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**Polar Biology**

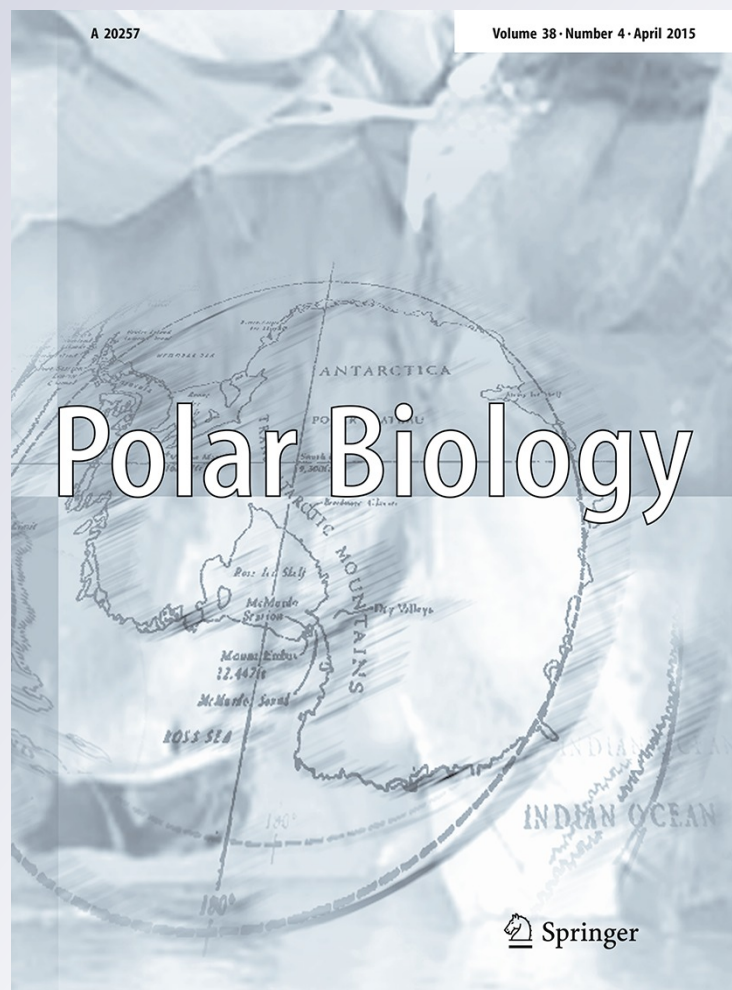
ISSN 0722-4060

Volume 38

Number 4

Polar Biol (2015) 38:517-527

DOI 10.1007/s00300-014-1614-7



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# A new *Parougia* species (Annelida, Dorvilleidae) associated with eutrophic marine habitats in Antarctica

Sergi Taboada · Maria Bas · Conxita Avila

Received: 19 June 2014/Revised: 22 October 2014/Accepted: 28 October 2014/Published online: 15 November 2014  
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**Abstract** In contrast to other areas of the planet, very little is known about Antarctic marine invertebrates associated with eutrophic marine benthic areas. Recently, several studies investigated this fauna by experimentally deploying whale bones, leading to the discovery of new opportunistic polychaetes. To investigate the Antarctic organisms associated with these substrates we experimentally deployed whale bones in the shallow waters of Deception Island (South Shetland Islands). We present here the formal description of *Parougia diapason* sp. nov., a dorvilleid found in remarkable abundance at some of the bones deployed for 1 year. This new *Parougia* species, the second described in the Southern Ocean, also occurred in moderate numbers at nearby organic-rich sediments close to the Spanish Antarctic Base, indicating that this may be an opportunistic species. *P. diapason* sp. nov. clearly differs from the rest of congeneric taxa described in the lack of dorsal cirrus as well as in other morphological characters related to the jaw apparatus and the shape of parapodial lobes. Phylogenetic analyses show that *P. diapason* sp. nov. is sister to the rest of the congeneric taxa whose sequences are currently available. The finding of *P. diapason* sp. nov. in an area which has been previously investigated using similar experiments suggests that a lot

remains to be discovered in Antarctic marine benthic invertebrate communities inhabiting eutrophic habitats.

**Keywords** Deception Island · Phylogeny · Taxonomy · Polychaeta · Opportunistic species · Whale bones

## Introduction

Marine invertebrate communities associated with polluted areas have been widely studied in the past, mainly in areas affected by anthropogenic activity. High organic matter loads and low oxygen concentrations characterize these habitats, which are generally distinguished by the occurrence of few ubiquitous opportunistic species, with annelid polychaetes as one of the most represented groups (Pearson and Rosenberg 1978). Due to the relatively low anthropogenic impact on Antarctic benthic communities and the consequent lack of eutrophic littoral zones, organisms associated with polluted habitats in the Southern Ocean have received little attention. However, as in other geographic areas, similar groups of opportunistic polychaetes in the families Capitellidae, Spionidae and Dorvilleidae also predominate in these altered habitats (e.g. Lenihan and Oliver 1995; Conlan et al. 2004, 2010).

Other than anthropogenically enriched habitats, natural habitats can also sustain organically enriched communities in Antarctic waters. One such habitat is natural patches created after the combined effects of ice-scouring and subsequent accumulation and decomposition of organic matter; however, the invertebrate fauna occurring in these habitats has not been deeply investigated yet (Richardson and Hedgpeth 1977; Powell et al. 2012). On the other hand, whale-falls have received a great deal of attention in the Southern Ocean lately, with several studies using shallow-

**Electronic supplementary material** The online version of this article (doi:10.1007/s00300-014-1614-7) contains supplementary material, which is available to authorized users.

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and deep-water experimentally deployed whale remains, which proved the occurrence of opportunistic and specialized fauna (Taboada et al. 2012, 2013; Glover et al. 2013). Both in natural patches mentioned above and in whale remains, the invertebrates appear to be primarily fueled by sulphophilic chemoautotrophic bacteria.

