

Research article

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Four new species and further records of Dorvilleidae (Annelida, Polychaeta) from deep-sea organic substrata, NE AtlanticAscensão RAVARA^{1,*}, Helena WIKLUND² & Marina R. CUNHA³^{1,3}CESAM - Centro de Estudos do Ambiente e do Mar, Departamento de Biologia, Universidade de Aveiro, Campus de Santiago, 3810-193 Aveiro, Portugal.²Department of Marine Sciences, University of Gothenburg, Carl Skottbergsgata 22B, 413 19 Gothenburg, Sweden.²Life Sciences Department, Natural History Museum, Cromwell Rd, London SW7 5BD, UK.*Corresponding author: aravara@ua.pt²Email: helena.wiklund@marine.gu.se³Email: marina.cunha@ua.pt¹urn:lsid:zoobank.org:author:677F8AB4-7FD3-483A-A047-C4BD5A6A449D²urn:lsid:zoobank.org:author:114C3853-7E48-42AC-88F3-F7AC327B24F3³urn:lsid:zoobank.org:author:553A98B5-0AE0-424F-9ED5-EC50F129519C

Abstract. Eight species of *Ophryotrocha* and one of *Parougia* were identified from organic substrata (wood and alfalfa) sampled at the Gulf of Cadiz and Western Iberian Margin (NE Atlantic). Morphological examination and molecular phylogenetic analyses, based on the nuclear gene H3 and the mitochondrial gene 16S, indicate the presence of four species new to science: *Ophryotrocha chemecoli* sp. nov., *O. nunezi* sp. nov., *O. geoffreadi* sp. nov. and *Parougia ougi* sp. nov. The geographic and/or bathymetric distribution is extended for four previously known species: *O. cantabrica*, *O. hartmanni*, *O. mammillata* and *O. scutellus*. Another species may also have its distribution extended, pending the molecular confirmation of its identity: *O. lipscombae*. Full descriptions and figures are given for all the new species and, when justified, also for the previously known ones. The original description of *O. scutellus* is amended. New DNA sequences are given for eight of the nine species studied here. The ecology and geographic distribution of the reported species is discussed.

Keywords. *Ophryotrocha*, *Parougia*, mud volcanoes, Gulf of Cadiz, Estremadura Spur.

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Introduction

The family Dorvilleidae Chamberlin, 1919 includes at present 203 species ascribed to 32 genera, most of them being monospecific or comprising only a few species (Chamberlin 1919; Read & Fauchald 2020; Yen & Rouse 2020). *Ophryotrocha* Claparède & Meczников, 1869, *Parougia* Wolf, 1986 and *Exallopus*

Jumars, 1974 are the main dorvilleid genera occurring in the deep sea (Claparède & Meczников 1869; Jumars 1974; Wolf 1986; Thornhill *et al.* 2012; Levin *et al.* 2013). Together, these three genera include more than 48% of the species within the dorvilleid family. *Ophryotrocha* is by far the most speciose genus, including at present 77 species (Read & Fauchald 2020), most of them (~80%) described from deep waters. The other two genera, *Parougia* and *Exallopus*, include nineteen and five species, respectively (Read & Fauchald 2020; Yen & Rouse 2020). These genera, and *Ophryotrocha* in particular, are known to thrive in all kinds of organically enriched habitats (e.g., Wiklund *et al.* 2009, 2012; Ravara *et al.* 2015; Taboada *et al.* 2016; Zhang *et al.* 2017; Vedenin *et al.* 2020). As new deep-sea organic-enriched places are studied (e.g., whale, wood or other organic falls), the rate of novel species of *Ophryotrocha* and related genera greatly increase when compared to the new records of already known species (e.g., Wiklund *et al.* 2009, 2012; Taboada *et al.* 2013; Salvo *et al.* 2014; Ravara *et al.* 2015). This denotes the incipient and fragmentary knowledge of these ephemeral habitats, thus limiting a comprehensive understanding of the diversity, distribution and dispersal of the species they support. For the NE Atlantic Ocean, only a couple of studies of dorvilleids on organic falls have previously been published, both reporting five *Ophryotrocha* species, three of which were new to science (Wiklund *et al.* 2009; Ravara *et al.* 2015). The present study adds three new species of *Ophryotrocha* and one new species of *Parougia* to the NE Atlantic organic-falls fauna. Five previously known species of *Ophryotrocha* are also reported for the first time in the Gulf of Cadiz (Moroccan margin) and the West Iberian margin, thus extending their geographic and bathymetric distributions. Full descriptions and images are given for the new species and, whenever considered necessary, also for some of the previously known species, based on the specimens studied here. Observed discrepancies regarding the original descriptions and distributions of the species are discussed. The original description of *O. scutellus* is amended based on the specimens studied here and a re-examination of some specimens from the original material (Wiklund *et al.* 2009). Molecular data is provided for eight out of the nine taxa studied.

Material and methods

Most of the biological material examined in this study was obtained from wood and alfalfa substrata experimentally deployed in the Gulf of Cadiz (NE Atlantic) from 2007 to 2009, with the aim of studying colonization and dispersal processes in deep-sea reduced habitats (Cunha *et al.* 2013). The experimental colonization devices (CHEMECOLI) contained two types of organic substrata – dried alfalfa grass and Douglas fir wood cubes – enclosed by a 2 mm mesh net and were deployed at three mud volcanoes (Mercator, Mèknes and Darwin), within a depth range of 354–1100 m, for a period of one to two years. Carbonate cubes were used as control samples. Table 1 includes site coordinates and cruises involved in the deployment and recovery of the colonization devices and Fig. 1 locates the sites on the map. Details on the experimental devices and sample processing can be found in Cunha *et al.* (2013). Additional material was retrieved from a small piece of sunken wood collected using the ROV hydraulic arm during a survey of a seemingly inactive pockmark field at the Estremadura Spur, West Iberian Margin, at a depth of 327 m (the sample was stored in the ROV biobox during ascent and immediately processed onboard). All the polychaete specimens were fixed either in 96% ethanol or in a 4% formaldehyde solution.

After a preliminary sorting into putative species, DNA of selected ethanol fixed specimens was extracted using a DNeasy Blood and Tissue Kit (Qiagen) following the protocol supplied by the manufacturer. About 450bp of the mitochondrial gene 16S were amplified with the primers Ann16SF 5'-GCGGTATCCTGACCGTRCWAAGGTA-3' (Sjölin *et al.* 2005) and 16SbrH 5'-CCGGTCTGAACTCAGATCACGT-3' (Palumbi 1996), and about 350bp of the nuclear coding gene H3 were amplified with the primers H3F 5'-ATGGCTCGTACCAAGCAGACVGC-3' (Colgan *et al.* 2000) and H3R 5'-ATATCCTTRGGCATRATRGTGAC-3' (Colgan *et al.* 2000). Attempts were made to amplify a fragment of the mitochondrial gene COI, but with low success. Only three sequences were obtained with the primers pollCO 5'-GAYTATWTTCAACAAATCATAAAGATATTGG-3' as

Table 1. Metadata of the deployment and recovery of the colonization experiments in the Gulf of Cadiz and of the sample recovered at the Estremadura Spur.

Site	Site coordinates			Deployment		Recovery		Sample	DD (days)
	Latitude	Longitude	Depth	Cruise-Dive	Date	Cruise-Dive	Date		
Mercator MV	35°17.916' N	06°38.709' W	354 m	JC10-D28	19 May 2007	64PE284-D8	2 Mar. 2008	01	731
						64PE284-D9	3 Mar. 2008		
						B09-14b-D01	19 May 2009		
Meknes MV	34°59.091' N	07°04.424' W	698 m	64PE284-D07	1 Mar. 2008	B09-14b-D03	20 May 2009	03	446
Darwin MV	35°23.523' N	07°11.513' W	1100 m	JC10-D33	21 May 2007	B09-14b-D02	19 May 2009	02	729
Estremadura Spur	39°17.295' N	10°01.045' W	327 m	NA	NA	PES-ROVL17-D01	1 Jun. 2017	pick#3W	NA

DD = deployment duration; MV = mud volcano; NA = not applicable.

well as PolyLCO and PolyHCO 5'-TAMACTTCWGGGTGACCAAARAATCA-3' (Carr *et al.* 2011). PCR mixtures contained 1 µl of each primer (10 µM), 2 µl of template DNA and 21 µl of Red Taq DNA Polymerase 1.1X MasterMix (VWR). The temperature profile was as follows: 96°C for 240 s, followed by (94°C for 30 s, 50°C for 30 s then 72°C for 60 s)*35 cycles, followed by 72°C for 480 s. PCR purification was performed using a Millipore Multiscreen 96-well PCR Purification System, and sequencing was performed on an ABI 3730XL DNA Analyser (Applied Biosystems) at the Natural History Museum Sequencing Facility, using the primers mentioned above. All sequences were deposited in GenBank (Table 2).

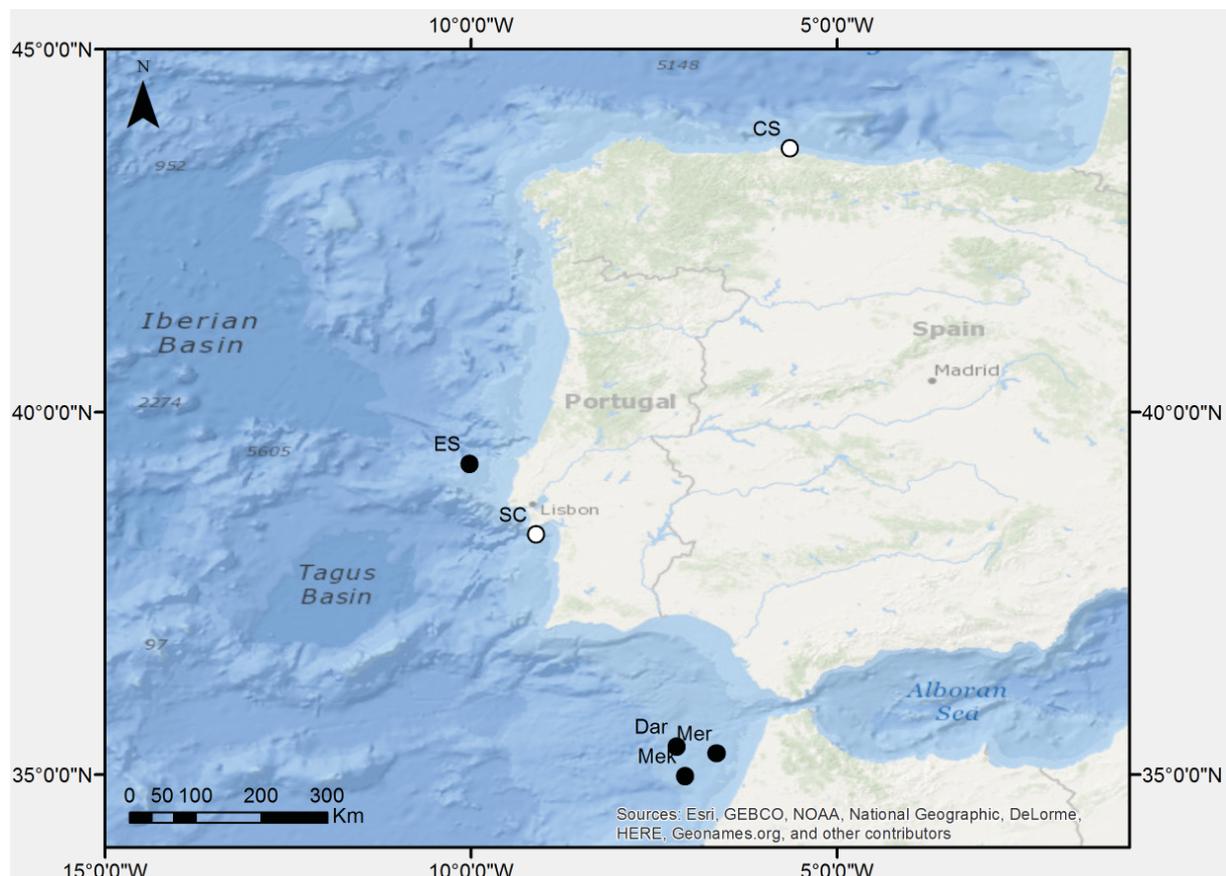


Fig. 1. Map with the location of the examined material. Full dots refer to this study, empty dots refer to previous studies (Nuñez *et al.* 2014; Ravara *et al.* 2015).

Table 2 (continued on next page). Names and Genbank accession numbers for taxa included in phylogenetic analyses and for the three excluded COI sequences.

Taxon name	16S	H3	COI	Water mass	Reference
cf. Dorvilleidae sp. DH 2009 3B3	GU227021.1	–	–	–	–
<i>Dorvillea erucaeformis</i>	DQ779611.1	–	–	–	–
<i>Dorvillea rubrovittata</i>	GQ415457.1	GQ415490.1	–	–	–
<i>Dorvillea similis</i>	DQ317915.1	–	–	–	–
<i>Eunice pennata</i>	AF321418.1	DQ779731.1	–	–	–
<i>Exallopus jumarsi</i>	JQ310744.1	–	–	Pacific	Wiklund <i>et al.</i> 2012
<i>Exallopus</i> sp. Seep	JX536712.1	–	–	Pacific	Thornhill <i>et al.</i> 2012
<i>Iphitime hartmanae</i>	GQ415458.1	GQ415491.1	–	Atlantic	Wiklund <i>et al.</i> 2009
<i>Ophryotrocha adherens</i>	AF321421.1	JQ310768.1	–	Mediterranean	Dahlgren <i>et al.</i> 2001
<i>Ophryotrocha</i> cf. <i>akessoni</i> sp. 1 GR 2017	KY701727.1	–	–	Pacific	Goffredi <i>et al.</i> 2017
<i>Ophryotrocha</i> cf. <i>akessoni</i> sp. 2 GR 2017	KY701728.1	–	–	Pacific	Goffredi <i>et al.</i> 2017
<i>Ophryotrocha alborana</i>	KY378403.1	GQ415492.1	–	Mediterranean	Taboada <i>et al.</i> 2017
<i>Ophryotrocha batillus</i>	JQ310745.1	JQ310769.1	–	Pacific	Wiklund <i>et al.</i> 2012
<i>Ophryotrocha birgittae</i>	AF321426.1	–	–	Pacific	Dahlgren <i>et al.</i> 2001
<i>Ophryotrocha cantabrica</i>	MW464897	MW464905	MW464902	Atlantic	This study
<i>Ophryotrocha chemecoli</i> sp. nov. (GoC)	MW464898	MW464907	–	Atlantic	This study
<i>Ophryotrocha chemecoli</i> sp. nov. (WIM)	–	MW464908	–	Atlantic	This study
<i>Ophryotrocha clava</i>	KC123175.1	KC123179.1	–	Antarctic	Taboada <i>et al.</i> 2013
<i>Ophryotrocha costlowi</i>	JQ310746.1	JQ310770.1	–	Atlantic	Wiklund <i>et al.</i> 2012
<i>Ophryotrocha craigsmitthi</i>	GQ415459.1	GQ415493.1	–	Atlantic	Wiklund <i>et al.</i> 2009
<i>Ophryotrocha cyclops</i>	KM979517.1	KM979518.1	–	Atlantic	Salvo <i>et al.</i> 2014
<i>Ophryotrocha diadema</i>	AF321425.1	JQ310771.1	–	Pacific	Dahlgren <i>et al.</i> 2001
<i>Ophryotrocha eutrophila</i>	GQ415460.1	GQ415494.1	–	Atlantic	Wiklund <i>et al.</i> 2009
<i>Ophryotrocha flabella</i>	JQ310747.1	JQ310772.1	–	Pacific	Wiklund <i>et al.</i> 2012
<i>Ophryotrocha geoffreadi</i> sp. nov.	MW464899	MW464909	–	Atlantic	This study
<i>Ophryotrocha geryoncola</i>	GQ415461.1	GQ415495.1	–	Atlantic	Wiklund <i>et al.</i> 2009
<i>Ophryotrocha globopalpata</i>	GQ415462.1	GQ415496.1	–	Pacific	Wiklund <i>et al.</i> 2009
<i>Ophryotrocha gracilis</i>	AF321424.1	GQ415497.1	–	Atlantic	Dahlgren <i>et al.</i> 2001
<i>Ophryotrocha hartmanni</i>	AF321419.1	JQ310773.1	–	Mediterranean	Dahlgren <i>et al.</i> 2001
<i>Ophryotrocha japonica</i>	GQ415463.1	GQ415498.1	–	Pacific	Wiklund <i>et al.</i> 2009
<i>Ophryotrocha jiaolongi</i>	MF398963.1	MF398968.1	–	Indian	Zhang <i>et al.</i> 2017
<i>Ophryotrocha labronica</i>	AF321429.1	GQ415499.1	–	Mediterranean	Dahlgren <i>et al.</i> 2001
<i>Ophryotrocha langstrumpae</i>	JQ310748.1	JQ310774.1	–	Pacific	Wiklund <i>et al.</i> 2012
<i>Ophryotrocha</i> cf. <i>lipscombae</i>	–	MW464906	–	Atlantic	This study
<i>Ophryotrocha lobifera</i>	GQ415464.1	GQ415500.1	–	Atlantic	Wiklund <i>et al.</i> 2009
<i>Ophryotrocha longicollaris</i>	JQ310749.1	JQ310775.1	–	Pacific	Wiklund <i>et al.</i> 2012
<i>Ophryotrocha longidentata</i>	GQ415471.1	GQ415501.1	–	Atlantic	Wiklund <i>et al.</i> 2009
<i>Ophryotrocha lusa</i>	–	KP731499.1	–	Atlantic	Ravara <i>et al.</i> 2015
<i>Ophryotrocha macrovifera</i>	AF321430.1	JQ310776.1	–	Mediterranean	Dahlgren <i>et al.</i> 2001
<i>Ophryotrocha maculata</i>	GQ415465.1	JQ310777.1	–	Atlantic	Wiklund <i>et al.</i> 2009
<i>Ophryotrocha magnadentata</i>	JQ310750.1	JQ310778.1	–	Pacific	Wiklund <i>et al.</i> 2012
<i>Ophryotrocha mammillata</i>	–	KP731523.1	–	Atlantic	Ravara <i>et al.</i> 2015
<i>Ophryotrocha mammillata</i> (GoC)	–	MW464910	MW464903	Atlantic	This study
<i>Ophryotrocha nauarchus</i>	JQ310751.1	JQ310779.1	–	Pacific	Wiklund <i>et al.</i> 2012
<i>Ophryotrocha notoglandulata</i>	AF321431.1	JQ310780.1	–	Pacific	Dahlgren <i>et al.</i> 2001
<i>Ophryotrocha nunezi</i> sp. nov.	MW464900	MW464911	–	Atlantic	This study
<i>Ophryotrocha orensanzi</i>	KC123176.1	KC123180.1	–	Antarctic	Taboada <i>et al.</i> 2013
<i>Ophryotrocha permanni</i>	AF321432.1	GQ415502.1	–	Atlantic	Wiklund <i>et al.</i> 2009
<i>Ophryotrocha puerilis</i>	GQ415466.1	GQ415503.1	–	Mediterranean	Wiklund <i>et al.</i> 2009
<i>Ophryotrocha puerilis</i> complex sp. ‘Deep’	KY378411.1	KY378627.1	–	Mediterranean	Taboada <i>et al.</i> 2017
<i>Ophryotrocha puerilis</i> complex sp. ‘Shallow’	KY378428.1	KY378644.1	–	Mediterranean	Taboada <i>et al.</i> 2017
<i>Ophryotrocha robusta</i>	AF321433.1	JQ310781.1	–	Mediterranean	Taboada <i>et al.</i> 2017
<i>Ophryotrocha rubra</i>	GQ415468.1	GQ415505.1	–	Atlantic	Ravara <i>et al.</i> 2015

