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Taxonomy and Biogeography of the Polychaetes of the Falkland Islands Critical Analysis of Published Works

Darbyshire, Teresa

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Taxonomy and Biogeography of the Polychaetes of the Falkland Islands

Critical Analysis of Published Works

Submission by Teresa L. Darbyshire

for the degree of Doctor of Philosophy (Published Works)

**School of Ocean Sciences
Bangor University**

2018

Declaration

I hereby declare that this thesis is the results of my own investigations, except where otherwise stated. All other sources are acknowledged by bibliographic references. This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree unless, as agreed by the University, for approved dual awards.

Yr wyf drwy hyn yn datgan mai canlyniad fy ymchwil fy hun yw'r thesis hwn, ac eithrio lle nodir yn wahanol. Caiff ffynonellau eraill eu cydnabod gan droednodiadau yn rhoi cyfeiriadau eglur. Nid yw sylwedd y gwaith hwn wedi cael ei dderbyn o'r blaen ar gyfer unrhyw radd, ac nid yw'n cael ei gyflwyno ar yr un pryd mewn ymgeisiaeth am unrhyw radd oni bai ei fod, fel y cytunwyd gan y Brifysgol, am gymwysterau deuol cymeradwy.



Teresa Darbyshire

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Finally, to my husband Brendan, who has encouraged me along the way and always had total faith in the importance of doing this work, even using his own holiday time to join me in the Falkland Islands, help me dig up worms on the shore and generally support me while I spent hours looking down the microscope in the evenings: thank you for being there and believing in me.

Teresa Darbyshire, 2018

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General Objectives and Thesis Structure

This submission in candidature of a PhD is based upon Bangor University's 'Regulations for the Award of the Degree of PhD by Published Works (Regulation 05 2009 Version 01)' ('the Regulations').

No part of this thesis has previously been or is currently submitted for another qualification.

In this submission the Published Works comprise a series of 4 papers in peer reviewed academic journals. Details of these papers are presented in Table 1. Copies of the full papers are presented in Appendices 1–4.

Throughout the text in this critical analysis, papers submitted as Published Works will be referred to by their numbering in Table 1 (e.g. '**Paper 1**'), rather than conventional academic referencing style.

Authorship and collaboration

In accordance with point 17 of the Regulations, it is noted that:

“Candidates may submit work(s) completed in collaboration with others in support of the candidature, but such work shall be accompanied by a detailed statement signed by each collaborator indicating the nature and amount of the work done by the candidate.”

Paper 3 is accompanied by a signed statement from the collaborator as to the amount of work contributed by the candidate.

Table 1. Details of peer-reviewed academic journal papers submitted as Published Works.

Paper	Chapter	Reference
1	2. Arenicolidae	Darbyshire, T. 2017. A re-evaluation of the <i>Abarenicola assimilis</i> group with a new species from the Falkland Islands and key to species. <i>Proceedings of the 12th International Polychaete Conference, Cardiff, Wales 2016. Journal of the Marine Biological Association of the U.K.</i> 97(5) : 897–910. doi: 10.1017/S0025315417000741.
2	3. Nereididae	Darbyshire, T. 2014. Intertidal and nearshore Nereididae (Annelida) of the Falkland Islands, southwestern Atlantic, including a new species of <i>Gymnonereis</i> . <i>ZooKeys</i> 427 : 75–108. doi: 10.3897/zookeys.427.7296.
3	4. Chrysopetalidae	Darbyshire, T. & Brewin, P. 2015. Three new species of <i>Dysponetus</i> Levinsen, 1879 (Polychaeta: Chrysopetalidae) from the South Atlantic and Southern Ocean, with a re-description of <i>Dysponetus bulbosus</i> Hartmann-Schröder, 1982. <i>Zootaxa</i> 4040 : 359–370. doi: 10.11646/zootaxa.4040.3.7.
4	5. Maldanidae	Darbyshire, T. 2013a. A new species of <i>Micromaldane</i> (Polychaeta: Maldanidae) from the Falkland Islands, southwestern Atlantic, with notes on reproduction. <i>Zootaxa</i> 3683 : 439–446. doi: 10.11646/zootaxa.3683.4.7.

