B** head, ventral **C** head, pro & mesothorax, lateral **D** pro, meso & metathorax, dorsal **E** metathorax and 1st abdominal segment, dorsal **F** lateral spacing hump, left lateral **G** pro, meso & metathorax, ventral **H** 1st, 2nd and 3rd abdominal sternites, ventral **I** 9th tergite & anal prolegs, dorsal.

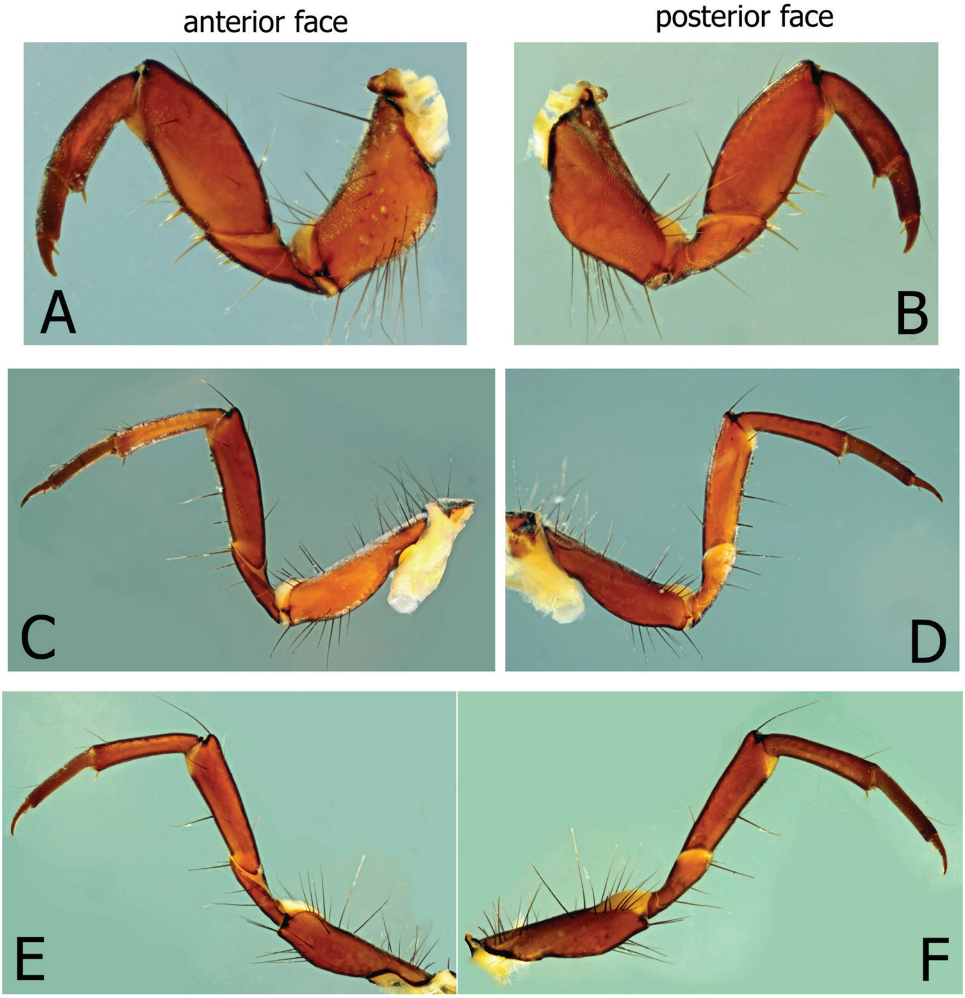

Figure 3. *Montiphylax albus*. Larval legs (**A–F**) **A** right side prothoracic leg, anterior face **B** right side prothoracic leg, posterior face **C** right side mesothoracic leg, anterior face **D** right side mesothoracic leg, posterior face **E** right side metathoracic leg, anterior face **F** right side metathoracic leg, posterior face.

D.W. Blinn, 13 August 2012, 2L, 1M, 1F; spring stream, ca. 150 feet southeast of outhouse at Mt. Baker Information Center parking lot, near top of Highway 542, 48.85378 –121.68543, D.E. Ruiter, 5 August 2012, 1L; meltwater stream on Fire and Ice trail, in Heather Meadows, Mt. Baker, D.W. Blinn, 31 July 2009, 13M, 3F (2M to National Museum of Natural History; 2M, 1F to S. Chuluunbat; 1M, 1F to Canadian National Collection, remainder in D.E. Ruiter personal collection); Terminal Lake on Mt. Baker Highway, D. W. Blinn, black light trap, 28 July 2009, 1M.

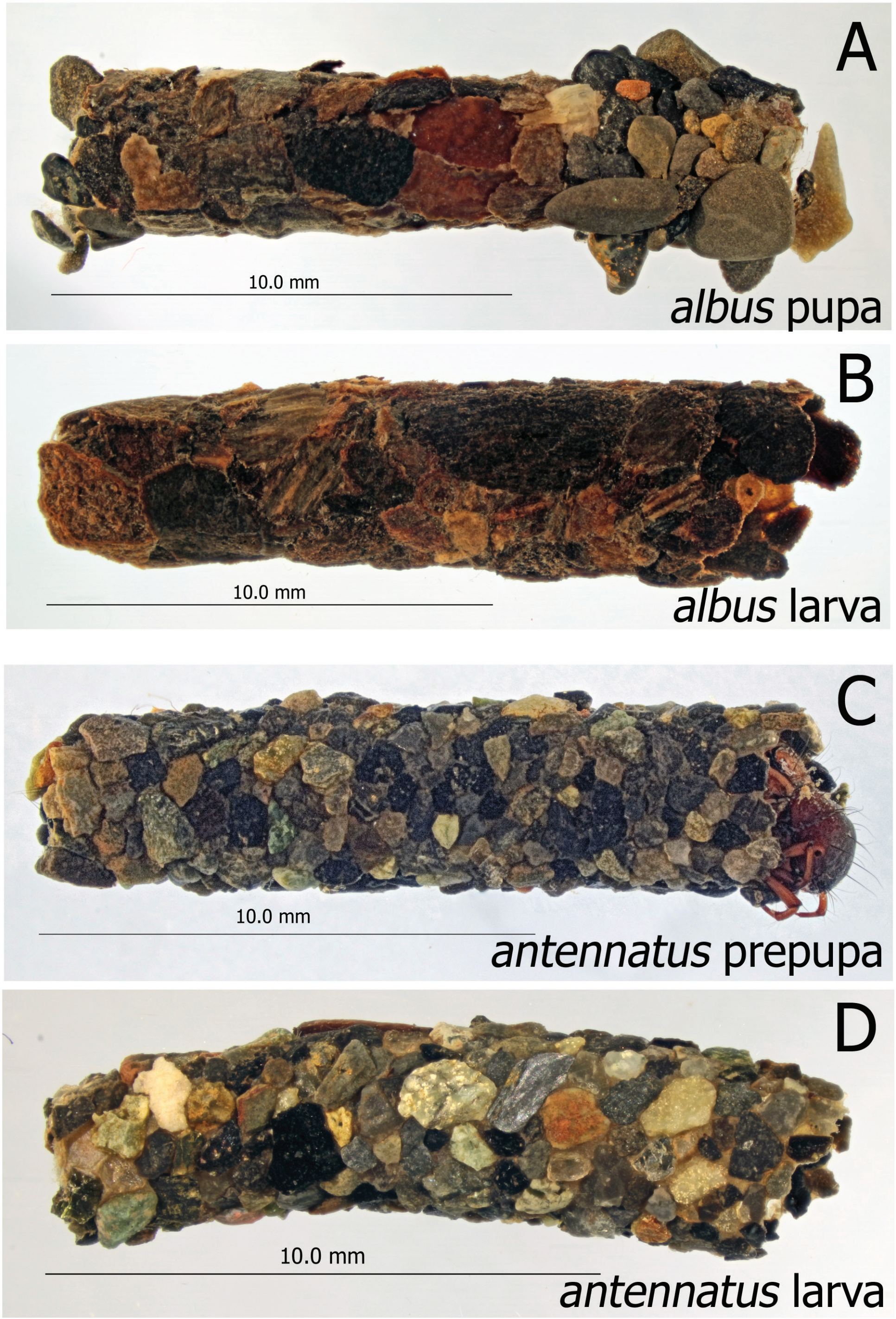

Figure 4. *Montiphylax*. Pupal and larval cases (**A–D**) **A** *M. albus* pupa case, lateral **B** *M. albus* larva case, lateral **C** *M. antennatus* prepupa case, lateral **D** *M. antennatus* larval case, lateral.