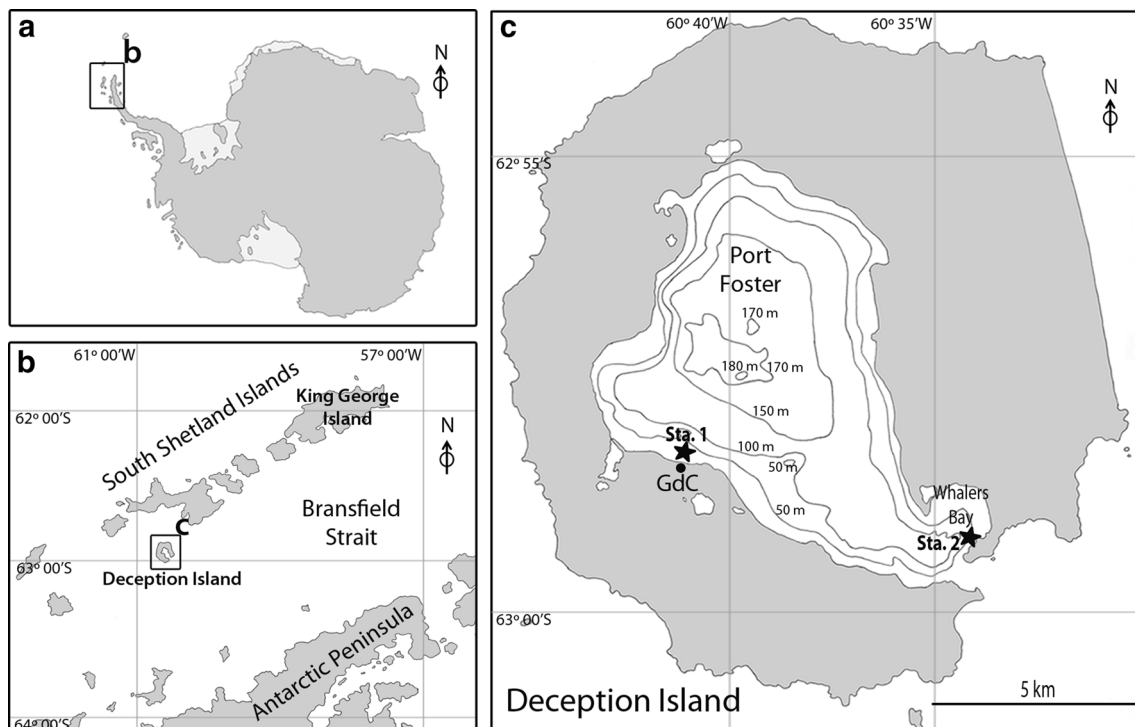
Polychaete dorvilleids are among the most represented families in natural and polluted environments, with representatives of the genus *Ophryotrocha* being some of the commonest organisms worldwide, including in Antarctic waters (e.g. Conlan et al. 2004, 2010; Taboada et al. 2013). Within this family, other dorvilleids are also known to have preferences for organically enriched habitats, such as species in the genus *Parougia*, which commonly occur in polluted harbours, anoxic sediments with H<sub>2</sub>S, cold seeps and hydrothermal vents (Oug 1978; Blake and Hilbig 1990; Åkesson and Rice 1992). To the best of our knowledge, only one species within this genus, *Parougia furcata* (Hartman 1953), has been reported from the Southern Ocean. Herein, we formally describe the species *Parougia diapason* sp. nov., collected from experimentally deployed whale bones as well as in association with adjacent polluted sediments at Deception Island (South Shetland Islands, Antarctica). In addition to the morphological description, we also provide a phylogenetic tree placing the new dorvilleid in its phylogenetic context using two

nuclear (18S and H3) and two mitochondrial (16S and COI) markers.

## Materials and methods

### Sample collection

Bones used in our experiments were obtained from a caudal fin of a common minke whale (*Balaenoptera acutorostrata*) stranded in Tarifa (SW Spain) in September 2011. They were defleshed, cut into pieces, and drilled to facilitate further attachment to experimental moorings. After this, bones were immediately frozen to  $-20^{\circ}\text{C}$  until deployment on the seabed. Experiments were deployed by SCUBA diving at about 10 m depth on the seabed of Deception Island (South Shetland Islands, Antarctica), attached to pieces of ballast (metallic chain) at two different stations during January 2012 (Fig. 1; Table 1). Some bones were put inside wire cages to avoid the effect of predation, if any. All bones were recovered by SCUBA diving in January 2013 after about 1 year of deployment (Table 1). After retrieval, bones were brought to the laboratory at the Gabriel de Castilla Spanish Antarctic Base (Deception Island), placed into separate containers with filtered sea water ( $0.22\ \mu\text{m}$ ), and kept at ambient



**Fig. 1** **a** Map of Antarctica showing the area where samples were collected, **b** South Shetland Islands area showing location of Deception Island, **c** Deception Island. GdC, Gabriel de Castilla

Spanish Antarctic Base. Sta. 1, station in front of the GdC Spanish Antarctic Base; Sta. 2, station at Whalers Bay

**Table 1** Summary of experimental bones analyzed during the study

Station	No. whale bones <sup>a</sup>	Deployment	Recovery
GdC	9 + 4	January 9, 2012	January 12, 2013
Whalers Bay	8 + 4	January 9, 2012	January 23, 2013

<sup>a</sup> Bones inside + outside wire cages. GdC, Gabriel de Castilla Spanish Antarctic Base

temperature (0–5 °C) without supplementary oxygen. This forced the system to become anoxic and provoked organisms to leave the bones. Prior to preservation, organisms were anaesthetized in 7 % MgCl<sub>2</sub> solution in fresh water, observed in vivo, and photographed using an Olympus compact camera.