Table 2 (continued). Names and Genbank accession numbers for taxa included in phylogenetic analyses and for the three excluded COI sequences.

Taxon name	16S	H3	COI	Water mass	Reference
<i>Ophryotrocha sadina</i>	–	KP731528.1	–	Atlantic	Ravara <i>et al.</i> 2015
<i>Ophryotrocha scutellus</i>	GQ415469.1	GQ415506.1	–	Atlantic	Wiklund <i>et al.</i> 2009
<i>Ophryotrocha scutellus</i> (GoC)	–	MW464912	–	Atlantic	This study
<i>Ophryotrocha shieldsi</i>	HM181932.1	JQ310782.1	–	Indian	Paxton & Davey, 2010
<i>Ophryotrocha socialis</i>	AF321420.1	JQ310783.1	–	Atlantic	Dahlgren <i>et al.</i> 2001
<i>Ophryotrocha</i> sp. n. 1 HW 2015	–	KP731549.1	–	Atlantic	Ravara <i>et al.</i> 2015
<i>Ophryotrocha</i> sp. NL	KJ833756.1	KJ833757.1	–	Atlantic	Mercier <i>et al.</i> 2014
<i>Ophryotrocha</i> sp. ‘Seep 1’	JX536696.1	–	–	Pacific	Thornhill <i>et al.</i> 2012
<i>Ophryotrocha</i> sp. ‘Seep 2’	JX536699.1	–	–	Pacific	Thornhill <i>et al.</i> 2012
<i>Ophryotrocha</i> sp. ‘Seep 3’	JX536701.1	–	–	Pacific	Thornhill <i>et al.</i> 2012
<i>Ophryotrocha</i> sp. ‘Seep 4’	JX536704.1	–	–	Pacific	Thornhill <i>et al.</i> 2012
<i>Ophryotrocha</i> sp. ‘Seep 5’	JX536711.1	–	–	Pacific	Thornhill <i>et al.</i> 2012
<i>Ophryotrocha vellae</i>	AF321434.1	–	–	Pacific	Dahlgren <i>et al.</i> 2001
<i>Ophryotrocha vivipara</i>	JQ310752.1	–	–	Atlantic	Wiklund <i>et al.</i> 2012
<i>Parougia albomaculata</i>	AF380115.1	JQ310784.1	–	Gibraltar Strait	Dahlgren <i>et al.</i> 2001
<i>Parougia bermudensis</i>	JQ310753.1	JQ310785.1	–	Atlantic	Wiklund <i>et al.</i> 2012
<i>Parougia diapason</i>	KX555630.1	KX555633.1	–	Antarctic	Taboada <i>et al.</i> 2015
<i>Parougia eliasoni</i>	GQ415470.1	GQ415507.1	–	Atlantic	Wiklund <i>et al.</i> 2009
<i>Parougia oregonensis</i>	JX536705.1	–	–	Pacific	Thornhill <i>et al.</i> 2012
<i>Parougia ougi</i> sp. nov.	MW464901	MW464913	MW464904	Atlantic	This study
<i>Parougia</i> sp. ‘Seep Clade CA’	JX536708.1	–	–	Pacific	Thornhill <i>et al.</i> 2012
<i>Parougia</i> sp. ‘Seep Clade OR’	JX536710.1	–	–	Pacific	Thornhill <i>et al.</i> 2012
<i>Parougia</i> sp. THS 2005	AY838841.1	–	–	unknown	Struck <i>et al.</i> 2006
<i>Pettiboneia urciensis</i>	AY838842.1	–	–	–	–
<i>Protodorvillea kefersteini</i>	DQ779634.1	DQ779759.1	–	–	–
<i>Pseudophryotrocha</i> sp. ‘Seep’	JX536713.1	–	–	Pacific	Thornhill <i>et al.</i> 2012

Overlapping sequence fragments were merged into consensus sequences using Geneious (Kearse *et al.* 2012). The sequences obtained in this study were aligned together with sequences from Genbank (Table 2) using MAFFT (Katoh *et al.* 2002) with default settings, provided as a plug-in in Geneious. Only 16S and H3 sequences were used in the analyses due to the greater coverage of those sequences. The 16S alignment consisted of 526 characters and the H3 alignment of 341 characters. In total, 77 terminal taxa were used in the phylogenetic analyses, with nine from *Parougia*, 57 from *Ophryotrocha*, ten from other Dorvilleidae genera and *Eunice pennata* (Eunicidae) as root (Table 2). The program jModelTest (Posada 2008) was used to assess the best model for each partition (16S and H3) with BIC, which suggested GTR+I+G as the best model for both genes. The data was partitioned into the two genes (16S and H3), and the evolutionary model mentioned above was applied to each partition. The parameters used for the partitions were unlinked. Bayesian phylogenetic analyses (BAs) were conducted with MrBayes ver. 3.2.6 (Ronquist *et al.* 2012). Analyses were run three times for 10 000 000 generations. Of these, 2 500 000 generations were discarded as burn-in. The tree files were interpreted with FigTree ver. 1.4.2 (available from <http://tree.bio.ed.ac.uk/software/figtree/>). The consensus tree is presented in Fig. 2.

Detailed morphological observations were carried out with stereo and compound microscopy. Stereo microscope images were taken with a Canon EOS1100D camera. Jaw and chaetal morphology was examined and imaged with a Zeiss Axioplan 2 imaging light microscope (Carl Zeiss, Oberkochen, Germany), equipped with a DP70 Olympus camera (Olympus Corp., Tokyo, Japan), after mounting the specimen on a slide preparation using Aquamount (Gurr) liquid. Measurements of body width were recorded from the widest part of the body (anterior region), excluding parapodia and chaetae, and body

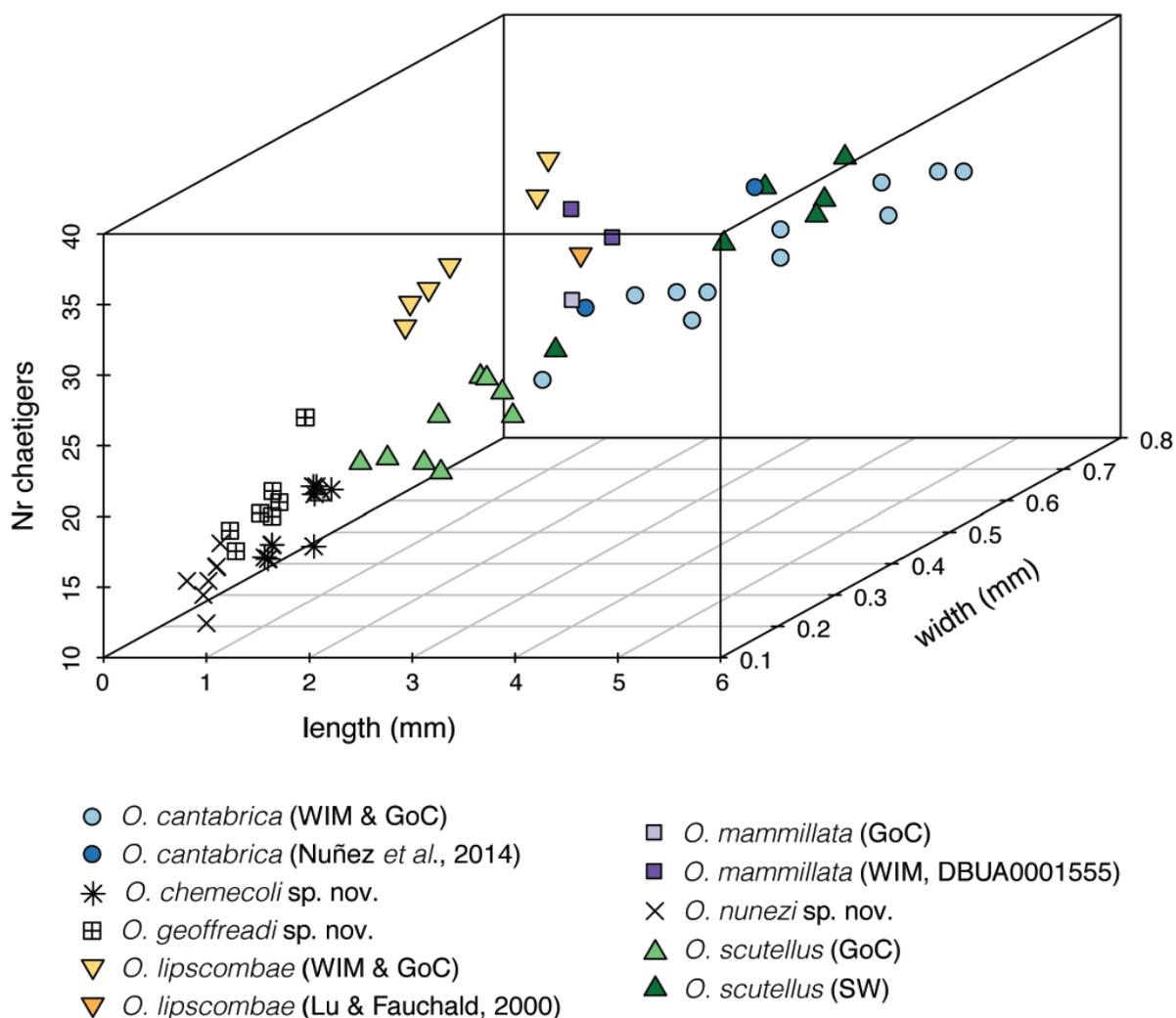
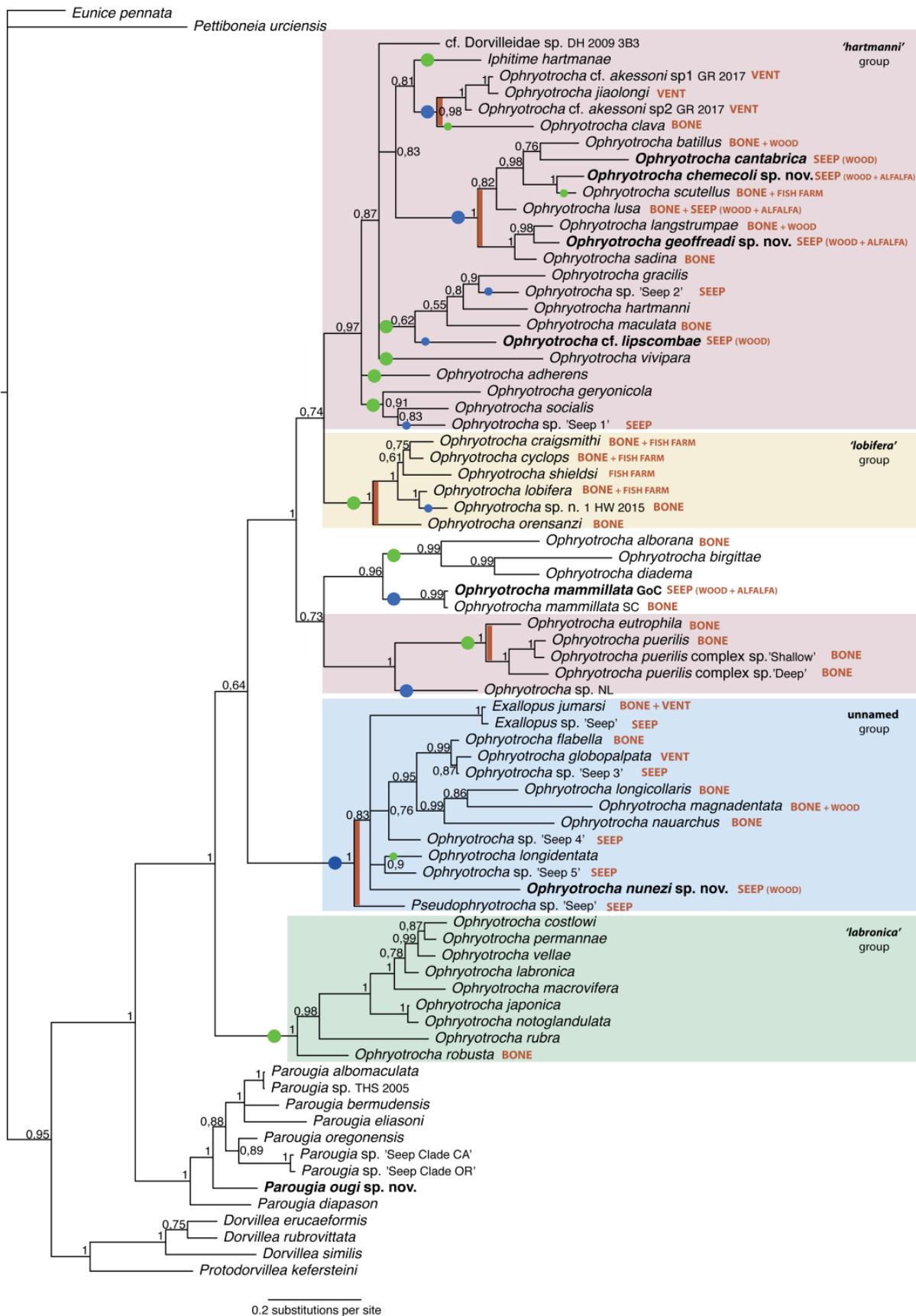


Fig. 3. Relationships between the number of segments, body length and body width.

Fig. 2 (next page). Majority rule consensus tree from the Bayesian analyses of a combined dataset with two genes (16S and H3). Posterior probability values near nodes result from the analyses in MrBayes. Taxon names highlighted in bold are new species or new sequences for already described species. Habitat specialization indicated by the text ‘VENT’ for hydrothermal vents, ‘SEEP’ for cold seeps, ‘BONE’ for whale/mammal-falls, ‘WOOD’ and ‘ALFALFA’ for wood- and alfalfa-falls, and ‘FISHFARM’ for the organically-enriched sediments beneath fish farms. Brown bars at the base of a clade indicate a specialization to a chemosynthesis-based ecosystem. Green and blue dots indicate depth distributions shallower and deeper than 200 m, respectively.



length excludes anal cirri. A 3D scatter plot was used to illustrate the relationship between the body length, width and the number of chaetigers for each species, including data from type material (Fig. 3). The plot was generated using the R program (R Core Team 2020) and the “scatterplot3d” package (ver. 0.3-41; Ligges & Mächler 2003). Whenever necessary, type material was requested from museum collections for comparison. The holotypes of the newly described species are deposited at the Natural History Museum of London (NHMUK). The remaining material is deposited at the Biological Research Collection (Marine Invertebrates) of the Department of Biology of the University of Aveiro (COBI-DBUA). DNA voucher terminology follows Pleijel *et al.* (2008).