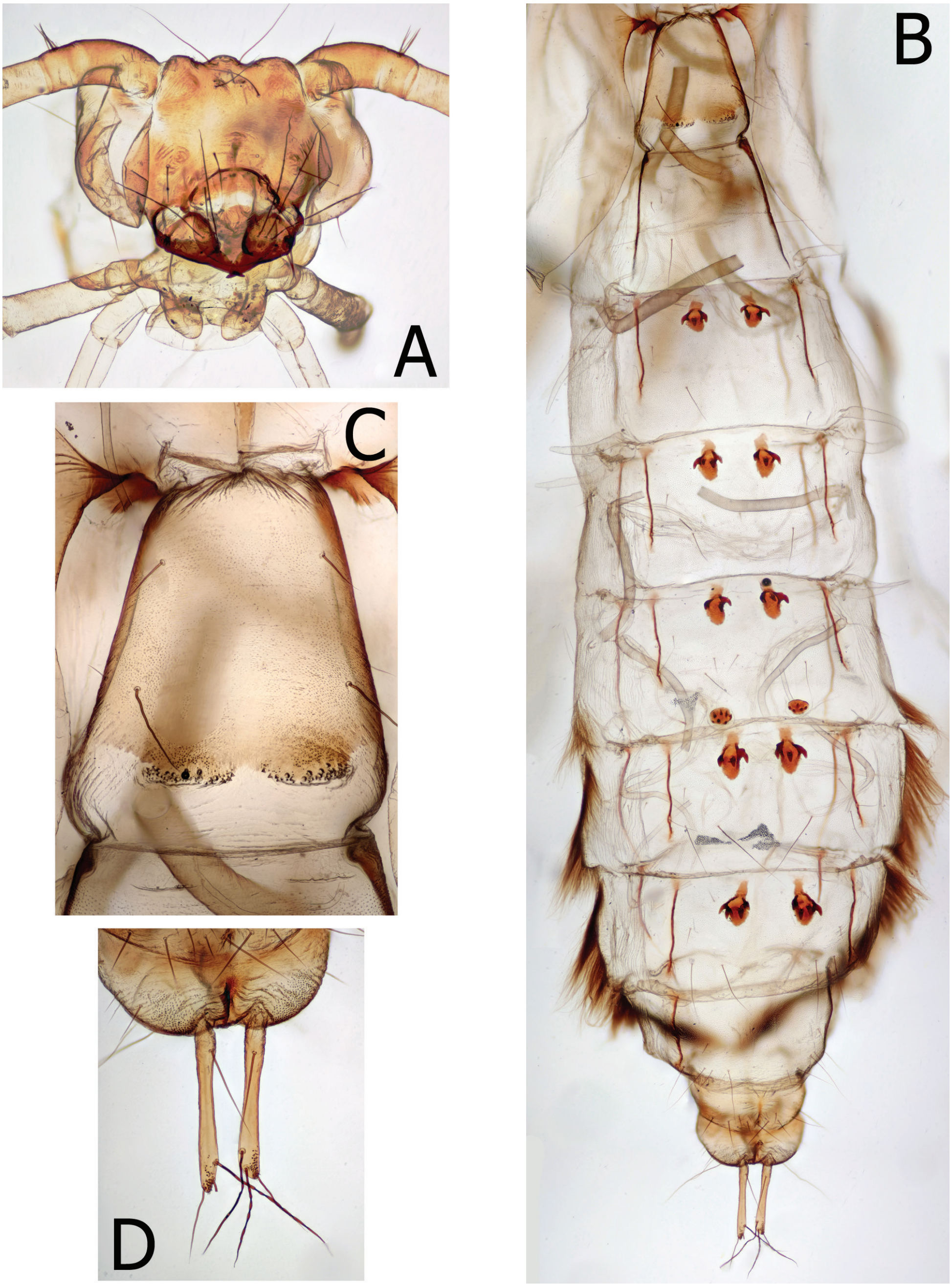

Figure 5. *Montiphylax albus*. Pupa (**A–D**) **A** head, anterior **B** abdomen, dorsal **C** 1st abdominal segment, dorsal **D** last abdominal segment, dorsal.