Structure of this document

The critical analysis presented here provides both a summary and context for the subject area within which the Published Works falls. It is divided into 7 main sections:

- Chapter 1: General Introduction
 - overview of the Falkland Islands and their geographic situation as well as an outline of the purpose of the project that was developed;
 - background of historic taxonomic work that has been carried out on the polychaetes of the Falkland Islands, illustrating the effort, or lack thereof, that has gone into their investigation;
 - the overarching biogeography of the region, its changing terminology and the role of polychaetes within the delineation of the region;
 - Methods and Materials.

- Chapter 2 (**Paper 1**): Arenicolidae

- Chapter 3 (**Paper 2**): Nereididae

- Chapter 4 (**Paper 3**): Chrysopetalidae

- Chapter 5 (**Paper 4**): Maldanidae

- Chapter 6: Revised situation of the knowledge on Falkland Islands Polychaeta
 - results from the fieldwork collections
 - summary of the updated knowledge of taxa in each family
 - cluster analyses and taxonomic distinctness measures illustrating the distribution and taxonomic spread of taxa around the Falkland Islands.

- Chapter 7: Discussion

Abstract

Taxonomic works relating to polychaetes from the Falkland Islands are few and little has been published specifically on them since the early to mid twentieth century. Unusually, the intertidal region has received less attention than subtidal sites with most information coming from Antarctic expeditions that used the Islands as a staging post on their journeys south. Works relating to the wider Magellan region, as well as the Antarctic, are far more numerous. The project detailed by this thesis was conceived to address this dearth of knowledge, put the information gleaned into context with the biogeographical region within which the Falkland Islands sit and to determine whether species distribution around the Islands is affected by the differing current regimes that influence the surrounding waters. In total, 218 taxa are reported, 52 of which have been named so far, including four new species whose published descriptions form part of this document. Over 85% of the named species are already known from the wider Magellan region and significant overlap with South Georgian and Antarctic faunas is also apparent. Cluster analyses and multi-dimensional scaling plots show depth (intertidal versus subtidal) to be the strongest influence on species composition with shore height and sediment type having limited effect and geographic location none. Taxonomic distinctness indices are used to assess the species lists and compare sample sites. Much of the diversity appears to centre on microhabitats such as epifaunal and algal turfs and biogenic encrustations. Syllidae are the most diverse family and dominate some samples, particularly those from epifaunal turf and sieved sediments. Other families appear to use microhabitats, such as epifaunal turf and biogenic encrustations, as nursery areas, with large numbers of juveniles in some samples. Comparisons are made with other intertidal diversity studies from the Scotia Arc and Antarctic.

Definitions

In the context of this document, the terms ‘**diversity**’ and ‘**dominant**’, including related forms of the words, are used according their respective dictionary definitions of ‘variety, multiformity’ and ‘predominant, major, main, chief’. No statistical values or support are inferred by their use. (Definitions taken from www.dictionary.com, accessed 15/10/ 2018).

Chapter 1: General Introduction

1.1 Overview of the Falkland Islands

The Falkland Islands (Las Malvinas) are an archipelago consisting of two larger islands, East and West Falkland, and over 700 smaller islands, situated between latitudes 51°S to 53°S (Figure 1). They are located off the southeast coast of South America in the southwest Atlantic Ocean, approximately 260 nautical miles east of Argentina. The archipelago sits on the Patagonian Shelf, which includes Burdwood Bank to the south (Figure 1), with the majority of the territorial sea reaching less than 100 m in depth and a maximum of less than 200 m (Figure 2).