All the material mentioned in this paper was examined by us. The notation ‘Other material’ refers to non-type material collected by us, whereas ‘Additional material’ refers to material loaned from other institutions.

List of locality and geological structure abbreviations

CS	=	Cantabrian Sea
DAR	=	Darwin mud volcano
ES	=	Estremadura Spur
GoC	=	Gulf of Cadiz
MEK	=	Meknès mud volcano
MER	=	Mercator mud volcano
MV	=	mud volcano
SC	=	Setúbal Canyon
Stn	=	station
SW	=	Sweden
WIM	=	West Iberian Margin

List of morphological abbreviations

a	=	apophyse
ac	=	accessory plates
bp	=	basal plate
cf	=	confer
d	=	denticles
dc	=	dorsal cirrus
f	=	forcep
fd	=	free denticles
lt	=	large teeth
mf	=	main fang
p	=	palp
pl	=	pre-acicular lobe
ps	=	palp scars
sl	=	sub-acicular lobe
spec.(s)	=	specimen(s)
st	=	small teeth
t	=	tooth
tr	=	teeth ridges
vc	=	ventral cirrus
wa	=	wing-like apophyse

List of repositories

COBI-DBUA	=	Biological Research Collection (Marine Invertebrates), Department of Biology, University of Aveiro, Portugal
GNM	=	Göteborgs Naturhistoriska Museum
NHMUK	=	Natural History Museum, London, UK

Results

Class Polychaeta Grube, 1850
Order Eunicida Dales, 1962
Family Dorvilleidae Chamberlin, 1919
Genus *Ophryotrocha* Claparède & Meczniow, 1869

Ophryotrocha cantabrica Nuñez, Riera & Maggio, 2014
Figs 4–5

Ophryotrocha cantabrica Nuñez, Riera & Maggio, 2014: 116, figs 1–3 (type locality: Gijón (Asturias), Bay of Biscay, Cantabrian Sea, NE Atlantic, 72–74 m depth).

Material examined

Holotype

SPAIN • Bay of Biscay, Cantabrian Sea; 43°37.71' – 43°38.36' N, 05°37.59' – 05°39.78' W; 72–74 m depth; 15 Jun. 1991; cruise Fauna II; Stn 114A; MNCN 16.0/14704.

Paratypes

SPAIN • 38 specs; same collection data as for holotype; MNCN 16.01/13633.

Other material

MOROCCO • 27 specs (ethanol), 44 specs (formalin), 1 spec. (slide preparation); GoC, Mercator MV; 35°17.916' N, 06°38.709' W; 354 m depth; 2 Mar. 2008; Stn 64PE284_12750W; wood substrata; DBUA0002281.01 • 7 specs (ethanol), 2 specs (formalin); same collection data as for preceding; 19 May 2009; Stn B09-14b_01W; wood substrata; DBUA0002282.01 • 1 spec. (ethanol), 3 specs (formalin); GoC, Meknès MV; 34°59.091' N, 07°04.424' W; 698 m depth; 20 May 2009; Stn B09-14b_03W; wood substrata; DBUA0002282.02.

PORTUGAL • 135 specs (ethanol); WIM, Estremadura Spur; 39°17.295' N, 10°01.045' W; 327 m depth; 1 Jun. 2017; Stn PES-ROVL17D01_pick#3W; sunken wood; DBUA0002283.01 (2 hologenophores and 133 paragenophores).

Description

Relatively large specimens in comparison to the majority of the species of *Ophryotrocha* (Fig. 3). Largest complete specimen 5.4 mm long and 0.8 mm wide for 35 chaetigers. Body compressed dorso-ventrally, wider sub-anteriorly and tapering posteriorly (Fig. 4A). A transversal band of cilia present in the middle of each segment. Prostomium broadly rounded, without eyes. Antennae and palps digitiform, sometimes retracted and with a more globulous appearance, subequal in length. Peristomium achaetous, with two rings subequal in length to the following segments. Mouth opens ventrally on the first peristomial ring (Fig. 4B). Mandibles rod-like; cutting plates straight and toothed; apophyses triangular, extending laterally right beneath the tip of the mandibula (Fig. 4B, D). Maxillae of P-type with a pair of forceps and seven pairs of free denticles (D1–7) (Fig. 4E); forceps and D1 comb-like with 13 large teeth alternating with two small teeth; D2–3 shovel-like, with long distal fang and serrated edge; D4–6 with coarsely serrated edge (~11 teeth); D7 shovel-like, broader than the others and with smaller and more numerous teeth (~40). Parapodia uniramous, with broadly conical acicular lobes, long digitiform pre-chaetal lamellae (in median parapodia), conical sub-acicular lobes slightly shorter than pre-chaetal lamellae, conical ventral cirri shorter than sub-acicular lobes, and ovoid to piriform dorsal cirri as long as pre-chaetal lamellae in anterior parapodia and greatly increasing in size posteriorly (Fig. 4A). Protruding acicula of sub-acicular lobes very thin and short. Supra-acicular chaetae simple, serrated, tapering distally to a thin pointed hook (Fig. 4F). Sub-acicular chaetae compound with serrated bidentate blades; secondary tooth tiny and difficult to see (Fig. 4G). Pygidium with terminal anus, two cirriform anal cirri inserted laterally and one short median cirrus (Fig. 4C).



Fig. 4. *Ophryotrocha cantabrica* Nuñez, Riera & Maggio, 2014. Stereo (A–C) and compound (D–G) microscope images. A, C–G: DBUA0002281.01; B: DBUA0002282.01. A. Complete specimen, dorsal view. B. Prostomium and mandibulae, ventral view. C. Pygidium with anal cirri, dorsal view. D. Anterior tip of mandibula, ventral view. E. Maxillae, ventral view. F. Supra-acicular chaetae, mid-body parapodium. G. Sub-acicular chaetae, mid-body parapodium. Numbers refer to free denticles.



Fig. 5. *Ophryotrocha cantabrica* Nuñez, Riera & Maggio, 2014, paratype (MNCN 16.01/13622). Compound microscope images. A. Mandibulae, ventral view. B. Maxillae, ventral view. C. Supra-acicular chaetae, mid-body parapodium. D. Sub-acicular chaeta, mid-body parapodium. The arrow points to a broken mandible. Numbers refer to free denticles.

Remarks

Ophryotrocha cantabrica was originally described from the Cantabrian Sea at 72–74 m depth (Nuñez *et al.* 2014). The holotype and paratypes were examined during this study and found to be similar in size (Fig. 3) and morphology to the material from GoC and WIM. Only the sub-acicular chaetae of the GoC and WIM specimens seem to have somewhat thicker and shorter blades (Fig. 5D) but this was not considered significant enough to establish a different species. Nuñez *et al.* (2014) described and illustrated the mandibulae of this species as being distally slightly bifid without serration on the anterior edge. However, a thorough examination of all the specimens (including type material) revealed that the mandibles are often broken at the tip (Fig. 5A), giving the appearance illustrated in the original description (Nuñez *et al.* 2014: fig. 3a). In fact, when not broken, the mandibles present a ridge of small teeth on its distal edge (Fig. 4D). Also in the forceps and denticle 1 of the maxillary apparatus, the large teeth were found to alternate with two small teeth (Figs 4E, 5B). The phylogenetic analysis segregates this species from the others within the tree (Fig. 2), but there are no DNA sequences from the type material to compare with. The two sequenced specimens were from WIM, the K2P value from the H3 alignment between the two specimens is 0.00 and the K2P value to the nearest species in the tree, *O. batillus* Wiklund *et al.*, 2012, is 0.10. This study extends the geographic and bathymetric distribution of *O. cantabrica* to WIM and GoC, where it was the most abundant species, and to a depth of 698 m. It is noteworthy that all our specimens were associated with wood samples only and not with alfalfa grass.

Ecology and distribution

NE Atlantic: from the Cantabrian Sea (Bay of Biscay) to the Gulf of Cadiz (Moroccan Margin). Found in muddy sand, 72–74 m depth, in the Cantabrian Sea (Nuñez *et al.* 2014), and in wood substrata, 327–698 m depth, at the West Iberian Margin and Gulf of Cadiz (present study).

Ophryotrocha chemecoli sp. nov.

urn:lsid:zoobank.org:act:4D7F8D13-207F-4E6F-A364-7F470A042F3D

Fig. 6

Etymology

The species name is an allusion to the colonization devices (CHEMECOLI) deployed in the GoC within the scope of the project CHEMECO (“Monitoring colonization processes in chemosynthetic ecosystems”). This species occurred in five of those devices containing wood and alfalfa, at all three mud volcanoes where the experiment was carried out. CHEMECOLI stands for “CHEMOSynthetic Ecosystem COLonization by Larval Invertebrates”.

Material examined

Holotype

MOROCCO • complete spec. (ethanol), 1.25 mm long, 0.24 mm wide, 18 chaetigers; GoC, Mercator MV; 35°17.916' N, 06°38.709' W; 354 m depth; 2 Mar. 2008; Stn 64PE284_12750W; wood substratum; NHMUK 2020.1510.

Paratypes

MOROCCO • 6 specs (ethanol); same collection data as for holotype; NHMUK 2020.1511 • 12 specs (ethanol), 38 specs (plus 3 cf.) (formalin), 2 specs (slide preparation); same collection data as for holotype; DBUA0002290.01.

Other material

MOROCCO • 1 spec. (formalin); same locality as for holotype; 3 Mar. 2008; Stn 64PE284_12752A; alfalfa substrata; DBUA0002290.02 • 1 spec. (formalin); same locality as for holotype; 19 May 2009; Stn B09-

14b_01W; wood substrata; DBUA0002291.01 • 1 spec. (ethanol); GoC, Mknès MV; 34°59.091' N, 07°04.424' W; 698 m depth; 20 May 2009; Stn B09-14b_03W; wood substrata; DBUA0002291.02 • 1 spec. (ethanol), voucher DNA, exhausted; GoC, Darwin MV; 35°23.523' N, 07°11.513' W; 1100 m depth; 19 May 2009; Stn B09-14b_02A; alfalfa substrata; DBUA0002291.03.

PORTUGAL • 6 specs (ethanol), 1 spec. (slide preparation); WIM, Estremadura Spur; 39°17.295' N, 10°01.045' W; 327 m depth; 1 Jun. 2017; Stn PES-ROVL17D01_pick#3W; wood substrata; DBUA0002289.01 (hologenophore).

Description

Relatively small specimens, 0.64–1.49 mm long and 0.16–0.26 mm wide for 10–19 chaetigers (Fig. 3). Body dorso-ventrally flattened, with the same width in the anterior half, gradually tapering posteriorly (Fig. 6A). Prostomium short and broadly rounded with a flattened anterior rim, without eyes (Fig. 6A). Antennae and palps long, digitiform; antennae inserted mid-dorsally on the prostomium; palps inserted laterally. Peristomium achaetous, with two short rings. Jaw apparatus heavily sclerotized, well visible through the specimen body (Fig. 6A–B). Mandibles rod-like, with straight and clearly dentate anterior edge; apophyse long, slightly surpassing the cutting edge, narrow and curved laterally (Fig. 6C). Maxillae of P-type (Fig. 6D); forceps falcate, comb-like with about 13 teeth, wider with thicker teeth on the right side and narrower with thinner teeth on the left side; eleven pairs of free denticles (D1–11), D1 similar to forceps with thick teeth on both sides, D2 and D3 broad, shovel-like, D4 to D11 shovel-like, narrower, usually directed inwards giving a rhomboid appearance to the maxillae; carrier-like structure with a toothed ridge on each side near the forceps, posterior end with a fimbriate handle. Parapodia

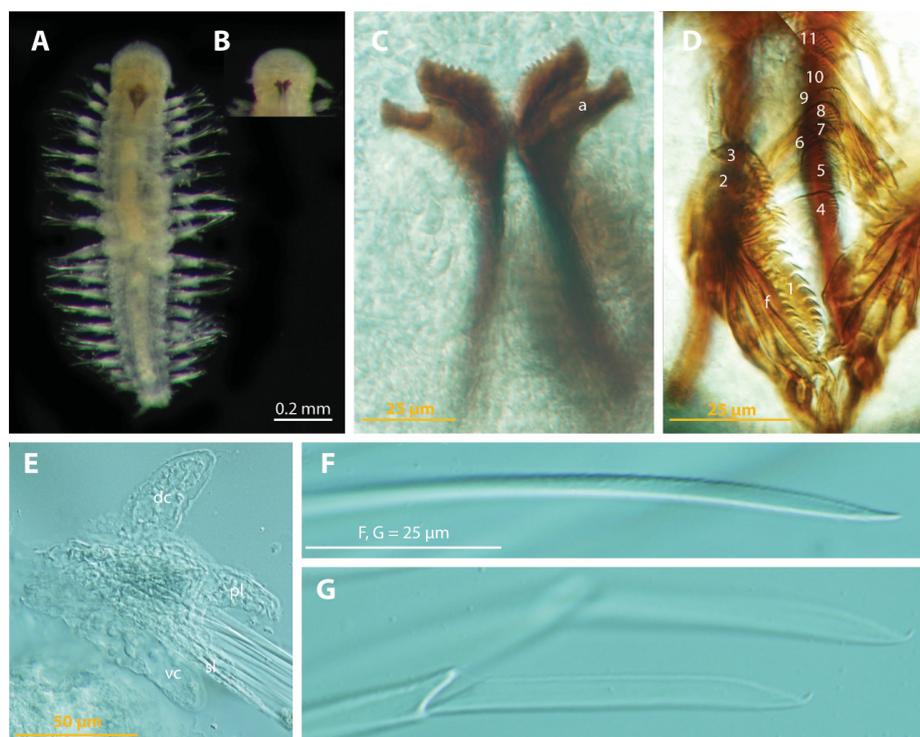


Fig. 6. *Ophryotrocha chemecoli* sp. nov. Stereo (A–B) and compound (C–G) microscope images. A–B: NHMUK 2020.1510; C–D, F–G: DBUA0002290.01; E: DBUA0002289.01.V01 (hologenophore). A. Holotype, entire specimen, dorsal view. B. Holotype, anterior end, ventral view. C. Mandibulae, ventral view. D. Maxillae, dorsal view. E. Mid-body parapodium, posterior view. F. Supra-acicular chaeta, mid-body parapodium. G. Sub-acicular chaetae, mid-body parapodium. Numbers refer to free denticles.

uniramous (Fig. 6E); pre-chaetal lamellae of the median parapodia long, conical; dorsal and ventral cirri conical (dorsal longer than ventral); sub-acicular lobes conical, similar in size to pre-chaetal lamellae, with a short, needle-like acicula protruding. Chaetae long and stiff; supra-acicular chaetae simple, slightly flattening and tapering distally to a fine tip, very lightly serrated (Fig. 6F); sub-acicular chaetae compound, with bifurcate, sub-distally serrated shafts and falcate, very lightly serrated blades (Fig. 6G). Pygidium with terminal anus, a pair of cirriform anal cirri and a very short, rounded median stylet.

Remarks

Ophryotrocha chemecoli sp. nov. is very close at molecular (Fig. 2) and morphological levels to the species *O. scutellus* Wiklund, Glover & Dahlgren, 2009, *O. lusa* Ravara, Marçal, Wiklund & Hilário, 2015 and *O. batillus* Wiklund *et al.*, 2012. *Ophryotrocha scutellus* and *O. lusa* are known to occur in the NE Atlantic (Wiklund *et al.* 2009; Ravara *et al.* 2015), whereas *O. batillus* occurs in the NE Pacific (Wiklund *et al.* 2012). Like *O. chemecoli* sp. nov., all of those species have a dorso-ventrally flattened body, a long parapodial pre-chaetal lobe and roughly rhombus-shaped maxillae. Also the chaetae of *O. scutellus* and *O. batillus* are very similar to those of the new species. However, *O. scutellus* differs from *O. chemecoli* sp. nov. by the larger body size, the flatter prostomium, the much longer pre-chaetal lobe and the mandibular morphology of the adult specimens; whereas *O. batillus* differs in the very large size of the parapodia and chaetae, the flatter and wider prostomium and, to some extent, also the mandibular shape. As in *O. chemecoli* sp. nov., *O. lusa* has eleven pairs of maxillary free denticles, while the other *Ophryotrocha* species usually have only eight or less (Paxton 2004, 2009; Ravara *et al.* 2015). Furthermore, the size of the specimens of the new species, as well as the neurochaetae and the mandibulae shape, are similar to those of younger specimens of *O. lusa*, making it difficult to distinguish between the two species. The adult specimens of *O. lusa*, however, have very different neurochaetae and mandibular morphology (see Ravara *et al.* 2015). Such variation in the mandibular morphology was not observed in the specimens of *O. chemecoli* sp. nov., although globular masses, indicating reproductive maturity, were detected at the base of median parapodia of some larger specimens. In the phylogenetic analysis, *O. cantabrica* also groups in the same clade as *O. chemecoli* sp. nov. (Fig. 2). At the morphological level, these species are very different, having only the morphology of the chaetae in common.

