

Research Article

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A review of Eunicoidea (Annelida) from Falkland Islands waters including a new species of *Hyalinoecia*

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Abstract

Historic species records of the families Onuphidae and Eunicidae, from the Falkland Islands region, are reviewed and updated, new records added from intertidal and nearshore localities on and around the Falkland Islands, and a new species of *Hyalinoecia* described. Eight genera are reported from around the region including eight taxa of Onuphidae and two of Eunicidae, although most are only known from deep offshore waters. *Kinbergonuphis dorsalis* is re-described from type material, *Kinbergonuphis* sp. from the Falkland Islands is described and discrepancies between the two descriptions are examined. *Hyalinoecia falklandica* sp. nov. is described and the history of the genus and its misidentification in the region is discussed. The new species is distinguished from all other species in the genus through a combination of simple, unidentical calcigers on chaetigers 1 and 2, ventral cirri present to chaetigers 3 or 4, and branchiae present from chaetigers 26 or 27 to the end of the body. The historic record of *Marphysa aenea* from the Falkland Islands is also shown to be a misidentification and the actual, as-yet-undetermined species present is described. Problems surrounding a correct identification of *Marphysa* species, other species that do not quite fit current descriptions, and additional Eunicoidea taxa that might be expected to occur in the region are also discussed.

Introduction

The Falkland Islands (Las Malvinas) are located off the southeast coast of South America in the southwest Atlantic Ocean, ~260 nautical miles east of Argentina. The archipelago, made up of two larger islands and over 700 smaller ones, sits on the Patagonian Shelf, which includes Burdwood Bank to the south (Figure 1). The majority of the territorial sea reaches <100 m in depth but the surrounding exclusive economic zone encompasses waters that extend below 4000 m. Biogeographically, the Islands sit within the Magellan biogeographic region (as defined by Koubbi *et al.*, 2014), sharing many species with southern Argentina, Chile, and Patagonia. Nevertheless, Darbyshire (2018) demonstrated an affinity of the Falkland Islands polychaete fauna with those of both South Georgia and Antarctica.

Falkland Islands polychaetes have been relatively poorly investigated with most specimens being recorded and published in the early 1900s by Pratt (1898, 1901), Pixell (1913), Ramsay (1914), Fauvel (1916), and Monro (1930, 1936). Between 2008 and 2012, multiple environmental baseline surveys were undertaken around the Islands with respect to oil exploration and these results have been compiled and published by Neal *et al.* (2020). Most of the baseline work was undertaken in deep waters to the north, east, and south of the Islands in the North and East Falkland Basins (~450–1800 m depths) providing a far more comprehensive record of the polychaete fauna in the region's deeper waters. More recently, in 2011, 2012, and 2015, extensive surveys were undertaken around the Islands which were a mix of intertidal and some limited shallow water sampling, further revealing previously unrecognized diversity of polychaetes from those shallow habitats (Darbyshire, 2018). The increased interest in oil exploration within the Falkland Islands area makes it more important than ever that accurate knowledge of the fauna should be available.

The families Eunicidae Berthold, 1827 and Onuphidae Kinberg, 1865 belong to the Order Eunicida Dales, 1962 along with five other families (Budaeva and Zanol, 2021) that all possess a ventral muscular pharynx with mineralized or sclerotized jaws (Tzetlin and Purschke, 2005). The two families are the only extant ones in the order to possess eulabidognath maxillae (Paxton, 2009) and, together with the additional synapomorphies of five prostomial appendages, peristomial cirri, and subacicular hooks in median and posterior parapodia (Struck *et al.*, 2006, 2015; Tilic *et al.*, 2016), recent genetic data supported the combination of the two families to form the superfamily Eunicoidea Orensanz 1990 (Tilic *et al.*, 2022). Eunicoidea species can be found from intertidal zones to the deep sea and play an important role in benthic communities including as both prey and predator species, by acting as a stabilizing force on the sediment through burrows and tube building and, in some cases, by enhancing surrounding biodiversity through epiphytic growth on tubes (Elgetany *et al.*, 2018; Budaeva, 2021; Zanol and Budaeva, 2021).



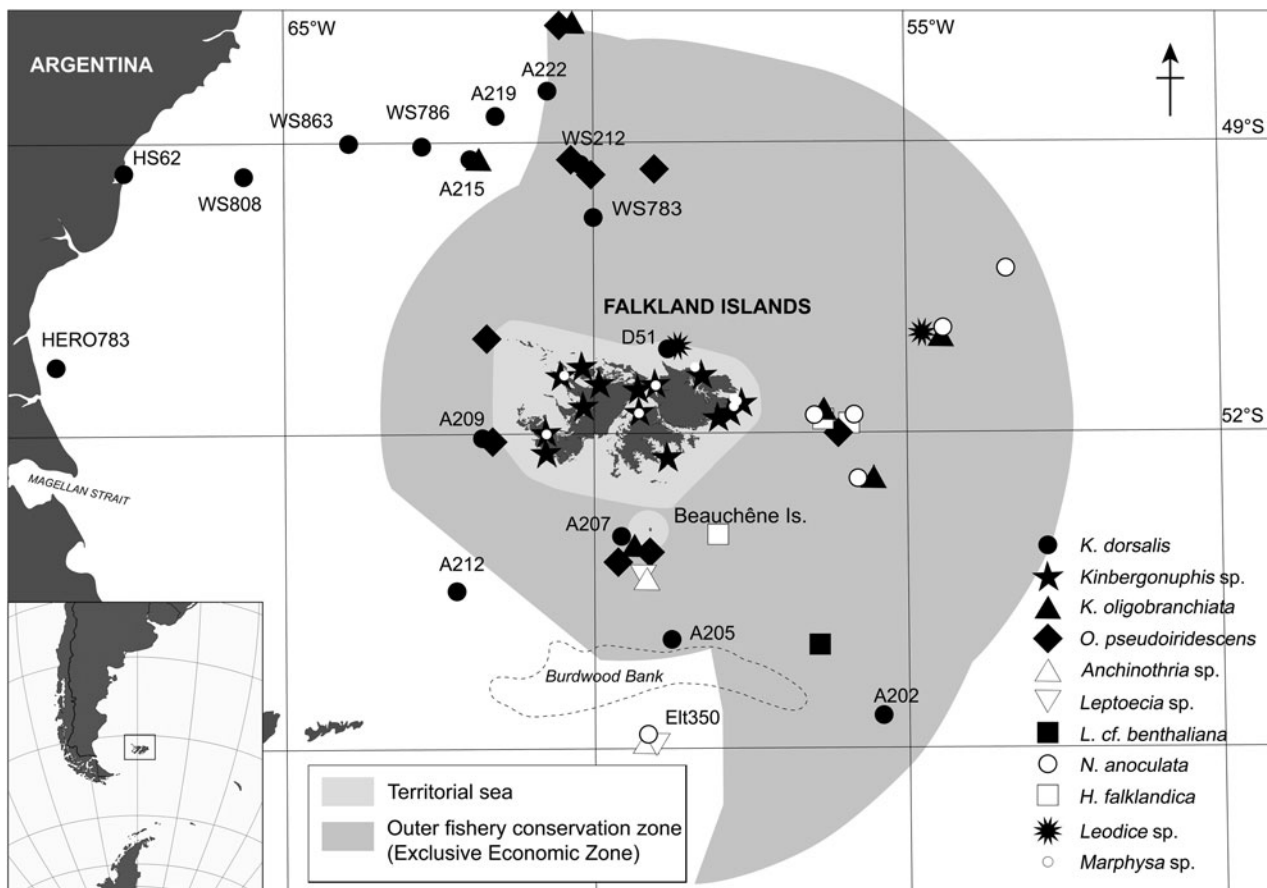


Figure 1. Map of Falkland Islands waters indicating the localities of each taxon record reported in this paper. Map inset shows the position of the Falkland Islands in the southwest Atlantic. Additional stations where *Kinbergonuphis dorsalis* was recorded by Monro (1930, 1936: D, WS), Hartmann–Schröder (1962: HS), Averincev (1972: A) and HERO783 are also indicated as well as those records from Hartman’s (1967) stn 350 (Elt).

Onuphidae consists of 22 valid genera containing over 300 species (Budaeva *et al.*, 2016) found from intertidal to abyssal depths, and the family has been described as one of the most successful deep-water families of polychaetes (Arias and Paxton, 2022). For the Magellan region specifically, Orensanz (1974b) listed eight species of Onuphidae as present. Around the Falkland Islands, Monro (1930, 1936), Hartman (1967), Averincev (1972), and Fauchald (1982c) all recorded species of Onuphidae, although none of these were from less than 100 m. Many of these identifications were later changed or synonymized with other species by Orensanz (1990), who conducted a detailed review of Antarctic and Subantarctic Eunicomorpha. The latter publication also reduced his original 1974(b) list of Magellan species from eight to six (plus one doubtful species). In a review of species in the Falkland Islands region, Darbyshire (2018) listed only two species as having previously been recorded, however, that review failed to take into account the many re-identifications made by Orensanz (1990) of specimens from the region. Since then, offshore exploration surveys in the area have additionally provided much greater knowledge of the deep-water species. Table 1 lists the different taxa recorded from Falkland Island waters and provides details on how their identification has changed from that first reported up until now.

Eunicidae is a large family containing 11 genera and more than 400 species (Zanol and Budaeva, 2021). Species occur in habitats from the intertidal to the deep sea, although around the Falkland Islands only one species of *Leodice* (as *Eunice*) and one species of *Marphysa* have previously been recorded from the region (Fauvel, 1916; Monro, 1930; Darbyshire, 2018), each

of those from very different habitats and depths (Table 1). A single species of *Marphysa* was reported by Fauvel in 1916, from specimens collected and sent to him by Rupert Vallerin from the intertidal region of West Falkland. Fauvel identified the species under the name *Marphysa corallina* (Kinberg, 1865), a species originally described from Hawaii, however, this identification was amended by Orensanz (1990) to *Marphysa aenea* (Blanchard in Gay, 1849), first described from the Pacific coast of Chile. This is the only species of Eunicidae currently reported from the intertidal and shallow regions of the Islands. Further offshore, *Leodice pennata* (Müller, 1776) was recorded by Monro (1930, as *Eunice pennata*) at 115 m depth and more recently it was also recorded from deeper water (1321–1842 m; Neal *et al.*, 2020).

In total, the current publication provides a review of ten taxa of Eunicioidea from the region: eight taxa (from six genera) of Onuphidae and two taxa (from two genera) of Eunicidae. Only five of the taxa can confidently be identified at species level at this time (Table 1). Figure 1 illustrates where each of the taxa was recorded around the Falkland Islands region. *Kinbergonuphis* sp. is described and figured and characters not quite conforming to the original description of *K. dorsalis* detailed. *Hyalinoecia falklandica* sp. nov. is newly described from specimens previously identified as *Hyalinoecia artifex* (Verrill, 1881), *Hyalinoecia stricta* Moore, 1911 and *Hyalinoecia tubicola* (Müller, 1776) and the relationship with those species discussed. Finally, the previous identification of *Marphysa aenea* is shown to be erroneous and a description and discussion of the as-yet undetermined species provided.

Table 1. Eunicidea species reported from the Falkland Islands region with details of who reported them, if records were subsequently re-assigned to a different name or taxon and who by, and the current assignation of that record

First reported as/by	Reassigned to/by	Reported here as
Onuphidae		
<i>Onuphis quadricuspis</i> /Monro (1930) <i>Onuphis dorsalis</i> /Monro (1936)	<i>Onuphis dorsalis</i> /Monro (1936) –	<i>Kinbergonuphis dorsalis</i> "
<i>Kinbergonuphis oligobranchiata</i> /Orensanz (1990), Neal et al. (2020) <i>Anchinothria</i> cf. <i>pycnobranchiata</i> /Neal et al. (2020) (in part)	– This paper	<i>Kinbergonuphis oligobranchiata</i> "
<i>Onuphis iridescens</i> /Monro (1936) <i>Nothria?</i> <i>iridescens</i> /Hartman (1967) <i>Onuphis pseudoiridescens</i> /Neal et al. (2020) <i>?Paronuphis antarctica</i> /Hartman (1967) (in part)	<i>Onuphis pseudoiridescens</i> /Orensanz (1990) 1. <i>Onuphis heterodentata</i> , <i>Onuphis lithobiformis</i> / Fauchald (1982) 2. <i>Onuphis pseudoiridescens</i> /Orensanz (1990) –	<i>Onuphis pseudoiridescens</i> " " "
<i>Leptoecia vivipara</i> /Neal et al. (2020) (in part)	This paper	<i>Anchinothria</i> sp.
<i>Leptoecia vivipara</i> /Neal et al. (2020) (in part)	This paper	<i>Leptoecia</i> sp.
<i>Hyalinoecia tubicola</i> /Hartman (1967) (in part)	<i>Leptoecia</i> cf. <i>benthaliana</i> /Orensanz (1990)	<i>Leptoecia</i> cf. <i>benthaliana</i>
<i>Hyalinoecia stricta</i> /Hartman (unpublished) <i>Hyalinoecia tubicola</i> /Hartman (1967) (in part) <i>Leptoecia vivipara</i> /Neal et al. (2020) (in part)	This paper <i>Hyalinoecia artifex</i> /Orensanz (1990) This paper	<i>Hyalinoecia falklandica</i> sp. nov. " "
<i>Nothria</i> nr <i>conchylega</i> /Hartman (1967) <i>?Paronuphis antarctica</i> /Hartman (1967) (in part) <i>Anchinothria</i> cf. <i>pycnobranchiata</i> /Neal et al. (2020) (in part) <i>Nothria anoculata</i> /Neal et al. (2020)	<i>Nothria anoculata</i> /Orensanz (1990) This paper This paper –	<i>Nothria anoculata</i> " " "
Eunicidae		
<i>Eunice pennata</i> /Monro (1930)	This paper	<i>Leodice</i> sp.
<i>Eunice</i> cf. <i>pennata</i> /Neal et al. (2020)	–	"
<i>Marphysa corallina</i> /Fauvel (1916)	<i>Marphysa aenea</i> /Orensanz (1990)	<i>Marphysa</i> sp.

Materials and Methods

Intertidal and shallow water specimens (Darbyshire, 2018) from the Falkland Islands were collected by digging, sieving sediments through a 0.5 mm sieve, opening rock crevices, turning rocks, and sampling algal crusts. Specimens collected by Neal et al. (2020) were obtained using a 0.25 m² USNEL box core or Van Veen grab, with samples sieved through a 0.5 mm mesh. Specimens were fixed in 4% formaldehyde in seawater (Darbyshire, 2018; Neal et al., 2020) and, in some cases, a sample of tissue was also preserved in 100% ethanol (Darbyshire, 2018). Where possible, those specimens collected by Darbyshire (2018) were relaxed in a 7% magnesium chloride solution prior to fixing. All specimens were transferred to 70–80% ethanol solution for long-term storage post-fixation.

Morphological examinations and measurements were made using a Nikon Eclipse E400 binocular microscope and a Nikon Labophot-2 compound microscope, and drawings were produced using camera lucida attachments on each microscope. Microscope photographs were compiled and stacked using a Leica Wild microscope and Helicon Focus™ software. Specimens used for scanning electron microscopy (SEM) were prepared using a Quorum K850 critical point drier and Agar sputter coater (AGB7341) with subsequent imaging undertaken on a JEOL Neoscope JCM-7000 benchtop SEM.

Lengths are provided as L10 (length at chaetiger 10), W10 (width at chaetiger 10 excluding parapodia), and TL (total length). Terminology relating to Onuphidae follows that of Budaeva (2021) and for Eunicidae that of Zanol and Budaeva (2021). Specific terminology of prostomial appendages follows that of Zanol et al. (2017) and for the pectinate chaetae of *Marphysa*, the classification proposed by Molina-Acevedo and

Carrera-Parra (2015, 2017) for the blade and teeth and that of Zanol et al. (2016) for the shaft are followed.

Specimens of *Kinbergonuphis* sp. and *Marphysa* sp. are accessioned in the zoological collections of Amgueddfa Cymru-Museum Wales (NMW.Z). The holotype and paratypes of *Kinbergonuphis dorsalis* were borrowed from the Zoological Museum Hamburg (ZMH) for examination along with comparative material, also identified as *K. dorsalis*, collected by Hartmann-Schröder (1962) and the HERO cruise (1983). A specimen identified by Fauvel (1916) as *Marphysa corallina* as well as Monro's specimens of *Kinbergonuphis dorsalis* (as *Onuphis quadricuspis* and *Onuphis dorsalis*) and *Eunice pennata* were borrowed from or examined at the Natural History Museum, London (NHMUK) along with those specimens of Onuphidae and Eunicidae recorded by Neal et al. (2020). Specimens collected by the USNS *Eltanin*, identified by Hartman and/or Orensanz, were borrowed from the Smithsonian National Museum of Natural History (USNM) including the now-designated holotype, paratypes, and non-type material of *Hyalinoecia falklandica* sp. nov. Museum accession numbers of specimens examined, with number of specimens in parentheses after, are provided in the Materials Examined section for each species. All locality details for examined specimens are provided in a supplementary spreadsheet (S1).

DNA extraction and amplification

A 524 bp region of the 16S large subunit mitochondrial ribosomal DNA was sequenced for three specimens of *Kinbergonuphis* sp. using the Palumbi (1996) primers 16SarL and 16SbrH. DNA was extracted using a Qiagen DNeasy kit and amplified using

GE Healthcare Illustra PuReTaq PCR beads with 1–2 µl of template and 0.25 µl of each primer (10 mM). Each reaction was made up to 25 µl using ultra-pure water and cycling conditions (Eppendorf Mastercycler) were as follows: 94°C for 150 s, 35 cycles of 94°C for 45 s, 51°C for 45 s, 72°C for 45 s, and finally 72°C for 10 min. Products were cleaned using a Sigma–Aldrich GenElute PCR clean up kit, quantified on agarose gels, and sequenced by DNA Sequencing and Services, Dundee University. Sequences were edited and compiled in ApE v.2.0.38 and sequences submitted to GenBank. Multiple unsuccessful attempts were also made to sequence the COI ‘barcoding’ gene using both the universal cytochrome oxidase subunit I (COI) primers (Folmer *et al.*, 1994) and a combination of the forward primer ACOIAF (Colgan *et al.*, 2001) and reverse primer COIEU-R (Zanol *et al.*, 2010).

Results

SYSTEMATICS

Order EUNICIDA

Superfamily EUNICOIDEA Orensanz, 1990

Family ONUPHIDAE Kinberg, 1865

Subfamily ONUPHINAE Kinberg, 1865

Genus *Kinbergonuphis* Fauchald, 1982a

Type species *Onuphis tenuis* Hansen, 1882

Diagnosis (modified from Budaeva, 2021)

Small to medium-sized worms with most species less than 10 cm long. Prostomium distally incised or extended with oval or ovoid frontal lips. Antennae with short to moderately long antennophores with 3–10 rings and long to moderately long styles reaching chaetigers 5–25. Median antenna shorter or equal to lateral antennae. Palpostyles longer than palpophores. Nuchal organs are straight with narrow middorsal separation. Anterior 3–7 pairs of parapodia slightly modified, not enlarged. Ventral cirri subulate on first 2–7 chaetigers. Branchiae usually present, from chaetiger 6, rarely before or after, single or pectinate with up to seven filaments. Pseudocompound falcigers on anterior parapodia unidentate to tridentate with short hoods. Large median hooks are present in transitional parapodia in some species. Pectinate chaetae oblique or transverse with up to 20 denticles. Bidentate hooded subacicular hooks from chaetigers 12–32, 2–3 per parapodium. Maxillae (Mx) V present; MxVI absent. Tubes are thin with inner mucous or parchment-like layer with outer layer of mud or sand grains.

Remarks

The above diagnosis has been modified to reflect that, although the majority of the nearly 40 species of *Kinbergonuphis* possess oblique pectinate chaetae, at least 10 have been described as transverse (straight) and the number of denticles ranges from 8 to 20.

Kinbergonuphis dorsalis (Ehlers, 1897)

Figure 1, 2A–G; Table 1; S1

Diopatra dorsalis Ehlers, 1897: 71–74, pl. 5: figs. 108–118.

Onuphis quadricuspis sensu Monro, 1930: 131–132, fig. 49. Not M. Sars, 1872.

Onuphis dorsalis. — Monro, 1936: 151–152.—

Hartmann-Schröder, 1962: 114–117, figs. 115–119.—

Averincev, 1972: 174, pl. 33, figs. 1–8 (in part).

Kinbergonuphis dorsalis.—Fauchald, 1982a: 18–19, fig. 7a–h.—Orensanz, 1990: 24–30, pl.3: a–h.

Type Locality

Strait of Magellan, Punta Arenas, Chile; intertidal.

Diagnosis

Ventral cirri on chaetigers 1–6. Branchiae from chaetiger 6, single filament; second filament usually present, third filament occasionally present. First five chaetigers with pseudocompound falcigers; unidentate on chaetiger 1, bidentate and/or tridentate on chaetigers 2–5. Two subacicular hooks from chaetigers 11 to 17 onward. Pectinate chaetae flat, slightly oblique, up to 18 denticles, 1–4 per parapodium.

Type Material

ZMH P-4806 (holotype); ZMH V-4808 (7 paratypes); ZMH V-4807 (1 paratype).

Additional Material Examined

as *Onuphis quadricuspis*: NHMUK 1930.10.8.1364–1365 (3); NHMUK 1930.10.8.1771–1772 (2); as *Onuphis dorsalis*: NHMUK 1936.2.8.2215–2217 (3); NHMUK 1936.2.8.2249–2250 (2); NHMUK 1936.2.8.2253–2255 (3); NHMUK 1936.2.8.2218–2227 (10); NHMUK 1936.2.8.2227–2232 (5); NHMUK 1936.2.8.2251–2252 (2); NHMUK 1936.2.8.2233–2236 (4); NHMUK 1936.2.8.2237–2247 (11); NHMUK 1936.2.8.2248 (1); as *Kinbergonuphis dorsalis*: ZMH P-14292 (2); ZMH P-18496 (4).

Description

Holotype complete with 163 chaetigers, L10 = 6.0 mm, W10 = 2.1 mm, TL = 69 mm. Four complete paratypes with 45–49 and 114 chaetigers, L10 = 1.35–4.3 mm, W10 = 0.65–1.5 mm, TL = 4.5–40 mm; four incomplete paratypes (juvenile) with 24–41 chaetigers. Colour of preserved specimens cream, no pigmentation present (present in original description); anterior body with iridescent cuticle, especially on palpo- and antennophores. Description based on holotype.