The background fauna was investigated for comparison with the bones fauna as part of an ongoing study on the infauna inhabiting the shallow-water platform of Deception Island. In this study, cores (ca. 380 cm<sup>2</sup>) were collected by SCUBA diving at 5 and 15 m depth at different stations. Sediment in the cores was sieved through 500- and 250- $\mu$ m meshes, subsequently preserved in 10 % formalin buffered in sea water, and then transferred to 70 % EtOH.

#### Morphological analysis

Organisms were preserved for scanning electron microscopy (SEM), DNA analysis and standard morphology. Specimens for SEM were prefixed in a solution of 2.5 % glutaraldehyde in 0.4 M phosphate-buffered saline (PBS) and 0.6 M NaCl for 24 h at 4 °C. Samples were then rinsed with PBS for 40 min, post-fixed in 1 % osmium tetroxide in PBS for 1 h, rinsed in PBS and distilled water for 1 h, and preserved in 70 % EtOH. SEM samples were dehydrated in a graded series of alcohol, critical-point dried, mounted, gold-coated, and imaged using a JSM-7100F field-emission SEM (University of Barcelona, UB). Organisms for DNA sequencing were preserved in 96 % EtOH and stored at –20 °C. Specimens for standard morphology were preserved in 10 % formalin buffered in sea water and then transferred to 70 % EtOH. Some specimens were submerged in a concentrated solution of Methyl Green and 80 % EtOH for a minimum of 60 s to observe staining patterns. Pictures of maxillae and mandibles were obtained after submerging several ethanol-fixed specimens in a 85 % lactic acid solution for 5 min, allowing tissue to become virtually invisible, thus enhancing visualization of jaws embedded in the animal.

Type material was deposited at the Natural History Museum of London (UK) and at the Centre of Biodiversity Resources (CRBA, formerly Museum of Zoology) in the Faculty of Biology, UB. All animals not deposited as type material or specimen vouchers are held by the first author at the Department of Animal Biology, Faculty of Biology, UB.

#### DNA extraction and amplification

Total DNA was extracted using a REExtract-N-Amp kit (Sigma Aldrich, St. Louis, MO, USA) from the posterior part of four specimens collected from one of the experimental bones, following the manufacturer's instructions. About 1,770 bp of the gene 18S ribosomal RNA (rRNA) (18S), 400 bp of cytochrome *c* oxidase I (COI), 310 bp of histone 3 (H3) and 520 bp of 16S rRNA (16S) were amplified using RED-taq (Sigma Aldrich) and polymerase chain reaction (PCR) recipes and temperature profiles indicated in Online Resources 1 and 2. PCR products were purified using microCLEAN (Microzone Ltd., Sussex, UK) and sequenced at the UB Scientific and Technological Centers (CCiT-UB) on an ABI 3730XL DNA analyzer (Applied Biosystems).

#### Phylogenetic analyses

Further molecular phylogenetic analyses were conducted using the sequence datasets of the genes mentioned above (Online Resource 3). In total, 13 terminal taxa were used in the analysis, including 7 *Parougia* operational taxonomic units (OTUs) (2 of which correspond to undescribed methane-seep species; see Thornhill et al. 2012) and 5 dorvilleids from the genera *Dorvillea*, *Ophryotrocha* and *Protodorvillea*, all of them rooted with *Eunice pennata* (Müller 1776). Overlapping sequence fragments were assembled into consensus sequences using the software Geneious (Drummond et al. 2010) and aligned using MAFFT with default settings (Katoh et al. 2002). The evolutionary model selected (GTR+I+G) was obtained by running the alignments in jModelTest (Posada 2008). Maximum-likelihood (ML) analyses were conducted with RAxML (Stamatakis 2006; Stamatakis et al. 2008), and Bayesian phylogenetic analyses (BA) with MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003). ML analyses were run using 10 heuristic searches [subtree pruning and regrafting (SPR) and nearest-neighbour interchange (NNI)], and robustness of nodes was determined with 500 replicates. BA analyses were run three times for each dataset with four chains for  $2 \times 10^6$  generations (with 1,500 trees discarded as burn-in), using partition codons for COI and H3 in both cases.