Ecology and distribution

NE Atlantic: from the Estremadura Spur (West Iberian Margin) to the Gulf of Cadiz (Moroccan Margin). Found in wood and alfalfa substrata at 327–1100 m depth.

Ophryotrocha geoffredi sp. nov.

urn:lsid:zoobank.org:act:F5023AAF-791B-47A3-90A2-824D50CC4826

Fig. 7

Etymology

The species is named after Dr Geoffrey Read, the chief taxonomic editor of Polychaeta at the World Register of Marine species (WoRMS) and founder of the Annelida mailing list. His tireless work in both these initiatives is an immense and invaluable aid to all polychaetologists.

Material examined

Holotype

MOROCCO • complete spec. (ethanol), 0.94 mm long, 0.17 mm wide, 16 chaetigers; GoC, Meknès MV; 34°59.091' N, 07°04.424' W; 698 m depth; 20 May 2009; Stn B09-14b_03W; wood substrata; NHMUK 2020.1512.

Paratypes

MOROCCO • 31 specs (formalin); same collection data as for holotype; NHMUK 2020.1513 • 1 spec. (ethanol), 2 specs (slide preparation); same collection data as for holotype; DBUA0002286.02.

Other material

MOROCCO • 5 specs (ethanol); same locality as for holotype; 20 May 2009; Stn B09-14b_03A; alfalfa substrata; DBUA0002286.03 (1 hologenophore, 4 paragenophores) • 2 specs (ethanol), 13 specs (formalin); GoC Darwin MV; 35°23.523' N, 07°11.513' W; 1100 m depth; 19 May 2009; Stn B09-14b_02A; alfalfa substrata; DBUA0002286.04 • 9 specs (ethanol), 1 spec. (slide preparation), 5 specs (formalin); same collection data as for preceding; 19 May 2009; Stn B09-14b_02W; wood substrata; DBUA0002286.05.

Description

Relatively small specimens compared to most species of *Ophryotrocha*. Most of the larger specimens are damaged or incomplete and were not measured. Measured specimens 0.73 to 1.46 mm long and 0.19 mm wide, for 17 to 25 chaetigers (Fig. 3). Body dorso-ventrally flattened, wider anteriorly and tapering posteriorly. Prostomium broadly rounded (Fig. 7A), without eyes. Antennae and palps short, cirriform; antennae inserted mid-dorsally on the prostomium; palps inserted laterally. Peristomium achaetous, with two rings of length similar to the following segments. Jaw apparatus brown, well visible through the specimen body. Mandibles rod-like, with straight, serrated cutting edge (with around 8 teeth in smaller specimens, Fig. 7B) and weakly sclerotized apophyses, shorter than cutting edges. In larger specimens, the cutting edge teeth are usually worn and the apophyses are enlarged longitudinally (Fig. 7E). Maxillae of P-type (also after moulting) with asymmetric forceps; left forceps narrow and finely toothed (up to 35? teeth), right forceps wider and coarsely toothed (~15 teeth) (Fig. 7F); seven free denticles (D1–7; Fig. 7C, F), D1 comb-like coarsely toothed, similar to right forceps, D2 shovel-like with an outer larger tooth and coarse teeth, D4–6 shovel-like with smaller teeth slightly increasing in number anteriorly, D7 shovel-like, much broader than the others; carrier-like structure with a toothed ridge on each side at the base of the bifurcation (Fig. 7F) and a posteriorly fimbriate handle (Fig. 7C). Parapodia uniramous, with conical acicular lobes, inconspicuous pre-chaetal lamellae, long sub-acicular lobes and conical dorsal cirri inserted sub-distally on the parapodia (Fig. 7D); ventral cirri absent. Sub-acicular lobes with a short needle-like protruding acicula (Fig. 7H). Chaetae relatively short and stiff; supra-acicular chaetae simple, tapering distally, smooth or very finely serrated, up to 7 per fascicle (Fig. 7I); sub-acicular chaetae compound with sub-distally serrated shafts and falcate, lightly serrated blades (Fig. 7G), up to 7 per fascicle. Pygidium with terminal anus, a pair of short cirriform anal cirri (spherical and almost inconspicuous in smaller specimens) and a median papilla.

Remarks

According to the phylogenetic analysis (Fig. 2), *O. geoffreadi* sp. nov. is close to the species *O. langstrumpae* Wiklund *et al.*, 2012, *O. sadina* Ravara, Marçal, Wiklund & Hilário, 2015, *O. cantabrica* Nuñez, Riera & Maggio, 2014, *O. scutellus* Wiklund, Glover & Dahlgren, 2009, *O. lusa* Ravara, Marçal, Wiklund & Hilário, 2015, *O. batillus* Wiklund *et al.*, 2012 and *O. chemecoli* sp. nov. (Wiklund *et al.* 2009, 2012; Nuñez *et al.* 2014; Ravara *et al.* 2015). However, unlike *O. geoffreadi* sp. nov., all those species have well-developed parapodial lobes and cirri, and only two of them (*O. langstrumpae* and *O. cantabrica*) have mandibulae with a straight cutting edge but without membranous apophyses. Three other species that are not included in the phylogenetic analysis have mandibulae with a straight, serrated cutting edge: *O. pachysoma* Hilbig & Blake, 1991 from the W Atlantic (604–2065 m depth), *O. natans* Pfannenstiel, 1975 from the Red Sea (intertidal) and *O. kagoshimaensis* Miura, 1997 from the W Pacific (197 m depth) (Pfannenstiel 1975; Hilbig & Blake 1991; Miura 1997). Nevertheless, the presence of a membranous apophyse below the cutting edge is not clear for the two latter species, and the cutting edge of the mandibulae of *O. pachysoma* is much wider and also serrated on its internal border. Furthermore, the maxillary, parapodial and chaetal morphology of all these species is different from that of *O. geoffreadi* sp. nov.

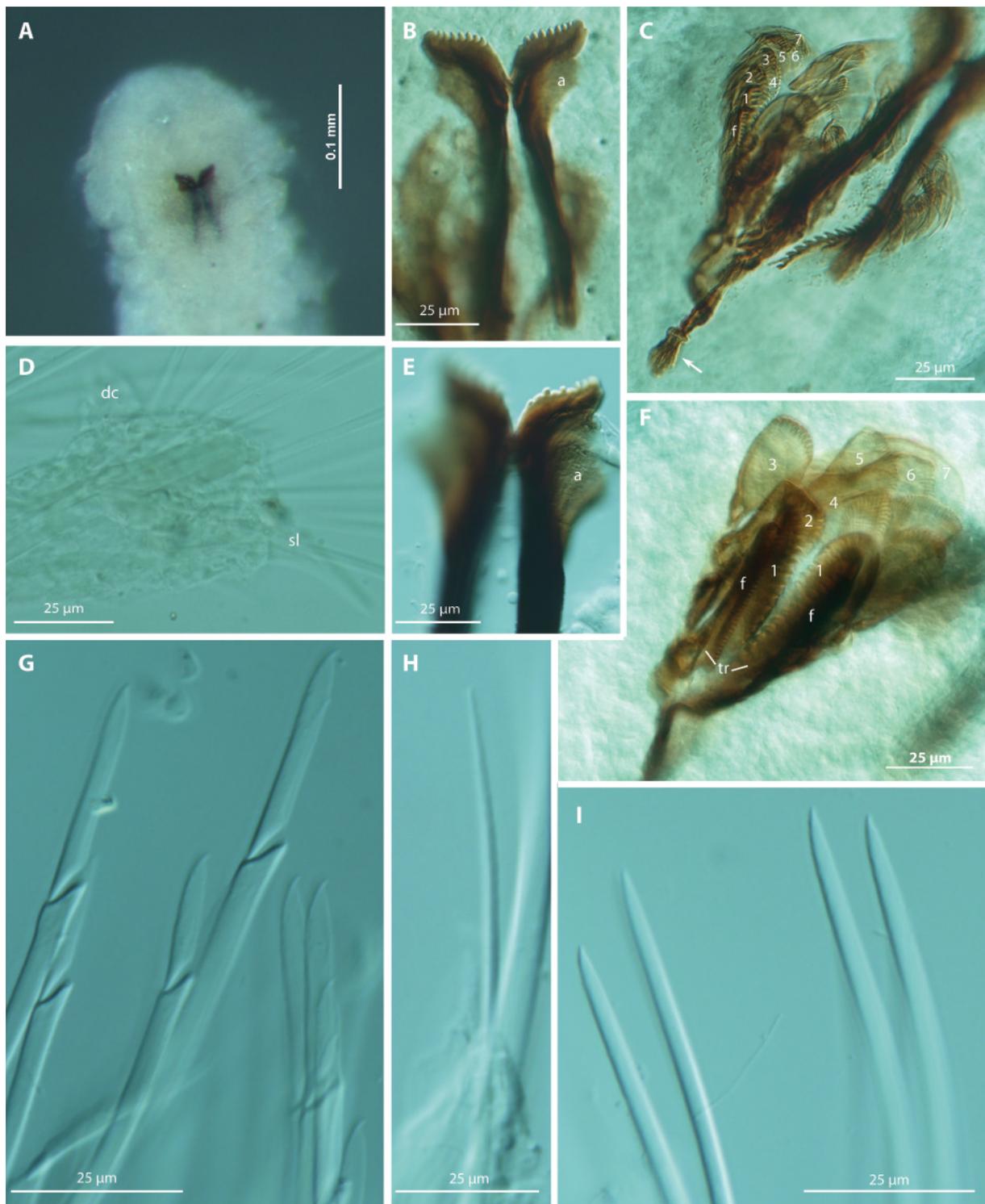


Fig. 7. *Ophryotrocha geoffreadi* sp. nov. Stereo (A) and compound (B–I) microscope images. A–D: DBUA0002286.02; E–I: DBUA0002286.05. **A.** Anterior region, ventral view. **B.** Mandibulae of a smaller specimen, ventral view. **C.** Maxillae of the same specimen with moulting pieces, ventral view. **D.** Median parapodia, anterior view. **E.** Mandibulae of a larger specimen, ventral view. **F.** Maxillae of the same specimen, dorsal view. **G.** Sub-acicular chaetae of mid-body parapodia. **H.** Simple chaeta protruding from the sub-acicular lobe of a mid-body parapodium. **I.** Supra-acicular chaetae, mid-body parapodium. Numbers refer to free denticles.

Ecology and distribution

NE Atlantic: Gulf of Cadiz (Moroccan Margin). Found in experimentally deployed wood and alfalfa substrata, at 698–1100 m depth (this study).

***Ophryotrocha hartmanni* Huth, 1933**

Fig. 8

Ophryotrocha hartmanni Huth, 1933: 309–381, fig. 1 (mentioned as a new species on page 311, but the description is mainly based on cytological characters; type locality: Plymouth)

Ophryotrocha hartmanni – Parenti 1961: 440–444, figs I6–11, II4–5 (re-description; Roscoff).

Material examined

MOROCCO • 1 spec. (ethanol), damaged; GoC, Mercator MV; 35°17.916' N, 06°38.709' W; 354 m depth; 19 May 2009; Stn B09-14b_01W; wood substrata; DBUA0002292.01 • 1 spec. (slide preparation), very damaged; same locality as for preceding; 3 Mar. 2008; Stn 64PE284_12752A; alfalfa substratum; DBUA0002293.01 • 1 spec. (ethanol); GoC, Darwin MV; 35°23.523' N, 07°11.513' W; 1100 m depth; 19 May 2009; Stn B09-14b_02W; wood substratum; DBUA0002292.02.

Additional material

GERMANY • 1 spec.; Helgoland, North Sea; shallow water; GNM: Polychaeta: 14698.

Remarks

The original description of *O. hartmanni* given by Huth (1933) is based mostly on cytological features. The only morphological details included reference to the specimens' average length (4–5 mm), to the body shape as being torpedo-like and to the position of the sperms and oocytes (sperms in the first three chaetigers and oocytes from the fourth chaetiger onwards). The specimens examined by Huth were collected at Plymouth and kept in laboratory conditions, but no information is given on type material or its deposition. Parenti (1961) provided a re-description of the same species based on material from Roscoff also kept in laboratory conditions. There is no mention to a re-examination of type material or other material from the type locality, but Parenti (1961) confirmed some of the cytological observations made by Huth (1933) and provided a complete morphological description, highlighting the differences between this and other species. Again, there is no indication regarding the deposition of the examined material. Åkesson (1973) studied the reproduction and larval morphology of *O. hartmanni* using specimens from Plymouth and Roscoff aquaria and from the harbours of Malaga (S Spain) and concluded that interbreeding of the three strains produced fertile progeny in all combinations, and also in subsequent generations. This denotes the widespread distribution of this species.

Only three specimens of *O. hartmanni* were found in the present study, two of which are not in good condition. The smallest (13 chaetigers, 0.76 mm long), and better preserved, and the larger (approximately 20 chaetigers, 2.3 mm long) specimens were mounted in a permanent slide where the jaw apparatus, parapodia and chaetae could be properly examined (Fig. 8). The molecular analysis performed with the posterior part of the third specimen failed, thus preventing molecular comparison. Except for the presence of small dorsal cirri on the parapodia (Fig. 8D), stated as absent for *O. hartmanni*, the GoC specimens have all the morphological diagnostic characteristics described by Parenti (1961). However, the DNA voucher of *O. hartmanni* included in our phylogenetic analysis, identified by Bertil Åkesson and also obtained from crossbreeding experiments with the previous strains, has very small dorsal cirri on its parapodia (H. Wiklund pers. obs.). Similarly to *O. hartmanni*, the antennae of our specimens are poorly developed, palps are absent and mandibulae are rod-shaped, widening distally into bifid serrated cutting

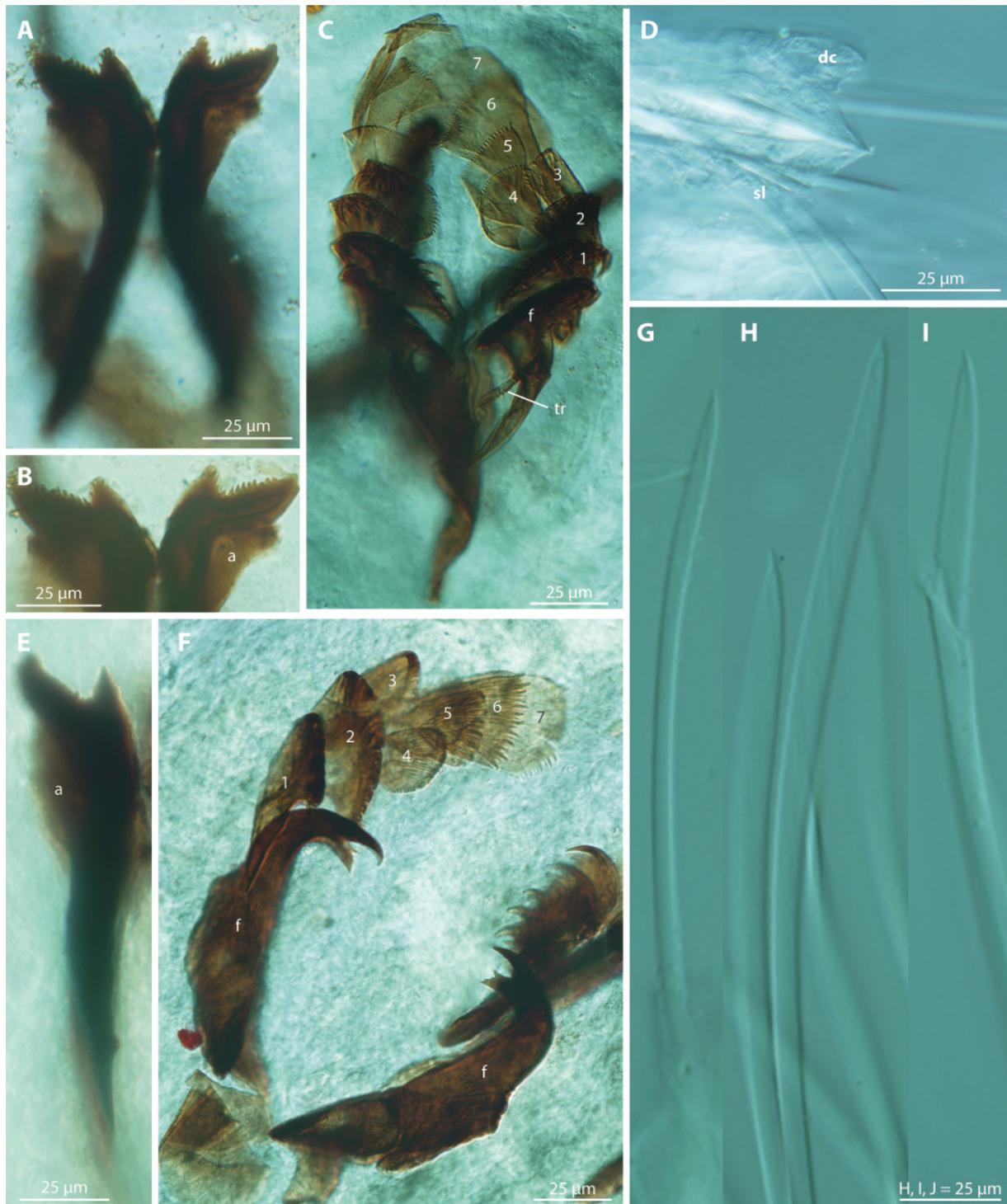


Fig. 8. *Ophryotrocha hartmanni* Huth, 1933 (DBUA0002293.01). Compound microscope images. **A.** Mandibulae of a small specimen, ventral view. **B.** Detail of the cutting edge of the same. **C.** P-type maxillae of the same specimen, dorsal view. **D.** Mid-body parapodium, anterior view. **E.** Mandibula of a larger specimen, ventral view. **F.** K-type maxillae of the same specimen, dorsal view. **G.** Acicular chaeta of sub-acicular lobe. **H.** Supra-acicular chaetae, mid-body parapodium. **I.** Sub-acicular chaeta, mid-body parapodium. Numbers refer to free denticles.