Prostomium with rounded anterior margin, very weakly incised; frontal and upper lips ovoid. Palps reaching chaetiger 1, lateral antennae reaching chaetiger 3, median antenna reaching chaetiger 2 (Figure 2A, B). Antennae and palps smooth with gradually tapering styles; palpo- and antennophores with three basal rings plus one long distal ring. Eyes not observed (present in original description). Peristomium half as long as first chaetiger. Peristomial cirri slender, slightly longer than peristomium, inserted distally on peristomium in line with lateral antennae.

First three pairs of parapodia modified, enlarged, and directed anteriorly. Parapodia of chaetiger 4 slightly enlarged, directed anterolaterally. Parapodia of chaetigers 5–6 directed posteriorly, from parapodia of chaetiger 7 onwards with no modification (Figure 2A, B). Prechaetal lobes ovate on chaetigers 1–5, reduced considerably on chaetiger 6. Postchaetal lobes long, triangular (Figure 2A, B), reducing in size, becoming more rounded by chaetiger 13, reduced to a low mound thereafter. Dorsal cirri present throughout, subulate and large on chaetigers 1–10; from chaetiger 11 onwards, dorsal cirri unchanged but appearing substantially less robust. Ventral cirri subulate on first four chaetigers, slightly reduced on chaetiger 5, in transitory form on chaetiger 6, replaced by ventral glandular pads from chaetiger 7 (Figure 2A, B). Branchiae present on chaetigers 6–132; two branchial filaments between chaetigers 10 and 56, single filament on all other chaetigers (Figure 2A, B).

First five pairs of parapodia with pseudocompound falcigers: unidentate (Figure 2C) on chaetigers 1–3, bidentate (Figure 2E) on chaetiger 3, tridentate with elongate, apical tip (Figure 2D) on chaetiger 4, tridentate with blunt, apical tooth on chaetiger 5. Simple falcigers absent. Limbate chaetae present on all chaetigers. Presence of pectinate chaetae unclear due to breakage but definitely present from at least chaetiger 19 to end of body, only 1 per parapodium apparent, slightly oblique with up to 18 denticles (Figure 2F). Aciculae present, two per parapodium on



Figure 2. *Kinbergonuphis dorsalis*: Holotype ZMH P-4806 (A) lateral view; (B) close-up lateral view; Paratype ZMH P-4807 (C) unidentate pseudocompound falciger, chaetiger 1; (D) tridentate pseudocompound falciger, chaetiger 3; (E) bidentate, pseudocompound falciger, chaetiger 4; (F) pectinate chaeta, chaetiger 90; (G) subacicular hook, chaetiger 91; dc, dorsal cirrus; gp, glandular pad; pol, postchaetal lobe; prl, prechaetal lobe; vc, ventral cirrus. Scale bars: A, 5 mm; B, 1 mm; C–E, 50 µm; F–G, 20 µm.

chaetigers 1–8, three from chaetiger 9. Bidentate subacicular hooks (Figure 2G) present from chaetiger 15, two per parapodium.

Pygidium with anus terminal; two pairs pygidial cirri ventral to anus, dorsal pair approximately three times longer than ventral pair.

Variation

All paratypes have subulate ventral cirri on parapodia of chaetigers 1–4 with transitory form on chaetiger 5 and glandular pads from chaetiger 6. Large paratype with single branchial filaments except on chaetigers 38–39 where rudimentary second branchial filaments are present. All juveniles except one were abranchiate; specimens with branchiae (46 chaetigers long, complete) possessed a few, single filaments only.

Large paratype with pseudocompound falcigers present on first four pairs of parapodia: unidentate on chaetigers 1–3, bidentate on chaetigers 3–4, tridentate with elongate, apical tip on chaetiger 3–4. Juveniles with pseudocompound falcigers present on first three or four pairs of parapodia and one short-bladed, bidentate compound falciger on a variable number of parapodia between chaetigers 4 and 11. Subacicular hooks start on chaetiger 16 on large paratype and chaetigers 11 or 12 on juveniles.

The three Falkland Islands specimens from stn 51 (Monro, 1930; Figure 1) are all posteriorly incomplete with 36–44 chaetigers, L10 = 4.7–7.5 mm, W10 = 1.5–1.7 mm, and TL = 20–28.5 mm. Eyes were not observed but present on all other specimens collected by Monro in 1930 and 1936 although sometimes hard to see. Some pigmentation is present on the largest specimen from stn 51 from chaetiger 4, forming transverse bands over the posterior half of each segment. Branchiae start from chaetiger 6 with a single filament followed by two filaments from chaetigers 7 or 10 and three from chaetiger 22, 24 or 28. Many anterior parapodia missing but unidentate pseudocompound falcigers are present on first four pairs of parapodia, bidentate and tridentate pseudocompound falcigers on parapodia of chaetigers 3–5. Bidentate subacicular hooks from chaetigers 15 or 16, two per parapodium. The only whole specimen collected by Monro was a small animal from station WS212 (Monro, 1936; Figure 1). This specimen consisted of 110 chaetigers, with maximally two branchial filaments (on chaetigers 19–29) and subacicular hooks from chaetiger 14. Pseudocompound falcigers were present on chaetigers 1–4 only.

Hartmann-Schröder's 1962 specimens (ZMH P-14292) consisted of one anterior fragment, four median fragments and one posterior fragment (one median fragment matches up with the anterior to form the specimen of 110 chaetigers described by Hartmann-Schröder) along with one complete juvenile (16.5 mm long, 67 chaetigers). In contrast with the original description, all specimens were uniformly dark brown with no pigmentation pattern and a glossy, iridescent cuticle in the anterior part of the body. Branchiae start from chaetiger 6, as single filaments to chaetiger 9, two filaments from chaetiger 10, and three from chaetiger 19; postchaetal lobes are clear to chaetiger 15. Unidentate pseudocompound falcigers were present on first five pairs of parapodia, tridentate pseudocompound falcigers present on chaetiger 4. The juvenile specimen has branchiae from chaetiger 6 to 40, single filaments only. Unidentate pseudocompound falcigers present on first three pairs of parapodia, bidentate pseudocompound falcigers on chaetigers 2 and 4 and tridentate pseudocompound falcigers on chaetigers 3–4. Two bidentate subacicular hooks from chaetiger 12. Pectinate chaetae are slightly oblique, 1–2 per parapodium, with up to 15 denticles. No eyes were observed although Hartmann-Schröder reported eyespots on the juvenile specimen.

Four specimens from the HERO cruise (stn783 A-B, Figure 1; ZMH P-18496), two adults and two juveniles, were also examined. The two adults are 61.3 mm long with 147 chaetigers (complete) and 31.7 mm long with 67 chaetigers (posteriorly incomplete). The complete specimen, which appeared to be at an earlier ontogenetic stage, had branchiae with a single filament on chaetigers 6–7 and two filaments from chaetiger 8. The incomplete specimen has two branchial filaments on chaetiger 6 and three filaments from chaetiger 7. Pseudocompound falcigers, unidentate or bidentate, present on first four pairs of parapodia, no tridentate pseudocompound falcigers present although several falcigers were broken. Subacicular hooks from chaetiger 15 or 17 and postchaetal lobes no longer prominent after chaetigers 14 or 17. The juvenile specimens are 5.7 mm long with 40 chaetigers and 6.2 mm long with 35 chaetigers, both complete. Branchiae absent on both juveniles. Pseudocompound falcigers present on first three or four pairs of parapodia (unidentate on chaetiger 1, bidentate on chaetiger 1–3 or 4) followed by 2–3 short-bladed, compound bidentate falcigers from chaetiger 4 to 12 with subacicular hooks from chaetiger 12. Pectinate chaetae slightly

oblique, up to 4 with 10–15 denticles present from at least chaetiger 3.

Remarks

Kinbergonuphis dorsalis is distinguished from all but one other *Kinbergonuphis* species through the combination of having subulate ventral cirri to chaetiger 5 (transitional form chaetiger 6), branchiae from chaetiger 6, and pseudocompound falcigers unidentate, bidentate, and tridentate. Only *Kinbergonuphis orensanzii* (Fauchald, 1982b) shares this combination of characters, but that species has large hooks present from chaetigers 3 to 6 that are absent in *K. dorsalis*. Around the Falkland Islands, both *K. dorsalis* and *Kinbergonuphis oligobranchiata* (Orensanz, 1974a) have been recorded (Figure 1). *Kinbergonuphis dorsalis* is recorded from just north of Falkland Sound (115 m: Monro, 1930) as well as to the south, west, and further north of the Islands (127–930 m: Monro, 1936; Averincev, 1972), and *K. oligobranchiata* from the east, south, and far north of the Island zone (512–1517 m: Averincev, 1972; Orensanz, 1990; Neal *et al.*, 2020). *Kinbergonuphis dorsalis* is easily distinguished through the ventral cirri (cirriform on chaetigers 1–4 only in *K. oligobranchiata* but present on chaetigers 1–5 in *K. dorsalis*) and the pseudocompound falcigers, which are only tridentate in *K. oligobranchiata* but uni-, bi-, and tridentate in *K. dorsalis*.

Since the original description of *K. dorsalis*, several other authors have provided detailed descriptions of the species from nearby regions. Augener (1931) reviewed and published details of Ehlers' type material as part of a description of his own specimens from Antarctica (published as *Onuphis dorsalis* but now dismissible as that species due to branchiae starting on chaetigers 11 or 12). Monro (1930, 1936) provided descriptions of specimens that he identified first as *Onuphis quadricuspis* and then later *Onuphis dorsalis* from the Falkland Islands region, as well as others from off the Argentinean coast (Figure 1). Hartmann-Schröder (1962) collected fresh material from further north in Argentina (Figure 1), but all collected specimens were incomplete and, abnormally, are a solid, dark brown-black colour (preserved material described as 'reddish-brown' in the original description) across the whole body with strong iridescence. Her description, but not specimens, was later reviewed by Orensanz (1974a) along with a description of additional specimens from Argentina. Averincev (1972) reported several records of *O. dorsalis* from samples taken around the region as part of the Soviet Antarctic expeditions. Fauchald (1982a), then transferred the species to *Kinbergonuphis* as a new combination but only reviewed the holotype in the work. Orensanz (1990) then reviewed the species and all records in a more comprehensive study, along with observations on additional specimens from the region, although he did not directly observe the type specimens or those collected from the Magellan region by Monro (1930, 1936), Hartmann-Schröder (1962) or Averincev (1972).

In Ehlers' (1897) original description, *K. dorsalis* was described as having brown pigmentation on anterior chaetigers and eyes present. Our observations of the holotype found all pigmentation to be absent, which is assumed to have faded as an artefact of the extended preservation period. The absence of eyes, which are generally very small in those species of *Kinbergonuphis* that have them, is possibly due to the same reason. Ehlers' description of the eyespots was that they were positioned close to the base of the 'middle antennae' although it is not clear whether he was talking about the median antenna or the lateral antennae which he also referred to as 'middle'. Later descriptions by Hartmann-Schröder (1962), Averincev (1972) and Orensanz (1974a), on fresh non-type material described eyes as being absent. Hartmann-Schröder's description (1962) did detail small eyespots on her juvenile specimen 'between the paired antennae' although we could not see these, either because they had faded over time or

due to the very dark pigmentation present on the specimens. Eyespots were present, although very faded in some cases, on most of Monro's 1936 publication specimens, but not on those from 1930. Fauchald's (1982a) review of the *K. dorsalis* holotype did not mention whether eyes were present or absent.

There are also discrepancies between the different descriptions of the chaetal complement of the species by different authors. Ehlers (1897) describes both unidentate and bidentate pseudocompound falcigers as present on chaetigers 1–5 although he doesn't specify the arrangement specific to chaetiger number. Tridentate pseudocompound falcigers are not described or figured as present. Our observations confirm all three types of pseudocompound falciger to be present on chaetigers 1–5 of the holotype and chaetigers 1–4 of the paratypes. Hartmann-Schröder (1962) described her specimens with 1–3 teeth present on the pseudocompound falcigers of the first five chaetigers and, again, our observations confirmed there to be uni-, bi-, and tridentate pseudocompound falcigers present in both of her specimens. Averincev (1972) reported pseudocompound falcigers on chaetigers 1–4 comprising unidentate (chaetigers 1–2), bidentate (chaetiger 3), and tridentate (chaetiger 4) forms while Orensanz (1974a) found unidentate pseudocompound falcigers present on chaetigers 1–5 and both bi- and tridentate pseudocompound falcigers present from chaetigers 2 to 5. Fauchald (1982a) on the other hand, stated that all falcigers in the studied holotype were unidentate except on chaetiger 5 where they were tridentate only, however this is shown here to be incorrect.

Another discrepancy in the descriptions concerns the number and the appearance of subacicular hooks. Ehlers (1897) description suggests that 5–6 subacicular hooks start 'with the appearance of the gills', decreasing in number to one or two posteriorly. Our observations, however, found only two hooks from chaetiger 15 to the end of the body (slightly earlier on smaller paratypes) with no other type of hook occurring between the end of the pseudocompound falcigers and the start of the subacicular hooks. On Monro's specimens they originate on chaetigers 14–16 and on chaetiger 12 or 17 on Hartmann-Schröder's specimens. Other literature reports the origin variably as chaetiger 20 (Averincev, 1972), chaetiger 12–16 (Orensanz, 1974a), and chaetiger 14 (Fauchald, 1982a). As with many other species, the start of the subacicular hooks has been demonstrated to show ontogenetic variation (Orensanz, 1990) and so must be treated with caution when comparing specimens and descriptions.

Similarly, pectinate chaetae were also variably described as either starting on chaetiger 16 (Hartmann-Schröder, 1962), chaetiger 5 (Averincev, 1972), or chaetiger 3 (Orensanz, 1974a) or the start was not mentioned (Ehlers, 1897; Fauchald, 1982a) and with either 13 denticles (Hartmann-Schröder, 1962), 14–17 denticles (Averincev, 1972), or 18 denticles (Fauchald, 1982a). On the juvenile specimen of Hartmann-Schröder, the first pectinate chaeta is actually present on chaetiger 5. Ehlers (1897) illustrated the pectinate chaetae as transverse and this was reiterated by Fauchald (1982a), however, Hartmann-Schröder (1962) illustrated her specimens as having oblique pectinate chaetae as did Orensanz (1974a, 1990). Examination of the type material confirmed the pectinate chaetae to be slightly oblique. The low angle of the denticles means that at some angles the chaetae can appear transverse so observation of the chaetae on several parapodia is recommended and could explain the discrepancy in the descriptions. Pectinate chaetae are very fragile and easily lost which makes determining the first chaetiger of their appearance difficult. However, an accurate description of whether pectinate chaetae are oblique or transverse, and the number of their denticles can aid in species description.

Orensanz (1990) described *K. dorsalis* as having branchiae with up to 3 (usually 2) filaments, unidentate pseudocompound

falcigers on chaetigers 1–4, pseudocompound falcigers with 1–3 teeth on chaetigers 3–4, tridentate or bidentate pseudocompound falcigers on chaetiger 5, subacicular hooks starting from chaetigers 14–16, and palpo- and antennophores with 3 basal rings. Juveniles (25 chaetigers) were found to possess short-bladed falcigers on chaetigers 1–12 that then transitioned to subacicular hooks. The latter character was confirmed in observations on two juveniles from the HERO cruise (783A-B) in the ZMH collection (P-18496), which were absent in larger specimens from the same sample, as well as Ehlers' juvenile paratypes. Hartmann-Schröder's juvenile specimen, with 67 chaetigers, did not possess such falcigers.

Although Fauchald (1982a) found the descriptive differences to be minor, the wide-ranging distribution and depths reported, combined with the differences in descriptions such as the dark pigmentation of Hartmann-Schröder's specimens and the different distribution of pseudocompound falcigers (no pseudocompound falcigers in chaetiger 5 and bidentate falcigers present in chaetiger 1) and more numerous pectinate chaetae in the HERO specimens, may point to a complex of species being involved that needs further investigation. Of the other *K. dorsalis* specimens detailed, those from the HERO cruise, from just north of Rio Gallegos, were collected closest to the original type locality at Punta Arenas. However, they also differ from the type specimens in several characters. A more comprehensive review of the species using a greater number of animals from closer to the type locality, in combination with molecular data, is desirable to help describe the degree of morphological variation present and the status of the species.

Distribution

Falkland Islands (Figure 1): north of Falkland Sound in 115 m (Monro, 1930) as well as to the south, west, and north of the wider region in 127–915 m (Monro, 1936; Averincev, 1972). Wider distribution: from intertidal habitats to 930 m depth (Orensanz, 1990), mainly in the Magellanic region of southern South America and off Argentina to as far north as the La Plata river. Wesenberg-Lund (1962) also reported one record of the species from the Pacific coast of Chile in Golfo Corcovado in 8 m.

Kinbergonuphis sp.

Figures 1, 3A–D, 4A–I; Table 1, 2; S1

Kinbergonuphis sp. Darbyshire, 2018: 38.

Diagnosis

Eyes present. Ventral cirri on chaetigers 1–6. Branchiae from chaetiger 6, single filament, second filament occasional, third filament rare. First five chaetigers with pseudocompound falcigers: unidentate on chaetiger 1–2, bidentate on chaetiger 3–4, tridentate on chaetigers 3–5. Two bidentate subacicular hooks from chaetigers 11–17 onward. Pectinate chaetae flat, slightly oblique, up to 18 denticles, 1 per parapodium.

Material Examined

East Falkland: NMW.Z.2011.039.0215–0217 (3); NMW.Z.2011.039.0230–0232 (4); NMW.Z.2011.039.0227–229 (106); NMW.Z.2011.039.0224–0226 (98); NMW.Z.2011.039.0218–0219 (9); NMW.Z.2011.039.0220 (1); NMW.Z.2011.039.0221,0223 (2); NMW.Z.2011.039.0222 (1); NMW.Z.2012.082.0218 (1); NMW.Z.2012.082.0150 (3); NMW.Z.2012.082.0151, 0152, 0160 (13); NMW.Z.2012.082.0153 (1); NMW.Z.2012.082.0154 (1); NMW.Z.2012.082.0155–0157, 0163 (10); NMW.Z.2012.082.0158–9, 0161–2 (8). *West Falkland*: NMW.Z.2012.082.0165–0166 (3); NMW.Z.2012.082.0167 (3); NMW.Z.2012.082.0164 (3); NMW.Z.2012.082.0170–201, 205 (126); NMW.Z.2012.082.0168–169 (3); NMW.Z.2012.082.0202–203, 0206 (16); NMW.Z.2012.

082.0208 (3); NMW.Z.2012.082. 0204, 0209, 0210 (14); NMW.Z.2012.082.0211 (2); NMW.Z.2012.082.0212 (2); NMW.Z.2012.082.0215 (2); NMW.Z.2012.082.0214 (4); NMW.Z.2012.082.0213 (4); NMW.Z.2012.082.0207 (9); NMW.Z.2012.082.0216 (1); NMW.Z.2012.082.0217 (1); NMW.Z.2015.002.0006 (2); NMW.Z. 2015.002.0007–0008 (9).

Description

Description based on 'best' (complete, well-preserved, representing all characters clearly; NMW.Z.2012.082.0170) specimen of 176 chaetigers (L10 = 7.5 mm, W10 = 2.5 mm, TL = 101 mm long) with additional images from selected specimens that best demonstrate particular characters (NMW.Z.2012.082.0158, 0163, 0186, 0204). Variation shown by remaining specimens and juveniles detailed in later section.

Live animals cream with pale orange-brown pigmentation, preserved specimens cream with reddish-brown pigmentation (Figure 3A, B). Prostomium pale with darker oval patch on posterior boundary of peristomium. Palpo- and antennophores slightly pigmented as well as bases of styles; palps with no pigmentation. Peristomium with light pigmentation across entirety. Chaetigers 1–12 with very light, dorsal horizontal bands in centre of each segment; parapodia with pigmented area on anterodorsal margin (chaetigers 1–10), bases of dorsal cirri (chaetigers 1–5), and bases of branchial filaments (chaetigers 6–13). Pigmentation reducing in intensity on posterior body, absent from chaetiger 18 onwards. Cuticle iridescent, particularly on palpo- and antennophores and lateral margins of anterior segments.

Prostomium with rounded anterior margin, weakly incised; frontal and upper lips ovoid. Palps reaching chaetiger 1, lateral antennae reaching chaetiger 4, median antenna reaching chaetiger 3 (Figure 3A). Antennae and palps smooth with gradually tapering styles; palpo- and antennophores with three basal rings plus one long distal ring. One pair of small, black eyes on outer posterolateral side of bases of lateral antennae. Peristomium $\frac{2}{3}$ as long as first chaetiger. Peristomial cirri slender, slightly longer than peristomium, inserted distally on peristomium in line with lateral antennae.

First three pairs of parapodia modified, enlarged, directed anteriorly. Parapodia of chaetiger 4 slightly enlarged, directed anterolaterally (Figure 3A, 4A). Parapodia of chaetigers 6–8 directed posteriorly; from parapodia of chaetiger 9 onwards with no modification. Prechaetal lobes broadly ovate on chaetiger 1, ovate on chaetigers 2–5, reduced from chaetiger 6 onward not extending beyond prechaetal fold. Postchaetal lobes long, triangular (Figure 3A), reducing in size from chaetiger 6–12, thereafter as a low mound. Ventral cirri subulate on first four chaetigers, slightly reduced on chaetiger 5, in transitory form chaetiger 6 (Figure 3B, 4A), replaced by ventral glandular pads from chaetiger 7. Single branchial filament on chaetigers 6–135 (Figure 3A, 4A).

First five pairs of parapodia with pseudocompound falcigers: unidentate (Figure 4B) on chaetigers 1–4, bidentate (Figure 3B) on chaetigers 3–4, tridentate with elongate, apical tooth on chaetigers 3–4 (Figure 4C), tridentate falcigers with blunt, apical tooth on chaetiger 5. Simple falcigers and large median hooks absent. Limbate chaetae (Figure 4B) present on all chaetigers, increasing in number to first branchial chaetigers then decreasing posteriorly. Pectinate chaetae (Figure 4D) present from chaetiger 4 or 5 to end of body, up to 4 per parapodium; slightly oblique with up to 16 denticles. Aciculae slender and curved, usually three per parapodia except on parapodia of first six chaetigers which have two. Bidentate subacicular hooks (Figure 4E) present from chaetiger 15, two per parapodium. Chaetal count and distribution provided in Table 2.