## Results

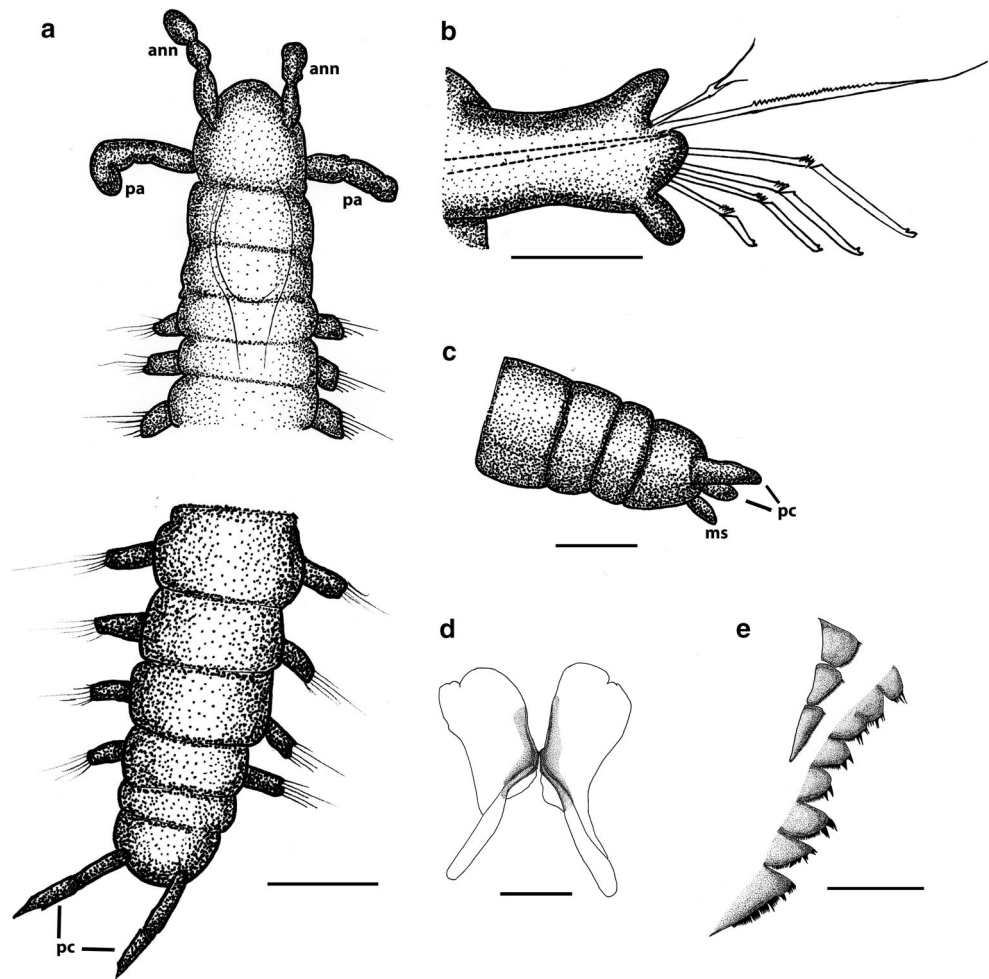
#### Systematics

Family Dorvilleidae Chamberlin, 1919

Genus *Parougia* Wolf, 1986

*Parougia diapason* sp. nov. (Figs. 2, 3)

**Fig. 2** *Parougia diapason* sp. nov. **a** Anterior and posterior regions, dorsal view (holotype NHMUK 2014.102). **b** Parapodium from mid-body chaetiger (paratype NHMUK 2014.106). **c** Posterior region, lateral view; parapodia not depicted, with incomplete pygidial cirri (paratype NHMUK 2014.107). **d** Mandibles. **e** Maxillae. *ann* antenna, *ms* median stylus, *pa* palp, *pc* pygidial cirri. Scale bars **a**, **c** = 100  $\mu$ m; **b** = 50  $\mu$ m; **d**, **e** = 20  $\mu$ m



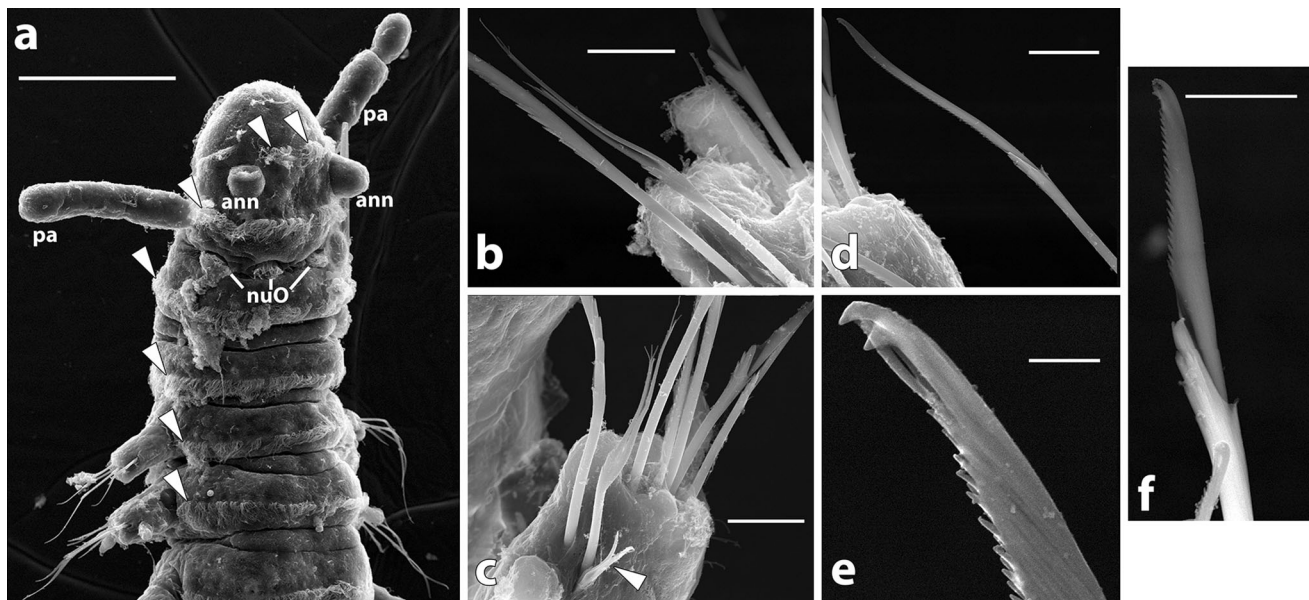
### Material examined

Port Foster, Deception Island (South Shetland Islands, Antarctica), from four different minke whale bones in front of the Gabriel de Castilla Spanish Antarctic Base (62° 58.532'S, 60°40.466'W; Fig. 1c). Holotype (NHMUK 2014.102), six complete paratypes (NHMUK 2014.103–104; CRBA.24827–24830), and four incomplete paratypes (NHMUK 2014.105–107; CRBA.24831) preserved in 10 % formalin, and transferred to 70 % EtOH. Paratypes NHM-2014.3–9 used for parapodia dissection. Five specimens used for SEM, four for molecular studies, and six specimens for jaw description. The rest of specimens collected comprise ca. 400 individuals preserved in 10 % formalin/70 % EtOH, and in absolute EtOH. Additional material collected from the sediment in front of the Spanish Antarctic Base at 5 and 15 m depth preserved in 10 % formalin, and transferred to 70 % EtOH (386 specimens) (Fig. 1c; Sta. 1). Material collected by S. Taboada, J. Cristobo, M. Bas, A. Riesgo and C. Avila.