plates with tiny pointed teeth (around 14 teeth in the smaller specimen spread along all the cutting edge, including around the inner peak, Fig. 8A–B; in the larger specimen, the teeth are worn out and the inner peak is almost smooth, Fig. 8E). The juvenile and adult forms of maxillae are also similar to those of *O. hartmanni*. The P-type forceps have a large distal tooth, the distal half is comb-like with alternating large and small teeth, and the posterior part has a ridge of tiny teeth (Fig. 8C). The K-type forceps have bifid tips strongly bent inwards (more gently curved in *O. hartmanni*, as illustrated in Parenti 1961: fig. II-4); the sub-apical tooth has a straight spine superiorly and is finely denticulated inferiorly (Fig. 8F). Denticles 1 to 7 (D1–7) are similar in shape for P- and K-type maxillae. Denticle 1 is similar in shape to the P-type forceps; D2 is shovel-shaped but also with a large tooth on the inner edge; D3 is shovel-shaped, narrow, with coarse teeth; and D4–7 are shovel-shaped, wider and with smaller teeth. According to Parenti (1961), *O. hartmanni* is particularly abundant in muddy sediments rich in organic detritus. This study provides a new record of *O. hartmanni* for the North Atlantic (at the GoC) and extends the bathymetric distribution of the species to 1100 m depth.

Ecology and distribution

N Atlantic: from Norway to northern France on soft bottoms from the intertidal down to around 100 m depth (Oug & Pleijel 2015 and references within), and in the Gulf of Cadiz (Moroccan Margin) in experimentally deployed wood and alfalfa substrata at 354–1100 m depth (present study); Mediterranean: Spain (Åkesson 1973), Italy (Simonini *et al.* 2010).

Ophryotrocha cf. lipscombae Lu & Fauchald, 2000

Fig. 9

Ophryotrocha lipscombae Lu & Fauchald, 2000: 486, figs 1–4 (type locality: continental slope 110 miles south of Woods Hole, Massachusetts, NW Atlantic, depth 1830 m).

Material examined

MOROCCO • 1 spec. (formalin); GoC, Mercator MV; 35°17.916' N, 06°38.709' W; 354 m depth; 2 Mar. 2008; Stn 64PE284_12750W; wood substratum; DBUA0002284.01.

PORTUGAL • 51 specs (2 hologenophores, 49 paragenophores; ethanol); WIM, Estremadura Spur; 39°17.295' N, 10°01.045' W; 327 m depth; 1 Jun. 2017; Stn PES_ROVL17D01-pick#3W; wood substrata; DBUA0002285.01.

Description of the material examined in this study

Body robust and compact (Fig. 9A), with the same width throughout, only tapering at the pygidium. Largest specimen 2.5 mm long and 0.43 mm wide for 38 chaetigers (Fig. 3). All segments with a transversal band of cilia. Prostomium short, broadly rounded, slightly trilobed (more evident in smaller specimens; Fig. 9B), without eyes. Antennae and palps spherical, very small, may appear to be absent (only visible under the microscope). Peristomium achaetous, with two rings half the length of the following segments. Delimitation between the prostomium and the first ring of the peristomium almost imperceptible. Jaw apparatus dark and relatively large (Fig. 9B). Mandibles rod-like; in larger specimens, the anterior end is cut in two levels, with the inner lower level toothed (teeth often worn) (Fig. 9C–E); in smaller specimens, the anterior end of mandibulae is mainly straight with small elevations at the outer tips and distinctly toothed (Fig. 9I). Maxillae with a pair of falcate forceps (Fig. 9F), seven pairs of free denticles (D1–7) (Fig. 9G–H) and five pairs of accessory plates (Fig. 9; the fifth plate was lost when detaching the denticles, Fig. 9G–H); forceps with a main fang followed by 1–2 large and several very small teeth (Fig. 9J); D1 comb-like, with about 18 large and small teeth alternating (Fig. 9F); distal denticles plate-like, with up to 8 large and small teeth irregularly alternating (Fig. 9G–H). Parapodia uniramous,

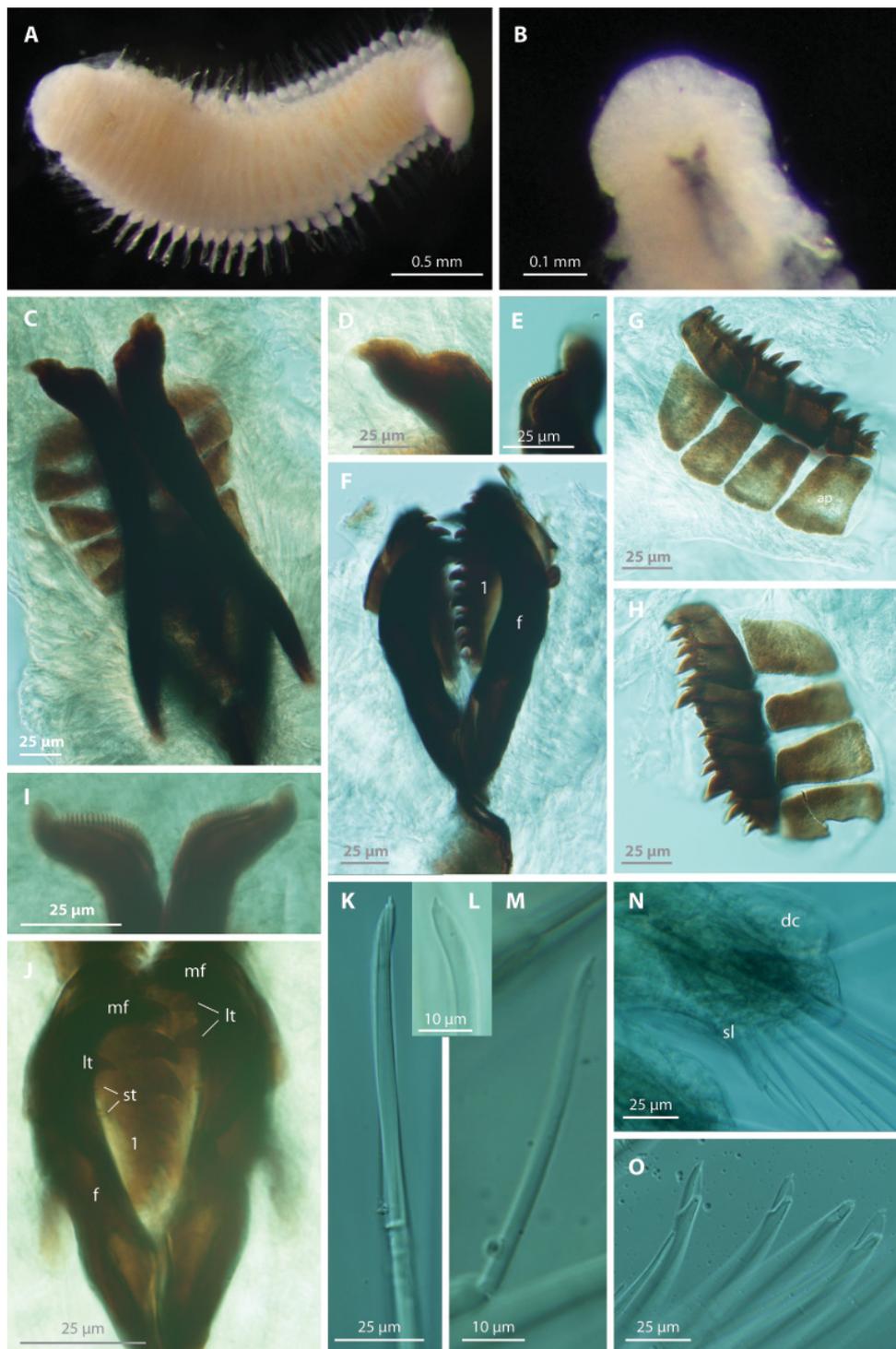


Fig. 9. *Ophryotrocha lipscombae* Lu & Fauchald, 2000 (DBUA0002285.01). Stereo (A–B) and compound (C–O) microscope images. **A.** Complete specimen, dorsal view. **B.** Prostomium of a smaller specimen, ventral view. **C.** Mandibular and maxillary apparatus, ventral view. **D–E.** Anterior tip of mandible of larger specimens. **F.** Maxillary carrier, forceps and basal denticles, dorsal view. **G–H.** Maxillarydistal denticles and accessory plates from right and left sides, respectively. **I.** Anterior tip of mandible of smaller specimen. **J.** Maxillary forceps and basal denticles, dorsal view. **K–L.** Supra-acicular chaetae, mid-body parapodium. **M.** Sub-acicular hook, mid-body parapodium. **N.** Anterior parapodium, posterior view. **O.** Sub-acicular chaetae, mid-body parapodium. Number 1 refers to free denticle 1.

with broadly conical acicular lobes, sub-acicular lobes and ovoid dorsal cirri fused to the acicular lobe (Fig. 9N); ventral cirri apparently absent. Aciculae slightly protruding in all parapodia. Sub-acicular lobes with harpoon-like protruding acicula with acute tip and subdistal tooth (Fig. 9M). Supra-acicular chaetae simple, subdistally serrated, tapering abruptly into a large main fang (Fig. 9K–L). Sub-acicular chaetae compound with very short serrated blades abruptly tapering into a main fang; heterogomph shafts distally serrated (Fig. 9O). Pygidium with terminal anus and 2 very small ovoid anal cirri.

Remarks

Ophryotrocha lipscombae is only known from its original description based on specimens collected from Woods Hole (NW Atlantic) at a depth of 1830 m (Lu & Fauchald 2000). This species is considered to be unique among the dorvilleids based on the presence of five pairs of accessory plates associated with the denticles of the maxillae (Lu & Fauchald 2000). Other distinctive characteristics are the presence of teeth below the main fang of the maxillary forceps and the clear fusion between the prostomium and the peristomium. All these characteristics are present in the specimens from the Estremadura Spur (WIM, NE Atlantic) and the single specimen from Mercator MV (GoC, NE Atlantic) examined in this study. The minor differences registered for the specimens from the NW Atlantic concern features that may have been overlooked or misinterpreted, such as: the absence of distal teeth on the mandibulae of larger specimens, which may be worn (in our specimens these teeth are mostly worn and the ones that are present are difficult to detect); the absence of prostomial palps (in our specimens the antennae and palps are tiny and could only be detected under the optical microscope); the absence of dorsal cirri on parapodia (in our specimens the dorsal cirri appear almost entirely fused with the acicular lobes and thus are difficult to distinguish (Fig. 9N); figure 1d of the original description illustrates a similar structure); and the tips of the supra- and sub-acicular chaetae, which in our specimens are more abruptly tapered into a distinct main fang (only visible under high magnification). The phylogenetic analysis segregates this species from the others within the tree (Fig. 2). The two sequenced specimens were from WIM, the K2P value from the H3 alignment between the two specimens is 0.00 and the K2P values to the nearest species in the tree, *O. maculata* and *O. hartmanni*, is 0.09. However, there are no DNA sequences for the West Atlantic *O. lipscombae* specimens to compare with. Furthermore, it was not possible to examine the type material that is deposited in the Smithsonian National Museum of Natural History. If the similarity at the morphological and molecular level is confirmed, then this study extends the geographic and upper limit of the bathymetric distribution of *O. lipscombae* to the NE Atlantic and to a depth of 327 m.

Ecology and distribution

NE Atlantic specimens: from the Estremadura Spur (West Iberian Margin) to the Gulf of Cadiz (Moroccan Margin) in wood substrata, at 327–354 m depth (present study).

Original distribution of *O. lipscombae*: NW Atlantic, south of Woods Hole, in sediment, at a depth of 1830 m (Lu & Fauchald 2000).

Ophryotrocha mammillata Ravara, Marçal, Wiklund & Hilário, 2015

Ophryotrocha mammillata Ravara *et al.*, 2015: 5, figs 4–12 (type locality: Setúbal Canyon, W Portugal, NE Atlantic).

Material examined

MOROCCO • 2 specs (ethanol), 1 spec. (slide preparation); GoC, Mercator MV, 35°17.916' N, 06°38.709' W; 354 m depth; 2 Mar. 2008; Stn 64PE284_12750W; wood substrata; DBUA0002279.01 • 1 spec. (ethanol); GoC, Meknès MV; 34°59.091' N, 07°04.424' W; 698 m depth; 20 May 2009; Stn B09-14b_03A; alfalfa substratum; DBUA0002280.01 • 1 spec. (ethanol); GoC, Darwin MV; 35°23.523' N, 07°11.513' W; 1100 m depth; 19 May 2009; Stn B09-14b_02W; wood substratum; DBUA0002280.02 •

2 specs (formalin), 3 specs (paragenophores, in ethanol); same collection data as for preceding; 19 May 2009; Stn B09-14b_02A; alfalfa substrata; DBUA0002280.03.

Additional material

PORTUGAL • 2 specs (ethanol); WIM, Setúbal Canyon; 38°16.856' N, 09°06.734' W; 1000 m depth; 22 Aug. 2012; on bone material from an experimentally deployed cow carcass; DBUA0001555.04.

Remarks

This species was recently described from an experimentally deployed mammal carcass for a similar amount of time (approximately 18 months) at the Setúbal Canyon (WIM) (Ravara *et al.* 2015). The morphological identification was confirmed with molecular analyses (Fig. 2). This study extends its distribution to the Gulf of Cadiz where it occurred associated with experimentally deployed wood and alfalfa substrata. Curiously, *O. mammillata* was not found in the wood-fall collected at Estremadura Spur (WIM), a site very close to its type locality. It is worth mentioning here that in the GoC only five specimens of *O. mammillata* were retrieved, compared to 198 specimens previously reported from the Setúbal Canyon (Ravara *et al.* 2015).

Ecology and distribution

NE Atlantic: from Setúbal Canyon (West Iberian Margin) to the Gulf of Cadiz. Found in experimentally deployed organic falls (mammal carcasses, wood and alfalfa substrata), at a depth of 354–1100 m (Ravara *et al.* 2015; present study).

Ophryotrocha nunezi sp. nov.

urn:lsid:zoobank.org:act:5526CBA2-A3C3-4E2E-9195-99E4BD6B04D2

Fig. 10

Etymology

The species is named after Dr Jorge Nuñez, who described several of the currently known *Ophryotrocha* species and first examined the specimens from the Cantabrian Sea. Dr Nuñez has always been very helpful in our requests for assistance on these taxa.

Material examined

Holotype

MOROCCO • complete spec. (formalin), 0.97 mm long, 0.14 mm wide, 16 chaetigers; GoC, Mercator MV; 35°17.916' N, 06°38.709' W; 354 m depth; 2 Mar. 2008; Stn 64PE284_12750W; wood substratum; NHMUK 2020.1514.

Paratypes

MOROCCO • 2 specs (formalin); same collection data as for holotype; NHMUK 2020.1515 • 2 specs (slide preparation), 1 spec. (ethanol); same collection data as for holotype; DBUA0002294.02 (paragenophores).