Maxillary apparatus (Figure 4F) and mandibles (Figure 4G) pale. Maxillary formula = 1 + 1, 6 + 7, 7 + 0, 9 + 11, 1 + 1. Maxillary carriers more than half as long as maxilla I (Figure 4F).

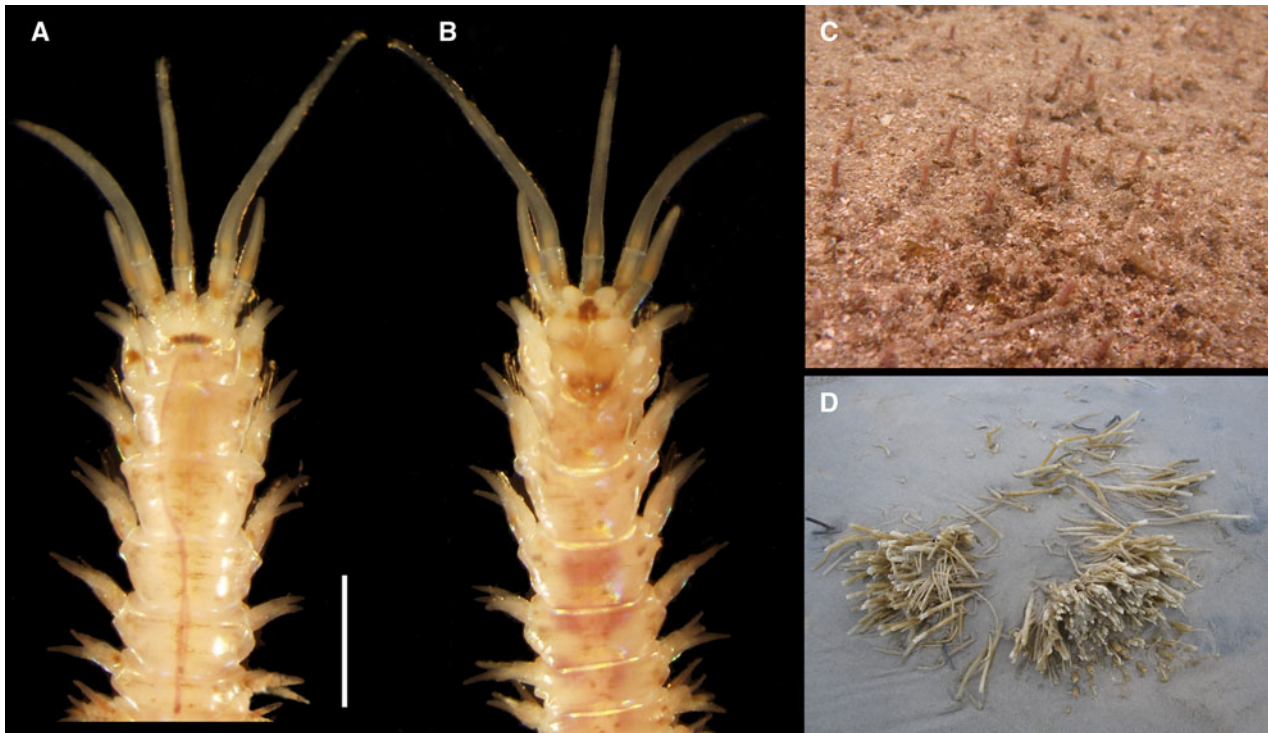


Figure 3. *Kinbergonuphis* sp.: NMW.Z.2011.039.0232 (A) dorsal view, live specimen; (B) ventral view, live specimen; (C) subtidal population, Kidney Island, fine-medium sand 4.6 m; (D) intertidal population, South Harbour, fine sand. Scale bar: A, B 1 mm.

Pygidium with anus terminal. Two pairs pygidial cirri ventral to anus, dorsal pair ~5 times longer than ventral pair.

Embryos found attached to inner wall of the tube of some specimens (Figure 4H); dark yellow in colour, 1–1.25 mm diameter, most at 4-cell stage of division or slightly later (Figure 4I).

GenBank accession numbers (16S): ON787615, OQ592145, OQ592146

Variation

Complete specimens with 37–190 chaetigers, L10 = 2.6–7.3 mm, W10 = 0.8–2.5 mm, TL = 18–116 mm. The start of the subacicular hooks varied with body size and ranged from chaetigers 11 to 17. Subulate ventral cirri were present on the first four pairs of parapodia only in smaller animals, with an intermediate/developing cirrus present on parapodia of chaetiger 5 and ventral glandular pads from chaetiger 6. The ‘developing’ ventral cirrus was still subulate unlike the transitory, rounded cirrus present on parapodia of chaetiger 6 of larger specimens. A clearly subulate ventral cirrus on parapodia of chaetiger 5 developed in animals at around 80–100 chaetigers.

Juvenile specimens (approximately 60 chaetigers or less) occasionally presented bidentate pseudocompound falcigers on chaetiger 2 (most specimens possessed only unidentate pseudocompound falcigers on the first two chaetigers), the median antenna could be longer than the lateral antennae (in larger animals the lateral antennae were always longer than the median), and an additional pair of eyespots were present on the anterior edge of the prostomium between the frontal palps and the lateral antennae. Of 13 juveniles (less than 60 chaetigers) examined, six possessed a single short-bladed, compound bidentate falciger on some or all of the parapodia of chaetigers 5–10 with subacicular hooks present on parapodia from chaetiger 11; four out of those six were abranched, all other juveniles showed developing branchiae to some extent.

Out of 468 specimens examined, both complete and incomplete, 61 specimens possessed two branchial filaments on at least one chaetiger. The second branchial filament first occurred

from chaetiger 8 to 44, with over 50% of animals first developing one between chaetigers 21 and 29. The smallest animal examined (of 7 complete specimens), on which two branchial filaments were found, was 45 mm long with 108 chaetigers, with the second filament starting on chaetiger 24; the largest was 116 mm long with 193 chaetigers, with the second filament first occurring on chaetiger 30. The earliest occurrence of the second filament, in a complete specimen, occurred on chaetiger 13 out of 178 (59 mm body length). There was no apparent relationship between length or number of chaetigers and where the second filament first occurred. After the additional filament first develops, presence is irregular and it may only occur on that single parapodium. The additional filament is frequently absent from subsequent individual parapodia or one or more segments but may, equally, occur consistently for a variable number of subsequent chaetigers. A third branchial filament was only identified in two separate parapodia (chaetigers 19 and 38) of a single posteriorly incomplete specimen (34 mm long with 46 chaetigers; NMW.Z.2015.002.0007).

Eyes were present on most specimens, varying from clear to very faint. Level of pigmentation was highly variable with a few animals showing very dark pigmentation similar to that of Hartmann-Schröder’s (1962) specimens of *K. dorsalis* (see above) with unclear pattern discernable through the pigment. Other specimens exhibited little or no pigmentation at all while the majority were of an intermediate level.

Remarks

Kinbergonuphis sp. demonstrates minor differences from *K. dorsalis* described above. All larger specimens examined of *K. dorsalis* possessed at least two branchial filaments, most had three filaments over a number of segments. The majority of the specimens reported or examined of *K. dorsalis* were incomplete, however, of those few available that were complete, the smallest was of 110 chaetigers and already had ten pairs of branchiae with two filaments (Monro, 1936, NHMUK1936.2.8.2216). Those specimens

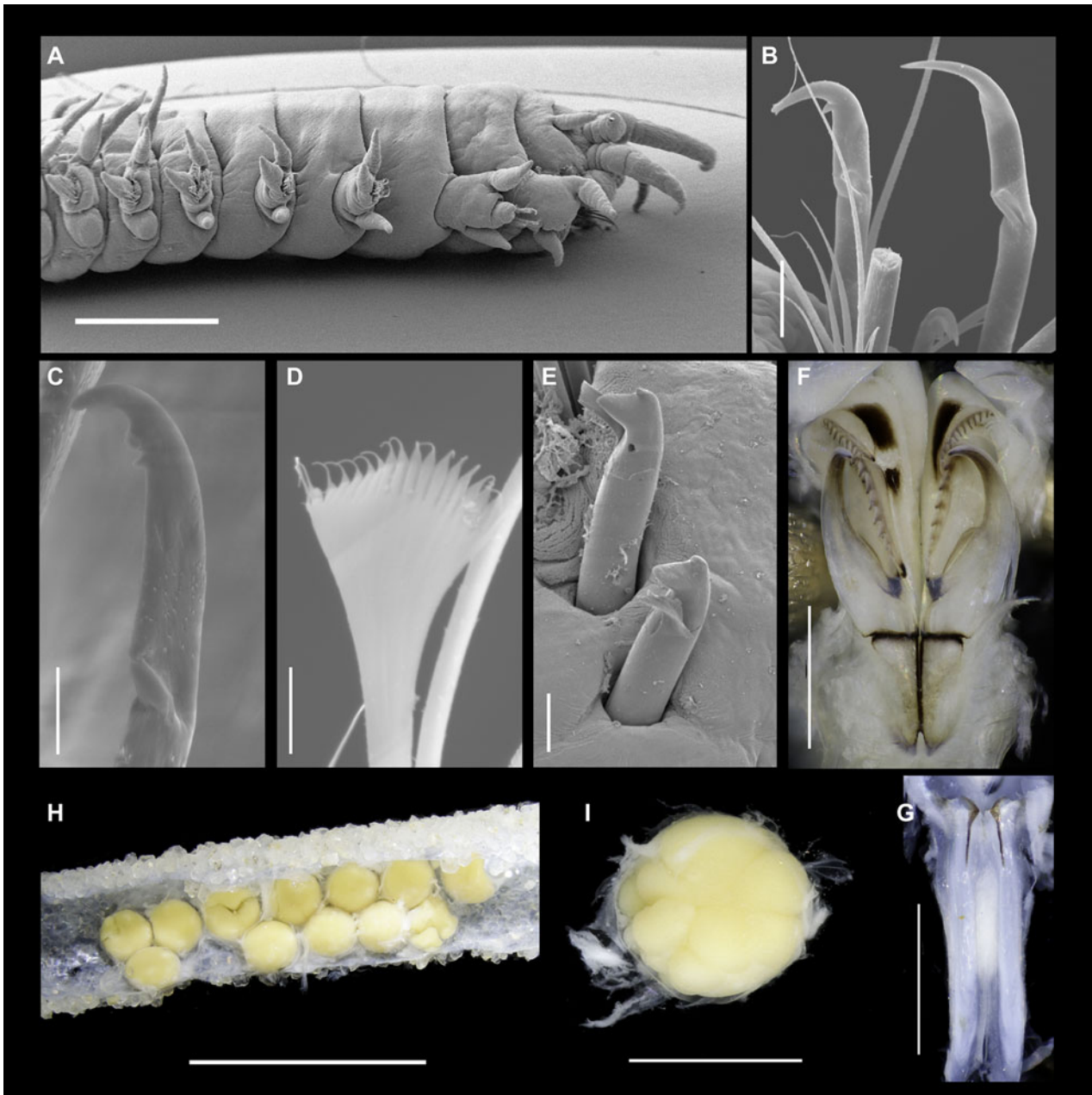


Figure 4. *Kinbergonuphis* sp.: NMW.Z.2012.082.0158 (A) lateral view; NMW.Z.2012.082.0163 (B) unidentate and bidentate pseudocompound falcigers, chaetiger 3; (C) tridentate pseudocompound falciger, chaetiger 3; NMW.Z.2012.082.0186 (F) maxillae; (G) mandibles; NMW.Z.2012.082.0204. (H) embryos attached to inside of tube; (I) multicell stage embryo. Scale bars: A, I, 1 mm; B, E, 20 μ m; C–D, 10 μ m; F–G, 0.5 mm; H, 5 mm.

examined, from Ehlers, Monro, Hartmann-Schröder, and the HERO cruise, demonstrated a consistent presence of the second branchial filament once developed, without skipping parapodia or segments before reverting back to a single filament. In *Kinbergonuphis* sp., however, the presence of an additional branchial filament is uncommon, present in only 61 of the 468 studied specimens, there seems to be no direct relationship to specimen size and second branchial filaments are first present in more posterior chaetigers than in *K. dorsalis*. A third branchial filament was only noted once – in two separate parapodia of one animal. Grimes *et al.* (2020) in studies on *Hermodice carunculata* (Pallas, 1766), found that animals would increase the number of branchial filaments in response to increased hypoxic conditions. When considered as a potential explanation for the discrepancy in the numbers of branchial filaments observed here between *Kinbergonuphis* sp. from the Falkland Islands and specimens of *K. dorsalis*

examined from previous studies, this is not thought to be a significant factor. The specimens of *Kinbergonuphis* sp. were collected from a range of sites around the Falkland Islands coastline that demonstrated differing sediment types including both anoxic sediments and cleaner sands with no apparent correlation between any habitat and the presence of additional branchial filaments. The type specimens of Ehlers were from intertidal sites as were those of Hartmann-Schröder (1962), while those from the HERO cruise were from only 30 m depth, all comparable to the habitats sampled here. Monro's specimens (1930, 1936) were from deeper waters (110 m) but showed no significant difference in branchial development to the intertidal specimens.

Additionally, *Kinbergonuphis* sp. specimens are longer than those of *K. dorsalis*. For equivalent sizes, *Kinbergonuphis* sp. specimens are longer than those few whole specimens of *K. dorsalis*

Table 2. Chaetal count and complement for *Kinbergonuphis* sp. (NMW.Z.2012.082.0207) for anterior chaetigers and selected chaetigers after

Chaetiger no.	Unidentate pseudocompound falcigers	Bidentate pseudocompound falcigers	Tridentate pseudocompound falcigers	Limbate chaetae	Aciculae	Subacicular hooks
1	6	–	–	2	2	–
2	5–6	–	–	4	2	–
3	3	1	1	5	2	–
4	2–3	2	3	6	2	–
5	–	–	3	10	2	–
6	–	–	–	18	2	–
7	–	–	–	19	3	–
10	–	–	–	19	3	–
20	–	–	–	11	3	2
50	–	–	–	6	3	2
100	–	–	–	8	3	2

that have been available to observe. The holotype of *K. dorsalis* is only 69 mm long with 163 chaetigers whereas specimens of *Kinbergonuphis* sp. are 80–100 mm in length for a similar number of chaetigers. Similarly, the specimens of *K. dorsalis* collected closest to the Falkland Islands, those of Monro (1930) from just north of Falkland Sound in 115 m depth, are posteriorly incomplete with three branchial filaments but show a smaller body size than specimens of *Kinbergonuphis* sp. that have the same relative number of chaetigers. Body size can, however, be affected by factors relating to preservation, including relaxation before fixing, and may not be a reliable character for comparison.

Amplification of the COI and 16S mitochondrial genes was attempted, however only 16S was successful. The three sequences retrieved were identical, representing a single haplotype. The only species of *Kinbergonuphis* with sequences currently available is *Kinbergonuphis pulchra* (Fauchald, 1980), which does not occur in the region and is distinguishable from both *K. dorsalis* and *Kinbergonuphis* sp. through multiple characters. No molecular analyses are provided here as no meaningful comparisons could be made due to the lack of sequences from congeners. The sequences have been submitted to GenBank, and the accession numbers are provided here for future use.

As mentioned previously, a review of *K. dorsalis*, from the actual type locality region, along with molecular data, would help clarify the morphological variability truly present and whether some of these specimens from further afield, that demonstrate inconsistencies with the types, are worthy of greater note. Until that time, the specimens reported here from the Falkland Islands are identified to genus only to highlight their differences from *K. dorsalis*.

Habitat

Intertidal and shallow water (less than 10 m) in fine to medium sandy sediments; often found in dense colonies both widely dispersed on the seabed (Figure 3C) or more discretely intertidally (Figure 3D).

Distribution

Recorded around the Falkland Islands archipelago in shallow and intertidal waters (0–10 m) (Figure 1).

Kinbergonuphis oligobranchiata (Orensanz, 1974a)

Figure 1, 5A–H; Table 1; S1

Onuphis oligobranchiata Orensanz, 1974a: 93–94, pl.6.

Kinbergonuphis oligobranchiata. – Fauchald, 1982a: 26–27, fig. 6c, table 6. – Neal *et al.*, 2020: 66.

Anchinothria cf. pycnbranchiata. – Neal *et al.*, 2020: 66 (in part).

Type Locality

Western Atlantic, off Argentina, Buenos Aires Province; –38.76667, –54.88333; 900 m.

Diagnosis

Eyes absent. Ventral cirri on chaetigers 1–4. Branchiae from chaetiger 6, single filament; second filament rare. First four chaetigers with pseudocompound falcigers: bidentate on chaetigers 1–4, tridentate on chaetigers 3–4. Two bidentate subacicular hooks from chaetigers 11–16. Pectinate chaetae flat, oblique, up to 15 denticles, 1–2 per parapodium.

Material Examined

as *Kinbergonuphis oligobranchiata*: USNM 97947 (1); USNM 97948 (5); NHMUK 2018.23537 (1); as *Anchinothria cf. pycnbranchiata*: NHMUK 2018.23591 (1).

Description

Description based on USNM specimens, details of Neal *et al.* (2020) specimens provided in Variation section.

Specimens all posteriorly incomplete with 13–33 chaetigers, L10 = 3–4.1 mm, W10 = 0.3–1.1 mm, TL = 3.8–9.8 mm. Body colour pale cream in alcohol, no pigmentation apparent. Prostomium with rounded anterior margin, weakly incised; frontal and upper lips ovoid. Palps reaching chaetiger 2, lateral antennae reaching chaetiger 6, median antennae reaching chaetiger 8 (Figure 5B–D). Antennae and palps with smooth, gradually tapering styles; palpo- and antennophores with two basal rings and one long distal ring. Eyes absent. Peristomium $\frac{2}{3}$ as long as first chaetiger. Peristomial cirri slender, slightly longer than peristomium, inserted distally on peristomium in line with lateral antennae (Figure 5B).

Parapodia of chaetiger 1 modified, enlarged and directed anteriorly (Figure 5B–D). Parapodia of chaetiger 2–5 directed anterolaterally. Postchaetal lobes long, subulate, reducing in size from chaetiger 6–12, equal to or shorter than acicular lobes from chaetiger 13 onward (Figure 5B–D). Dorsal cirri long, subulate with slight ventral expansion at base; shorter than postchaetal lobes on chaetigers 1–5, longer thereafter. Ventral cirri subulate on first four chaetigers, replaced by glandular pad from chaetiger 5

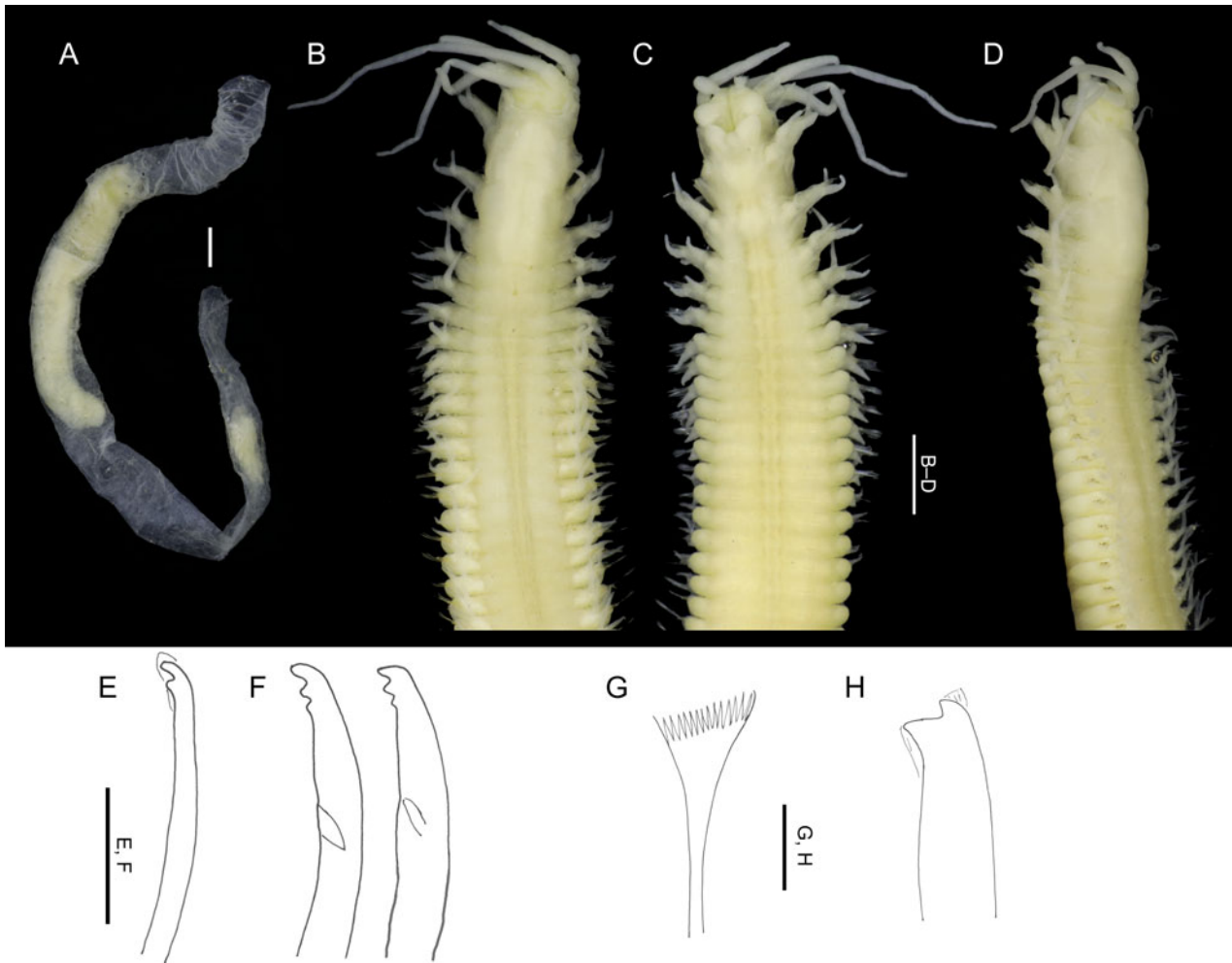


Figure 5. *Kinbergonuphis oligobranchiata*: USNM 97948 (A) tube with specimen fragment; (B) dorsal view; (C) ventral view; (D) lateral view; (E) bidentate falciger, chaetiger 2; NHMUK 2018.23537 (F) tridentate falcigers, chaetiger 3; USNM 97948 (G) pectinate chaeta, chaetiger 24; (H) subacicular hook, chaetiger 24. Scale bars: A, 5 mm; B–D, 1 mm; E–F, 50 μ m; G–H, 20 μ m.