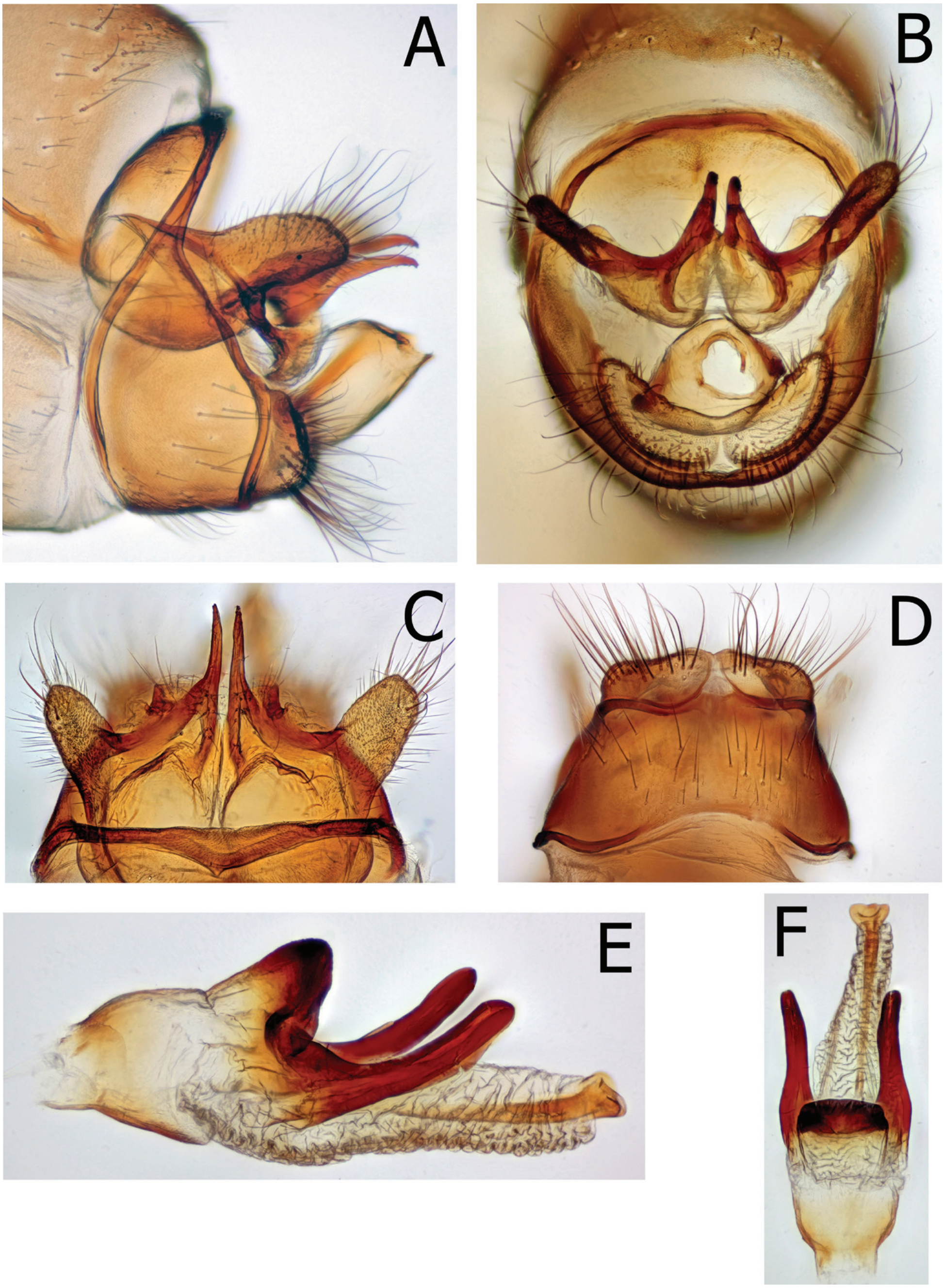

Figure 6. *Montiphylax antennatus.* Male **(A–F) A** genitalia, left lateral **B** genitalia, caudal **C** genitalia, dorsal **D** genitalia, ventral **E** aedeagus, left lateral **F** aedeagus, dorsal.

***Montiphylax thor* (Nimmo, 1971)**

Figure 7–8

Philocasca thor Nimmo, 1971: 147–148, figs 143a, b, 545–547, 653.

Notes. Nimmo (1971) described *M. thor* from a single specimen collected within Jasper National Park, Alberta. The Barcode of Life project has collected additional males from the Willmore Wilderness in Alberta, ca. 150 km northwest of the *M. thor* type locality. This Barcode of Life material was compared to the *M. thor* holotype and found to be the same. To date, females or larvae of *M. thor* have not been located.

Wiggins and Anderson (1968) mentioned the dark ventral surface of the *M. antennatus* scape described by Banks (1900) was absent on the Idaho *M. antennatus* specimen that Banks (1943) described, implying it was present on the *M. antennatus* type. The darker ventral surface of the antennal scape is present on the Mt. Baker *M. antennatus* males and females examined here. However, it is absent on our *M. albus* material, that have a concolorous scape. *Montiphylax thor* males have a darkened scape with the ventral surface pale - the exact opposite coloration pattern from *M. antennatus*. The Banks (1943) Idaho specimen was examined and it has the light ventral surface of the scape and upturned, acute parameres of *M. thor*. Neither Banks (1943) nor Wiggins and Anderson (1968) recognized this Idaho specimen as a new species. Our genetic comparisons of *M. antennatus* and *M. thor* also support Nimmo's conclusion that *M. thor* is a valid species. Our determination that the Banks (1943) Wallace, Idaho, record represents *M. thor* extends the *M. thor* range another 600km farther south along the Rocky Mountains. This also results in *M. thor* occurring both further north and south than *M. albus* along the Rockies. Wallace, Idaho, is a historic silver mining city in the South Fork of the Coeur d'Alene River Valley. It is likely the *M. thor* specimen was collected at higher elevations in the surrounding area.

Description. Male genitalia (Fig. 8): The dark, conical, ventral sclerite of the phallic apparatus illustrated by Nimmo (1971) is absent from the holotype and the other *M. thor* specimens examined in this study. It is unknown what the Nimmo (1971) dark ventral sclerite represents. Eighth tergite without dorsal modified spines or projections. Ninth segment annular with tergite narrow and strap-like; remainder of 9th broad in lateral view, directed posteroventrad at ca. a 45 degree angle from the narrow tergite, with tall, narrow inferior appendages nearly fused to 9th. In caudal view, inferior appendages slightly cupped around phallic apparatus and slightly separated mesally. Tenth segment cupped anteriorly, appearing as two hemispheres extending broadly anteriad within the 9th. Tenth segment appears fused mesally along anterior margin. Superior appendages approximately as long as tall, triangular in lateral view directed upward. Intermediate appendages arise ventrally, strongly sclerotized and extending as two long, tapered, parallel projections, curving downward at apex. In posterior view, below the intermediate appendages are paired, curved,

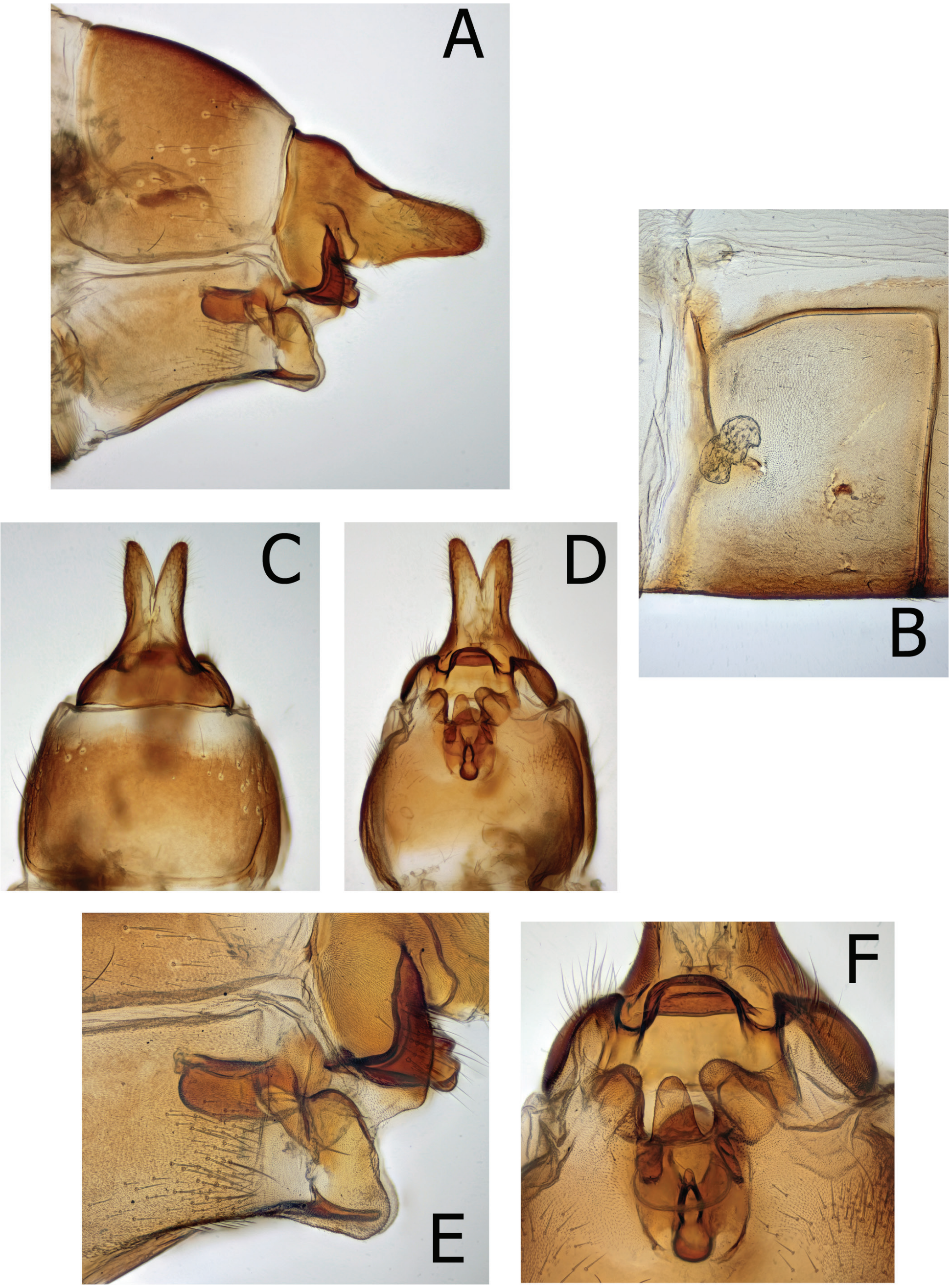

Figure 7. *Montiphylax antennatus*. Female **(A–F)** **A** genitalia, left lateral **B** 5th sternite, left lateral **C** genitalia, dorsal **D** genitalia, ventral **E** genitalia, left lateral **F** genitalia, ventral.