Other material

MOROCCO • 3 specs (formalin); same locality as for holotype; 19 May 2009; Stn B09-14b_01W; wood substrata; DBUA0002295.01.

Additional material

SPAIN • 4 specs; Bay of Biscay, Cantabrian Sea; 43°22.18' – 43°23.14' N, 02°15.00' – 02°15.21' W; 93–101 m depth; 22 Jun. 1991; cruise Fauna II; Stn 150A; MNCN 16.9/13680.

Description

Relatively small specimens compared to most *Ophryotrocha* species, with proportionally long chaetae. Larger specimens measure from approximately 0.70 to 0.99 mm long and 0.12 mm wide, for 12 to 17 chaetigers (Fig. 3). Prostomium broadly rounded (Fig. 10A), without eyes. Antennae small, spherical, inserted dorsally in mid prostomium; palps bi-articulated with spherical palpophores and ovoid palpostyles, inserted laterally on the posterior part of prostomium (Fig. 10A). Peristomium achaetous, with two rings of similar length to the following segments; anterior ring apparently fused to prostomium. Jaw apparatus light brown, almost inconspicuous (Fig. 10A). Mandibles rod-like, weakly sclerotized, with curved, serrated cutting edge (with 14 teeth) and large, wing-like apophyses confined to the anterior part of the mandibulae, giving a butterfly-like appearance (Fig. 10C). Maxillae with falcate forceps with a large subdistal tooth below the main fang and transversal ridges posteriorly, giving a wrinkled appearance (Fig. 10D–E), basally fused to the maxillary carrier; approximately seven free denticles (D1–7) very weakly sclerotized and difficult to examine (Fig. 10D); D1 elongated and lightly serrated, parallel to forceps, D2–7 apparently small and compacted above the forceps (Fig. 10E); the small size of the specimen and the poor sclerotization makes it impossible to count the exact number of free denticles and to observe their morphology more thoroughly. Parapodia long, uniramous, with conical acicular lobes, inconspicuous pre-chaetal lamellae, long sub-acicular lobes and conical dorsal cirri inserted subdistally on the parapodia (Fig. 10H). Anterior parapodia (chaetigers 1–3 or 1–4) with a single compound chaeta (similar to the sub-acicular chaetae) protruding from the sub-acicular lobe (Fig. 10H); following parapodia with simple chaetae protruding from the sub-acicular lobe (Fig. 10I). Supra-acicular chaetae simple, slightly curved sub-distally, coarsely serrated, 2–3 per fascicle (Fig. 10G). Sub-acicular chaetae compound with lightly serrated blades, all of subequal length; shafts distally serrated (Fig. 10F), 3 per fascicle. Pygidium with terminal anus and two clavate anal cirri (Fig. 10A–B).

Remarks

Ophryotrocha nunezi sp. nov. can be distinguished from all other species by the combination of four characteristics: bi-articulated palps, winged mandibulae, falcate maxillary forceps with internal tooth, and clavate anal cirri. According to the phylogenetic analysis (Fig. 2), six described species of *Ophryotrocha* and one of *Exallopus* are placed in the same clade as *O. nunezi* sp. nov.: *O. longidentata* Josefson, 1975, *O. nauarchus* Wiklund *et al.*, 2012, *O. magnadentata* Wiklund *et al.*, 2012, *O. longicollaris* Wiklund *et al.*, 2012, *O. globopalpata* Blake & Hilbig, 1990, *O. flabella* Wiklund *et al.*, 2012 and *E. jumarsi* Blake, 1985 (Josefson 1975; Blake 1985; Blake & Hilbig 1990; Wiklund *et al.* 2012). All these species of *Ophryotrocha* have bi-articulated palps, but, unlike the others, *O. longicollaris* does not have winged mandibulae. Furthermore, of all of them, only *O. flabella* has toothed K-type forceps and only *O. magnadentata* has clavate anal cirri. The latter species also has sub-acicular lobes sustained by a compound falciger similarly to *O. nunezi* sp. nov. However, all the other characteristics of both species are different. There are two more species of *Ophryotrocha* with bi-articulated palps and winged mandibulae (not included in the phylogenetic analysis), *O. paragerlachi* Brito & Nuñez, 2003 and *O. platykephale* Blake, 1985, but both these species have long cirriform anal cirri and different parapodial and chaetal morphology (Blake 1985; Brito & Nuñez 2003). Two other species, *O. mammillata* Ravara, Marçal, Wilund & Hilário, 2015 and *O. wubaolingi* Miura, 1997, have bi-articulated palps but different mandibulae and anal cirri as well as other morphological features (Miura 1997; Ravara *et al.* 2015). *Ophryotrocha labidion* Hilbig & Blake, 1991, from the US Atlantic coast, have bi-articulated palps, winged mandibulae and clavate anal cirri, but strongly differs in the maxillary, parapodial and chaetal morphology (Hilbig & Blake 1991). Another species from the West Atlantic coast, *O. atlantica* Hilbig & Blake, 1991, with winged mandibulae, falcate forceps with teeth and clavate anal cirri, have simple palps and different maxillary and chaetal morphology (Hilbig & Blake 1991). Paxton & Morineaux (2009) gave a brief description of an undetermined species (*Ophryotrocha* sp.) reported from the Mid-Atlantic Ridge (Menez Gwen vent field, 865 m depth), that although larger in size, had a similar appearance to this species but with simple palps and mandibulae with a smooth cutting edge. The genus *Exallopus* also includes species with bi-articulated palps, although this is not the case for the species *E. jumarsi*, which

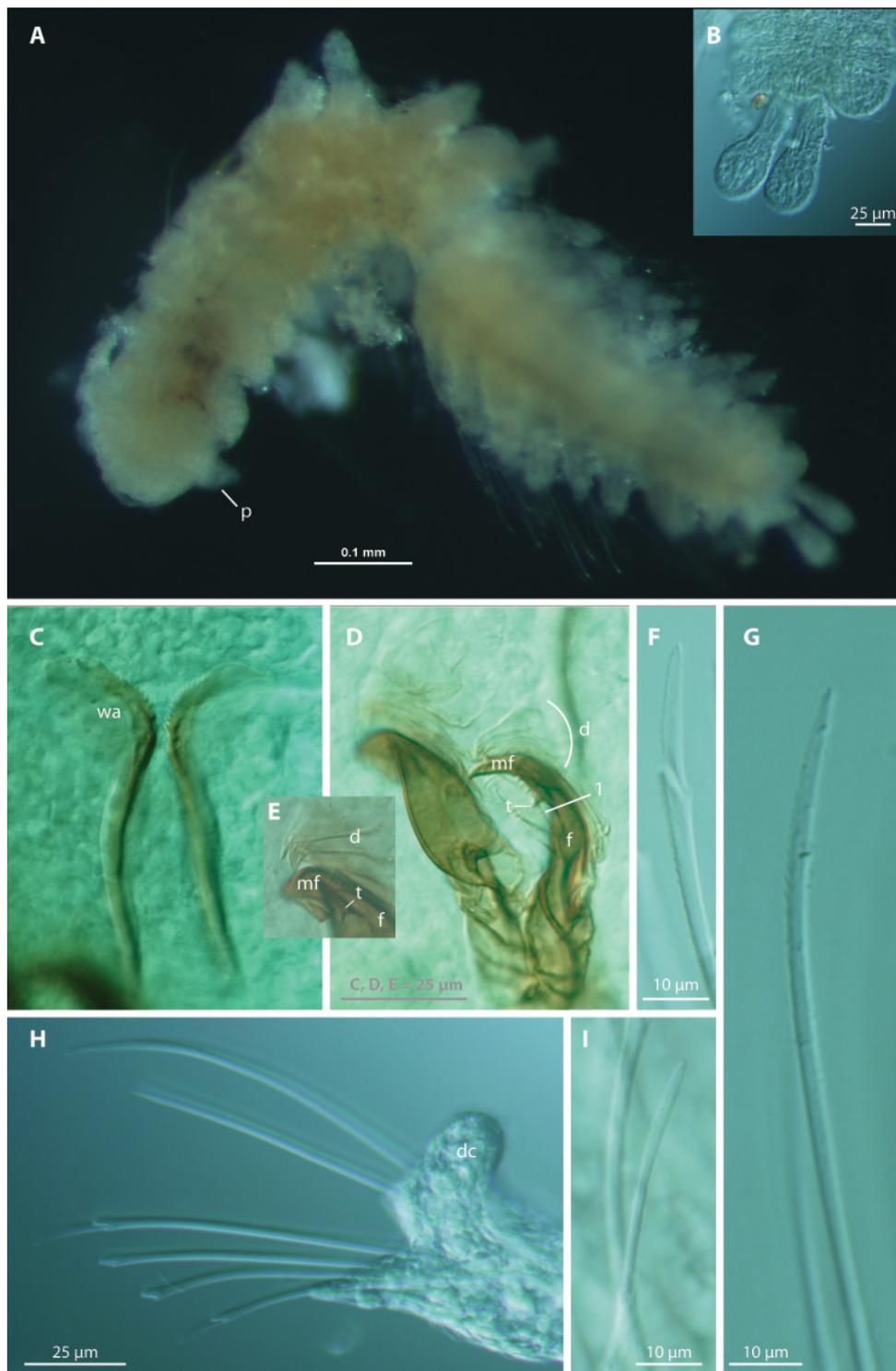


Fig. 10. *Ophryotrocha nunezi* sp. nov. Stereo (A) and compound (B–I) microscope images. A: holotype, NHMUK 2020.1514; B–I: paratypes, DBUA0002294.02. A. Complete specimen, ventral view. B. Pygidium with anal cirri, ventral view. C. Mandibulae, ventral view. D. Maxillae, ventro-lateral view. E. Detail of the tips of maxillary forcep and free denticles. F. Sub-acicular chaeta, mid-body parapodium. G. Supra-acicular chaeta, mid-body parapodium. H. Anterior parapodium with compound chaetae protruding from the sub-acicular lobe. I. Simple chaeta protruding the sub-acicular lobe of a mid-body parapodium. Number 1 refers to free denticle 1.

further differs from *O. nunezi* sp. nov. by having the antennae weakly annulated, the P-type maxillae and by the presence of strongly modified chaetae in the first chaetigerous segment. This latter characteristic is the main morphological difference between the genera *Exallopus* and *Ophryotrocha*. Nevertheless, based on the molecular analyses done to date, the two genera cannot be separated at the molecular level (Fig. 2; Wiklund *et al.* 2012). The lack of molecular data for the type species of the genus *Exallopus* (*Exallopus cropion* Jumars, 1974) has prevented concluding the synonymy of the two genera. Four other non-described species (*Ophryotrocha* ‘Seep 3, 4 and 5’ and *Exallopus* ‘seep’, Fig. 2) are placed in the same clade as *O. nunezi* sp. nov., but no morphological descriptions are available for comparison.

When examining the material of *O. cantabrica* deposited in the MNCN, Madrid, a vial with additional material was found under the collection number MNCN 16.9/13680 (see Nuñez *et al.* 2014), containing four specimens of the new species described here. It was not possible to perform molecular analyses with this material. Nevertheless, all the morphological characteristics are the same as the specimens from the GoC.

Ecology and distribution

NE Atlantic: from the Cantabrian Sea (Bay of Biscay) to the Gulf of Cadiz (Moroccan Margin). Found in sandy sediments with shells and experimentally deployed wood substrata, at 93–354 m depth.

Ophryotrocha scutellus Wiklund, Glover & Dahlgren, 2009
Figs 11–12

Material examined

MOROCCO • 11 specs (plus 2 cf.) (formalin), 2 specs (slide preparation); GoC, Mercator MV; 35°17.916' N, 06°38.709' W; 354 m; 2 Mar. 2008; Stn 64PE284_12750W; wood substrata; DBUA0002288.01 • 1 spec. cf. (formalin); same locality as for preceding; 3 Mar. 2008; Stn 64PE284_12752A; alfalfa substratum; DBUA0002288.02 • 1 spec. (ethanol); same collection data as for preceding; 19 May 2009; Stn B09-14b_01W; wood substratum; DBUA0002287.05 • 1 spec. (ethanol), 7 specs (formalin), 3 specs (slide preparation); GoC, Meknès MV; 34°59.091' N, 07°04.424' W; 698 m; 20 May 2009; Stn B09-14b_03W; wood substrata; DBUA0002287.03 • 3 specs (ethanol), 1 spec. (formalin); same locality and date as for preceding; Stn B09-14b_03A; alfalfa substrata; DBUA0002287.04 • 4 specs (ethanol), 1 spec. (formalin), 1 spec. (slide preparation, hologenophore); GoC, Darwin MV; 35°23.523' N, 07°11.513' W; 1100 m; 19 May 2009; Stn B09-14b_02A; alfalfa substrata; DBUA0002287.01 • 1 spec. (ethanol); same locality and date as for preceding; Stn B09-14b_02C; carbonate substratum; DBUA0002287.02.

Additional material

PORTUGAL • 6 specs (ethanol); WIM, Setúbal Canyon; 38°16.856' N, 09°06.734' W; 1000 m depth; 22 Aug. 2012; on bone material from a cow carcass; DBUA0001557.01-02.

SWEDEN • 12 specs (ethanol); coastal Skagerrak; 58°53.1' N, 11°06.4' E; 125 m depth; on bone material from a minke whale carcass; DBUA0002348.

Description (amended)

Size of WIM and GoC specimens varies within 1.55–2.70 mm long and 0.24–0.39 mm wide for 18–24 chaetigers. Skagerrak specimens are larger, up to 3.60 mm long and 0.75 mm wide for 31 chaetigers (Fig. 3). Body dorso-ventrally flattened, with similar width throughout the body, abruptly ending with pygidium in smaller specimens (Fig. 11A) or tapering slightly at posterior end in larger ones. Prostomium broadly rounded, dorso-ventrally flattened, with a transverse ridge between the antennae, without eyes (Fig. 11A). Antennae and palps long, digitiform; antennae inserted mid-dorsally on the prostomium; palps inserted laterally. Peristomium achaetous, with two rings slightly narrower and shorter than the

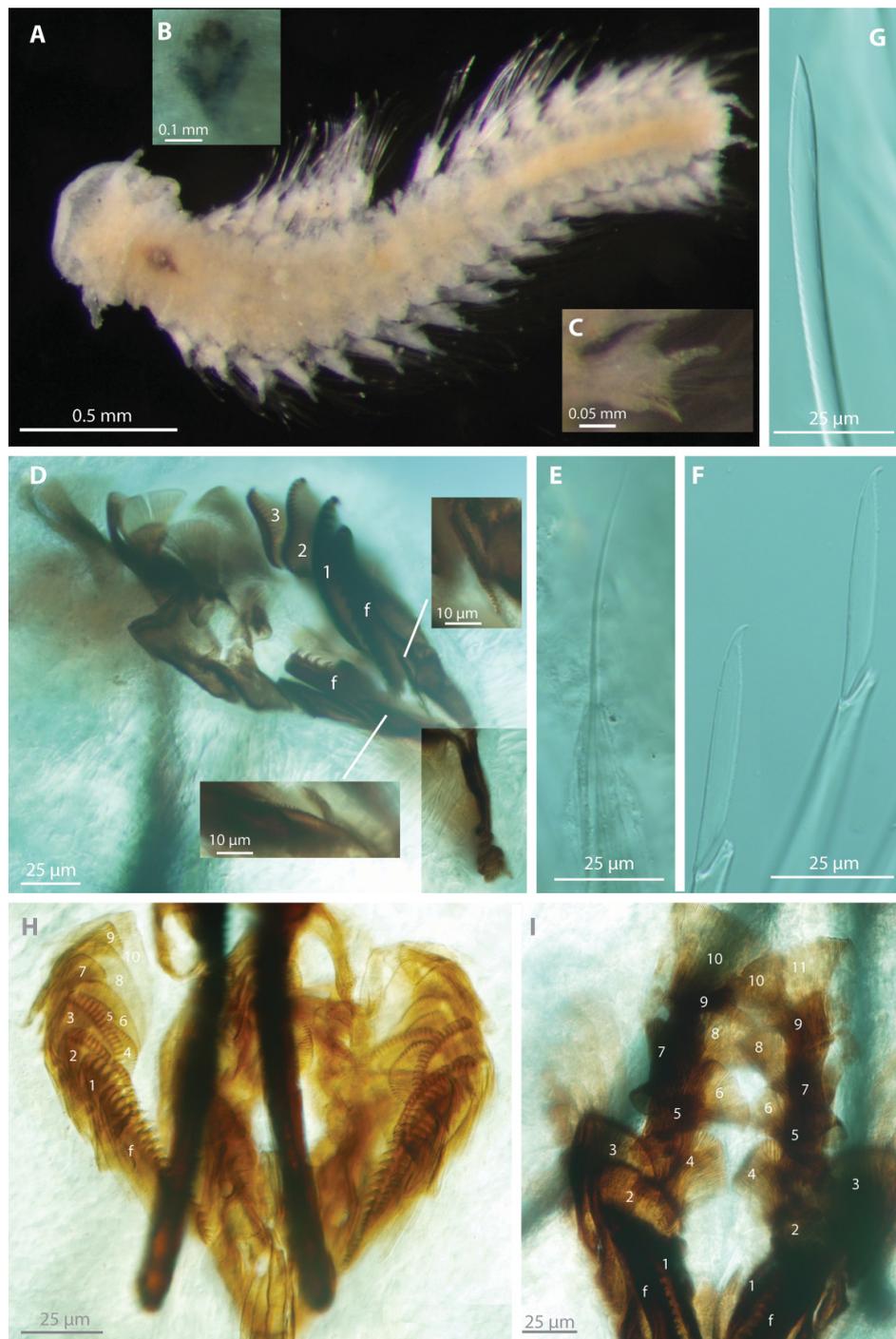


Fig. 11. *Ophryotrocha scutellus* Wiklund, Glover & Dahlgren, 2009. Stereo (A, C) and compound (B, D–I) microscope images. A–C: DBUA0002288.01; D–G: DBUA0002287.03 (L1); H: DBUA0002287.03 (L3); I: DBUA0002348. A. Entire specimen, dorsal view. B. Maxillary apparatus through body tissue, dorsal view. C. Mid-body parapodium, posterior view. D. Maxillae, dorsal view (left forcep and first denticles broken), arrows show details of the teeth ridges at the base of the maxillary carriers. E. Needle-like chaeta of sub-acicular lobe. F. Compound sub-acicular chaetae, mid-body parapodium. G. Supra-acicular chaeta, mid-body parapodium. H. Maxillae of a specimen from GoC, dorsal view. I. Maxillae of a specimen from off Sweden, dorsal view. The maxillae in H and I are in the process of moulting, thus including functional and replacement sets. Numbers refer to free denticles.