(Figure 5B). Single branchial filament from chaetiger 6 (Figure B, D), second branchial filament on one specimen from chaetiger 13.

First two pairs of parapodia with bidentate and tridentate pseudocompound falcigers, with hoods (Figure 5E–F); tridentate pseudocompound falcigers on chaetigers 3–4. Smallest specimen (USNM 97947) with pseudocompound falcigers on first two pairs of parapodia only. Unidentate falcigers absent. Pectinate chaetae oblique, 1–2 per parapodium, from chaetiger 5, with up to 15 denticles (Figure 5G). Bidentate subacicular hooks (Figure 5H) from chaetiger 11 or 14 onward.

Maxillary apparatus not seen. Tube soft, membranous, translucent (Figure 5A).

Variation

Although *Kinbergonuphis oligobranchiata* was reported from two of the Falkland Islands offshore exploration stations (Neal *et al.*, 2020), only one of those specimens was available for investigation which was in poor condition and showed evidence of previous dehydration. Some observations could be made however and variations from that detailed above are as follows: specimen posteriorly incomplete with 56 chaetigers, L10 = 4.53 mm, W10 = 0.8 mm, TL = 20.8 mm. No second branchial filament was observed. First four pairs of parapodia with bidentate (possibly subtridentate, observations difficult due to preservation) and tridentate pseudocompound falcigers, with hoods, in contrast to tridentate pseudocompound falcigers only on chaetigers 3–4 of the USNM

specimens. Bidentate subacicular hooks present from chaetiger 15 onward, slightly later than observed on the USNM specimens.

Another specimen, previously identified as *Anchinothria cf. pycnobranchiata*, was also found to be *K. oligobranchiata*. Morphology was consistent with the other specimens detailed above with the following additions: posteriorly incomplete with 48 chaetigers, L10 = 3.9 mm, TL = 14.5 mm, W10 = 0.7 mm; stained pink, no pigmentation or eyes observed. Lateral and median antennae reaching chaetiger 6. Branchiae present on chaetigers 9–34, single filament. First four pairs of parapodia with pseudocompound falcigers, up to 4 per parapodium, all tridentate except for one bidentate pseudocompound falciger on chaetiger 2. Pectinate chaetae mostly broken, flat, oblique with up to 15 denticles. Two bidentate subacicular hooks present from chaetiger 16 to end of body.

Remarks

Kinbergonuphis oligobranchiata had not been described when Hartman published her 1967 volume, but there is no listing of onuphid specimens from stn 339 in the publication and only a mention of 7 unidentified onuphids from stn 557. Orensanz (1990), however, examined the specimens, identified them as *K. oligobranchiata* and included them in his review and on the distribution maps. He did not, however, reference them in the distribution he provided for the species which was given only as 'off Argentina'.

The description of specimens presented by Neal *et al.* (2020) on the Marine Flora and Fauna of the Falkland Islands website (<https://falklands.myspecies.info>) is simple and lacks details, thus the present description attempts to remedy that given the condition of the available specimen. Contrary to the description provided, the specimen investigated was found to only possess single branchial filaments from chaetiger 6 (none bifurcate) although the other characters observed matched the limited detail provided. However, as there were clearly more specimens collected originally it is assumed that this description probably refers to those unavailable specimens. The studied specimen agrees in morphology with the specimens listed by Hartman (1967). The specimen mis-identified as *Anchinothria* cf. *pycnobranchiata* showed characters consistent with the other specimens examined and all specimens were collected from the same region to the east of the Falkland Islands.

The original description of the species (Orensanz, 1974a) was limited and appeared to be based on poorly preserved juvenile specimens (Fauchald, 1982a), however, Orensanz (1990) provided more detail and demonstrated the characters subject to ontogenetic variation to be based on adult specimens. The specimens observed here all fall within the variation range of those characters detailed in the updated description. Pectinate chaetae are described by Orensanz (1974a, 1990) as oblique although Fauchald (1982a) described them as transverse, apparently from the same specimens. Pectinate chaetae on the specimens examined from the Falkland Islands were clearly oblique.

Kinbergonuphis oligobranchiata can be distinguished from *K. dorsalis* and *Kinbergonuphis* sp. by having ventral cirri on the first four chaetigers, instead of five, and by having bidentate and tridentate falcigers on the first four chaetigers, as opposed to uni-, bi-, and tridentate falcigers on the first four or five chaetigers.

Distribution

Falkland Islands (Figure 1): East of the Falkland Islands, East Falklands Basin and south of Beauchêne Island in 512–1517 m (Neal *et al.*, 2020). Wider distribution: off Argentina 142–900 m (Orensanz, 1990).

Genus *Onuphis*

Type species *Onuphis eremita* Audouin and Milne Edwards, 1833

Diagnosis (from Budaeva 2021)

Small- to medium-sized worms up to 30 cm long with about 200 chaetigers. Prostomium often anteriorly extended; with ovoid or oval frontal lips. Antennae and palps with 10–25 rings and short to moderately long styles reaching chaetiger 5–25. Median antenna shorter than lateral antennae. Palpostyles shorter than palpophores. Nuchal organs straight with narrow to wide middorsal separation. Peristomial cirri present. Anterior 2–5 pairs of parapodia modified but not enlarged. Ventral cirri subulate on anterior 4–6 chaetigers. Branchiae rarely absent, usually present from chaetiger 1, rarely from chaetiger 3–6; single or pectinate with up to 12 filaments. Pseudocompound falcigers on modified parapodia usually tridentate (rarely only bidentate, sometimes bi- to multidentate) with short, pointed hoods. Pectinate chaetae flat. Paired bidentate hooded subacicular hooks from chaetiger 10–12. Maxillae V present; MxVI absent. Tubes cylindrical, with thin mucous or tough parchment-like inner layer covered with sediment particles.

Onuphis pseudoiridescens Averincev (1972)

Figure 1, 6A–I; Table 1; S1

Onuphis (*Nothria*) *pseudoiridescens* Averincev, 1972: 176, pl.32, figs 1–9.

Onuphis iridescens. — Monroe, 1936: 150–151.

Nothria ?iridescens. — Hartman, 1967: 91.

?*Paronuphis antarctica*. — Hartman, 1967: 96–97 (in part).

Onuphis heterodentata Fauchald, 1982c: 241–243, fig.2, table 2.

Onuphis lithobiformis Fauchald, 1982c: 243–245, fig.3.

Onuphis pseudoiridescens. — Orensanz, 1990: 20–23, pl. 1a–i, fig. 8. — Neal *et al.*, 2020: 66.

Type Locality

Western Atlantic: off Argentina, Uruguay & Falkland Islands; 202–659 m

Diagnosis

Palpostyles shorter than palpophores. Eyes absent. Ventral cirri on chaetigers 1–5. Branchiae from chaetiger 1, single filament. Tridentate pseudocompound falcigers present on chaetigers 1–4 with short, pointed hoods. Two bidentate subacicular hooks from chaetigers 11–15. Pectinate chaetae flat, oblique, 13–18 denticles, 1–3 per parapodium.

Material Examined

as ?*Paronuphis antarctica*: USNM 58439 (20); as *Onuphis pseudoiridescens*: NHMUK 2018.24031, 2018.19091–19100 (5); NHMUK 2018.23563 (1).

Description

Six specimens from Neal *et al.* (2020) were available for examination, the following description is based on and encompasses all of them. Details in parentheses relate to specimens from Hartman (1967) although most are in poor condition with many structures missing or degraded, absence of additional data indicates that it matches that already detailed.

Specimens posteriorly incomplete, 42–99 (37–62) chaetigers; L10 = 2.7–5.9 (5.3–8.0) mm, W10 = 0.7–1.6 (0.9–1.1) mm, TL = 12–40.4 (14.9–32.0) mm. Prostomium anteriorly extended (Figure 6B); frontal and upper lips oval (Figure 6A, B). Palpophores with 11–15 (12) rings and one slightly longer ring, palpostyles shorter than palpophores (Figure 6A, B) reaching to chaetiger 1. Lateral antennae with 10–14 (13) rings and one slightly longer ring, antennal styles reaching to chaetiger 5–10 (5–7), longer than median antenna (Figure 6A–C). Median antenna with 5–7 (7) rings and one slightly longer ring, antennal styles reaching to chaetiger 3–6 (5–6). Eyes absent. Peristomium half as long as first chaetiger. Peristomial cirri very slender, nearly twice as long as peristomium, inserted distally on peristomium in line with lateral antennae.

First four parapodia with tridentate, pseudocompound falcigers, up to 4 (5) in each parapodium, with short, pointed hoods (Figure 6D–G). Limbate chaetae from chaetiger 1, up to 12 in anterior chaetigers; pectinate chaetae flat, oblique, with 13–15 (12–18) denticles (Figure 6H), up to 3 per parapodium, start unclear but present from at least chaetiger 6 (5). Bidentate subacicular hooks (Figure 6I) from chaetiger 11 or 14 (10–15). Tube thin, soft, covered in silt particles.

Remarks

Monro (1936) reported five specimens of this species (as *Onuphis iridescens* (Johnson, 1901)) from a single station (WS212, Figure 1) north of the Falkland Islands (242–249 m). Hartman (1967) identified 22 specimens from samples taken in 567–595 m directly south of the Islands as *Nothria? iridescens* that were later re-described as two new species (*Onuphis* (*Nothria*) *heterodentata* and *Onuphis* (*Nothria*) *lithobiformis*) by Fauchald (1982c). Orensanz (1990) later synonymized both *O. heterodentata* Fauchald, 1982c and *O. lithobiformis* Fauchald, 1982c with *O. pseudoiridescens* and also attributed Monro's records (1930, 1936) to the species. In his remarks, Orensanz (1990) found

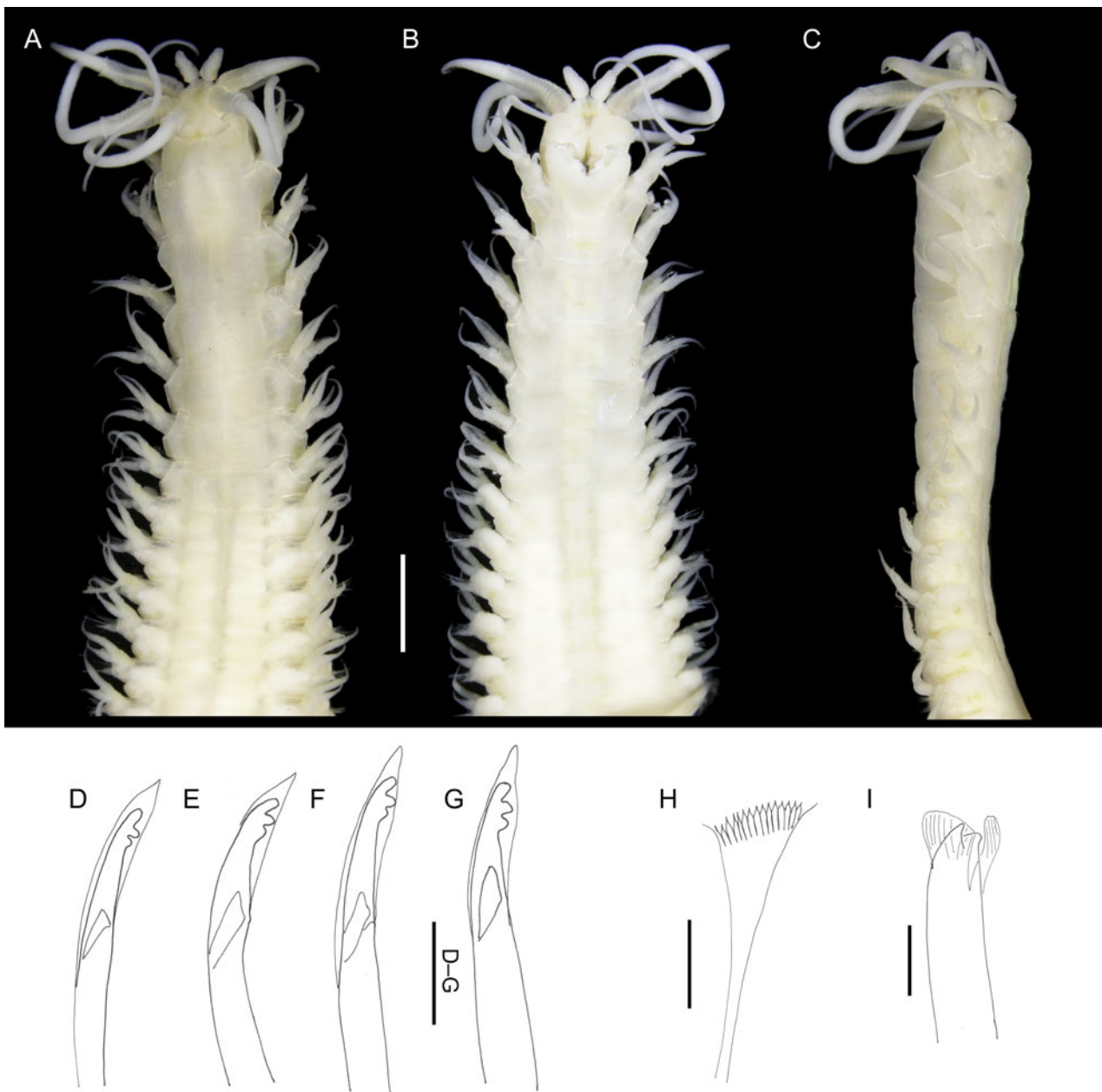


Figure 6. *Onuphis pseudoiridescens*: NHMUK 2018.24031 (A) dorsal view; (B) ventral view; (C) lateral view; (D) tridentate pseudocompound falciger, chaetiger 1; (E) tridentate pseudocompound falciger, chaetiger 2; (F) tridentate pseudocompound falciger, chaetiger 3; (G) tridentate pseudocompound falciger, chaetiger 4; (H) pectinate chaeta, chaetiger 39; (I) subacicular hook, chaetiger 40. Scale bars: A–C, 1 mm; D–G, 50 μ m; H, 20 μ m; I, 25 μ m.

that *O. pseudoiridescens* and *O. iridescens* were indistinguishable morphologically but inhabited separate geographic regions, with *O. pseudoiridescens* present in southwest Atlantic localities and *O. iridescens* present in the northeast Pacific. No other species of *Onuphis* have been reported from the Falkland Islands region.

The record of ?*Paradiopatra antarctica* (Monro, 1930), published by Hartman (1967) as ?*Paronuphis antarctica*, is here reassigned to *O. pseudoiridescens*. Orensanz (1990) reassigned all of Hartman's (1967) records of *Paronuphis antarctica* (Monro, 1930), *en masse*, to *Notonuphis antarctica* (Monro, 1930) including those from the single station near the Falkland Islands from which she recorded the species (Table 1). However, Hartman's specimens from station 558, east of the Falkland Islands, were only tentatively identified as that species and were not commented on further nor were they examined by or commented on by Orensanz. Orensanz (1990) described the distribution of *P. antarctica* as endemic to the South Shetland and South Orkney

Islands and the adjacent southern Scotia Sea, omitting the Falkland Islands from both the text and the map provided. In 2011, Budaeva and Fauchald made *Notonuphis* a junior synonym to *Paradiopatra* and included Hartman's record in their distribution map for the species, an outlying point to an otherwise limited Antarctic distribution. New examination of the specimen lot found the specimens to be in a very poor condition with many structures difficult to discern due to significant degradation or loss. However, the majority of the specimens were determined to be *Onuphis pseudoiridescens* although an additional juvenile *Nothria anoculata* was also identified (see later). The removal of the record from *Paradiopatra antarctica*, leaves the species with a more discrete distribution around the northwest Antarctic peninsula and South Shetland Islands (Budaeva and Fauchald, 2011).

Neal *et al.* (2020) found *O. pseudoiridescens* to be one of the most common taxa in samples from the SeaLion field exploration area to the north of the region (450–463 m) and also recorded it

from the Toroa site to the southeast in 615 m. Details of actual abundance are not provided on the Marine Flora and Fauna of the Falkland Islands website (<https://falklands.myspecies.info>) or in their publication and only six specimens were available to examine so a full accounting of potential variation cannot be given. Branchiae are described as normally starting from chaetiger 1, but Orensanz (1990) did find that they could start as far back as chaetiger 4. In one small SeaLion specimen, branchiae did not start until chaetiger 5 but this does not seem a significant variation. Variation in the presence of ventral cirri and the start of the subacicular hooks was almost identical to that reported by Orensanz (1990). Although the species is reported from depths as shallow as 21 m (Orensanz, 1990), all records from around the Falkland Islands are from depths greater than 200 m but fall within the currently accepted depth range.

Distribution

Falkland Islands (Figure 1): north, south, and east of the Islands in 212–845 m (Monro, 1936; Hartman, 1967; Neal *et al.*, 2020). Wider distribution: southern South America, southern Chile, Strait of Magellan and off Argentine Patagonia, 21–861 m (Orensanz, 1990).

SUBFAMILY Hyalinoeciinae Paxton, 1986a
Genus *Anchinothria* Paxton, 1986a
Type species *Diopatra pourtalesii* Ehlers, 1879

Diagnosis (from Budaeva, 2021)

Body short, up to 100 segments. Median antenna longer than lateral antennae. Palpo- and antennophores short, consisting of 2–5 rings. Nuchal grooves straight. Peristomial cirri present. Anterior 2–3 pairs of parapodia enlarged, directed anteroventrally with bi- to trilobed prechaetal lobes. Ventral cirri subulate on anterior 2–3 chaetigers. Branchiae present or absent, single or dichotomously branched with up to 10 filaments. Uni- or bidentate simple or pseudocompound falcigers on first 2–4 pairs of anterior parapodia, in one species on first seven pairs of parapodia. Pectinate chaetae wide with rolled margins, so-called ‘scoop-shaped’, from chaetigers 2–3, in one species from chaetiger 14. Subacicular hooks from chaetigers 4–16. Maxillae V present; Mx VI absent. Tubes dorsoventrally flattened with parchment-like inner layer covered with mud and often incrustated with scattered large elongated foraminiferans, glass sponge spicules, or echinoid spines attached along longitudinal margins.

Anchinothria sp.

Figure 1, 7A–F; Table 1; S1

Leptoecia vivipara. – Neal *et al.*, 2020: 66 (in part).

Diagnosis

Eyes absent. Ventral cirri on chaetigers 1–2. Branchiae absent. Bidentate pseudocompound falcigers present on chaetigers 1–2. Two bidentate subacicular hooks from chaetigers 9–10. Pectinate chaetae scoop-shaped, oblique, 8–14 denticles, 1–2 per parapodium.

Material Examined

as *Leptoecia vivipara*: NHMUK 2018.23504 (1).

Description

One specimen complete (Figure 7A) with 49 chaetigers; L10 = 1.7 mm, W10 = 0.5 mm, TL = 7.6 mm. Preserved colour white; pigmentation absent. Prostomium with rounded anterior margin, weakly incised; frontal and upper lips oval. Palps short, to chaetiger 2; lateral antennae long, thin, to chaetiger 9 (Figure 7A–C); median antenna long, thin, to chaetiger 6; palpo- and

antennophores with three short rings and one longer ring. Eyes absent. Peristomium half as long as first chaetiger. Peristomial cirri slender, degraded, inserted distally on peristomium just lateral to lateral antennae.

First two pairs of parapodia enlarged, directed anteriorly. Ventral cirri subulate, present chaetigers 1–2 (Figure 7C). Branchiae absent. First two pairs of parapodia with bidentate, pseudocompound falcigers (Figure 7D), up to 4 per parapodium; one simple, bidentate falciger present in one parapodium of chaetiger 1 (Figure 7D). Pectinate chaetae from chaetiger 3, 1–2 per parapodium, scoop-shaped, oblique with 8–14 denticles (Figure 7E). Two bidentate, subacicular hooks (Figure 7F) from at least chaetiger 9 or 10 to end of body. Maxillae not observed.

Pygidium with two pairs of anal cirri, both ventrally inserted, one pair short, one pair long, thin. Tube not present.

Remarks

Of the two specimens originally identified by Neal *et al.* (2020) as *Anchinothria* cf. *pycnobranchiata* one specimen proved to be *Nothria anoculata* Orensanz, 1974a (see later) and the second specimen was re-identified as *Kinbergonuphis oligobranchiata* (see earlier). However, a small specimen was examined that had been mis-identified as *Leptoecia vivipara* and is here re-assigned to *Anchinothria* sp.

The description of the Falkland Islands specimens on the Marine Flora and Fauna of the Falkland Islands website appears to be based on the mis-identified *N. anoculata* specimen leading to the discrepancies noted there from the original description of *Anchinothria pycnobranchiata*. Those include branchiae present (actually absent), pseudocompound falcigers present beyond chaetiger 2 (first two pairs of parapodia only) and subacicular hooks from chaetiger 6 (actually chaetiger 9 or 10). Orensanz (1990) agreed with Pettibone (1970) on presence or absence of branchiae not being a diagnostic character due to variability even within specimens from the same sample. *Anchinothria pycnobranchiata* is reported as reaching 70–75 mm in length for 70–80 chaetigers (Orensanz, 1990), and the specimen described here is less than 8 mm long with only 49 chaetigers. The lack of falcigers on chaetiger 3 could well be due to the small size and likely juvenile condition of the specimen. Similarly, the presence of one simple falciger amongst the other pseudocompound falcigers also suggests that pseudocompound is a juvenile trait with development just starting toward a simple form. Orensanz (1990) also discusses the first appearance of the subacicular hooks, stating that they actually appear from chaetiger 4, but are frequently broken in earlier chaetigers due to their slender stature until they become more robust in later segments.

Two specimens were also recorded from a single station (350, see Figure 1) just south of the region by Hartman (1967) as *Nothria abranchiata* (reassigned by Orensanz, 1990 to *A. pycnobranchiata*) and are mentioned here due to the proximity of the locality. No other publications that have examined specimens from the region (Monro, 1930, 1936; Hartman, 1953; Hartmann-Schröder, 1983) recorded the species. The type locality for *A. pycnobranchiata* is the eastern Pacific, off Chile (–34.11667, –73.93333) at a depth of 4069 m, far deeper than the specimen described here was recorded from (1782 m). The distant type locality and much deeper type locality depth, along with the morphological variation between this specimen and the known details for *A. pycnobranchiata*, give cause to provide an identification to genus only for this specimen.