narrow projections nearly surrounding the anus. Phallus large, with strongly sclerotized phallicata; membranous endophallus with dorsal, strongly sclerotized band, projected upward and distad apically; strong, thick parameres originate at the base

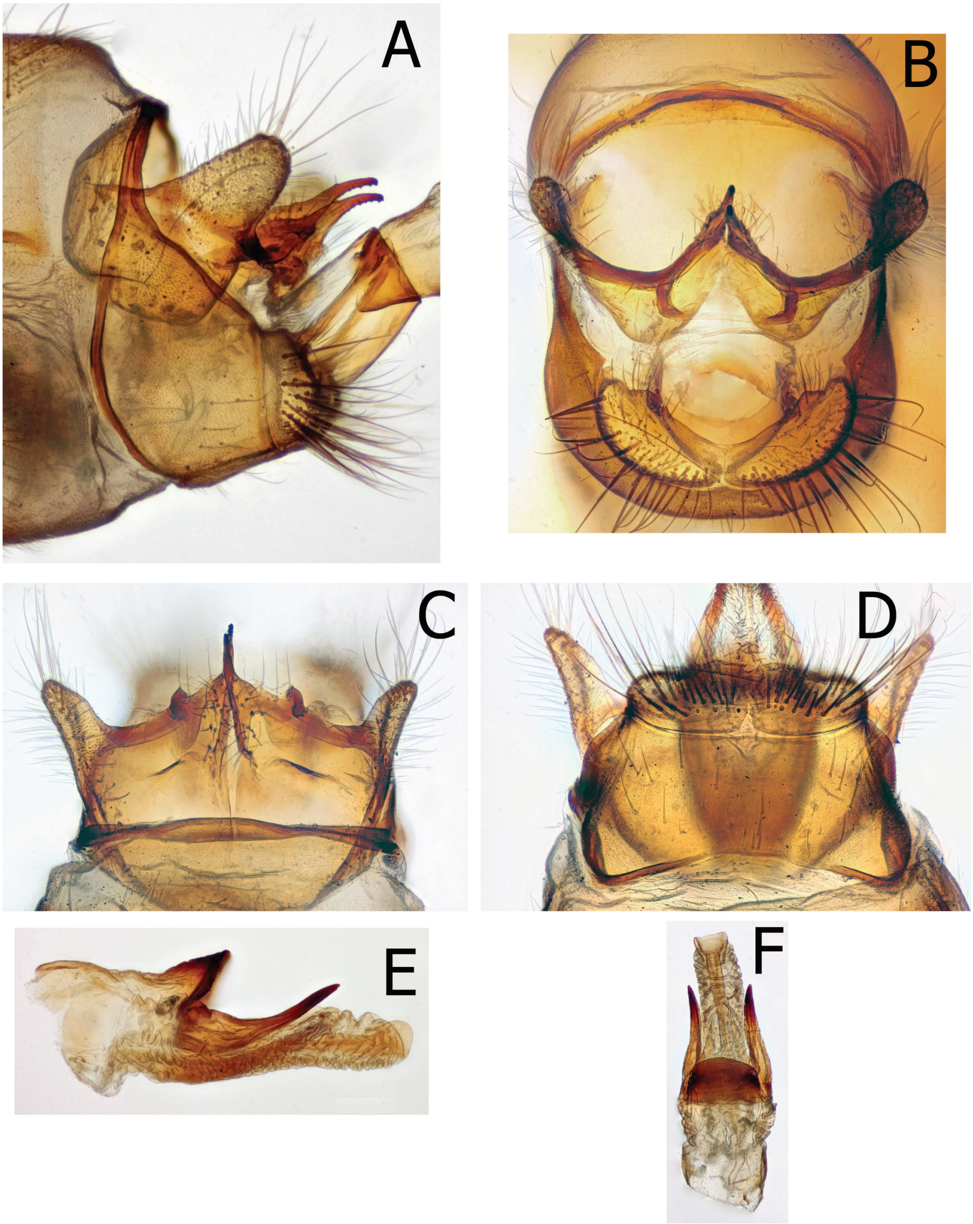

Figure 8. *Montiphylax thor*. Male **(A–F) A** genitalia, left lateral **B** genitalia, caudal **C** genitalia, dorsal **D** genitalia, ventral **E** aedeagus, left lateral **F** aedeagus, dorsal.

of the dorsal band, extend distally; tapered to acute apex in lateral view and slightly curved upward throughout. Parameres originate dorsolaterally and extend posteriorly ca. 3 times as long as wide; tapering evenly throughout to acute apex in dorsal view. Aedeagal apex a sclerotized tube within an extensile sheath; ending in the bottom of an upward directed sclerotized cup.

Material examined. Holotype male - Canadian National Collection Type # 10,588, Alpine Meadows, east of Mt. Edith Cavell, Jasper National Park, Alberta, habitat: Mountain Tarn, A. P. Nimmo, 10–12am, 4 July 1975; Alberta, Willmore Wilderness, 53.6858, -119.419, Hilchie & MacAuley, 21 July 2007, 3 males (Bold # 10ABCAD-004, 10ABCAD-006, & 10ANCAD-007).

Montiphylax albus (Nimmo, 1977)

Figs 2, 3, 4A, B, 5, 9, 10

Philocasca alba Nimmo, 1977: 45–46, 49, figs 102–105, 121; Mutch, 1981: 222–228, fig. 43.

Notes. Nimmo (1977) described *M. albus* and included characters to separate *M. albus* from *M. thor*. The second author reared from associated pupae (Alberta, Middle Fork Creek, Marmot Creek Experimental watershed, 1800 meters altitude, 50.94820 –115.15151) the male and female of *M. albus*, and provided figures of the male, female, and pupa. These are from the same watershed as the Nimmo paratype collection. Based on this *M. albus* material, we add descriptions and images for the *M. albus* adults, pupa and larva.

Description. Head to wingtip length: male - 18–19 mm (n = 8); female - 18–20 mm (n = 3). General description of adults, pupa, and larva contained in genus description above.

Male genitalia (Fig. 9): 8th tergite without dorsal modified spines or projections. Ninth annular with tergite narrow and strap-like; remainder of 9th broad in lateral view; with tall, narrow inferior appendages nearly fused to 9th. In caudal view, inferior appendages curved around margin of 9th base to meson of 9th, appearing fused mesoventrally. Tenth segment cupped anteriorly, appearing as two hemispheres extending broadly anteriad within the 9th. Tenth segment appears split mesally. Superior appendages taller than long in lateral view, directed downward and distad at ventral margin. Intermediate appendages arise ventrally, strongly sclerotized and extending as two long, tapered, parallel projections, curving downward at apex. In caudal view, ventrad to the intermediate appendages paired, curved, narrow projections nearly surround the anus. Phallus large, phallicata strongly sclerotized; endophallus with strongly sclerotized band dorsally, projected upward and distad apically; strong, thick parameres originate at the base of the dorsal band, extend distally, tapered to acute apex in lateral view and slightly curved downward throughout. In dorsal view, parameres originate dorsolaterally and extend posteriorly ca. 3 times width, tapering evenly to bluntly curved apex. Aedeagus apex a sclerotized tube within an extensile sheath, ending in the bottom of an upward directed sclerotized cup.