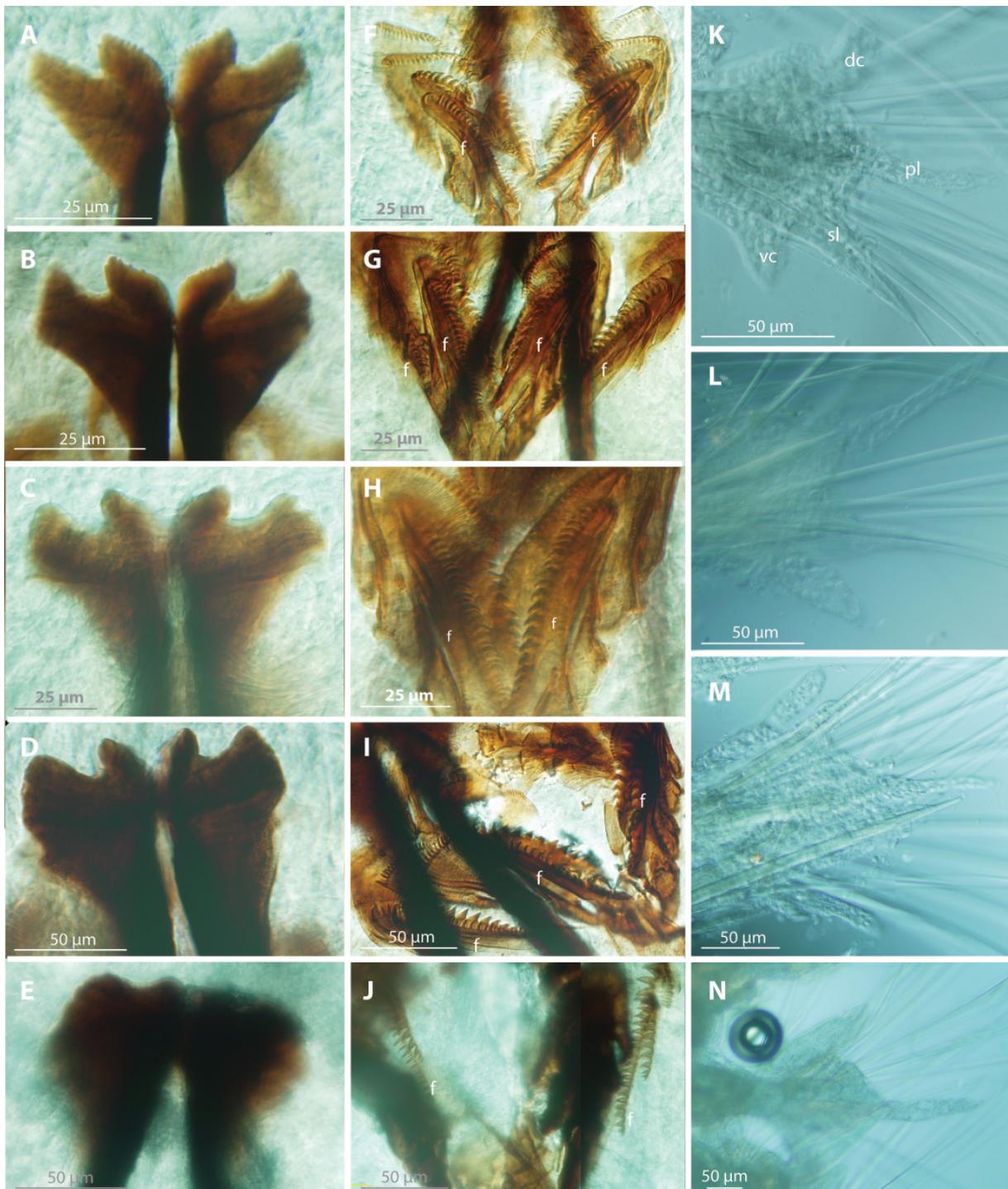


Fig. 12. *Ophryotrocha scutellus* Wiklund, Glover & Dahlgren, 2009. Mandibulae, maxillae and parapodial development from smaller to larger specimens. Compound microscope images. A, F, K: DBUA0002288.01 (L5); B, G: DBUA0002287.03 (L3); C, H, L: DBUA0002288.01 (L6); D, I, M: DBUA0002287.03 (L2); E, J, N: DBUA0002348. A–E. Mandibulae, ventral view. F–J. Maxillae, dorsal view. K–N. Mid-body parapodia. The maxillae in G, I–J are in the process of moulting, thus including functional and replacement sets.

following segments. Jaw apparatus heavily sclerotized, well visible through the specimen body, usually with an apparent rhombus shape (Fig. 11A–B). The morphology of mandibles and maxillary forceps varies with the specimen size (Fig. 12A–J). Mandibles rod-like; smaller specimens with straight and clearly dentate anterior end and long apophyse, well surpassing the cutting edge, with a diagonal connection to the shaft (Fig. 12A); with growth, the teeth wear out (Fig. 12B) and the cutting edge becomes short and more curved forward, without teeth, the apophyse becomes thicker with an almost vertical connection to the shaft (Fig. 12D–E). Maxillae of P-type; forceps falcate, comb-like, slightly wider with up to 20 large teeth on the right side, and narrower with up to 26 thinner teeth on the left side (Fig. 12F–G); with growth, the teeth of the left forcep become irregular (Fig. 12H) resulting in a clear alternation in size in larger specimens (Figs 11D, 12I–J); eleven free denticles (D1–11), D1 similar to forceps (always with even teeth), D2 to D11 shovel-like, D4 to D11 usually directed inwards (Fig. 11H–I); carrier-like structure with a toothed ridge on each side near the forceps (see details in Fig. 11D) and with a posteriorly fimbriate handle (Fig. 11D). Parapodia uniramous (Fig. 11C); pre-chaetal lamellae of median parapodia very long, cirriform; dorsal and ventral cirri digitiform, long (dorsal longer than ventral); sub-acicular lobes conical, about two-thirds the length of pre-chaetal lamellae in smaller specimens, becoming shorter in larger specimens (Fig. 12K–N), with a needle-like acicula (Fig. 11E). Chaetae long and stiff; supra-acicular chaetae simple, slightly flattening and tapering distally to a fine tip, very lightly serrated, 7 per fascicle (Fig. 11G); sub-acicular chaetae compound with bifurcate, sub-distally serrated shafts, and falcate, very lightly serrated blades (Fig. 11F), 7–9 per fascicle. Pygidium with terminal anus, a pair of cirriform anal cirri and a very short (almost imperceptible) median stylet.

Remarks

This species was originally described from a minke whale carcass deployed at a depth of 125 m off Sweden and organically enriched sediments beneath a fish farm in Norway, at a depth of 104 m (Wiklund *et al.* 2009). Later, seven specimens of the same species were retrieved from an experimentally implanted cow carcass at the Setúbal Canyon (WIM), 1000 m depth (Ravara *et al.* 2015). The present study extends the distribution of *O. scutellus* to GoC where it occurred associated with experimentally deployed alfalfa and wood substrata and control samples (carbonate cubes), at a depth of 354–1100 m. The specimens from the GoC and WIM are overall smaller than the ones originally described from Sweden and Norway (Fig. 3) and exhibit some variation in the mandibular and maxillary morphology, apparently associated with growth (Fig. 12). However, the larger specimens of the southern locations entirely match the morphology of the northern ones. The morphological identification was furthermore confirmed with molecular analyses for both the larger and the smaller specimens. The specimen from GoC (DBUA0002287.01) sequenced here falls among previously published *O. scutellus* sequences (Genbank accession numbers GQ415506 and KP731544-48) with within-species K2P values from the H3 alignment of 0.009–0.01, and a K2P value of 0.10 to the nearest species in the tree, *O. chemecoli* sp. nov. A similar variability in length and corresponding variation in the mandible morphology has earlier been described for other species, such as *O. sadina* and *O. lusa* (Ravara *et al.* 2015: figs 15, 25, respectively). Differing from what was stated in the original description, the specimens of *O. scutellus* studied here have eleven pairs of free denticles (instead of seven) in the maxillary apparatus, and the left forcep of the larger specimens have uneven teeth. These characters were also found in the specimens from off Sweden examined here (Figs 11–12). Thus, the original description is here amended accordingly.

Ecology and distribution

NE Atlantic: from Norway to the Gulf of Cadiz (Moroccan Margin). Found in mammal carcasses, organically enriched sediment beneath fish farms, wood, alfalfa and carbonate substrata, at a depth of 104–1100 m (Wiklund *et al.* 2009; Ravara *et al.* 2015; present study).

Genus *Parougia* Wolf, 1986*Parougia ougi* sp. nov.

urn:lsid:zoobank.org:act:C91E1B58-1DB0-49E4-B3A9-0DB4290AB587

Fig. 13

Etymology

The species is named after Dr Eivind Oug, who made a thorough revision and described several species within the genus *Parougia*.

Material examined**Holotype**

MOROCCO • incomplete spec. (ethanol, anterior region mounted in a slide preparation); GoC, Mercator MV; 35°17.916' N, 06°38.709' W; 354 m depth; 2 Mar. 2008; Stn 64PE284_12750W; wood substrate; NHMUK 2020.1516 (hologenophore).

Description

Incomplete specimen, with 43 chaetigers. Body cylindrical, long and slender (Fig. 13A). Prostomium rounded, longer than wide, without eyes (Fig. 13A–B). Antennae and palps missing; palp scars detected on slide mount under light microscopy (Fig. 13E); antennal scars not detected. Peristomium achaetous, with two rings of roughly the same length as following segments, with transversal ciliary bands. Jaws located at peristomium level, weakly sclerotized. Mandibles roughly square anteriorly, with smooth and lightly trilobed margin (median lobe much smaller than outer ones); handles short and widely divergent (Fig. 13C–D). Maxillae with four similar rows of denticles; both inferior and superior rows with basal plates and free denticles (Fig. 13F–G); basal plates formed by the fusion of 6 square denticles homogeneously toothed, left and right plates fused posteriorly (Fig. 13G); at least 16 free denticles, shovel-like with finely toothed margin, anterior ones very weakly sclerotized and barely visible; maxillary carriers absent. Parapodia sub-biramous, long in median chaetigers (Fig. 13H); dorsal cirri present from the second chaetiger, similar in length or slightly longer than acicular lobes, digitiform, indistinctly biarticulated, supported by an internal acicula in cirrophore (Fig. 13J); neuropodial acicular lobes conical, pre- and postchaetal lamellae poorly developed; ventral cirri shorter than dorsal cirri, inserted subdistally on the acicular lobe. Supra-acicular chaetae simple, wider and coarsely serrated basally, tapering to fine tips distally (Fig. 13I), ca 4 per fascicle (2 long and 2 short). Supra-acicular furcate chaetae present from third chaetiger, with coarsely serrated shaft and thin asymmetric tines (Fig. 13K), one per parapodium. Sub-acicular chaetae compound, with sub-distally strongly serrated shafts and bidentate, very lightly serrated blades (Fig. 13L), 7 per fascicle. Pygidium not examined.

Remarks

The genus *Parougia* includes, at present, nineteen nominal species (Yen & Rouse 2020). Five of these species (*P. albomaculata* (Åkesson & Rice, 1992), *P. bermudensis* (Åkesson & Rice, 1992), *P. diapason* Taboada, Bas & Avilla, 2015, *P. eliasoni* (Oug, 1978) and *P. oregonensis* Hilbig & Fiege, 2001) are represented in the phylogenetic reconstruction (Fig. 2) and are found to be molecularly different from the one studied herein (Oug 1978; Åkesson & Rice 1992; Hilbig & Fiege 2001; Taboada *et al.* 2015). Twelve species of *Parougia* are known to occur in chemosynthetic habitats: one in whale-falls in Antarctica (*P. diapason*, 10 m depth), eight in methane seeps in the NE Pacific (*P. batia* (Jumars, 1974), also in whale-falls, 587–1229 m depth; *P. billiemiroae* Yen & Rouse, 2020, 587 m depth; *P. ceruleibohorum* Yen & Rouse, 2020, 588–1433 m depth; *P. indiareinhardtiae* Yen & Rouse, 2020, 650 m depth; *P. oregonensis*, also in whale-falls, 595–850 m depth; *P. sulleyi* Yen & Rouse, 2020, ~600–1600 m depth; *P. theloniousblueski* Yen & Rouse, 2020, ~1000 m depth; *P. zairahae* Yen & Rouse, 2020, 514–809 m depth), and three in hydrothermal vents in the SW Pacific (*P. chutsaoi* Yen &

Rouse, 2020, 1991 m depth; *P. jessieae* Yen & Rouse, 2020, 1821–1845 m depth) and in the NE Pacific (*P. wolfi* Blake & Hilbig, 1990, 1545–2200 m depth) (Jumars 1974; Blake & Hilbig 1990; Yen & Rouse

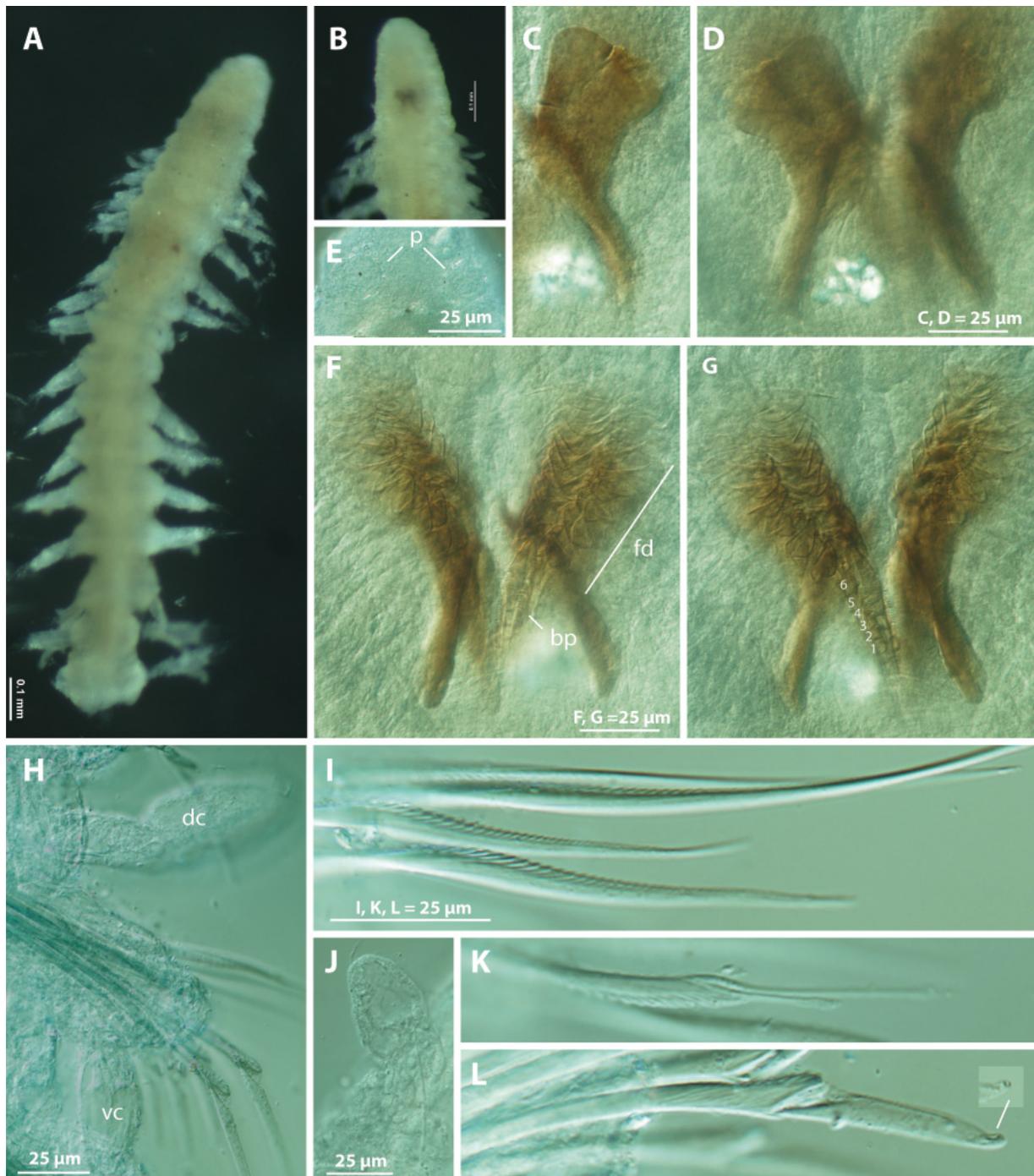


Fig. 13. *Parougia ougi* sp. nov., holotype (NHMUK 2020.1516). Stereo (A–B) and compound (C–L) microscope images. **A.** Anterior fragment, dorsal view. **B.** Anterior end, ventral view. **C.** Right mandibula, dorsal view. **D.** Mandibulae, ventral view. **E.** Palp scars. **F.** Maxillae, dorsal view. **G.** Maxillae, ventral view. **H.** Parapodium from the second chaetiger, posterior view. **I.** Supra-acicular chaetae, anterior parapodium. **J.** Dorsal cirrus, sixth parapodium. **K.** Furcate chaeta, sixth parapodium. **L.** Sub-acicular chaetae, anterior parapodium.