Distribution

Falkland Islands (Figure 1): East Falklands Basin (southern end, north of Burdwood Bank) in 1782 m (Neal *et al.*, 2020).

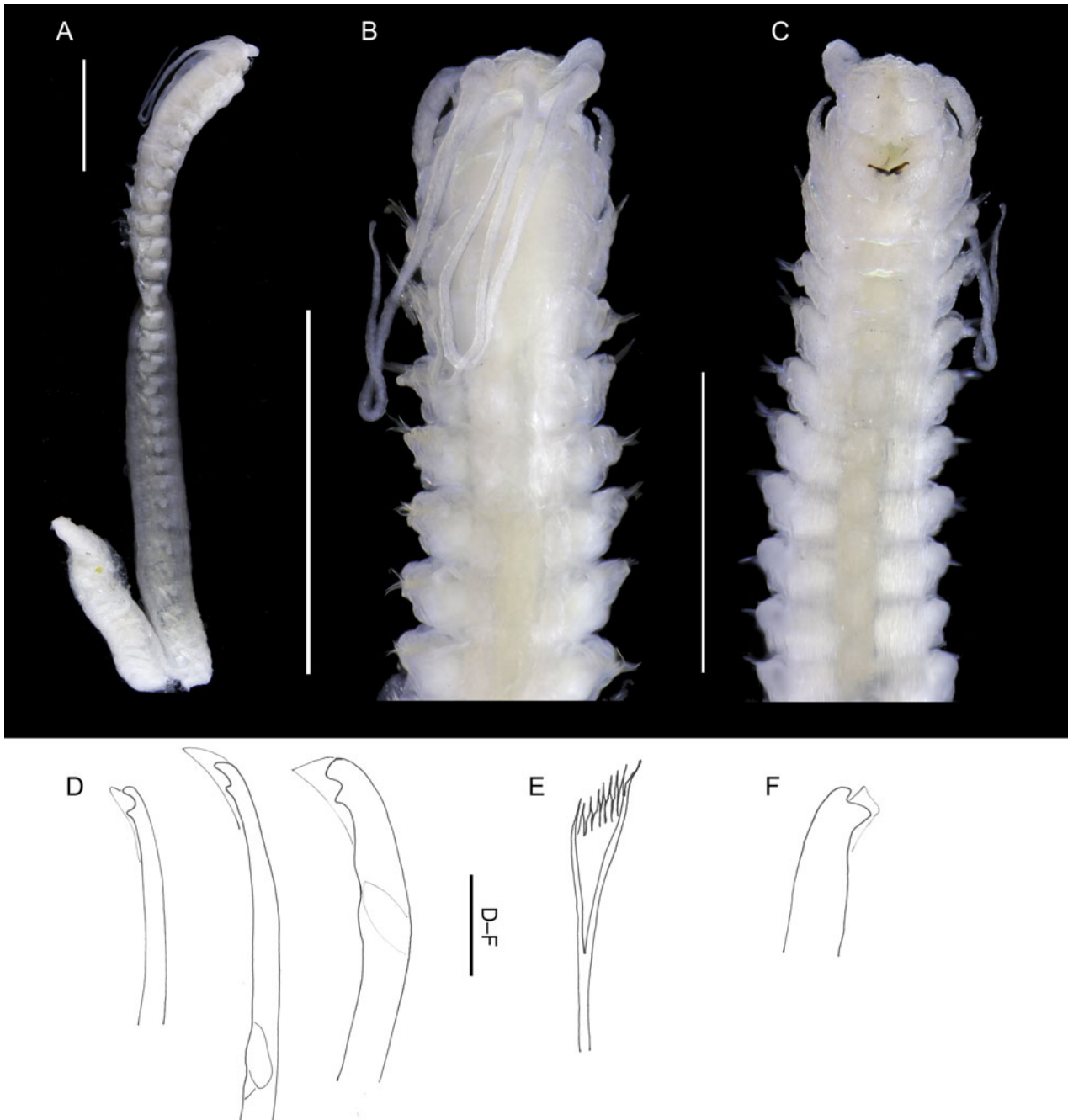


Figure 7. *Anchinothria* sp.: NHMUK 2018.23504 (A) whole specimen, lateral view; (B) dorsal view; (C) ventral view; (D) bidentate, simple and pseudocompound falcigers, chaetiger 1; (E) pectinate chaeta, chaetiger 40; (F) subacicular hook, chaetier 24. Scale bars: A–C, 1 mm; D–F, 20 µm.

Genus *Leptoecia* Chamberlin, 1919

Type species *Leptoecia abyssorum* Chamberlin, 1919

Diagnosis (from Budaeva, 2021)

Small-sized worms 10–40 mm long with up to approximately 80 chaetigers. Prostomium rounded, conical, or pointed with reduced or absent frontal lips. Antennae with short 1–4 ringed antenno-phores and long styles. Nuchal organs slightly curved with wide middorsal separation, may be absent in some species. Peristomial cirri absent. Anterior 1–2 pairs of parapodia modified, first pair prolonged with auricular prechaetal lobe and digitiform postchaetal lobe. Ventral cirri subulate on first two chaetigers. Branchiae absent. Simple or pseudocompound uni- to bidentate falcigers with short blunt hoods on 1–2 pairs of anterior parapodia. Pectinate chaetae flat with about ten denticles. Paired bidentate

hooded subacicular hooks from chaetigers 12 to 50. Maxillae V and VI absent. Tubes secreted, quill-like, circular in cross-section or flattened dorsoventrally, with two longitudinal ribs.

Leptoecia sp.

Figure 1, 8A–H; Table 1; S1

Leptoecia vivipara. – Neal *et al.*, 2020: 66 (in part).

Diagnosis

Prostomium pointed; peristomial cirri absent. Eyes absent. Ventral cirri on chaetigers 1–2. Branchiae absent. Pseudocompound falcigers present on chaetigers 1–2: unidentate on chaetiger 1, bidentate on chaetiger 2. Bidentate subacicular hooks from chaetiger 4, 1 anteriorly, 2 from chaetiger 16.

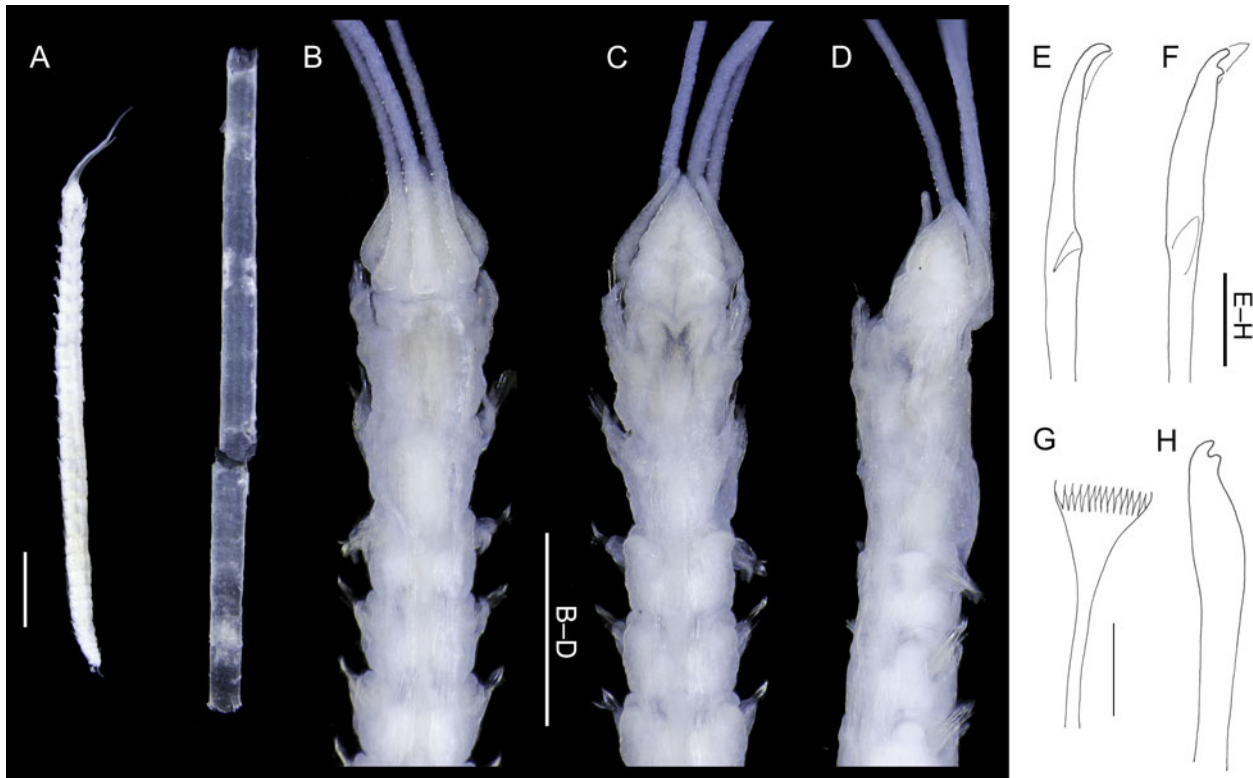


Figure 8. *Leptoecia* sp.: NHMUK 2018.23503 (A) whole specimen with tube, dorsal view; (B) dorsal view; (C) ventral view; (D) lateral view; (E) unidentate, pseudo-compound falciger, chaetiger 1; (F) bidentate, pseudo-compound falciger, chaetiger 2; (G) pectinate chaeta, chaetiger 3; (H) subacicular hook, chaetiger 18. Scale bars: A, 1 mm; B–D, 0.5 mm; E–H, 20 μ m.

Pectinate chaetae flat, transverse, up to 12 denticles, up to 5 per parapodium in anterior chaetigers, reduced posteriorly.

Material Examined

as *Leptoecia vivipara*: NHMUK 2018.23503 (1).

Description

Single, complete specimen (Figure 8A–D) of 28 chaetigers, L10 = 7.1 mm, W10 = 0.25 mm, TL = 6.4 mm. Prostomium pointed (Figure 8B–D), peristomial cirri absent (Figure 8B), frontal lips absent (Figure 8D). Antennae with short, single-ringed antennophores and long, slender styles. Eyes absent. Peristomium $\frac{1}{3}$ as long as first chaetiger; peristomial cirri absent.

First two pairs of parapodia modified, directed anteriorly; first pair enlarged, elongated. Dorsal cirri reduced to nodule from chaetiger 9 onwards but present to end of body. Ventral cirri subulate on chaetigers 1–2 (Figure 8D); branchiae absent.

First pair of parapodia with 2–3 unidentate pseudo-compound falcigers (Figure 8E) with short, blunt hoods. Second pair of parapodia with four, bidentate pseudo-compound falcigers (Figure 8F) and flat, transverse pectinate chaetae with up to 12 denticles (Figure 8G). Up to five pectinate chaetae in parapodia of chaetiger 3, reduced in number thereafter. Limbate chaetae present from chaetiger 3, up to three in each parapodium. Subacicular hooks (Figure 8H) from chaetiger 4: one from chaetiger 4–15, two from chaetiger 16. Tube cylindrical, smooth, straight, translucent (Figure 8A).

Remarks

Of the three specimens previously identified as *Leptoecia vivipara* by Neal *et al.* (2020), one was reassigned to *A. pycnobranchiata* (see earlier), one to the new species of *Hyalinoecia* (see later) and the remaining specimen, described here, to *Leptoecia* sp.

Leptoecia vivipara has previously only been reported from Antarctica, and the records reported by Neal *et al.* (2020) would be the first for the Falkland Islands and the most northerly records to date. However, the characters present in the specimen described, although aligning it with *Leptoecia*, do not conform to any of the currently described species or their known variations. It differs from *L. vivipara* in the shape of the prostomium (pointed not rounded), having pseudo-compound falcigers on two anterior chaetigers (not one) and dorsal cirri reduced to a nodule by chaetiger 9 (not 20).

The pseudo-compound falcigers on both chaetigers 1 and 2 set the specimen apart from all the other described Antarctic species except for a single, incomplete specimen of '*Leptoecia* sp.' from the Wilkes abyssal plain mentioned by Orensanz (1990). However, on that specimen, all falcigers were bidentate whereas those on chaetiger 1 are unidentate in the present specimen.

The pointed ('helmet'-shaped) prostomium is as described and illustrated for *Leptoecia oxyrincha* (Kucheruk, 1978), although there is no dorsal tubercle (as described for the species in Orensanz, 1990). It also differs from that species in several characters including the start of the subacicular hooks (chaetiger 4 not 15–17), presence of dorsal cirri (reduced but continuing to posterior in *Leptoecia* sp., absent from posterior in *L. oxyrincha*) and the anterior falcigers (parapodia of chaetigers 1–2 in *Leptoecia* sp. as opposed to just parapodia of chaetiger 1 in *L. oxyrincha*). *Leptoecia benthaliana* (McIntosh, 1885) is described as having a variable prostomial shape with some specimens having a blunter, bilobed form and others a more pointed one. The 'pointed' form is not as smoothly-shaped as in *Leptoecia* sp. and anterior falcigers are present on first pair of parapodia only and are bidentate (unidentate on chaetiger 1 in *Leptoecia* sp. as well as having bidentate falcigers on parapodia of chaetiger 2).

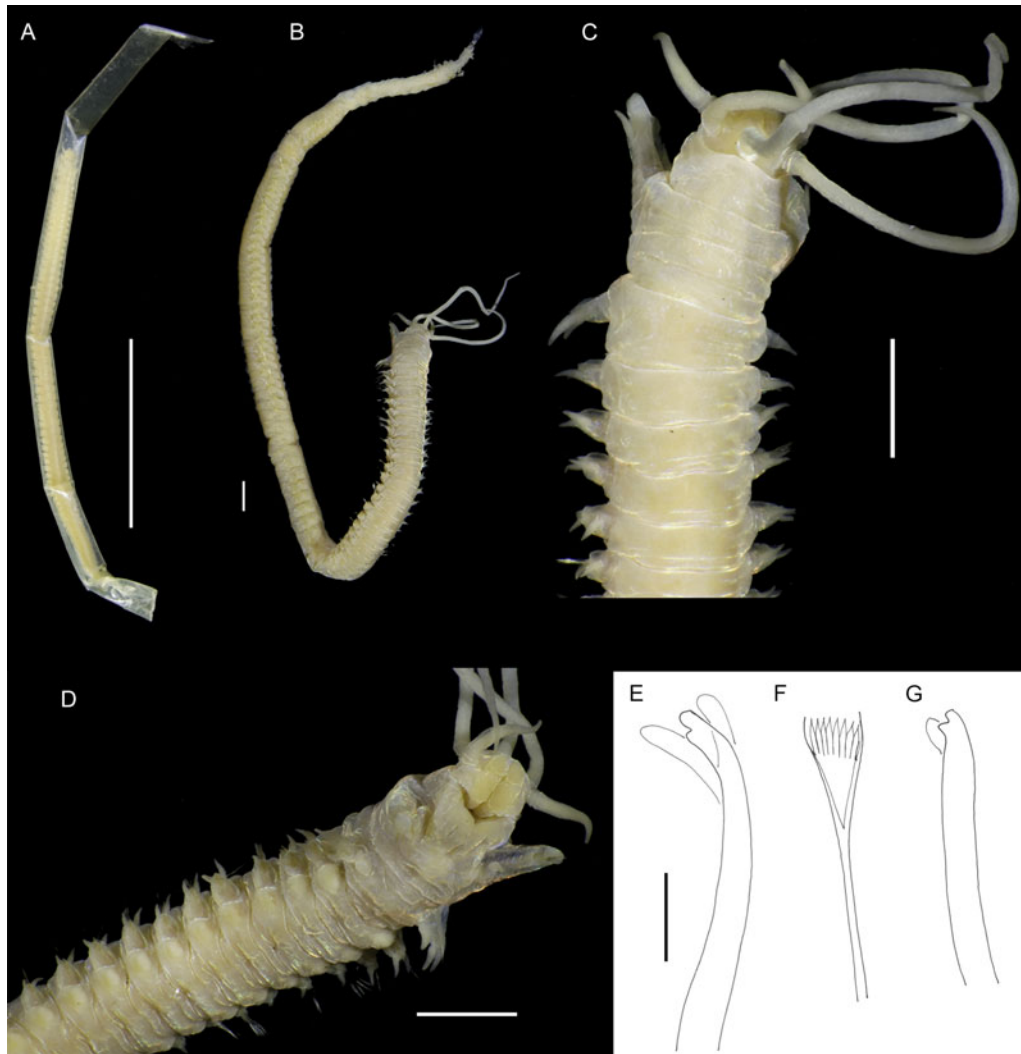


Figure 9. *Leptoecia* cf. *benthaliana*: USNM 58018 (A) whole specimen in tube; (B) whole specimen; (C) dorsal view; (D) ventral view; (E) simple, bidentate falciger, chaetiger 1; (F) pectinate chaeta, chaetiger 74; (G) subacicular hook, chaetiger 73. Scale bars: A, 10 mm; B–D, 1 mm; E–G, 20 μ m.

The very small size of the specimen of *Leptoecia* sp. (less than 7 mm long) makes it unclear as to whether it is a juvenile or not and thus how characters such as the start of the subacicular hooks, and the presence of branchiae and dorsal cirri may develop. The prostomial shape and presence of pseudocompound falcigers on two anterior chaetigers clearly set it apart from the other known species of *Leptoecia*, however without further specimens, *Leptoecia* sp. is considered the best identification possible at this time.

Distribution

East Falklands Basin in 1842 m (Neal *et al.*, 2020) (Figure 1).

Leptoecia cf. *benthaliana* (McIntosh, 1885)

Figure 1, 9A–G; Table 1; S1

Hyalinoecia benthaliana McIntosh, 1885: 339, pl.21a, figs 15,16

Hyalinoecia tubicola. — Hartman, 1967: 89 (in part: stn 377)

Leptoecia cf. *benthaliana*. — Orensanz, 1990: 55–58, fig. 16, pl.13a–n

Type Locality (*Leptoecia benthaliana*)

Southeast Indian Ocean; -50.016667 , 123.066667 ; 3240 m

Diagnosis

Prostomium pointed or bilobed; peristomial cirri absent. Eyes absent. Dorsal cirri present throughout. Ventral cirri on

chaetigers 1–2. Branchiae absent. Bidentate simple falcigers present on chaetiger 1 only. Bidentate subacicular hooks from chaetiger 48. Pectinate chaetae flat, transverse, 8–10 denticles, up to 10 per parapodium.

Material Examined

USNM 58018 (2).

Description

Two complete specimens (Figure 9A, B), 80 and 95 chaetigers, L10 = 4.1–4.9 mm, W10 = 0.8–1.1 mm, TL = 23.1–30.4 mm. Prostomium pointed on one specimen with frontal lips absent, slightly bilobed on the other with reduced frontal lips (Figure 9C, D). Antennae with short antennophores with two rings and long, slender styles (Figure 9C). Palps short, to chaetiger 1 only, median antenna long, reaching to chaetiger 11 or 14, lateral antennae to chaetiger 7 or 9 (Figure 9B, C). Eyes absent. Peristomium half as long as first chaetiger; peristomial cirri absent.

First pair of parapodia modified, enlarged, directed anteriorly, elongated with auricular prechaetal lobes (Figure 9C, D); postchaetal lobes digitiform. Second pair of parapodia modified, slightly enlarged (Figure 9C), not directed anteriorly. First chaetiger twice length of second (Figure 9C). Dorsal cirri reduced from chaetiger 18 onwards but present to end of body. Ventral cirri subulate, chaetigers 1–2 (Figure 9D). Branchiae absent.

First pair of parapodia with three simple bidentate falcigers with short, blunt hoods (Figure 9E). Second pair of parapodia with up to four limbate chaetae only. Third pair of parapodia with limbate chaetae and up to 10 flat, transverse pectinate chaetae with up to 8–10 denticles (Figure 9F). Subacicular hooks (Figure 9G) from chaetiger 48: one on chaetigers 48–49 or 50, two from chaetiger 50 or 51. Tube quill-like (Figure 9A).

Remarks

Hartman (1967) identified specimens from three stations around the Falkland Islands as *Hyalinoecia tubicola* (Müller, 1776), including three from a sample taken in a deep trench north of Burdwood Bank in the southern part of the Falkland Islands zone. Orensanz (1990) examined and re-identified the specimens from that station (377), stating that they ‘may belong to’ *Leptoecia* cf. *benthaliana* (the remaining specimens from the other samples were attributed to *Hyalinoecia artifex* Verrill, 1881 as discussed later). Re-examination of the specimens does not find any reason to suspect Orensanz’ original placement of the specimens and it is thought that his tentative placement was more due to their locality, *L. benthaliana* being originally described from south of the Great Australian Bight. The different prostomial shapes exhibited in the specimens are as described by Orensanz for the other specimens he discussed, and all other characteristics fall within the ranges described. Most records of the species are from the Antarctic, particularly the deep southeast Pacific Basin (Orensanz, 1990), but it is also reported from the Scotia Sea, south of the Falkland Islands region. The record is also at the shallow end of the reported depth range and so a more tentative assignment is considered appropriate. This is the first and, so far only, report of the species from the Falkland Islands region and differs from the only other specimen here attributed to the genus (*Leptoecia* sp., see earlier) in having simple, unidentate falcigers on chaetiger 1 only (*Leptoecia* sp. has pseudocompound falcigers on first two pairs of parapodia with those on chaetiger 1 being unidentate and those on chaetiger 2 bidentate) and a pointed, ‘helmet-shaped’ prostomium (as opposed to slightly bilobed or pointed).

Distribution

Falkland Islands (Figure 1): Northeast of Burdwood Bank (south of the Islands) in 1879–1886 m (Hartman, 1967). Wider distribution: circum-Antarctic in deep water (1879–4946 m; Orensanz, 1990).