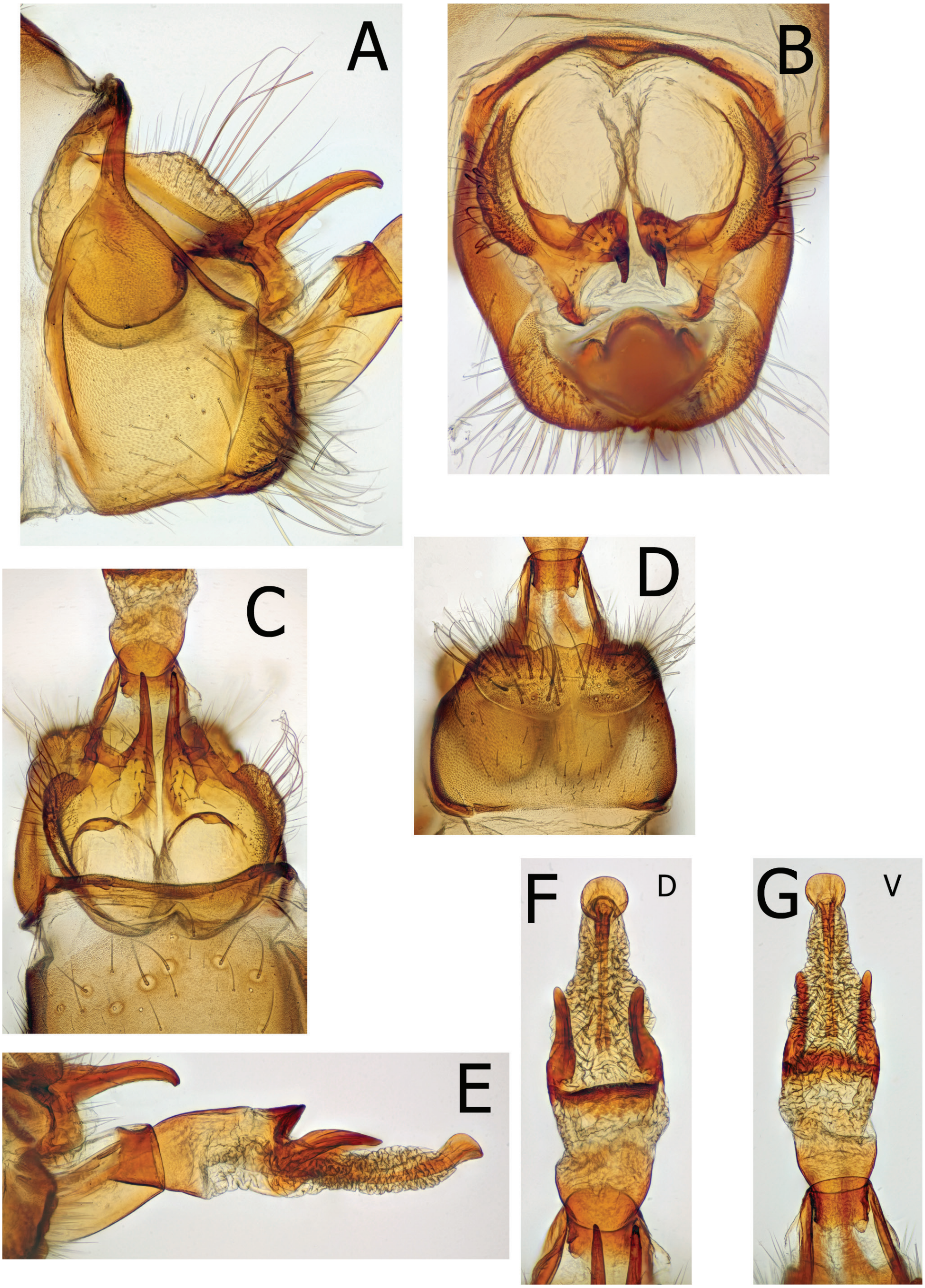

Figure 9. *Montiphylax albus*. Male **(A–G) A** genitalia, left lateral **B** genitalia, caudal **C** genitalia, dorsal **D** genitalia, ventral **E** aedeagus, left lateral **F** aedeagus, dorsal **G** aedeagus, ventral.

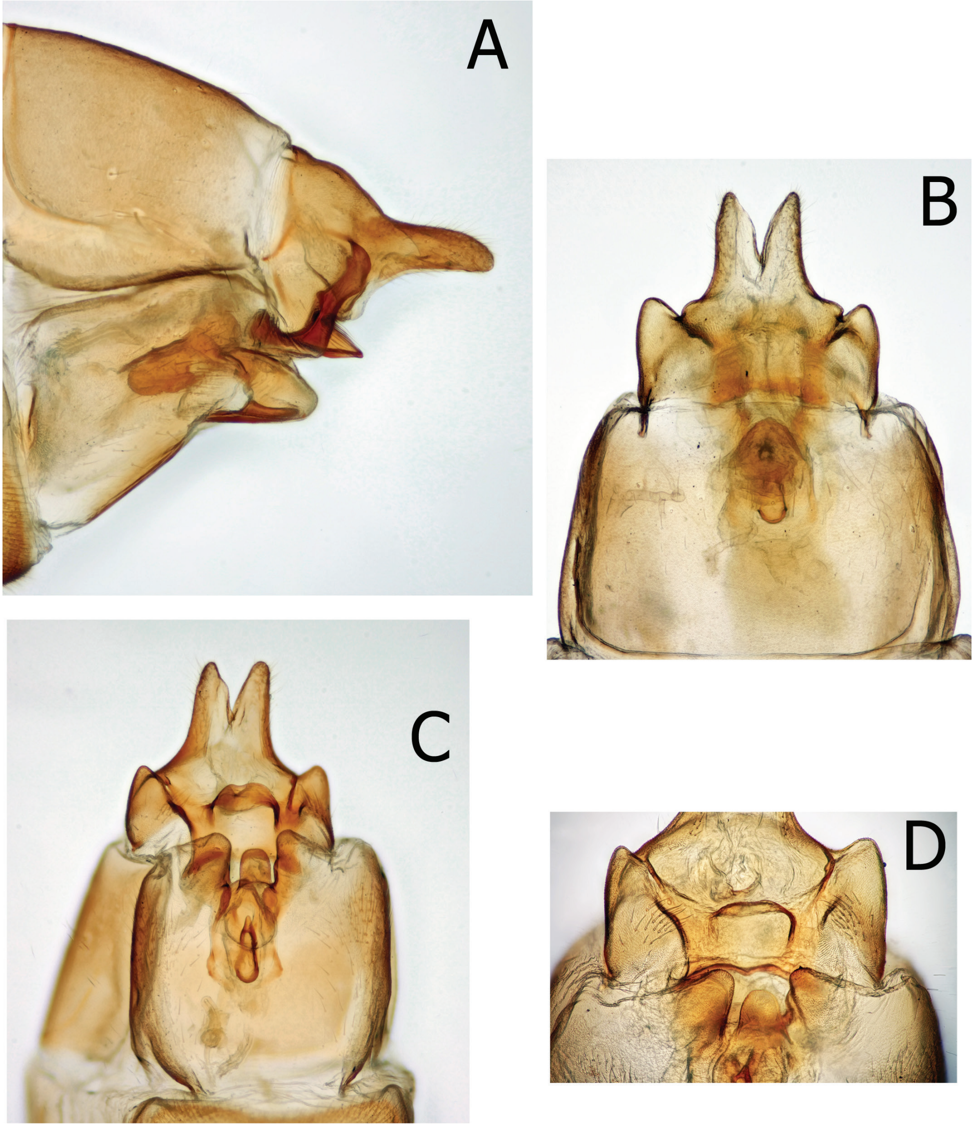

Figure 10. *Montiphylax albus*. Female **(A–D) A** genitalia, left lateral **B** genitalia, dorsal **C** genitalia, ventral **D** genitalia, ventral.