### Description

Holotype (NHMUK 2014.102) 3.5 mm long, 0.22 mm wide for 37 chaetigers; paratypes (NHMUK 2014.103–107; CRBA.24827–24830) 3.9–2.7 mm long, 0.24–0.16 mm wide for 38–26 chaetigers. Other complete specimens in ethanol and formalin 1.6–3.5 mm long, 0.14–0.24 mm wide for 37–21 chaetigers. Body shape elongated, cylindrical, uniform width throughout the body, slightly tapering at the posterior end (Fig. 2a). In life, body white-greenish (Online Resource 4), becoming opaque white after preservation. No distinctive Methyl Green staining pattern observed.

Prostomium rounded, longer than wide, dorso-ventrally slightly flattened, without eyes. Pair of smooth, digitiform antennae inserted dorsally in the anterior part of prostomium with 2–3 articles. Smooth, cylindrical paired palps inserted ventro-laterally, slightly longer and thicker than antennae; palpophores about twice as long as the two articles present. Two peristomial achaetous rings, as long



**Fig. 3** *Parougia diapason* sp. nov. SEM micrographs. **a** Anterior region, dorsal view. Only base of antennae present. Bundles of cilia and ciliary bands arrowed. **b** Furcate and capillary chaetae. **c** Two furcate and one capillary chaeta. Emerging furcate chaeta arrowed.

**d** Long composite heterogomph falciger. **e** Detail of the anterior blade of long composite heterogomph falciger. **f** Short composite heterogomph falciger. *ann* antenna, *nuO* nuchal organs, *pa* palp. Scale bars **a** = 100  $\mu$ m; **b–d** = 10  $\mu$ m; **e** = 1  $\mu$ m; **f** = 5  $\mu$ m

as subsequent chaetigers (Fig. 2a). Prostomium with two bundles of cilia close to the base of antennae and a band of cilia located at posterior part; three nuchal organs located dorsally between prostomium and peristomium (Fig. 3a). Peristomium and subsequent chaetigers with well-defined ciliary bands at the posterior part of each segment (Fig. 3a).

Parapodia uniramous lacking dorsal cirrus, with dorsal triangular, distally rounded suprachaetal lobe, rounded acicular lobe, and digitated ventral lobe (Fig. 2b); suprachaetal and ventral lobe with scattered cilia. Supra-acicular chaetae composed by 1–2 long capillary chaetae with double serration rows and 1–2 furcate chaetae (Figs. 2b, 3b, c); capillaries up to three times as long as furcate chaetae (Figs. 2b, 3b, c). Furcate chaetae with distally serrated shaft and asymmetric pubescent tines (Fig. 3b, c). Both furcate and capillaries emerging from the same area (Figs. 2b, 3c). Sub-acicular chaetae composite heterogomph falcigers numbering 3–5, with blades decreasing in length ventrally (Figs. 2b, 3d, f); blades with double serration rows, two terminal teeth and a subterminal elongated sheath (Fig. 3e, f); shafts serrated at the base (Fig. 3d, f). Pygidium rounded with two lateral pygidial cirri with two articles (Fig. 2a) and a short median stylus inserted ventrally (Fig. 2c); anus ventral.

Jaws situated within the first ring of the peristomium, slightly visible through body wall. Mandibles without teeth 63–68  $\mu$ m long, with anterior wing-like parts divided into two lobes; weakly chitinized in the articulation area and

part of the handles (Fig. 2d). Maxillae slightly longer than mandibles (82–98  $\mu$ m long) and homogeneously chitinized. Superior elements numbering 6–7 squarish denticles (each finely serrated with 2–4 prominent teeth; with grooves in its concave part) and a basal plate with fused articles prominently serrated at the cutting edge. Three inferior elongated to squarish elements finely serrated (Fig. 2e).

One mature female with eggs (holotype) 21–26  $\mu$ m in diameter in the coelomic cavity from chaetigers 12–31.

#### Habitat and ecology

*Parougia diapason* sp. nov. is known from Port Foster, Deception Island (South Shetland Islands, Antarctica) in front of the Gabriel de Castilla Spanish Antarctic Base at depths of 5–15 m. This species occurred not only in experimentally deployed fresh whale bones, but also in association with organically enriched sediments nearby (Fig. 1c). *Parougia diapason* sp. nov. co-occurred in the bones with the polychaete *Microphthalmus antarcticus* (Bick 1998), and an unidentified oligochaete, which also appeared at remarkable densities (Table 2). In the nearby sediment, *P. diapason* sp. nov. was one of the most abundant species, sharing habitat with *Mesospio moorei* (Gravier, 1911), an unidentified cirratulid and the same unidentified oligochaete found in the bones, as well as *M. antarcticus*, amongst others (authors' unpublished data).

**Table 2** Absolute abundances of invertebrates found in the experimental bones at station 1 (Fig. 1c)

Taxon	Cage 1	Cage 2	Cage 3	Cage 4	Cage 5	Cage 6	Cage 8	Cage 9	Exposed 1	Exposed 2	Exposed 3	Exposed 4
Annelida												
<i>Capitella perarmata</i> (Gravier, 1911)	3	–	–	–	1	–	–	–	4	1	–	–
<i>Cirratulus balaenophilus</i> Taboada et al., 2012	–	–	–	–	–	–	–	–	–	1	–	–
<i>Leitoscoloplos kerguelensis</i> (McIntosh, 1885)	2	–	–	–	–	–	–	–	1	–	–	–
<i>Microphthalmus antarcticus</i> Bick, 1998	283	206	2	–	–	–	–	–	214	18	–	–
<i>Mesospio moorei</i> Gravier, 1911	–	–	–	–	1	–	–	–	1	–	–	–
Nerillidae sp.	–	–	–	–	–	–	–	–	16	–	–	–
Oligochaeta sp.	130	5	4	25	–	–	–	–	85	7	3	–
<i>Ophryotrocha</i> sp.	–	–	–	–	–	–	–	–	–	1	–	–
<i>Parougia diapason</i> sp. nov.	135	10	–	–	–	–	–	–	170	87	–	–
<i>Polygordius</i> sp.	2	–	–	–	–	–	–	–	8	2	–	–
Others												
Amphipoda sp.	11	25	2	–	–	–	–	–	9	10	–	–
Isopoda sp.	1	1	–	–	2	–	1	–	1	–	–	–
Crustacea sp.	–	–	–	1	1	–	–	–	–	–	–	–
Nematoda sp.	–	–	–	–	–	–	–	–	1	–	–	–
Nemertea sp.	–	–	–	–	–	–	–	1	–	–	–	–
Platyhelminthes sp.	–	–	–	–	–	–	1	–	–	–	–	–