Genus *Nothria* Malmgren, 1867

Type species *Onuphis conchylega* Sars, 1835

Diagnosis (from Budaeva, 2021)

Body short, up to 100 segments. Antennae with antennophores consisting of 2–5 rings and short to moderately long styles. Median antenna longer than lateral antennae. Nuchal organs straight with narrow middorsal separation. Anterior 2–3 pairs of parapodia enlarged, directed anteroventrally with large auricular prechaetal lobes. Ventral cirri subulate on first 2–3 chaetigers. Branchiae present or absent, single to up to five filaments. Uni-, bi- or tridentate simple or pseudocompound falcigers on first 2–3 pairs of anterior parapodia. Pectinate chaetae wide with rolled margins, so-called ‘scoop-shaped’, from chaetigers 2–3, in one species from chaetiger 9; rarely pectinate chaetae flat. Paired hooded subacicular hooks from chaetigers 7–15. Maxillae V present; Mx VI absent. Tubes dorsoventrally flattened with thin inner parchment-like layer covered with large shell fragments, small stones, and shells foraminiferans.

Nothria anoculata Orensanz (1974a)

Figure 1, 10A–H; Table 1; S1

Nothria conchylega anoculata Orensanz, 1974a: 99, pl. 8.

Nothria nr *conchylega*. — Hartman, 1967: 90 (in part: stns 350, 369).
 ?*Paronuphis antarctica*. — Hartman, 1967: 96–97 (in part).
Nothria anoculata. — Orensanz, 1990: 44–48, pl. 9a–m, fig. 14. — Neal *et al.*, 2020: 66.

Type Locality

Western Atlantic: off Argentina, Buenos Aires Province; 700–900 m.

Diagnosis

Eyes absent. Ventral cirri on chaetigers 1–2. Branchiae present from chaetiger 10–14, single filament. Simple and pseudocompound falcigers present: unidentate, simple on chaetiger 1; unidentate simple and unidentate and bidentate pseudocompound on chaetiger 2; bidentate pseudocompound on chaetiger 3. Bidentate subacicular hooks from chaetigers 12 or 13. Pectinate chaetae scoop-shaped, flat, up to 10 denticles, up to 19 per parapodium, number reducing posteriorly.

Material Examined

as ?*Paronuphis antarctica*: USNM 58439 (1); as *Nothria anoculata*: USNM 58193 (32); USNM 98048 (1); NHMUK 2018.23592 (1); NHMUK 2018.23473 (1); NHMUK 2018.23538 (1).

Description

Three specimens were available to examine from Neal *et al.* (2020), two originally identified as *Nothria anoculata* and one that had been re-identified from *Anchinotthria* cf. *pyncnobranchiata*. In addition, 34 specimens from Hartman (1967) were examined – one juvenile re-identified from ?*Paronuphis antarctica* (see earlier), one from east of the Islands and 32 from stn 350, south of Burdwood Bank just outside of the region. The two specimens from Neal *et al.* (2020), correctly identified as *Nothria anoculata*, were complete, one with eggs. The remaining specimens, that had previously been misidentified, were posteriorly incomplete. The following description encompasses all specimens excluding those from stn 350 outside of the region although those are discussed in the Remarks.

Two complete specimens (Figure 10A) with 30 and 36 chaetigers, L10 = 2.5–3.6 mm, W10 = 1.1–1.5 mm, TL = 11.6–14.7 mm; three posteriorly incomplete specimens with 15–21 chaetigers, L10 = 2.4–4.6 mm, W10 = 1.1–1.3 mm, TL = 3.8–5.75 mm. Prostomium with rounded anterior margin, very weakly incised; frontal and upper lips oval. Palpo- and antennophores with two short and one long ring with moderately long styles. Palps reaching chaetiger 1, lateral antennae reaching chaetiger 7–9 (4 in juveniles), median antenna reaching chaetiger 12–13 (6 in juveniles) (Figure 10B, C). Eyes absent. Peristomium half as long as first chaetiger. Peristomial cirri slender, slightly longer than peristomium, inserted distally on peristomium in line with lateral antennae.

First two pairs of parapodia modified, enlarged, directed anteroventrally (Figure 10B), first pair more than second, with large auricular prechaetal lobes. Ventral cirri subulate on chaetigers 1–2 (Figure 10B). Branchiae present, from chaetiger 10–14, single strap-like filament only.

First pair of parapodia with 3–5 simple, unidentate falcigers (Figure 10D). Second pair of parapodia with 1–2 simple, unidentate falcigers (Figure 10E) and 2–3 pseudocompound, uni- or bidentate falcigers, 1–2 limbate chaetae and 10–17 flat, scoop-shaped pectinate chaetae with up to 10 denticles. Third pair of parapodia with 3 bidentate, pseudocompound falcigers (Figure 10F), 2 limbate chaetae, and up to 19 scoop-shaped pectinate chaetae (Figure 10G). From chaetiger 4 with up to 4 limbate and 3–8 pectinate chaetae; bidentate subacicular hooks (Figure 10H) from chaetiger 12 or 13. Tubes with thin, inner parchment-like layer with large irregular pebbles attached (Figure 10A).

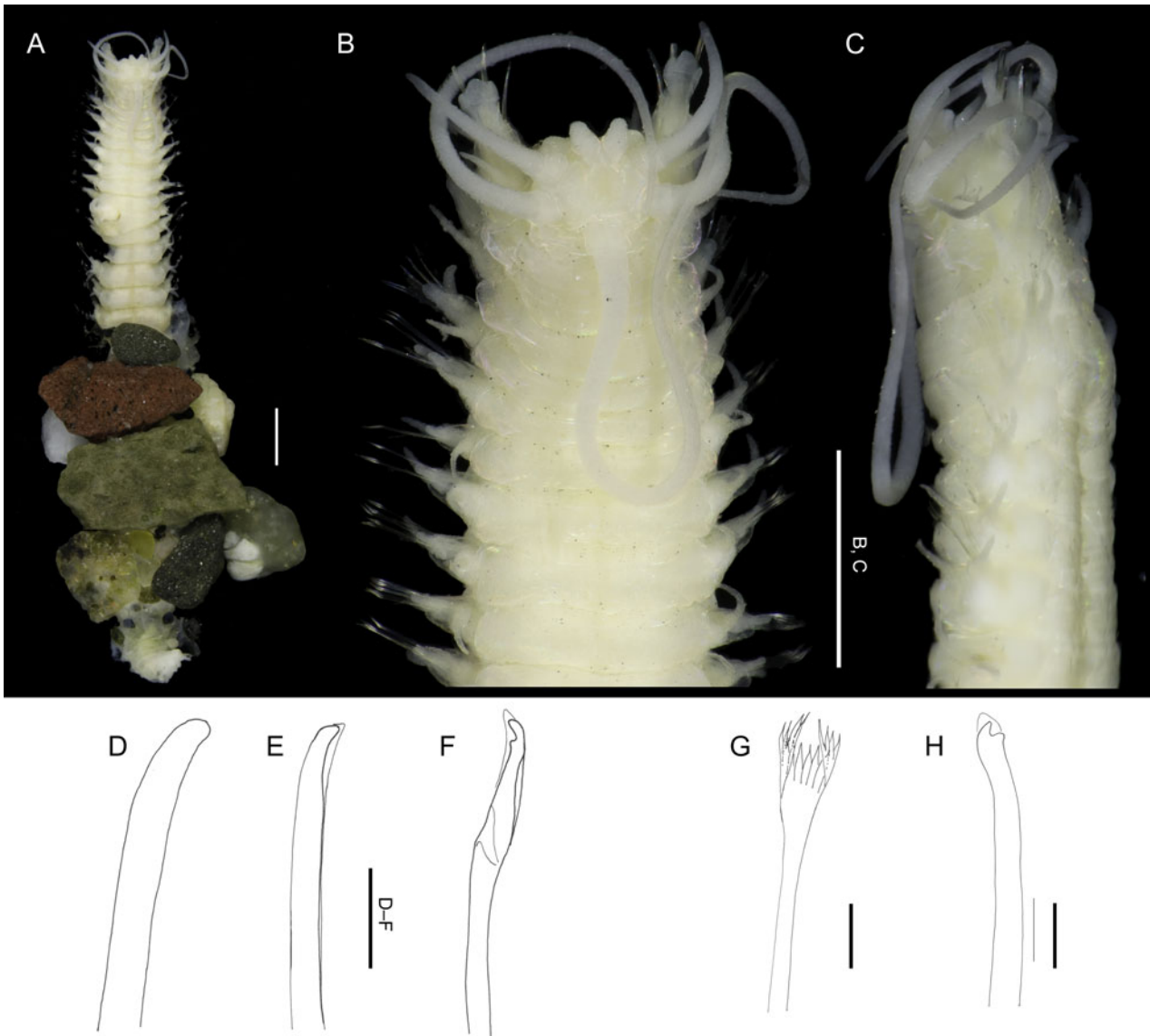


Figure 10. *Nothria anoculata*: NHMUK 2018.23473 (A) whole specimen in tube; (B) dorsal view; (C) lateral view; (D) simple, unidentate falciger, chaetiger 1; (E) simple, unidentate falciger, chaetiger 2; (F) bidentate pseudocompound falciger, chaetiger 3; (G) pectinate chaeta, chaetiger 5; (H) subacicular hook, chaetiger 11. Scale bars: A–C, 1 mm; D–F, H, 50 µm; G, 50 µm.

Remarks

Nothria anoculata was not described when Hartman identified the specimens for her 1967 publication and she clearly recognized that they did not fit any description available at the time, placing those from stn 350, just outside the Falkland Islands region, as *Nothria* nr *conchylega* but not reporting those from station 558. Orensanz (1990) noted that several specimens from Hartman's stn 350 showed some variation and could represent a different species, however, of those specimens examined, all fit within the description for *Nothria anoculata* and were consistent with the specimens examined from the other stations. The Falkland Islands specimens (Neal *et al.*, 2020), from up to 1837 m depth just within Orensanz' considered range, also conform to the original description. Some falcigers in chaetiger 1 of the smallest specimens, did demonstrate a 'semi-pseudocompound' appearance as opposed to having simple hooks only in chaetiger 1. Orensanz (1990), however, illustrated three stages of development in the species, the second of which could demonstrate both simple and pseudocompound hooks in chaetigers 1 and 2. He also stated that the pseudocompound falcigers of chaetiger 2 were replaced

by simple ones later in development, as also documented in more detail by Budaeva and Paxton (2013). Due to the small size of the Falkland Islands specimens, it is likely that the variation noted in chaetiger 1 is due to the incomplete development of the specimen and, in the mature specimen (indicated by the presence of eggs in the tube), simple falcigers are evident in chaetiger 2 as well as pseudocompound ones. These variations in the falcigers are therefore considered to be due to the incomplete development of the specimens and are not considered significant. All specimens fit the description for the species in all other respects.

Distribution

Falkland Islands (Figure 1): East of the Falkland Islands and East Falklands Basin, 646–1837 m (Neal *et al.*, 2020) and just outside the region to the south of Burdwood Bank in 2452 m. Wider distribution: subantarctic areas around Tierra del Fuego, off Argentina, north of Drake Passage, South Georgia shelf, Pacific-Antarctic, and Macquarie ridges, Antipodes-Bounty and Prince Edward-Marion shelves (75–1887 m) (Orensanz, 1990).

Genus *Hyalinoecia* Malmgren, 1867
Type species *Nereis tubicola* Müller, 1776

Diagnosis (from Budaeva, 2021)

Small to large-sized worms up to 20 cm long with up to 200 chaetigers. Prostomium anteriorly rounded with oval or ovoid frontal lips. Antennae with antennophores with 2–5 rings and long styles reaching chaetiger 8–20. Median antennae longer and thicker than lateral antennae. Nuchal organs are straight with small to moderately large middorsal separation. Peristomial cirri absent. Anterior 2–3 pairs of parapodia modified, moderately prolonged, with large auricular prechaetal and subulate postchaetal lobes. Ventral cirri are subulate on anterior 3–4 chaetigers. Branchiae from chaetiger 18–33, single, strap-like filaments, or absent. Pseudocompound falcigers on modified parapodia uni- to bidentate, simple to pseudocompound, with or without hoods. Flat pectinate chaetae from chaetiger 2, with up to 20 denticles. Paired bidentate hooded subacicular hooks from chaetiger 15–30. Maxillae V present; MxVI absent. Tubes round in transverse section, translucent quill-like, completely secreted by worm and lacking external covering of foreign particles. Anterior and posterior ends of the tube with 2–4 internal valves.

Hyalinoecia falklandica sp. nov.

Figure 1, 11A–E, 12A–I; Table 1, 3; S1

Hyalinoecia tubicola. – Hartman, 1967: 89 (in part: stns 557, 558).

Hyalinoecia artifex. – Orensanz, 1990: 52–54, pl.12a–l, fig. 15.

Leptoecia vivipara. – Neal *et al.*, 2020: 66 (in part).

Type Locality

East Falkland Islands; –51.942, –56.642; 855–866 m.

Diagnosis

Peristomial cirri absent. Eyes absent. Ventral cirri on chaetigers 1–3 or 4. Branchiae present from chaetiger 26–27, single filament.

Simple, unidentate falcigers on chaetigers 1–2. Two bidentate subacicular hooks from chaetigers 23–37. Pectinate chaetae flat, transverse, up to 12 denticles, up to 5 per parapodium.

Type Material

USNM 1682921 (holotype); USNM 1682922 (2 paratypes).

Additional Material Examined

as *Hyalinoecia stricta*: USNM 058016 (9); as *Hyalinoecia artifex*: USNM 058019 (6); as *Leptoecia vivipara*: NHMUK 2018.23562 (1).

Description

Description based on holotype unless otherwise stated. Holotype complete (Figure 11A) with 153 chaetigers, L10 = 15 mm, W10 = 4 mm, TL = 97 mm, tube = 175 mm; two paratypes complete with 105 chaetigers, L10 = 14–15 mm, W10 = 4 mm, TL = 80–85 mm.

Dark brown pigmentation is present (holotype only) on anterodorsal and anteroventral region of prostomium (Figure 11B, C), dorsal region of upper lips around the posterior edge of ventral lips, around ventral and lateral border of palpophores and on anterior surface of parapodia from chaetiger 1; cuticle iridescent. Prostomium with rounded anterior margin; frontal lips and upper lips globose. Palpo- and antennophores short (Figure 11B, C) with two basal rings and one slightly longer ring, styles long; palps reaching to chaetiger 1, lateral antennae to chaetiger 9, median antenna to chaetiger 12 (Figure 11B, C). Eyes absent. Peristomium less than half as long as first chaetiger, with middorsal anterior fold. Peristomial cirri absent.

First four pairs of parapodia are modified, enlarged, with auricular prechaetal and subulate postchaetal lobes, directed anteroventrally (Figure 11B–D). Chaetiger 1 $\sim\frac{1}{3}$ longer than chaetiger 2. Postchaetal lobes long, reducing in size from about chaetiger 13, shorter than the prechaetal and acicular lobes

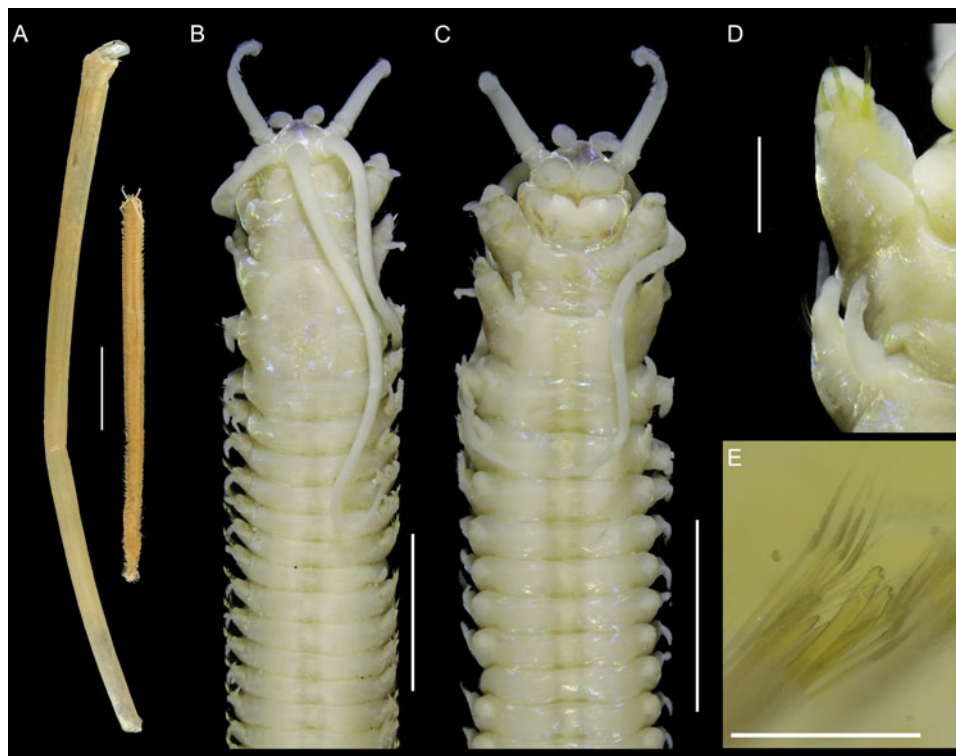


Figure 11. *Hyalinoecia falklandica* sp. nov.: Holotype USNM 1682921 (A) whole specimen, dorsal view, with tube; (B) dorsal view; (C) ventral view; Paratype USNM 1682921 (D) close-up view of chaetiger 1, illustrating auricular prechaetal lobe and simple falcigers; Holotype USNM 1682921 (E) subacicular hooks, emergent aciculae and limbate chaetae of chaetigers 88–89. Scale bars: A, 10 mm; B–E, 1 mm.

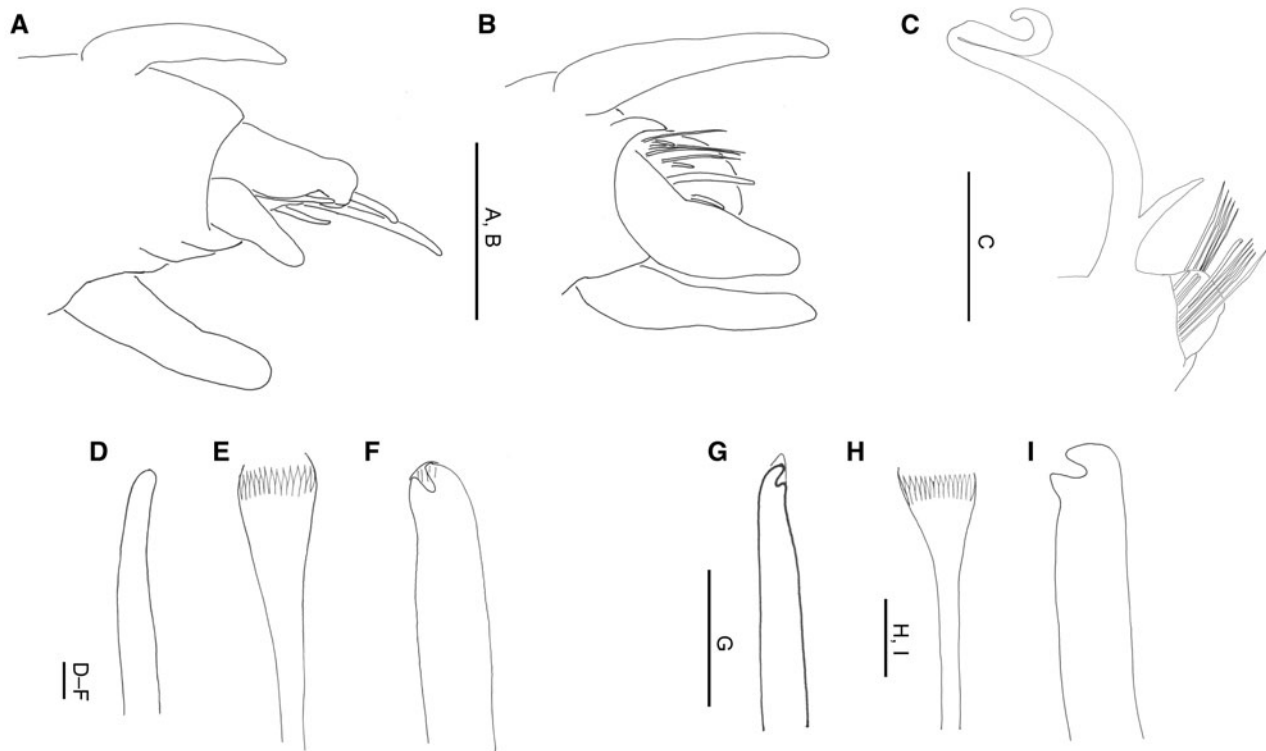


Figure 12. *Hyalinoecia falklandica* sp. nov.: Paratype USNM 1682921 (A) chaetiger 1, posterior view; (B) chaetiger 2, posterior view; (C) chaetiger 37, anterior view; USNM 58019 (D) simple, unidentate falciger, chaetiger 1; (E) pectinate chaeta, chaetiger 105; (F) subacicular hook, chaetiger 105; USNM 58016 (G) simple, bidentate falciger, chaetiger 2; (H) pectinate chaeta, chaetiger 79; (I) subacicular hook, chaetiger 80. Scale bars: A–C 1 mm; D, 100 μ m; E–F, 10 μ m; G, 20 μ m; H–I, 20 μ m.

from around chaetiger 30–35, absent by chaetiger 50. Ventral cirri subulate on chaetiger 1–3 or 4 (Figure 11C, 12A–B). Branchiae from chaetiger 27 to end of body, single strap-like filament (Figure 12C), reaching to or just past mid-line of body.

First two pairs of parapodia with simple, unidentate falcigers (Figures 11D, 12A–B, 12D), 4 or 5 in each parapodium; limbate and pectinate chaetae present from chaetiger 2. Limbate chaetae (Figure 11E) present throughout body, except chaetiger 1, up to 14 per parapodium. Pectinate chaetae flat, transverse (Figure 12E, H), up to 5 per parapodium in anterior chaetigers with up to 12 denticles. Three blunt aciculae emerging from chaetiger 7, to end of body (Figure 11E); bidentate subacicular hooks (Figures 11E, 12F, 12I) from chaetiger 37, two per parapodium, teeth angled approximately 45° to main axis.

Pygidium with two long, thin anal cirri, ventrally inserted. Tube tough, translucent, cylindrical, smooth, slightly curved.

Variation

USNM 58016 consists of nine specimens in tubes, all of similar size, most in poor condition due to inadequate in-tube preservation; USNM 58019 consists of six specimens, none with tubes. In addition, a single juvenile specimen from Neal *et al.* (2020), previously mis-identified as *Leptoecia vivipara* (see earlier) is here re-assigned to *Hyalinoecia falklandica* sp. nov.