Allotype female genitalia (Fig. 10): 9th segment fused laterally and incomplete ventrally. In lateral view, 9th fused with, and nearly as long as 10th. Tenth with dorsal and ventral margins parallel throughout most of its length until rounded apex. In dorsal view 10th cleft to approximately midlength. In lateral view, ventrolateral corners of 9th clearly shorter than remainder of 9th; in ventral view, broadly rounded at apex and directed outward. Medial lobe of the vulval scale shorter than lateral lobes, approximately as wide as long. Vaginal apparatus rectangular in lateral view, ca. twice as long as tall; in ventral view, rectangular with anterolateral corners projecting outward.

Material examined. Holotype male: Canadian National Collection # 151765, Rowe Brook, near Lower Rowe Lake, 6350', Waterton National Park, Alberta, 12 June 1975, D.B. Donald [near 49.054706, -114.052434]; Alberta, Twin Creek, Marmot Creek Experimental watershed, 1800 meters elevation, R. Mutch, 1978, 4L, 50.94820 -115.15151; light trap, 1 July 1979 4M4F; 16 April 1980, 1 pupa reared to male; 16 April 1980 1 female pupa; 26 April 1980, 1 larva reared to female; 26 April 1980, 1 larva reared to male; 1 May 1980, 1 larva reared to male.

Distribution and life history

Like *Philocasca,* all species of *Montiphylax* are known only in the Western Cordillera of North America. *Montiphylax* is the more northern of the two genera and has been found in locations ranging in latitude from ca. 46 to 54 degrees north. *Montiphylax* is known from the Cascade Range of Washington (*M. antennatus*), the Shoshone Range of Idaho (*M. thor*), the Selkirk Range of British Columbia (*M. thor*) and the eastern slopes of the Canadian Rocky Mountains in Alberta (*M. thor* & *M. albus*).

Adults of the three species of *Montiphylax* have been found at altitudes ranging from 1354m (4,442') in the Cascade Mountains *(M. antennatus* Whatcom Co. Washington) to 1936m (6,350') in the Rocky Mountains (*M. thor* Waterton National Park). The larvae of *M. antennatus* and *M. albus* inhabit small cold sub-alpine streams. The larva of *M. thor* is unknown but given the locations the adults have been taken, it seems highly likely the larvae of this species will be found in high mountain streams.

A detailed life history is known only for *M. albus*. To date this species has only been associated with small, cold sub-alpine mountain streams in the Eastern Slope of the Rocky Mountains of Canada. In these streams the life cycle is three years but the presence of a few intermediate sized larvae suggests that the life cycle is flexible. There are five instars. All instars build cases of detritus, predominately of cone bracts, bark, small bits of conifer needles and wood. Instars I – IV have a case with a non-curved triangular cross-section. The V instar case is cylindrical in cross section and is made principally of the same materials as earlier instars except that some small stones are added. The emergence period is from mid-May until mid-June and the flight period lasts until the last week of July. Egg masses have not been located in the field. Growth of larvae is confined to the ice-free period (June – early November). The larvae are detritivores but moss may play a significant role in the diet of the V instars (Mutch 1981).

The flight periods of *M. thor* and *M. antennatus* are not known but adults of *M. thor* have been collected in July and adults of *M. antennatus* collected in June/July/early August.

Final instar larvae of *M. antennatus* build a case that has more mineral content than that of *M. albus.*

Discussion

Montiphylax forms a closely allied group with *Homophylax*. *Montiphylax*, *Chyranda*, *Clostoeca*, *Homophylax,* and *Phanocelia* all fall within the Limnephilidae Genera *Incertae Sedis* A of Vshivkova et al. (2007), and they all lack larval forked lateral lamellae. This lack of lateral lamellae is a rare condition within the Limnephilidae. During preparation of the enclosed key we also noted that larvae of *Pycnopsyche gentilis* group also lack the larval forked lateral lamellae. Adult *Montiphylax* will track to couplet 21 in Schmid (1998) and then fail, not matching either choice. In Ruiter (2000) *Montiphylax* tracks to *Chyranda*. *Montiphylax* can be readily separated from *Chyranda* by the presence of irrorate wings in *Montiphylax*. *Montiphylax* larvae will track to *Homophylax* or *Philocasca* in Wiggins (1996) depending on how strongly sclerotized the lateral hump sclerites are. In Morse and Holzenthal (2008) *Montiphylax* will key to *Homophylax*, *Pycnopsyche*, or *Psychoglypha* for the same reason. The problem with current larval keys is that the arrangement and size of sclerites around the lateral spacing hump is more variable than presented in the keys. As more larval specimens of these western taxa are examined it has become obvious that the lateral hump sclerite spacing and size are not consistent within the genera, particularly within *Psychoglypha*. We have provided a new key for the North American Limnephilidae larvae that possess gill clusters comprised of only a single filament. Hopefully this will provide for more consistent results within these taxa and lead to improved larval species associations. The pupae of *Montiphylax* we have will not key to the limnephiloids in Wiggins and Currie (2008) because of the non-hooked labral setae. It is possible that all our specimens (n = 4) possess broken setae since these setae are often broken on pupal material. Since caddis pupae are still poorly described, further work at the family level will be needed.

Key to the North American Limnephilidae larvae which possess gill clusters consisting of a single filament*

1 In lateral view pronotum distinctly inflated at midlength (Wiggins 1996: fig.20.31) **2**
– In lateral view pronotum not inflated, with transverse furrow in anterior half (Wiggins 1996: fig.20.34) **3**
2 Large flattened scale-hairs along anterior margin of pronotum (Wiggins 1996: fig. 20.31) .... **Philocascinae: *Philocasca***
– Pronotal scale hairs absent, margins of head pebbled, without carina, (Wiggins 1996: fig. 20.13) .... ***Ecclisocosmoecus***
3 Metanotal setal area 1 & setal area 2 sclerites large in relation to metanotum, distance between setal area 2 sclerites less than 3 times width of one setal area 2 sclerite, usually much less (Wiggins 1996: fig. 20.14) .... ***Ecclisomyia***

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* † The larvae of *Chilostigmodes* remain un-described although it is expected to have single filament gill clusters. *Chilostigmodes* records occur throughout northern North America from Alaska to Newfoundland.

– Metanotal sclerites small, distance between setal area 2 sclerites greater than 3 times width of setal area 2 sclerite (Wiggins 1996: fig. 20.7)........................**4**

4 Abdominal lateral lamellae absent (Wiggins 1996: fig. 20.7)........................**5**

– Abdominal lateral lamellae present (Wiggins 1996: fig. 20.11) **10**

5 Lateral line gills absent (Wiggins 1996: fig. 20.14) ....***Montiphylax***

– Lateral line gills present (Wiggins 1996: fig. 20.7) **6**

6 Setae present on metatergal membrane between setal area 2 sclerites (Wiggins 1996: fig. 20.11)................................***Pycnopsyche* in part (*gentilis* group)**

– Setae absent on metatergal membrane between setal area 2 sclerites (Wiggins 1996: fig. 20.9)..**7**

7 Strong, pale, spines absent on anal proleg sclerite (Wiggins 1996: fig. 20.9)......**8**

– Pale spines present on anal proleg sclerite (Wiggins 1996: fig. 20.22) **9**

8 Dorsal and ventral lateral gills present (Wiggins 1996: fig. 20.9) .....***Clostoeca***

– Only ventral lateral gills present (Wiggins 1996:fig.20.7).............***Chyranda***