Cage, refers to bones inside wire cages; Exposed, refers to bones outside wire cages



**Table 3** Comparative list of selected characters for species of the genus *Parougia*

Species/taxon	Area, depth range	Habitat	No. chaetigers	Antennae (no. articles)	Supra-acicular chaetae	Mandibles	Basal plates	Superior free denticles	Inferior free denticles
<i>P. albomaculata</i> (Åkesson & Rice, 1992)	SW Mediterranean, N Atlantic, shallow water	Mud in polluted harbours	30–78	10–18	Long/short capillaries and furcates	3–4 teeth	Row of fused denticles	Clavate, main tooth, serrated edge	Spoon-shaped, serrated edge
<i>P. batia</i> (Jumars, 1974)	NE Pacific, 1,223–1,229 m	Silty mud	44	–	Capillaries; no furcates	Bifurcate, denticulate antero-medially	Row of fused denticles	Rounded, main tooth, serrated edge	Rounded, serrated edge
<i>P. bermudensis</i> (Åkesson & Rice, 1992)	Bermuda (N Atlantic), shallow water	Old pieces of wood	30–62	15–20	Short capillaries; no furcates	6 teeth	Row of fused denticles	Spoon-shaped, serrated edge	Spoon-shaped, serrated edge
<i>P. caeca</i> (Webster & Benedict, 1884) <sup>a</sup>	N American coast (N Atlantic), 7–10 m	Dark mud with detritus	45–51	12–15	Capillaries and furcates	Up to 5 teeth	Row of imbricated fused denticles	Squarish, main tooth, serrated edge	Oval, serrated edge
<i>P. eliasoni</i> (Oug, 1978)	Norway (N Atlantic), 7–410 m	Dark mud with detritus	52–57	ca. 25	Capillaries, short and stout simple chaetae and furcates	Up to 7 teeth	Row of large fused denticles	Squarish, main tooth, serrated edge	Rounded, serrated edge
<i>P. fiurcata</i> (Hartman, 1953) <sup>b</sup>	South Georgia (Antarctica), 250–310 m	Soft mud with stones	ca. 50	Undefined	Capillaries and furcates	No teeth/5–7 teeth	Row of imbricated fused denticles	Squarish, main tooth, serrated edge	Oval, serrated edge
<i>P. macilenta</i> (Oug, 1978)	Lindaspollene (N Atlantic), 30–35 m	Sandy mud	30–44	14–17	Capillaries and furcates	No teeth, partially subdivided	Row of imbricated fused denticles	Squarish, 1–2 large teeth, serrated edge	Triangular, serrated edge
<i>P. nigridentata</i> (Oug, 1978)	Lindaspollene (N Atlantic), 20–70 m	Black mud with SH <sub>2</sub>	48–56	10–15	Capillaries and furcates	Up to 8 teeth, heavily chitinized	Row of imbricated fused denticles	Elongate, main tooth, coarsely serrated edge	Oval, serrated edge
<i>P. oregonensis</i> Hilbig & Fiege, 2001	Cascadia Margin off Oregon (NE Pacific), 600–800 m	Cold seeps	47–80	Unknown, scars only	Capillaries and furcates	No teeth, wing-like	Row of small fused denticles	Squarish, heavy accessory dorsal tooth	Rounded, serrated edge, some with whip-like tooth
<i>P. wolffi</i> Blake & Hilbig, 1990	NE Pacific, 1,545–2,200 m	Hydrothermal vents	37–56	Unknown, scars only	Simple chaetae with bidentate tip; no furcates	5 large/5 small teeth, triangular heavily chitinized	2 rows of imbricated fused denticles	Elongate, whip-like tooth, slanted edge	Elongate, some with slanted edge
<i>P. diapason</i> sp. nov.	Deception Island (Antarctica), 10 m	Whale bones	21–38	2–3	Capillaries and furcates	No teeth, wing-like divided into 2 lobes	Row of small fused denticles	Squarish, main teeth, serrated edge	Elongate/squarish, serrated edge

Papers used to complement original descriptions: <sup>a</sup> Oug (1978); <sup>b</sup> Oug (1978), Orensanz (1990)

### Remarks

The main character that distinguishes *P. diapason* sp. nov. from the rest of congeneric species described so far is the absence of a dorsal cirrus (i.e. it is the only species described so far with uniramous parapodia) and the shape of neuropodial lobes. Type material of *P. furcata*, the only previously known congeneric Antarctic species, was not examined by us due to its poor condition (see Oug 1978). The description of this species used for comparative purposes was based on the original description by Hartman (1953) and the additional information provided by Oug (1978) after his investigations on the type material. The description of *P. furcata* given by Orensanz (1990), who collected organisms at the type locality, widely coincides with that given by Hartman (1953) and Oug (1978) but differs in the mandible characteristics: Orensanz (1990) describes mandibles as bearing 5–7 teeth, while Oug (1978) describes mandibles as weakly chitinized and resembling those of *Parougia macilenta* (Oug, 1978) (i.e. without teeth). However, all of them coincide in describing the presence of a prominent dorsal cirrus (Hartman 1953; Oug 1978; Orensanz 1990), lacking in *P. diapason* sp. nov. Other characters distinguish *P. diapason* sp. nov. from *P. furcata*, such as the absence of eyes (two pairs in the latter), the maximum number of chaetigers recorded and their bathymetric range (Table 3). Toothless mandibles are found in *P. diapason* sp. nov., *P. macilenta* and *Parougia oregonensis* Hilbig & Fiege, 2001; those of *P. diapason* sp. nov. resemble those of *P. macilenta* but clearly differ in having two marked lobes (Fig. 2d; Table 3). Finally, the occurrence of furcate chaetae appears to be a common character shared by most species in the genus (Table 3). Information about shafts (most of them serrated) or the tip of the tines (most of them pubescent) in furcate chaetae was not considered here because of the distinct informative detail given by the different authors.