Twelve incomplete specimens with 64–112 chaetigers, L10 = 6.7–18 mm, W10 = 1.6–5 mm, TL = 22–82 mm; four complete specimens with 66–174 chaetigers, L10 = 4.7–16 mm, W10 = 0.8–4 mm, TL = 22.5–135 mm; tubes 48–76 mm long. Antennophores with 1–2 basal rings, lateral antennae reaching to chaetiger 5–14, median antenna to chaetiger 9–14. Branchiae present from chaetiger 26 or 27, consistent across all sizes examined. Smaller specimens (USNM 58016: TL 23–34 mm) with up to four simple, bidentate falcigers (Figure 12G) with short, pointed hoods on chaetiger 1, chaetiger 2 with up to three simple,

bidentate falcigers on each side; smallest specimen (NHMUK 2018.23562) with both pseudocompound and simple bidentate falcigers in chaetigers 1 and 2. Bidentate, subacicular hooks present from chaetiger 23–37, from chaetiger 12 in the smallest specimen; up to four in posterior chaetigers of some larger specimens. Small specimens (USNM 58016) with teeth of subacicular hooks angled at 30° to main axis (Figure 12I).

Remarks

Specimens identified by Hartman (1967) as *Hyalinoecia tubicola*, from the station 558, were re-assigned to *H. artifex* by Orensanz (1990) after his examination, along with others from station 557 that he did not examine. Specimens of *H. tubicola* from the station 377, he re-assigned to *Leptoecia* cf. *benthaliana* (see earlier). A search of the collection catalogue at the Smithsonian National Museum of Natural History also brought to light additional specimens that had been identified as *Hyalinoecia stricta* by Hartman, also from stations 557 and 558, although never published as such nor mentioned by Orensanz in his later works. Orensanz (1990) recorded in his publication that he did not examine the *Hyalinoecia* specimens from station 557, however, he re-assigned them to *H. artifex* along with those from station 558. No other specimens of *Hyalinoecia* from stations 557 or 558 were found when searching the catalogue, suggesting that those examined here are the same as those recorded by both Hartman and Orensanz.

Morphological characters were consistent between specimens from station 557 and those from station 558 that Orensanz (1990) had re-identified as *H. artifex*. Eyes are absent from all specimens, branchiae are consistent in their start on either chaetiger 26 or 27 and the large falcigers of chaetiger 1 are all simple and unidentate. Small specimens, previously identified as *H. stricta* from stn 558, differ slightly from the larger '*H. stricta*' and '*H. artifex*' (also from station 558), in the presence of simple bidentate

falcigers on chaetiger 2 and subacicular hooks with teeth at a more acute angle (30° vs 45°) to the main axis; all other characters however fell within the same boundaries.

The smallest specimen, a specimen previously misidentified as *L. vivipara* (NHMUK 2018.23562), bears some resemblance to Orensanz' (1974a, 1990) southwest Atlantic variety of *H. tubicola*, with more rounded frontal lips and subacicular hooks starting from chaetiger 12, well before the earliest start of chaetiger 23 on the smallest of the USNM specimens. However, on the aforementioned NHMUK specimen, branchiae start from chaetiger 26 as with the other specimens documented (as opposed to chaetigers 23–24 in Orensanz' southwest Atlantic *H. tubicola*) and the apical tooth of the bidentate anterior falcigers is larger and more rounded than that figured by Orensanz (1974a) for his southwest Atlantic variety. The specimen is therefore included within the new species as it is considered that these characters are most likely a result of the very small size and juvenile status of the specimen, although the potential of there being more than one taxon represented is noted.

Despite Orensanz' comparison to *H. artifex*, several differences are apparent between that description and the current specimens. In Table 3 selected characters are compared for *H. falklandica* sp. nov. *H. artifex*, *H. stricta* and *H. tubicola*. From the table, it can be seen that *H. falklandica* differs from *H. artifex* in the reduction of the postchaetal lobes, number of anterior chaetigers with ventral cirri and the shape of the subacicular hooks, from *H. stricta* in the shape of the falcigers of chaetigers 1 and 2 and the subacicular hooks and from *H. tubicola* in the presence of eyes, the shape of the chaetiger 1 and 2 falcigers and the shape of the subacicular hooks. Orensanz (1974a) considered characters such as the start of the branchiae (within limits) and relative sizes of cirri and antennae to be unimportant due to individual variation, however, when such characters show a consistent and reliable difference, particularly for animals of an equivalent size, they are here considered of high taxonomic value. Ontogenetic variation in falcigers is noted by Orensanz (1990), and further detailed by Budaeva and Paxton (2013), for *Nothria anoculata*, with falcigers developing from pseudocompound to simple and from bidentate to unidentate. Although not specifically detailed for *Hyalinoecia*, this genus may have a similar chaeta progression pattern in ontogeny explaining the discrepancy in the falcigers between the small and the large animals that otherwise share other characters. The start of the subacicular hooks was also noted as having significant variation by Orensanz (1990), and by Mangum and Rhodes (1970) for *H. artifex* although not for *H. tubicola*, however, the shape and presence of a notch proximal to the teeth in *H. tubicola* provide further distinction between the species.

Amongst the currently described species of *Hyalinoecia*, the combination of simple unidentate falcigers, ventral cirri present to chaetigers 3 or 4, branchiae present from chaetigers 26 or 27 to the end of the body (a consistent character across the size range investigated) and subacicular hooks with teeth positioned at an acute angle to the main axis is unique. The presence of some pseudocompound falcigers in the smallest specimen is considered a juvenile character, especially as some simple falcigers are also in place. The presence of bidentate falcigers in the USNM 58016 lot is more problematic and it is not clear if this indicates the presence of a different species in the examined material. The specimens are, however, from the same station as USNM 58019, in which the much larger specimens align with the type specimens here described and so are believed to be part of the same population, just separated due to their size.

None of the currently described species of *Hyalinoecia* were originally described from the southwest Atlantic: 10 of the 19 species were described from the Pacific, two from Australia and New Zealand, six from the north Atlantic, and one from South Africa.

Recent investigation of the reproductive traits of *Hyalinoecia robusta* (Arias and Paxton, 2022) found them unlikely to support widespread dispersal of the species with the conclusion that reports of that species from outside of its native northeast Atlantic range are unlikely to be correct. Although *H. artifex* has been recorded from Patagonia, Strait of Magellan, and the Argentinean slope (Orensanz, 1990) and *H. tubicola* reported as present further north from San Sebastian Island to Uruguay (Orensanz, 1974a), the type locality of *H. tubicola* is off Norway in the northeast Atlantic and the type locality of *H. artifex* is off New England in the northwest Atlantic. The research by Arias and Paxton (2022) adds to the doubt that either taxa might be likely to occur in the southwest Atlantic or any of the other currently described taxa. Despite the lack of molecular data, the morphological data is deemed strong enough to warrant the description of *H. falklandica* as a new species and promote a start toward a more accurate knowledge of *Hyalinoecia* in the southwest Atlantic and reduce the perpetuation of inaccurate species records. All other southwest Atlantic records of *Hyalinoecia*, including those recorded by Orensanz (1974a, 1990) and Hartmann-Schröder (1983), should now be re-evaluated.

Etymology

Hyalinoecia falklandica is named for the Falkland Islands region from where the specimens were collected.

Habitat

Habitat type unknown; slope depths in 571–866 m.

Distribution

Falkland Islands (Figure 1): eastern slope in 646–866 m (Hartman, 1967) and southeast sector of the region in 571 m (Neal *et al.*, 2020).

Family Eunicidae Berthold, 1827

Genus *Leodice* Lamarck, 1818

Type species *Leodice antennata* Lamarck, 1818

Diagnosis (from Zanol and Budaeva, 2021)

Median, lateral antennae and palps present with regular or irregular articulations. Prostomium steep truncate or round. Peristomial cirri present. Maxillae with four or five paired plates and one unpaired plate. Mandibles flat. Limbate chaetae, thin pectinate chaetae, compound bidentate or tridentate falcigers, aciculae, and subacicular hooks present. Aciculae light or dark. Dark aciculae vary in colour along body; anteriormost always lightest but maintain same colour shade. Subacicular hooks light or dark, bidentate, or tridentate. Lateral black dots between parapodia present or absent.

Leodice sp.

Figure 1, 13A–K; Table 1; S1

Eunice pennata: Monro (1930): 118–120, fig. 42. – Orensanz (1990): pl. 17a–f, fig. 18.

Eunice cf. *pennata*. – Neal *et al.* (2020): 60.

Diagnosis

Ventral cirri present. Branchiae pectinate, up to five filaments, from chaetiger 3. Bidentate, compound, hooded falcigers present from chaetiger 1. Aciculae yellow with bent tip. Single subacicular hook, yellow, from chaetigers 15 to 37, start size dependent. Pectinate chaetae present from chaetiger 2, up to 3 per parapodium.

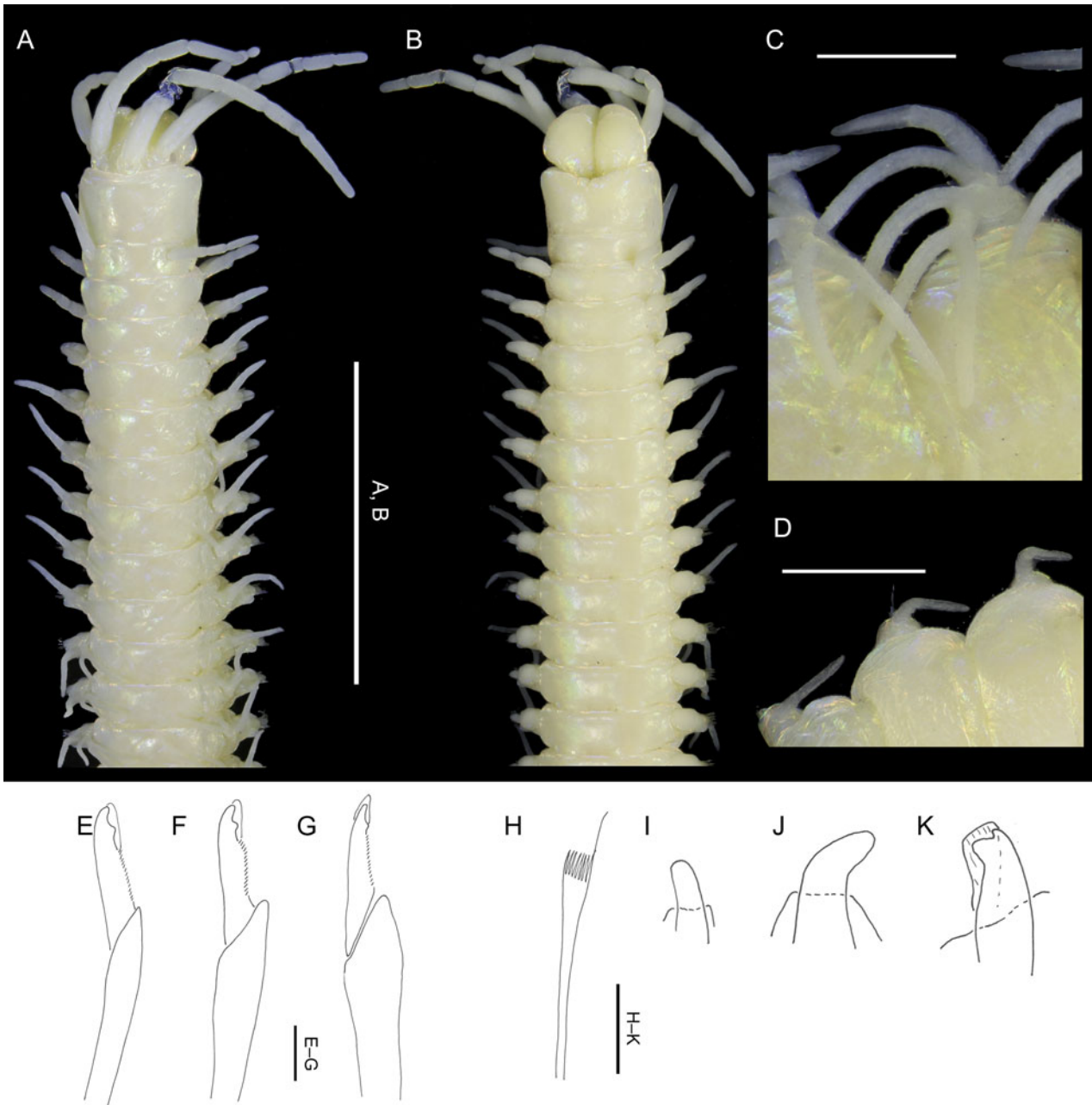


Figure 13. *Leodice* sp.: NHMUK 1930.10.8.1434 (A) dorsal view; (B) ventral view; (C) mid-body region showing pectinate branchiae, chaetigers 26–29; (D) post-branchial end of specimen, chaetigers 46–48; (E) pseudocompound falciger, chaetiger 3; (F) pseudocompound falciger, chaetiger 21; (G) pseudocompound falciger, chaetiger 47; (H) pectinate chaeta, chaetiger 3; (I) aciculum, chaetiger 21; (J) aciculum, chaetiger 44; (K) subacicular hook, chaetiger 47. Scale bars: A–B, 5 mm; C–D, 1 mm; E–H 20 µm; I–K, 50 µm.

Material Examined

as *Eunice pennata*: NHMUK 1930.10.8.1434 (1); as *Eunice* cf. *pennata*: NHMUK 2018.23524 (1); NHMUK 2018.23525 (1); NHMUK 2018.23547 (2).

Description

Description based on Monro’s (1930) specimen. Additional notes in Variation section detail Neal *et al.*’s (2020) specimens.

Single specimen posteriorly incomplete with 48 chaetigers, L10 = 9.5 mm, W10 = 2.35 mm, TL = 36 mm. Colour cream in alcohol, no pigmentation present. Prostomium bilobed, lobes frontally rounded (Figure 13A, B). Prostomial appendages in semicircle. Palps, lateral, and median antennae long with irregular, long articulations, with ring-shaped bases. Median antenna

reaching chaetiger 4, lateral antennae reaching chaetiger 3, and palps reaching to first peristomial ring (Figure 13A, B).

Second peristomial ring approximately half length of first, shorter than following chaetigers; rings clearly separated all round. Peristomial cirri long, articulated, inserted anteromedially on segment, reaching middle of chaetiger 2 (Figure 13A).

Branchiae pectinate with up to five filaments (Figure 13C), from chaetiger 3 to 40; filaments shorter than notopodial cirri to chaetiger 7, thereafter equal to or longer than notopodial cirri. Notopodial cirri long, articulated, increasing in length from chaetigers 1 to 3 (Figure 13A) afterwards stable to end of fragment; articulation clear in the pre-branchial region, becoming fainter to almost indistinguishable in the remaining fragment. Ventral cirri present, digitate on chaetigers 1–4 (Figure 13B), developing defined conical tips over chaetigers 5–8, with oblong

Table 3. Comparison of morphological characters for *H. falklandica* sp. nov. with *H. artifex* (as defined by Mangum and Rhodes (1970)), *H. stricta* (as defined by Moore (1911) with additions from Fauchald (1968*)) and *H. tubicola* (as defined by Mangum and Rhodes (1970)). Range of some characters provided in brackets where known.

Character	<i>H. falklandica</i> sp. nov.	<i>H. artifex</i>	<i>H. stricta</i>	<i>H. tubicola</i>
Type locality	Falkland Islands, 855–866 m	Northwest Atlantic, off New England, 351–668 m	Northwest Pacific, off San Diego, 1937 m	Northeast Atlantic, Norway
Length (mm) recorded during study	23–135	15–180	72–236	35–130
Eyes	Absent	Absent	Absent	Present
Rings on ceratophores	3–4	3–4	3–4	3–4
Lateral antennae reach chaetiger	14	30	13–17	16
Chaetiger 1&2 falcigers	Simple; unidentate or bidentate (juv. only)	Simple; unidentate	Simple; bidentate with globular distal tooth*	Simple; bidentate or tridentate
Postchaetal lobe	Rudimentary by ch.30–35, absent from ch. 50	Rudimentary by ch.50	Not documented	absent from ch. 35
Ventral cirri	1–3 (4)	1–6	Not documented	1–4
Start of branchiae	26–27	29 (26–33)	26–30 (28–31*)	24 (23–28)
Subacicular hooks	(12) 23–37, up to 4; notch absent, teeth at 45° angle to main axis	24–45, up to 3; notch absent, teeth parallel to main axis	Start and number not documented; notch absent, teeth almost parallel to main axis	23–28, up to 5; notch proximal to teeth, teeth at acute angle to main axis

Range of some characters provided in brackets where known.

inflated bases, and conical tips from chaetiger 9. In postbranchial chaetigers, ventral cirri reverting back to digitate over several chaetigers and reducing in size. Prechaetal lobes short, postchaetal lobes as long as or very slightly shorter than chaetal lobes along length of fragment, chaetal lobes rounded.

First pair of parapodia with compound hooded, bidentate falcigers (Figure 13E, F, G) with short blade, ventral to aciculae. Limbate chaetae supra-acicular only, from chaetiger 1. Pectinate chaetae (Figure 13H) from chaetiger 2, up to 3 per parapodium. Aciculae yellow, darkening slightly in post-branchial region; stout, single on first chaetiger, two thereafter, developing pronounced bent tips (Figure 13I–J). Subacicular hooks (Figure 13K) from chaetiger 31, yellow (of similar hue to aciculae), one per parapodium.

Variation

The specimens from Loligo station 1MFA are very small, one whole specimen of 38 chaetigers and one anterior fragment of 11 chaetigers. Both have branchiae from chaetiger 3. In the complete specimen, branchiae end on chaetiger 16 with maximally two filaments. Antennae and palps are articulated. Aciculae are yellow, blunt with bent tips. Subacicular hooks are bidentate, starting from chaetiger 15.

Remarks

Only three specimens represent this species from the Falkland Islands region, one of those is posteriorly incomplete, two more are juvenile. Two additional specimens, published as *Eunice* cf. *pennata* by Neal *et al.* (2020) from the Inflexible exploration area, were re-assigned to Onuphidae indet. and are not discussed here.

Fauchald (1974) noted a wide variability in reports of *Leodice pennata* and suggested that they indicated that more than one species may be involved. Later (1992), Fauchald discussed the wide-ranging bi-polar distribution, stating that reports of the species from the southern hemisphere (Hartman, 1964, 1967) required confirmation. Zanol and Budaeva (2021) state that although worldwide distribution has been reported for some species, more modern

investigative work is now finding that such taxa are, generally, complexes of cryptic species with more narrow distributions. Orensanz (1990) also referred to Fauchald's comments regarding the potential for additional species but could not find any definitive differences in those specimens he determined as *L. pennata* to identify them as a different species. In a review of *Eunice* species (1992), Fauchald stated the identifying character for *L. pennata* as the presence of ring-shaped bases in posterior notopodia (a character only shared by one other species). Orensanz (1990) did provide a figure of a posterior parapodium (the 60th) as part of the description of his *L. pennata* specimens, however, a ring-shaped base was not apparent nor mentioned. Examination of Monro's (1930) and Neal *et al.*'s (2020) specimens found no evidence of ring-shaped bases in posterior notopodia (Figure 13D) either. Fauchald's description of ring-shaped bases was only that they were 'post-branchial', and, except for the short anterior fragment, specimens still had a significant portion of post-branchial chaetigers so it is therefore assumed that this feature should have been present for them to represent *L. pennata sensu stricto*.

Leodice antarctica (Baird, 1869), described from Antarctic Seas (actual type locality unclear), also has branchiae starting on chaetiger 3, yellow aciculae and subacicular hooks, and cylindrical articulations on the antennae. Historically, *L. antarctica* has been synonymized with *L. pennata* (Monro, 1936; Hartman, 1964) and, after examining the type of material, Orensanz (1990) also considered it so. Fauchald (1992), however, also found the species to be very similar to *L. pennata* but determined there to be verifiable differences in the branchiae (up to five filaments that are shorter than notopodial cirri in *L. antarctica* but up to 12 filaments that are longer than notopodial cirri in *L. pennata*) and the articulations of the notopodial cirri (present throughout the body in *L. antarctica* but absent from the branchial region on *L. pennata*). Arguably, the specimens here are closer to *L. antarctica* than to *L. pennata*, with branchiae with five filaments and the absence of the post-branchial cirrophores. However, there are still discrepancies with *L. antarctica*: the branchial filaments are only shorter than the notopodial cirri in the

pre-branchial region and articulation of notopodial cirri becomes unclear through the branchial region with most of the post-branchial region absent. This, combined with the limited distribution capacity of most *Eunice* species (Zanol and Budaeva, 2021) making the presence of *L. antarctica* around the Falkland Islands doubtful, means that identification was deemed better left at genus level than to assign a poorly-matched species name and potentially introduce another doubtful record to the area.

In the wider Magellan region, *Eunice magellanica* McIntosh, 1885, is recorded from southwest Chile to Argentina (Rozbaczylo, 1985; Orensanz, 1974b, 1990) but has branchiae from chaetiger 7 and black aciculae. *Eunice frauenfeldi* Grube, 1866, also recorded from the region, has branchiae from chaetiger 6 but was originally described from St Paul's Island in the Indian Ocean, with records probably incorrectly attributed to the name due to the previous synonymy of *E. magellanica*.

Distribution

Falkland Islands (Figure 1): east (115 m; Monro, 1930) and north-east (1321 m; Neal *et al.*, 2020) of the Islands.

Genus *Marphysa* de Quatrefages, 1866 (1865)
Type species *Nereis sanguinea* Montagu, 1813

Diagnosis (from Zanol and Budaeva, 2021)

Median antenna, lateral antennae, and palps present. Peristomial cirri absent. Maxillae with four paired plates and one unpaired plate. MxI falcate arch extended rectangular; basal inner edge lacking a curvature. Mandibles flat. Branchiae distributed along most of the body. Neuropodial postchaetal lobes longer than chaetal lobes at least in anteriormost parapodia. Limbate chaetae, pectinate chaetae, aciculae, and subacicular hooks present; bidentate falcigers and spinigers present or absent. Thin pectinate chaetae with both outer teeth longer than inner teeth; inner teeth of equal length. Thick pectinate chaetae present. Subacicular hooks light or dark, falcate, or bidentate.

Marphysa sp.

Figure 1, 14A–J; Table 1; S1

Marphysa corallina. – Fauvel, 1916: 432–3, Pl.XI fig. 50–52

Marphysa aenea. – Orensanz, 1990: 70, Pl.18, figs a–f. – Darbyshire, 2018: 31, 37.