2020). Three other species are known from shallow waters of the North Atlantic: *P. caeca* (Webster & Benedict 1884), *P. macilenta* (Oug, 1978) and *P. nigridentata* (Oug, 1978) and another species was described from soft sediments of the southern ocean: *P. furcata* (Hartman, 1953) (Hartman 1953; Oug 1978; Webster & Benedict 1884). All of these species differ from *P. ougi* sp. nov. at the morphological level, especially in the maxillary apparatus. In *P. ougi* sp. nov. all free denticles are shovel-shaped with numerous small teeth of similar size, while in the majority of the other species, at least the posterior free denticles of the superior row have a large main tooth followed by several smaller ones. The only exception is *P. jessieae*, for which the free denticles are very similar to those of *P. ougi* sp. nov. Also, the mandibles of this species have smooth anterior margins as in *P. ougi* sp. nov., although with a prominent median peak and slightly different shape. However, *P. ougi* sp. nov. differs from *P. jessieae* by the coarsely serrated supra-acicular chaetae and the presence of furcate chaetae (absent in *P. jessieae*). Another species from a closely related genus, *Ougia tenuidentis* Wolf, 1986, described from shallow sandy sediments from Florida, presents the same kind of mandibulae as *P. ougi* sp. nov. and is otherwise very similar (Wolf 1986). But again, the free denticles of that species bear both small and large teeth. *Ougia tenuidentis* also differs from *P. ougi* sp. nov. in the basal plates of the maxillary superior row, which are serrated rather than composed of fused free denticles, and the presence of maxillary carriers, which are distinctive characteristics of the genus *Ougia* Wolf, 1986 (Wolf 1986). *Parougia ougi* sp. nov. presents what apparently are basal plates on the inferior rows of maxillary denticles. Yen & Rouse (2020) recently referred to these structures as being possible moults, although their identification as either the inferior or a replacement row was considered to be ambiguous for some species. None of these hypotheses can be confirmed in the single specimen examined in this study. Also *P. wolffi* was originally described as having superior basal plates with double vertical rows of teeth fused to each other and to a horny base (Blake & Hilbig 1990). This structure may be equivalent to the presence of both inferior and superior basal plates, but further studies are needed to confirm this. *Parougia wolffi* clearly differs from *P. ougi* sp. nov. by the distinct shape of the anterior free denticles of the maxillary apparatus.

Ecology and distribution

NE Atlantic: Gulf of Cadiz (Moroccan margin). Found in experimentally deployed wood at a depth of 354 m.

Discussion

Phylogenetic results

A total of 477 dorvilleid specimens were examined in this study: 284 from GoC and 193 from WIM (Table 3). These specimens were ascribed to eight *Ophryotrocha* and one species of *Parougia*. Four of these species are described here as new to science. Seventeen new DNA sequences (nine H3, five 16S and three COI) were obtained, ten for the four newly described species, six for the new records of three previously known species and one for a specimen herein referred as *O. cf. lipscombae* (Table 2). Although morphologically similar to *O. lipscombae*, known from Woods Hole (NW Atlantic), a putative extension of the species distribution to the NE Atlantic, combined with our inability to examine the type material and the absence of sequences from the original location to compare with the one obtained herein, all add uncertainty to the identification that must be considered with caution. Only the specimens of *O. hartmanni* failed to produce viable sequences. The Bayesian phylogenetic analyses (including the genetic markers 16S and H3) supported the species *O. chemecoli* sp. nov., *O. nunezi* sp. nov., *O. geoffreadi* sp. nov. and *P. ougi* sp. nov. as being new to science, and confirmed the identity of the previously known species *O. mammillata* and *O. scutellus* (Fig. 2). No sequences were previously known for the species *O. cantabrica*.

Similarly to other studies (Wiklund *et al.* 2012; Taboada *et al.* 2013; Salvo *et al.* 2014; Zhang *et al.* 2017), the phylogenetic analysis retrieved a well-supported ‘*Ophryotrocha*’ clade which also includes species from the genera *Exallopus*, *Iphitime* Marenzeller, 1902 and *Pseudophryotrocha* Hilbig & Blake, 1991

Table 3. Number of specimens for each species at the four studied sites.

Site	Gulf of Cadiz								WIM
	Mercator MV			Meknes MV		Darwin MV			ES
Cruise	64PE284	B09-14b	64PE284	B09-14b	B09-14b	B09-14b	B09-14b	B09-4b	PES-ROVL17
Sample	12750W	01W	12752A	03W	03A	02W	02A	02C	pick#3W
<i>O. cantabrica</i>	–	9	–	4	–	–	–	–	135
<i>O. chemecoli</i> sp. nov.	59(+3 cf.)	1	1	1	–	–	1	–	7
<i>O. geoffreadi</i> sp. nov.	–	–	–	35	5	15	15	–	–
<i>O. hartmanni</i>	–	1	1	–	–	1	–	–	–
<i>O. cf. lipscombae</i>	1	–	–	–	–	–	–	–	51
<i>O. mammillata</i>	3	–	–	–	1	1	5	–	–
<i>O. nunezi</i> sp. nov.	6	3	–	–	–	–	–	–	–
<i>O. scutellus</i>	13(+2 cf.)	1	1 cf.	11	4	–	6	1	–
<i>Parougia ougi</i> sp. nov.	1	–	–	–	–	–	–	–	–

MV = mud volcano; A = alfalfa substrate; W = wood substrate; C = carbonate substrate.

(Fig. 2), but the non-existence of DNA data for the type species of these genera prevents their synonymy with *Ophryotrocha*, as previously discussed by Wiklund *et al.* (2012) (Marenzeller 1902; Hilbig & Blake 1991). The ‘*Parougia*’ group, where the new species *P. ougi* sp. nov. is included, is well supported and sister to the ‘*Ophryotrocha*’ group. Within the *Ophryotrocha* clade, the tree shows a low degree of resolution with only 58.8% of the nodes having posterior probability support values of 95 or above. Still, the analysis retrieved the three main clades known within *Ophryotrocha*, namely ‘*hartmanni*’, ‘*lobifera*’ and ‘*labronica*’ (Salvo *et al.* 2014; Taboada *et al.* 2017; Zhang *et al.* 2017), along with a fourth unnamed clade previously defined by Wiklund *et al.* (2012) as clade ‘D’ (Fig. 2). All these clades are well supported, although the ‘*hartmanni*’ group seems to be paraphyletic, as already shown by Dahlgren *et al.* (2001).

Ecological results

Previous studies have suggested a possible bathymetric segregation of the fauna from reduced environments, with the shallow-water naturally reduced habitats being more similar to other shallow-water organic-rich sulphidic substrata, such as fish farms or sewage discharges (Wiklund *et al.* 2009; Danise *et al.* 2014; Taboada *et al.* 2016), while deep-water organic falls would have strong affinities with hydrothermal vents and cold seeps (Bennett *et al.* 1994; Smith 2006). This is not validated by our analysis, where close affinities between species of various habitat types, depths and biogeographical regions are patent in several clades (Fig. 2, see also Table 2). In fact, species from reduced environments are present in several clades, indicating that the adaptation to such environments happened multiple times independently, as already suggested by Thornhill *et al.* (2012) and Wiklund *et al.* (2012) for the dorvilleids and by Eilertsen *et al.* (2017) for the NE Atlantic ampharetids.

All the nine species reported herein were found in the colonization devices from one or more mud volcanoes of GoC, but only three species (*O. cantabrica*, *O. chemecoli* sp. nov. and *O. cf. lipscombae*) were also present in the sunken wood fragment sampled at WIM (Table 3). The geographic and bathymetric distribution is extended for four species (*O. cantabrica*, *O. hartmanni*, *O. mammillata* and *O. scutellus*). As mentioned before, the putative extension of *O. lipscombae* must be considered with caution. However, both *O. scutellus* and *O. hartmanni* were already known to have a wide distribution (from Norway to Portugal and from the English Channel to the Mediterranean, respectively) (Åkesson 1973; Ravara *et al.* 2015), compatible with the new records from the Iberian and Moroccan margins. Although uncommon, these wide geographic distributions are not unprecedented, and there are similar reports for other species (e.g., *O. orensanzi* Taboada *et al.*, 2013 in Paxton *et al.* 2017, *O. bifida* Hilbig & Blake, 1991 and *P. ceruleibohorum* Yen & Rouse, 2020). Given the known limited larval dispersal capability of *Ophryotrocha* species (Paxton & Åkesson 2007), a possible explanation for such wide

distributions is the existence of ephemeral or long-lasting spots of organic enrichment across those distribution areas, capable of sustaining viable populations of those species (Cunha *et al.* 2013). Species of *Ophryotrocha* are considered as omnivores or unspecialized opportunists, able to inhabit non-enriched environments and to rapidly increase their abundances when nutrient conditions become more favourable (Paxton *et al.* 2017). This seems to be the case for *O. orensanzi*, which was described from a whale-fall in W Antarctica and later reported from non-enriched sediments at the other side of the continent (Taboada *et al.* 2013; Paxton *et al.* 2017). The species *O. cantabrica* was first reported from non-enriched sediments and it is reported here as the dominant dorvilleid both in naturally occurring and experimentally deployed sunken wood at Estremadura Spur (327 m deep) and Mercator MV (354 m deep), respectively. These two shallower locations also showed overall the highest number of dorvilleids (177 specs in Mercator MV and 193 in Estremadura Spur), mostly in association with wood substrata colonised by the wood-borer bivalve *Xylophaga* W. Turton, 1822, known for its role in the breakdown of refractory organic materials into more readily available food sources (Voight 2015).

The genus *Ophryotrocha* was always represented by several species in all samples: Mercator MV presented the highest species diversity, with the presence of eight different species, two of which were only found at this location (*O. nunezi* sp. nov., *Parougia ougi* sp. nov.); at the deeper sites five species were retrieved in each mud volcano, represented by a total of 61 and 44 specimens, respectively, in Mèknes MV (698 m) and Darwin MV (1100 m). Three species, *O. chemecoli* sp. nov., *O. mammillata* and *O. scutellus*, were found at all three mud volcanoes, in wood and alfalfa substrata. *Ophryotrocha chemecoli* sp. nov. was also found at Estremadura Spur in sunken wood. Only one species, *O. geoffreadi* sp. nov., was found exclusively in the deeper mud volcanoes (Mèknes and Darwin), both in alfalfa and wood substrata. The outstanding diversity of *Ophryotrocha* taxa in organically-enriched, reduced environments is patent in the frequent occurrence of several sympatric congeners, also reported in previous studies (e.g., California methane seeps – Levin *et al.* 2003; an Italian harbour – Prevedelli *et al.* 2005; NE Atlantic and NE Pacific organic falls – Wiklund *et al.* 2009, 2012; Antarctic whale falls and eutrophic sediments – Taboada *et al.* 2013, 2017; experimentally deployed organic falls in the NE Atlantic – Cunha *et al.* 2013; Ravara *et al.* 2015; this study). This co-existence is often explained by adaptive mechanisms leading to niche differentiation via specialization and resource partitioning (Cunha *et al.* 2013; Ravara *et al.* 2015 and references therein). Previous studies indicate that organically-enriched habitats are heterogeneous environments supporting diverse food sources including different bacterial communities that, in turn, feed distinct species of *Ophryotrocha*, as revealed by isotopic analyses (Levin *et al.* 2013). Resource partitioning (e.g., food, space occupancy) may arise from differences in body size, as appears to be the case in our samples, where the most abundant species are segregated by size (Fig. 14; see also Table 3 and Fig. 3). At the shallower sites the largest species (*O. cantabrica*: 5.4 mm) is dominant but one intermediate size species (*O. scutellus*: 2.7 mm in Mercator MV; *O. cf. lipscombae*: 2.5 mm in Estremadura Spur) and a smaller-sized species (*O. chemecoli* sp. nov.: 1.5 mm), also are well represented. At the deeper sites (Meknès and Darwin MVs) a small-sized species (*O. geoffreadi* sp. nov.: 1.5 mm) is dominant and seconded by one intermediate size species (*O. scutellus*). In most cases, other species are represented by a single or few specimens in each sample. Studies over time have revealed an overlap of successional stages in the colonization process of whale-falls (Ravara *et al.* 2015; Taboada *et al.* 2017) that may also explain the locally high species richness encountered in organically-enriched habitats. Both adaptive (e.g., niche differentiation) and non-adaptive mechanisms (founder effect, genetic drift, hybridization) have been invoked as contributors to the global speciation of *Ophryotrocha* in organic falls and other reducing environments (Cunha *et al.* 2013 and references therein). Life history traits of species of *Ophryotrocha* play an essential role in these processes but little is known about their reproductive strategies (e.g., fecundity, dispersal potential, population growth rates) or feeding behaviour (e.g., type and size of food particles). Although there are some studies based on live observations of single species of *Ophryotrocha* feeding behaviour (e.g., Mercier *et al.* 2014), more comprehensive studies are crucial to better understand the ecology and distribution of this genus.

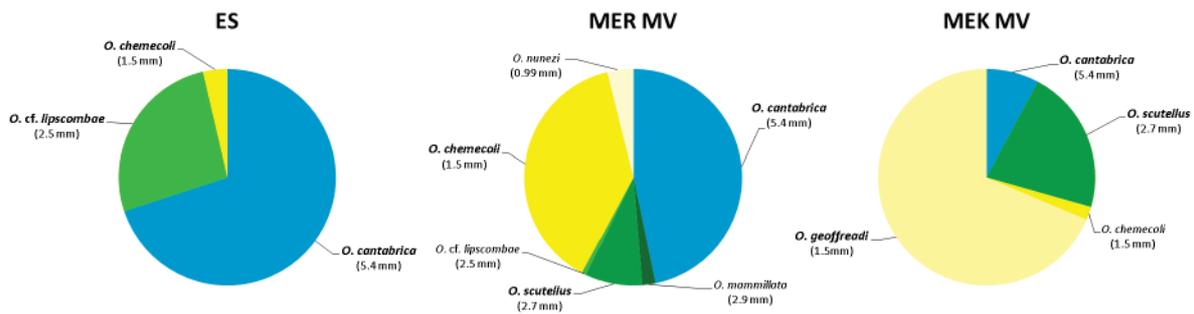


Fig. 14. Relative abundance of species of *Ophryotrocha* Claparède & Meczniow, 1869 in the three most abundant samples (> 50 specimens) suggesting niche differentiation by body size. The assemblages are dominated by one larger species (in blue), one smaller species (in yellow) and one intermediate size species (in green). Body size of adults (maximum) is indicated in brackets (see also Fig. 3 for variability in size). Abbreviations: ES = Estremadura Spur (WIM), wood, PES-ROVL17_pick#3W; Mer MV = Mercator MV (GoC), wood, 64PE284_12750W; Mek MV = Meknès MV (GoC), wood, B09-14b_03W.

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