### Etymology

The species is named based on the resemblance of its furcate chaetae to a diapason (acoustic resonator in the form of a two-pronged fork). The name was proposed by one of the visitors after a contest organized by the authors to name the species in the 2014 Live Research Fair organized by the University of Barcelona.

### Molecular analysis

The concatenated alignment consisted of 3,128 characters, of which 18S had 1,599 characters, 16S had 535 characters, COI had 651 characters, and H3 had 343 characters. ML and BA analysis recovered a tree with strong support for

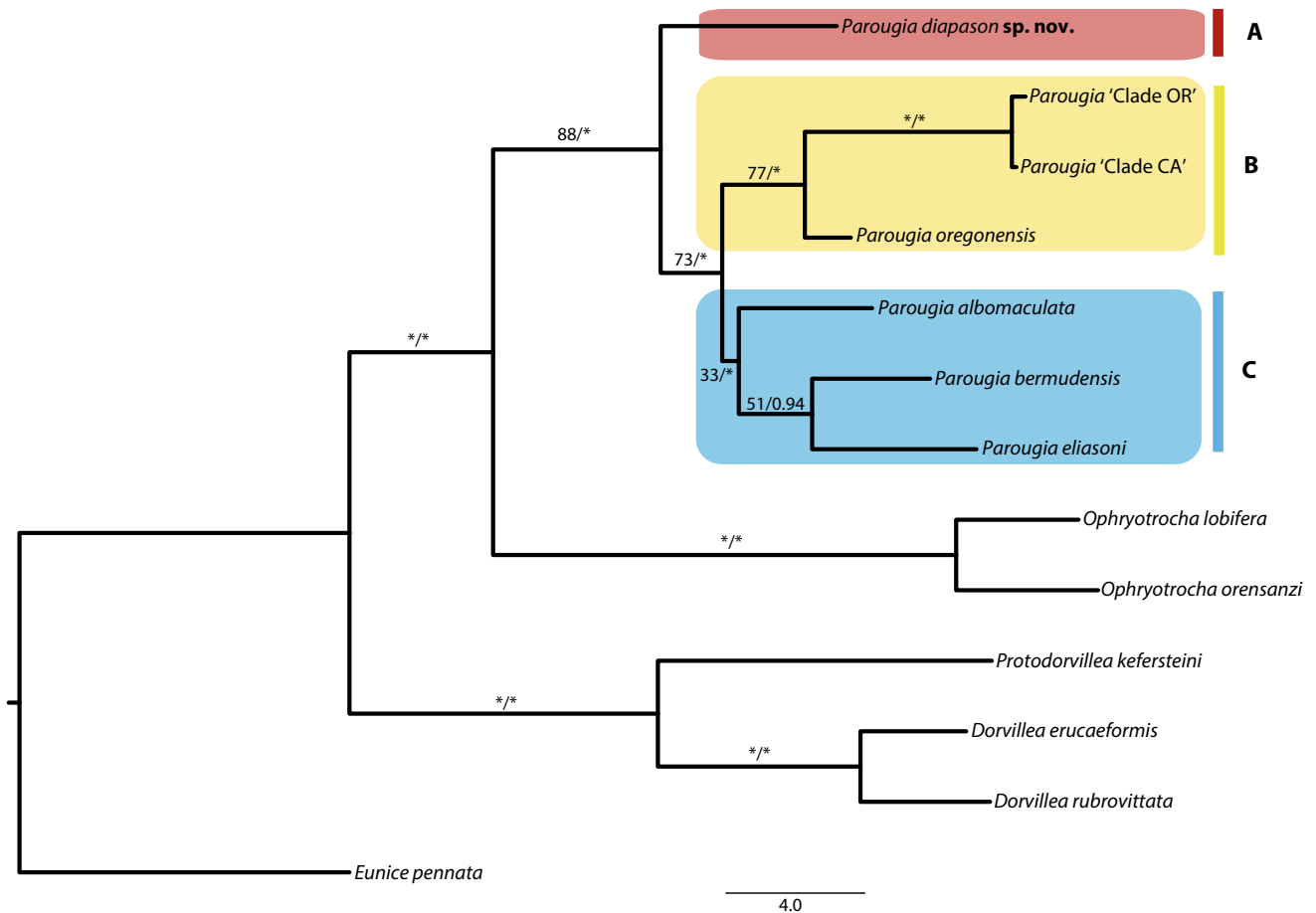
monophyletic *Parougia*. Three clades were distinguished (Fig. 4): clade A, including just *P. diapason* sp. nov. branching basally to the rest of the congeneric taxa; clade B, including *P. oregonensis* and the undescribed *P.* ‘Clade OR’ and *P.* ‘Clade CA’ (see Thornhill et al. 2012); and clade C, with less support than the previous ones, including *P. albomaculata* (Åkesson & Rice, 1992), *P. bermudensis* (Åkesson & Rice, 1992) and *P. eliasoni* (Oug, 1978).