Diagnosis

Ventral cirri on chaetigers 1–2. Branchiae present from chaetiger 10 to 14, single filament. Supra-acicular limbate chaetae and bidentate compound falcigers with short blade on all parapodia. Anterior chaetigers with isodont pectinate chaetae with thin shafts, narrow blade, and short teeth; median chaetigers with isodont pectinate chaetae with thin shafts and narrow and wide blades. Posterior chaetigers with isodont pectinate chaetae with thin shafts and wide blade and up to three asymmetrical anodont chaetae, with thick, short shaft and wide blade and up to 6 long, thick teeth. Subacicular hooks single, unidentate from chaetiger 16–34.

Material Examined

East Falkland: NMW.Z.2011.039.0233 (1); NMW.Z.2011.039.0234–235 (2); NMW.Z. 2011.039.0236 (1); NMW.Z.2012.082.0232–235 (8); NMW.Z.2012.082.0236–237 (4); NMW.Z.2012.082.0219, 0220, 0223 (24); NMW.Z.2012.082.0224 (1); NMW.Z.2012.082.0225–227 (3); NMW.Z.2012.082.0221 (1); NMW.Z.2012.082.0228 (2); NMW.Z.2015.002.0009 (1); *West Falkland*: NMW.Z.2012.082.0222, 0238–240 (6); NMW.Z.2012.082.0229 (1); NMW.Z.2012.082.0230–231 (4).

Comparative Material Examined

Marphysa corallina: NHMUK 1928.4.26.181 (1); *Marphysa aenea*: NHMUK 1963.3.1 (1).

Description

Complete specimens with 58–255 chaetigers, L10 = 2.15–16.25 mm, W10 = 0.5–6.25 mm, TL = 10–169 mm. Description based on best specimen (complete, best representing all characters: NMW.Z.2012.082.0232) with variations shown detailed in following section.

Prostomium bilobed, 1.5 mm long, 3.5 mm wide, lobes anteriorly rounded (Figure 14A, B); median sulcus shallow, reaching $\frac{1}{3}$ length of prostomium, and ventral sulcus deep (Figure 14A, B). Palps, lateral and median antennae short, blunt (but see Variation below), reaching second peristomial ring where complete (Figure 14A). Palpo- and antennophores ring-shaped, short, thick; styles tapering, without articulation. Eyes present, situated between palps and lateral antennae.

Peristomium slightly longer than prostomium, first ring nearly twice as long as second, separation between rings distinct on all sides (Figure 14A–C). Second peristomial ring slightly shorter than first chaetiger. Peristomial ventrolateral lips present as elevated surfaces (Figure 14B).

Maxillary apparatus (Figure 14D, E) with MF = 1 + 1, 6 + 5, 7 + 0, 4 + 6, 1 + 1. Maxillary carriers half the length of MI with pair of oval wings situated at lateral margins. MI forceps-like, maxilla with falcate arch extended, well developed; MII with distal teeth largest; MIII short, curved, with blunt teeth. Left MIV longer than wide, teeth blunt; right MIV with second and third teeth larger. MV rectangular, longer than wide (Figure 14E). Mandibles dark, rectangular with whitish cutting plates (Figure 14F).

Branchiae pectinate, up to 4 filaments, from chaetiger 14, absent from posterior fifth of body. Branchial filaments longer than notopodial cirri except in posteriormost parapodia.

Notopodial cirri without articulation; longer than ventral cirri, digitiform, decreasing in size after branchiae start. Prechaetal lobes as transverse folds in all chaetigers. Chaetal lobes rounded, with aciculae emerging in midline, longer than other lobes. Postchaetal lobes best developed in pre-branchial chaetigers then reduced in size, becoming shorter than acicular lobe by chaetiger 40. Ventral cirri elliptical in chaetigers 1–2, becoming globular with obtuse tip from chaetiger 4 onwards then more pad-like with small tip from start of branchiae; digitiform in posteriormost chaetigers. Aciculae blunt, straight, black (Figure 14G), up to 5 per parapodium, highest number of aciculae in pre-branchial chaetigers.

Limbate chaetae supra-acicular only. Pectinate chaetae present: isodont chaetae with thin shafts, narrow blade, and short teeth in both anterior and median chaetigers; wide blade isodont chaetae with thin shafts and short teeth in both median chaetigers and posterior chaetigers. Up to three asymmetrical anodont chaetae, with thick, short shaft and wide blade and up to 6 long, thick teeth (Figure 14H) present in posterior chaetigers also. Compound falcigers bidentate with short blade, both teeth blunt, distal marginally smaller, no significant variation along body. Subacicular hooks unidentate (Figure 14I), paler than aciculae, slightly curved distally, from chaetiger 33 (L), 31 (R), one per parapodium.

Pygidium with anus terminal. Two pairs of ventral cirri, dorsal pair longer than ventral pair (Figure 14J). Ventral pair missing in majority of specimens.

Variation

Several morphological features of *Marphysa* have previously been shown to vary relative to body size (Molina-Acevedo and Carrera-Parra, 2015, 2017) including first branchial chaetiger (12–24), number of branchial filaments (1–4), number of aciculae

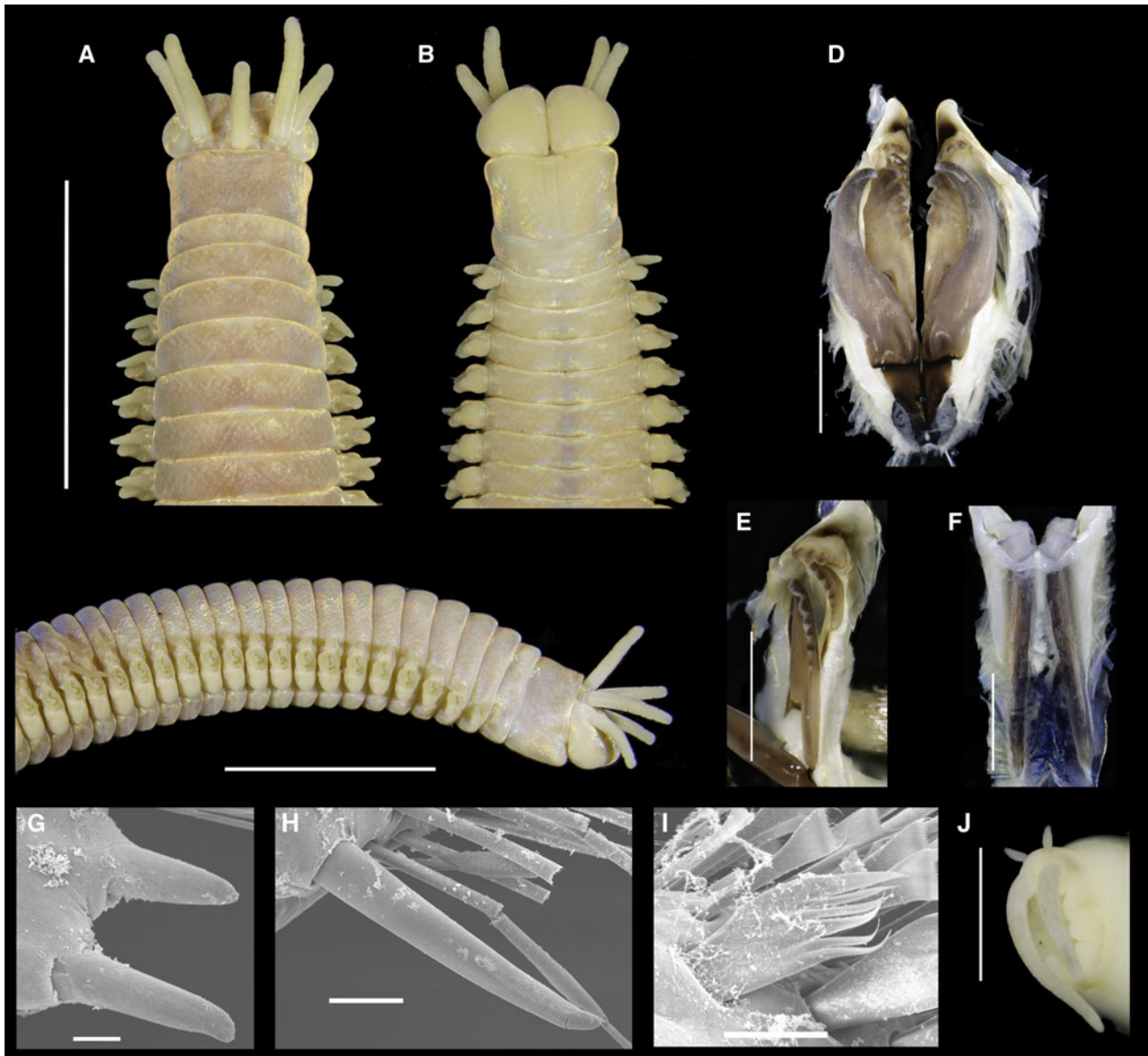


Figure 14. *Marphysa* sp.: NMW.Z.2012.082.0225. (A) dorsal view; (B) ventral view; (C) lateral view; NMW.Z.2012.082.0226 (D) Maxillae; (E) lateral view of left maxillae II–IV; (F) mandibles; NMW.Z.2011.039.0234. (G) aciculae, chaetiger 71; (H) subacicular hook, chaetiger 71; (I) anodont pectinate chaeta, chaetiger 212; NMW.Z.2012.082.0231. (J) pygidium. Scale bars: A–C, 5 mm; D–F, J, 1 mm; G, 20 μ m; H–I, 50 μ m.

(1–6), and start of subacicular hooks (chaetigers 16–34) which frequently appear on different segments of an animal by 1–2 chaetigers.

Juveniles with less than around 60 chaetigers possessed a second pair of minute eyespots at the anterior of the prostomium (larger animals with single pair only as in main description) as well as occasionally lacking or having poorly developed lateral antennae. Palps and antennae on larger animals frequently appeared blunted giving a generally digitiform appearance, however the tips of the styles are easily broken.

Subacicular hooks were bidentate in smaller specimens of less than around 100 chaetigers, becoming unidentate thereafter, generally 1 per parapodium, occasionally 2. Aciculae were always unidentate, even in juveniles.

Remarks

Fauvel (1916) described specimens of *Marphysa* from a single intertidal location in the Falkland Islands, calling the species *Marphysa corallina*, a species originally described from Hawaii (Kinberg, 1865). Orensanz (1990) later re-assigned Fauvel's specimens to *Marphysa aenea*, a species described from the Pacific

coast of Chile, although he did not re-examine any of the specimens. One specimen from Fauvel's original description was available from Natural History Museum, London and was examined and confirmed as the same as those described here.

The specimens from the Falkland Islands are part of the *Marphysa-aenea* group (sensu Glasby and Hutchings, 2010) with composite falcigers only in the sub-acicular region and branchiae present into the posterior of the body (Group C2 of Fauchald, 1970). Within that group, the deeply divided prostomium, dark (black) unidentate aciculae and pale subacicular hooks that are slightly curved distally, distinguish it from most other species in the group and place it as most similar to *Marphysa aenea*, *Marphysa capensis* (Schmarda, 1861), *Marphysa gayi* Quatrefages, 1866 and *Marphysa peruviana* Quatrefages, 1866. *Marphysa quadrioculata* (Grube, 1856) would also fall into this category however it was designated as indeterminate by Fauchald (1970) as well as being described as lacking branchiae.

In agreement with Orensanz (1990), *M. corallina* is discounted for the identification due to having bidentate aciculae (unidentate in *Marphysa* sp.) but *M. aenea*, described with bidentate

subacicular hooks (unidentate in *Marphysa* sp. for equivalent sized specimens), can also be discounted. Unfortunately, the other comparable species (*M. gayi*, *M. peruviana*, *M. capensis*) are represented by very old descriptions lacking details and are in need of modern re-description. The type specimens of *M. gayi* and *M. peruviana*, housed in Paris, were unavailable for loan and no type of material of *M. capensis* could be located. Most, if not all, currently accepted diagnostic characters are missing from the descriptions and no genetic work has been carried out making a definitive identification impossible at the current time. Collaboration is now planned with other researchers looking into these species to provide a more definitive identification in the future.

Distribution

Around the Falkland Islands in intertidal and shallow water rocky habitats (0–18 m) (Figure 1).

Discussion

The majority of publications that have reported taxa of Eunicoidea from the Falkland Islands region date back to the 1960s and earlier. Since that time, taxonomy and knowledge of the two families have changed substantially, many new taxa have been described and others have been synonymized or revised and, consequently, much of the information in those early publications is out of date. The ten taxa reviewed here were represented by another 17 taxon names in the past that were either incorrectly used for them or changed since the original publications, resulting in a challenge for anyone attempting to determine the current situation.

The genus *Kinbergonuphis* currently includes around 40 species and is found worldwide, with most species reported from the western Atlantic Ocean in shallow and intertidal waters (Fauchald, 1982a). Six species are recorded from the southwest Atlantic in particular, although only two of these were recorded specifically from the Falkland Islands region, *Kinbergonuphis dorsalis* in shallow slope depths (around 100 m, Monroe, 1930) and *Kinbergonuphis oligobranchiata* in deep water (1000 m+, Neal et al., 2020). The other four species, *Kinbergonuphis fragilis* (Kinberg, 1865), *Kinbergonuphis difficilis* (Fauchald, 1982b), *Kinbergonuphis orensanzii* (Fauchald, 1982b), and *Kinbergonuphis tenuis* (Hansen, 1882) occur off northern Argentina and Uruguay. No Onuphidae have previously been recorded from shallow (50 m or less) or intertidal habitats around the Islands, although *K. dorsalis* has been recorded intertidally from Punta Arenas (Magellan Strait) and the Argentinean coast (Ehlers, 1897; Hartmann-Schröder, 1962). Previous studies have shown a high similarity between Falkland Islands fauna and other areas of the Magellan biogeographic region (Knox and Lowry, 1977; Montiel et al., 2005a, 2005b; Darbyshire, 2018) as well as a high affinity between Falkland Islands and South Georgia polychaetes (Knox and Lowry, 1977). It might therefore be expected that, similar to *K. dorsalis*, other onuphid taxa that occur along the Atlantic coasts of Chile and southern Argentina also occur in the Falkland Islands. It is less likely to find the species reported from north of the Magellan region boundary. The majority of *Kinbergonuphis* species are either known only from their original type locality or local region and so *K. dorsalis* is unusual in its wide distribution, being recorded from the Pacific coastline of Chile (Wesenberg-Lund, 1962) as well as the Atlantic coasts of Chile and Argentina (Ehlers, 1897; Monroe, 1936; Hartman-Schröder, 1962; Orensanz, 1974a, 1974b, 1990) and the Falkland Islands. No other *Kinbergonuphis* taxa occur along the Magellan Atlantic coast, although others, as previously mentioned, are recorded north of the area as well as from the

Pacific coast of Chile. The wide geographic distribution and variability of several characters, demonstrated by *K. dorsalis*, could indicate a species complex.

A recent study by Hektoen et al. (2022) on *Diopatra* in the East Atlantic, found that despite the genus being well-studied globally, morphological similarities and high intraspecific variation of characters have led to diversity in the genus potentially being significantly underestimated. Using molecular techniques, the study recovered an additional 17 undescribed species, many of which were found to have restricted distributions. The findings are no longer unusual in the field of polychaete research with many species previously thought to be widely distributed, being instead found to represent multiple species with more narrow distributions, sometimes affecting species knowledge over a wide geographic area (e.g. Bleidorn et al., 2006; Barroso et al., 2010; Simon et al., 2019) but sometimes in more localized areas too (e.g. Nygren et al., 2018; Grosse et al., 2020). Although attempts to sequence COI in *Kinbergonuphis* sp. were unsuccessful, despite attempts with more than one set of primers, sequences of 16S were obtained. Unfortunately, in the case of *Kinbergonuphis*, genetic information is only available for one other species, *K. pulchra* (Budaeva et al., 2016), and so cannot help resolve the question of whether multiple species exist under the *K. dorsalis* species name. In the future though, perhaps those sequences obtained will be able to offer some help to other studies.

Except for *O. pseudoiridescens* and *K. dorsalis*, the other onuphid species reported by Orensanz (1974b), for the Atlantic portion of the Magellan region, were originally described from Pacific or northern hemisphere localities. All have since been re-assigned (Orensanz, 1990) to other southern hemisphere species (Table 1) whose distribution in the region is more generally accepted or, in the case of *H. artifex*, re-described as a new species.

Other species that occur within close-by parts of the Antarctic and subantarctic that could be considered as having potential to occur within the Falkland Islands zone include one other species of *Kinbergonuphis*, *Kinbergonuphis notialis* (Monro, 1930), found in Antarctic waters and the Scotia Sea, including South Georgia, but it is not known outside of the Antarctic convergence (Orensanz, 1990). Other subantarctic taxa reported from the Scotia Sea, South Georgia, or other nearby subantarctic islands are, in fact, few. The removal of Hartman's 1967 record from the Falkland Islands now restricts the distribution of *Paradiopatra antarctica* (Monro, 1930) to Antarctic and sub-Antarctic waters (Budaeva and Fauchald, 2011). *Paradiopatra ehlersi* (McIntosh, 1885), a widely distributed taxon around deep areas of the Southern Ocean and elsewhere, is not currently known from the South Atlantic above the subantarctic zone (Budaeva and Fauchald, 2011). Additionally, a single unidentified species of *Diopatra* (for the most part, a warmer water genus: Paxton et al., 1995) was recorded from South Georgia (Orensanz, 1990), *Rhynchobranchium ehlersi* Monro, 1930 is also known from South Georgia and other subantarctic islands (Paxton, 1986b; Orensanz, 1990) and *Nothria abyssia* Kucheruk, 1978 is recorded widely including from the Scotia Sea (Orensanz, 1990) and the Atlantic sector of Antarctica (Budaeva and Paxton, 2013).

The situation in the Eunicidae is much the same as for Onuphidae, with very few additional species reported for the Magellan region, although more records are known for northern Argentina and the Pacific coast of Chile. *Eunice magellanica* was originally described from muddy sediment in the Magellan Strait (McIntosh, 1885) and is also noted as having an association with *Macrocystis* holdfasts (Orensanz, 1990), neither of which habitat was sampled around the Falkland Islands. Mud is uncommon but *Macrocystis* holdfasts offer a wealth of potential habitat that has not yet been investigated so it is feasible that the species

could be present in the shallow waters of the Islands but so far unsampled. Hartman (1964) synonymized *E. magellanica* with *Eunice frauenfeldi* (Hartman, 1964) until it was re-established by Fauchald (1992). *Eunice frauenfeldi*, though, was described from the Indian Ocean and is not considered a valid species for the region here, records more likely to have been incorrectly attributed due to the synonymy of *E. magellanica*. Further south, *Leodice antarctica*, as discussed earlier, is also considered unlikely to occur outside of the region due to the limited distribution capacity of most *Eunice* species (Zanol and Budaeva, 2021). No other *Eunice* or *Leodice* taxa are currently reported for the Magellan region, or any other Eunicidae genera except for *Marphysa*.

The identification of the *Marphysa* specimens collected from the Falkland Islands remains in question. Originally identified as *M. corallina* by Fauvel (1916) and then reassigned to *M. aenea* by Orensanz (1990), the species is shown here to clearly not be the latter either, although *M. aenea* is the only *Marphysa* species currently reported for the Magellan Atlantic coasts. Species of *Marphysa* have come under scrutiny in recent years following the re-description (Hutchings and Karageorgopoulos, 2003) of the widely recorded and considered-to-be cosmopolitan species *Marphysa sanguinea* (Montagu, 1813), with that species now considered far more restricted in its distribution. In South Africa too, another place where *M. sanguinea* had previously been recorded but is now known to be a different species (Lewis and Karageorgopoulos, 2008), research is showing that other *Marphysa* species recorded there have been historically misidentified and have more restricted distributions than previously believed (Kara *et al.*, 2020). One of those species, *M. capensis*, is part of the poorly described group that is most similar to the Falkland Islands specimens. It is hoped that collaboration with researchers in South Africa, as well as South America where the other closely related but poorly defined species *M. gayi* and *M. peruviana* originate, albeit from the Pacific, may resolve taxonomic issues for all the species. It seems apparent that *Marphysa* species generally, are not found over wide geographic areas, but those from South Africa and South America must still be investigated appropriately and so it is essential to get new morphological and molecular data to resolve the situation.

The lack of clarity in some of the species included in this review is a reflection of the problems of working with damaged or juvenile specimens where that is the only material available. Many of the Neal *et al.* (2020) specimens are from deep water sites where retrieval of good quality specimens is more challenging, some taxa were small-bodied or juvenile and generally few specimens were available to enable a comprehensive comparison of characters. Polychaete diversity in the deep sea is known to be highly underestimated and deep sea investigations often report large numbers of new species (e.g. Fiege *et al.*, 2010; Brasier *et al.*, 2016) with misidentifications common due to physically damaged specimens and the pressures involved in identifying large numbers of specimens in a restricted timeframe (Brasier *et al.*, 2016). The vast majority of specimens collected are also fixed or preserved with formaldehyde or other denaturing solutions, as was the case here for all the comparative material borrowed from other institutions, rendering them unusable for genetic studies that might have mitigated the problem of damaged or juvenile specimens. The correction of several misidentified specimens, the description of a new species of *Hyalinoecia*, and a thorough review of the current names of confirmed taxa will help to improve current and future knowledge of the Eunicidea in the Falkland Islands and facilitate more accurate identification. It is to be hoped that the information provided here may also prompt further research or provide a stepping stone for further descriptions if new specimens become available. The fauna of the Falkland Islands region is shown to be more diverse than previously recognized and potentially harbours undescribed species.

Supplementary material. The supplementary material for this article can be found at <https://doi.org/10.1017/S0025315423000966>.

Data availability. The authors confirm that the data supporting the findings of this study are available within the article [and/or its supplementary materials].

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Author contributions. Teresa Darbyshire: collection and preliminary identification of specimens, project concept, DNA sequencing and analysis, review of *Kinbergonuphis* specimens and description of all non-*Kinbergonuphis* specimens; manuscript preparation. Jacob Cameron: analysis, imaging and illustration of *Kinbergonuphis* specimens; DNA sequencing and analysis; manuscript preparation

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Conflict of interest. The authors declare none.

Ethical standards. No vertebrates or regulated invertebrates were involved in this study.

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