9 Meso and metafemora with numerous major ventral setae, stout, pale spines absent on 9th tergal sclerite (Wiggins 1996: fig. 20.29)................***Phanocelia***

– Meso and metafemora with only two major ventral setae, stout, pale spines present on 9th tergal sclerite (Wiggins 1996: fig. 20.22) .... ***Homophylax***

10 Basal segment of hind trochanter with more than 1 seta along the ventral surface (image 11A this paper)..**11**

– Basal segment of hind trochanter with only 1 seta on ventral margin, located at distal margin near suture (image 11B this paper) **12**

11 Setae between metanotal setal area 2 sclerites in a straight line near posterior margin of segment (Wiggins 1996: fig. 20.33)...............***Pseudostenophylax***

– Setae scattered near middle of metanotal segment between setal area 2 sclerites (Wiggins 1996: fig. 20.11)...***Desmona***

12 Lateral hump of abdominal segment 1 without sclerites near base of hump (Wiggins 1996: fig. 20.19)...**13**

– Lateral hump of abdominal segment 1 with sclerites near base of hump (Wiggins 1996: fig. 20.23)..**14**

13 Head and pronotum covered with small spines (Wiggins 1996: fig. 20.19)... .... ***Grensia***

– Head and pronotum without small spines (Wiggins 1996: fig. 20.6) .... ***Chilostigma***

14 Abdominal lateral spacing hump with several small sclerites variously positioned near base (Wiggins 1996: fig. 20.34)............................***Psychoglypha***

– Lateral spacing hump with a single, large sclerite along posterior margin (Wiggins 1996: fig. 20.36)...**15**

15 Mesonotal setal area 1 sclerites fused mesally (Wiggins 1996: fig. 20.23) .... ***Hydatophylax***

– Mesonotal setal area 1 distinctly separated (Wiggins 1996: fig. 20.36).......... ....***Pycnopsyche* in part**

History of *Philocasca* and *Montiphylax* systematic placement

Banks (1900) described *Stenophylax antennatus* from a Mt. Rainier, Washington, specimen. At the time he pointed out it was not a true *Stenophylax* but was waiting for more specimens with which to describe a new genus. *Stenophylax antennatus* was not mentioned again until the major review of the Limnephilidae (Milne 1935) where Milne placed *S. antennatus* within *Anisogamus* based on the forewing shape with long apical cells.

Denning (1941) described *Anisogamus banksi* from a single Wallace, Idaho, male and mentioned that Banks (in lit.) thought it was near *Pseudostenophylax edwardsi*. Denning's *A. banksi* type information is: male, Wallace Idaho, 29 April 1938, Otto Huellemann; deposited at University of Minnesota collection. This locality and collector are the same as mentioned by Banks (1943), for a specimen of *S. antennatus*, although the date is different. Denning's (1941) aedeagal figure (Fig. 11a) is upside down. The Denning holotype was examined during this study, is pinned and in good condition with the cleared abdomen and separated aedeagus within a separate microvial on the pin.

Ross (1941) created the genus *Philocasca* for a single male (*P. demita*) and placed it within the Limnephilidae, Limnephilinae, Stenophylacini. This placement was based on his conclusion of a close association between *P. demita* and *Anisogamus*, and followed Milne's (1935) conclusion. [Until the recent description of a second species (Graf et al. 2015), *Anisogamus* was a monospecific genus based on *A. difformis* (McLachlan 1867) known from only a small area in Europe and thought to be most closely related to *Stenophylax*.] The *P. demita* type information is: Boyer, Oregon, Hood Craven Cabin, September 30, 1933, J.A.A.

The Boyer type locality is questionable as Hood Craven Cabin is not at Boyer. By 1933, Boyer, Oregon, had been relocated from the original locality in Lincoln County to its current location along Highway 18 (Benton County Museum 1981) in far southeast Tillamook County (45.06990 –123.72656) at ca. 600 feet altitude. Ross (1941) described both *Limnephilus ectus* and *Rhyacophila ecosa* from Boyer that were collected 6 May 1934 and 15 July 1934 respectively by M.L.H. The identity of M.L.H. is unknown to the authors. These *L. ectus* and *R. ecosa* descriptions did not include Hood Craven Cabin as part of the type locality. In a summary of Oregon Tipuliidae collection records, Alexander (1954) indicates Hood Craven Cabin is the same as Saddle Mountain, Lincoln County, at 3,000 feet. Saddle Mountain is actually 2,220 feet elevation, and located ca. 60 miles SSW of Boyer. Wiggins and Anderson (1968) indicated that Boyer is in Lincoln County, possibly following the Alexander information, or the original post office location. It is likely an error was introduced by connecting Hood Craven Cabin with Boyer.

Banks (1943) indicated that the type of *Stenophylax antennatus* Banks was a male and provided a re-description and clear, representative figures. He also indicated he had another male from Wallace, Idaho, 12 June (Huellemann) - the same locality/collector (although different date) as Denning's *Anisogamus banksi*. Banks (1943) did

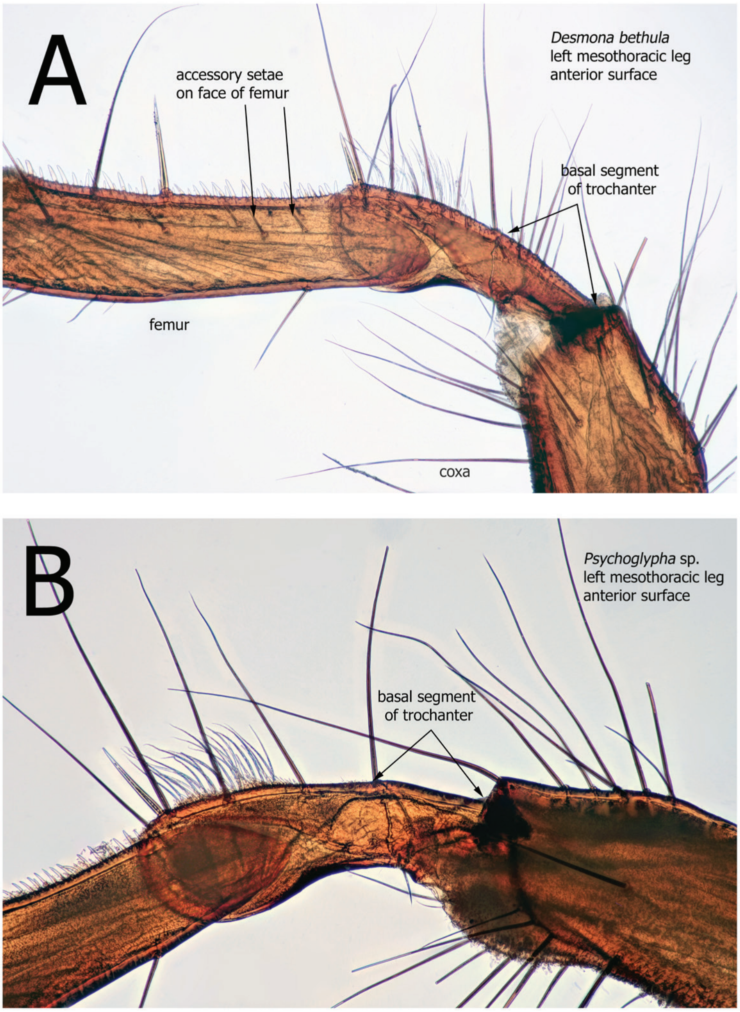

Figure 11. Mesothoracic trochanter. Larvae **(A, B) A** *Desmona bethula*, left side, anterior surface **B** *Psychoglypha* species, left side, anterior surface.

not mention Denning's (1941) *Anisogamus banksi* description, or where he thought *S. antennatus* should be placed.