### Discussion

*Parougia diapason* sp. nov. is the second species of the genus described from Antarctic waters and the first to occur in association with organically enriched environments. In order to investigate these habitats, experimentally deployed whale bones have been successfully used in the recent past to describe the Antarctic fauna commonly present in eutrophic habitats (Taboada et al. 2012, 2013; Glover et al. 2013). The occurrence of new species using these substrates, even in previously surveyed areas such as Deception Island (South Shetland Islands), suggests that a lot remains to be discovered in Antarctic marine benthic invertebrate communities naturally occurring in these extreme environments.

*Parougia furcata*, the only previously known member of the genus from Antarctic waters, was originally described from the South Georgia region at moderate depths (Table 3). After its description, it has occasionally been reported in the South Shetland Islands area, associated with silt and clay sediments, although in most cases it was identified with taxonomical doubts (Sicinski 2000, 2004). The presence of *P. diapason* sp. nov. at moderate densities at some of the bones experimentally deployed at Deception Island, as well as in nearby organic-matter-rich sediments, suggests that this may be an opportunistic species, as proposed for other sympatric dorvilleids such as *Ophryotrocha clava* Taboada et al., 2013 and *Ophryotrocha orensanzii* Taboada et al., 2013 (Taboada et al. 2013). Thus, all these dorvilleid opportunistic species may occur in other natural habitats, such as sediment from patches created after ice-scouring and subsequent accumulation and decomposition of organic matter (Richardson and Hedgpeth 1977; Powell et al. 2012) as well as associated with anthropogenically enriched marine areas, to the best of our knowledge never studied in the South Shetland Islands or the Antarctic Peninsula.

The new *Parougia* did not appear in all the experimentally deployed bones from station 1 (Fig. 1c), but it was one of the most abundant species when present, showing no apparent differences in terms of absolute abundance when comparing bones in cages versus exposed



**Fig. 4** Phylogenetic tree of *Parougia* resulting from the concatenated analyses of *H3*, *COI*, *18S*, and *16S*, combining maximum-likelihood (ML) and Bayesian analysis (BA). Numbers on nodes indicate bootstrap support values (ML) and posterior probability values (BA) out of 100 and 1, respectively. Values of 95 and over for bootstrap and values of 0.95 and over for posterior probability are marked by

asterisks. Clades A, B and C marked in red, yellow and blue, respectively. *Parougia* 'Clade CA', undescribed *Parougia* occurring in deep-water methane seeps along the California margin (see Thornhill et al. 2012); *Parougia* 'Clade OR', undescribed *Parougia* occurring in deep-water methane seeps along the Oregon margin (see Thornhill et al. 2012)

bones (Table 2). It also occurred at remarkable densities associated with eutrophic sediments (ca. 20 % organic matter) in front of the Spanish Antarctic Base (authors' unpublished data). At the bones and the sediments, *P. diapason* sp. nov. co-occurred with the hesionid polychaete *Microphthalmus antarcticus*, a common inhabitant of the rocky and sandy intertidal areas of the South Shetland Islands (Bick 1998; Bick and Arlt 2013). Interestingly, no *P. diapason* sp. nov. was found associated with the bones deployed during the same period and at a similar depth at Whalers Bay (Fig. 1c; Sta. 2), the bay's closest area to the open sea; among other marine invertebrates, the only dorvilleids inhabiting these bones were two species of the genus *Ophryotrocha* (*O. clava* and *O. orensanzi*), with similar polychaete assemblages as those reported by Taboada et al. (2013) in the same area. The fact that *P. diapason* sp. nov. only occurred at the experimental bones deployed at the inner part of the bay as well as in the

adjacent sediments remains unexplained, but could be related to the heterogeneous physical and oceanographic characteristics or the geochemical composition of the waters of Deception Island, an active volcano (Somoza et al. 2004).

The new *P. diapason* sp. nov. clearly differs from the rest of previously described congeneric species in the lack of a dorsal cirrus; in fact, it is the only species in the genus with uniramous parapodia (all other species having sub-biramous parapodia). Other morphological characters distinguish the new Antarctic *Parougia* from the rest of species in the genus (Table 3), which is also supported by differences in molecular data. Although molecular data are missing for some of the congeneric species/taxa (including the sympatric *P. furcata*), *P. diapason* sp. nov. clusters within the rest of *Parougia* whose sequences are currently available, branching basally to all of them (Fig. 4). *Parougia diapason* sp. nov. is sister to clade B including

*P. oregonensis* and the undescribed *P.* ‘Clade OR’ and *P.* ‘Clade CA’, all of them occurring in deep-water methane seeps along the Oregon and California margins (Thornhill et al. 2012), and also to clade C, including the shallow-water species *P. albomaculata*, *P. bermudensis* and *P. eliasoni*, preferentially associated with polluted habitats (Oug 1978; Åkesson and Rice 1992). Further molecular information is needed in order to clarify the phylogenetic relationships within the genus, with special emphasis on inclusion of molecular data from *P. furcata*.

**Acknowledgments** Thanks are due to R. de Stephanis, P. Gauffier, J. Giménez and E. Fernández and the institutions EBD-CSIC, CIRCE and Junta de Andalucía, who kindly provided the fresh whale vertebrae for our experiments. We also thank the Gabriel de Castilla Spanish Antarctic Base crew of the 2011–12 and 2012–13 seasons for their help during deployment and recovery of the experiments. We are highly grateful to our ACTIQUIM project colleagues J. Cristobo, A. Riesgo, J. Moles, C. Angulo, B. Figuerola and L. Núñez-Pons, and also to G. Paterson, from the National History Museum of London. Two anonymous reviewers as well as the editor are acknowledged for their comments, which helped to improve a previous version of the manuscript. This research received support from the SYNTHESYS Project (<http://www.synthesys.info/>), which is financed by the European Community Research Infrastructure Action under the FP7 Integrating Activities Programme, and from the Spanish Government, through the research project ACTIQUIM-II (CTM2010-17415/ANT). This paper is part of the AntEco (State of the Antarctic Ecosystem) Scientific Research Programme.

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