Banks (1943), in his following description of *Drusinus frontalis* [moved to *Eocosmoecus* Wiggins and Richardson, 1989], has a note indicating: "We have no species closely congeneric with *Anisogamus*, and [*Anisogamus*] *edwardsi* and [*Anisogamus*] *atripennis* are better in *Drusinus*". [*Drusinus* Betten (1934) is a synonym of *Pseudostenophylax*; see Schmid (1955).] Then Banks (1943), in a discussion focused on *Philocasca*, disagreed with Ross' conclusion that *Philocasca* was close to *Anisogamus* and proposed *P. demita* may be a member of *Phacopteryx* Kolenati (1848) [currently a synonym of *Anabolia* Stephens (1837); see Betten and Mosely 1940, Schmid 1950].

Banks also stated that Milne's placement of *Anisogamus disjuncta*, and *Asynarchus costalis* as *Anisogamus* was incorrect, resulting in Banks' conclusion that no North American taxa belonged within *Anisogamus*. In the following paragraph, Banks (1943) created the genus *Clostoeca* for *Clostoeca sperryae* and moved *Anisogamus disjuncta* to *Clostoeca*. It is clear that Banks had concluded *S. antennatus* did not belong within *Philocasca* Ross.

Ross (1944), without comment, moved *Anisogamus banksi* to *Philocasca* along with *P. demita* and left *S. antennatus* as *Stenophylax*, apparently agreeing with Banks (1943).

Ross (1949) described *Philocasca oron* and pointed out (although did not illustrate) the aedeagal structure was typical for the genus. The primary characters Ross listed to separate *P. oron* from *P. demita* were width and thickness of mesal cerci processes (thin and curved ventrad) and reduced spur count (1-2-2). The *P. oron* type locality is Bear Creek, Clatsop County, Oregon, 12 April 1947, S.G. Jewett, Jr. [likely near 45.78172 -123.43585 C. Kerst and R. Wisseman pers. comm. 2018]. Wiggins and Anderson (1968) noted the collection of a 1-3-4 spur count *P. oron* specimen. During research for this paper, DER has also noted inconsistent spur counts in *P. demita* and *P. rivularis*. Often one hind leg preapical spur is totally absent while the second preapical spur is reduced to a nub. We have been unable to locate fresh Clatsop County, Oregon, *Philocasca* specimens for DNA analysis. The male and female differences presented to separate *P. oron* and *P. demita* are minor variations in shape of a couple structures. A larva distinguishable from *P. demita* has not been found, although the larvae of the other *Philocasca* species are readily separated. We suspect *P. oron* is a synonym of *P. demita*. The type locality is in an area that has been extensively clear-cut and developed for residential/recreational housing over the intervening years (C Kerst, pers. comm. 2018).

Schmid (1955) was the first to formally move *Stenophylax antennatus* to *Philocasca*. It is not clear why Schmid did this as he indicated he had not examined any of the Ross *Philocasca* taxa and that the *S. antennatus* male was admittedly different from the rest of the *Philocasca*. Schmid also indicated that females, that would have improved his decision, were not available to him. Schmid (1955), in the discussion of *Stenophylax*, referenced a paper (Schmid 1955 in press) where he reviewed the genus *Stenophylax*. The Schmid (1955 in press) *Stenophylax* paper was essentially completed in 1952 but not published until 1957 (see Schmid 1957). Therefore, Schmid had the *Stenophylax* information in 1955. In the 1957 (1952) paper Schmid did not mention *S. antennatus* or his 1955 placement of *S. antennatus* within *Philocasca*. This appears to indicate Schmid no longer agreed with his own 1955 placement of *S. antennatus* within *Philocasca*.

It is fascinating that this long, convoluted taxonomic history resulting in the placement of *Stenophylax antennatus* within *Philocasca* appears to be based on the one male type from Mt. Rainier National Park, Washington, and the description of another *S. antennatus* male by Banks (1943) from Wallace, Idaho (see discussion under *M. thor* above). The Banks (1943) description of the irrorate wings, "dark crescentic lobe" dorsally on the aedeagus, and upturned spines (parameres) are clearly not characteristic of *Philocasca*.

Subsequent authors (Flint 1966, Wiggins and Anderson 1968, Wiggins 1977, Anderson et al. 1982, Wiggins 1996, Schmid 1998, etc.) followed Schmid's 1955 placement of *Stenophylax antennatus* within *Philocasca*, rather than Banks (1943).

Wiggins and Anderson (1968) summarized the known *Philocasca* species. They provided re-descriptions and illustrations for the holotypes of *P. demita*, *P. oron*, *P. antennata,* and *P. banksi* males. They also provided new descriptions and figures for the *P. demita* female and larva; *P. oron* female; and *P. rivularis* male, female and larvae. There is also a description for an unknown *Philocasca* larva. Additional specimens representing this unknown *Philocasca* species have been examined from Idaho and Montana and, with the association of the *Stenophylax antennatus* larva, we conclude the unknown larva of Wiggins and Anderson (1986) is *P. banksi*.

Nimmo (1971) described *P. thor* from a single Alberta collection. The first author examined this holotype and compared it to three additional Alberta *P. thor* males in the Barcode of Life DNA voucher collection, Guelph. They are the same. The female and larvae of *P. thor* have yet to be associated.

Nimmo (1977) described *P. alba* from three collections in southern Alberta; including, as paratypes, material the second author collected.

During his studies on litter processing and insect life history within a small Alberta stream, Mutch (1981) discovered that the primary insect litter processor was *P. alba*. Mutch also noted that the larva associated with *P. alba* was not similar to the other known *Philocasca* larvae. He conducted a review of *Philocasca* (Mutch 1981) and concluded that the seven *Philocasca* species belong within two separate groups, suggesting that *P. antennata*, *P. alba*, and *P. thor* belonged within a different genus. Further studies planned at that time to resolve the issue ceased until now. The first author compared the *P. alba* holotype to material from this southern Alberta population and they are the same, resulting in associations of larvae, pupae, males and females for *P. alba*.

Schmid (1998) provided an additional description and illustrations of the *P. thor* male and the *P. demita* female.

It was not until the Blinn and Ruiter (2013) collections of *P. antennata* from Mt. Baker, Washington, that *P. antennata* material other than the holotype was located. This is likely due to the difficulty of collecting high altitude, isolated habitats early in the season. The Mt. Baker material contained males, females and associated *P. antennata* larvae and also led to the conclusion that *P. antennata*, *P. alba*, and *P. thor* did not belong within *Philocasca*.

Acknowledgments

Foremost, we want to recognize Norm Anderson (recently deceased) for his diligence in storing Bob Mutch's thesis and ultimately passing it on to Dave Ruiter. This brought the authors together to focus on a mutual effort. Much additional *Philocasca* material examined in the work has been provided by Bob Wisseman, Jon Lee, Cary Kerst and

Greg Courtney. The first author greatly appreciates their assistance and friendship for many years now. We thank Suvdtsetseg Chuluunbat, Mongolian State University of Education, for assistance with initial clarification of *S. antennatus* taxonomy. Jon Lee and Terry Ruiter also provided needed reviews of the draft and we are very grateful. We also thank several museum curators for providing necessary material, including holotypes, etc., for study: Robin Thomson, University of Minnesota, St. Paul (*Philocasca banksi* holotype); Owen Lonsdale, Canadian National Collection (*Montiphylax albus* and *Montiphylax thor* holotypes); Phil Perkins and Charles Farnum, Museum of Comparative Zoology for the loan of the Banks (1943) Idaho *Montiphylax thor* specimen; and Jayme Sones, Collections Manager, Centre for Biodiversity Genomics, University of Guelph for the loan of *Montiphylax thor* specimens. We thank Joe Giersch and two anonymous reviewers for the comments and suggestions during the editorial process.

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