Geographically, the Islands lie between the Antarctic Polar Front (formerly the Antarctic Convergence) to the south and the Sub-Tropical Front (formerly the Sub-Tropical Convergence) to the north and are classed as cold temperate. The main oceanographic influence is the Falklands (Malvinas) Current, a north-flowing offshoot of the Antarctic Circumpolar Current (ACC; formerly known as ‘West Wind Drift’), which circumnavigates the Southern Ocean

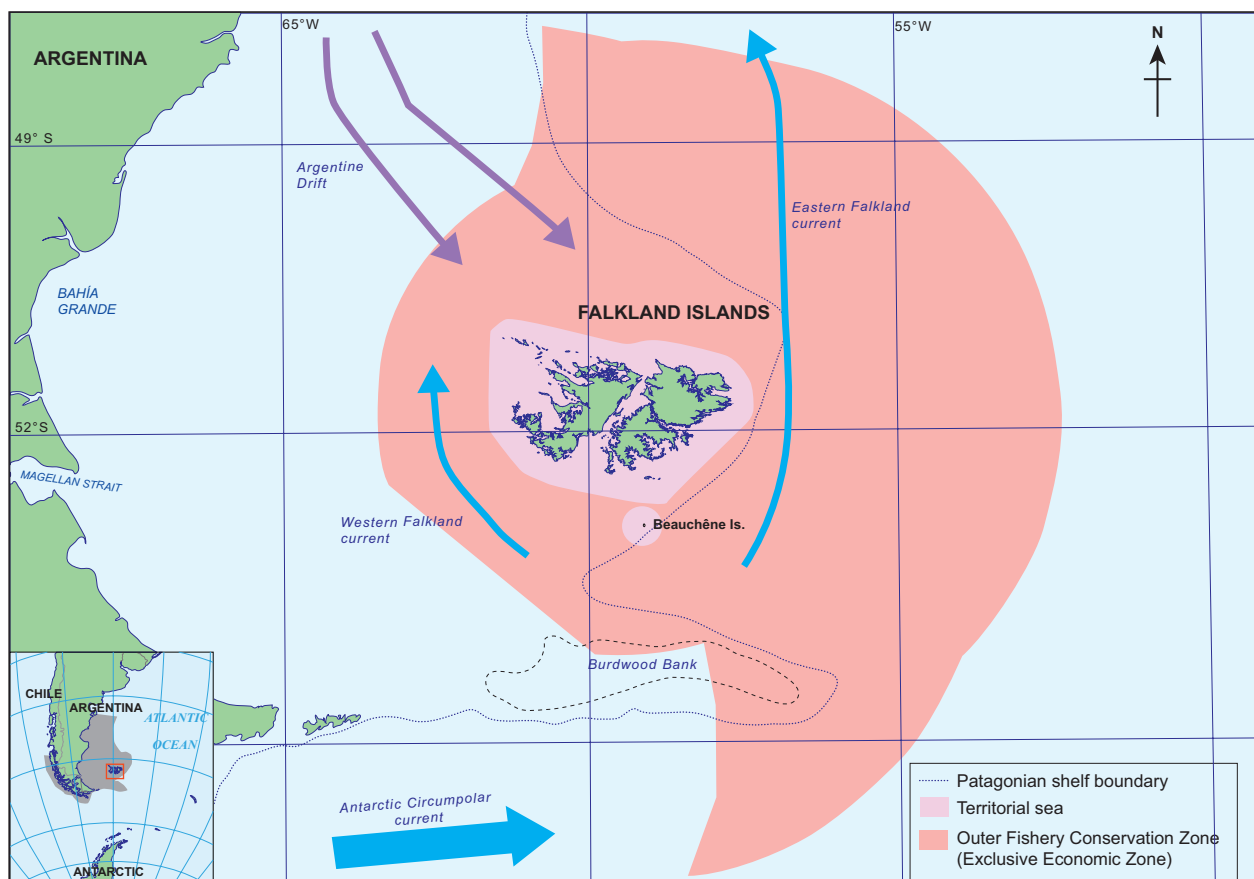


Figure 1. Map showing the location of the Falkland Islands in the South Atlantic (inset, bottom left, with associated Magellan biogeographic region (Koubbi et al. 2014) shaded grey) and the demarcation of the UK claimed area. Arrows depict the general direction of the major oceanographic currents (position of Falkland Islands currents and Argentine drift taken from Arkhipkin et al. 2013). Dotted line represents the approximate edge of the Patagonian shelf.

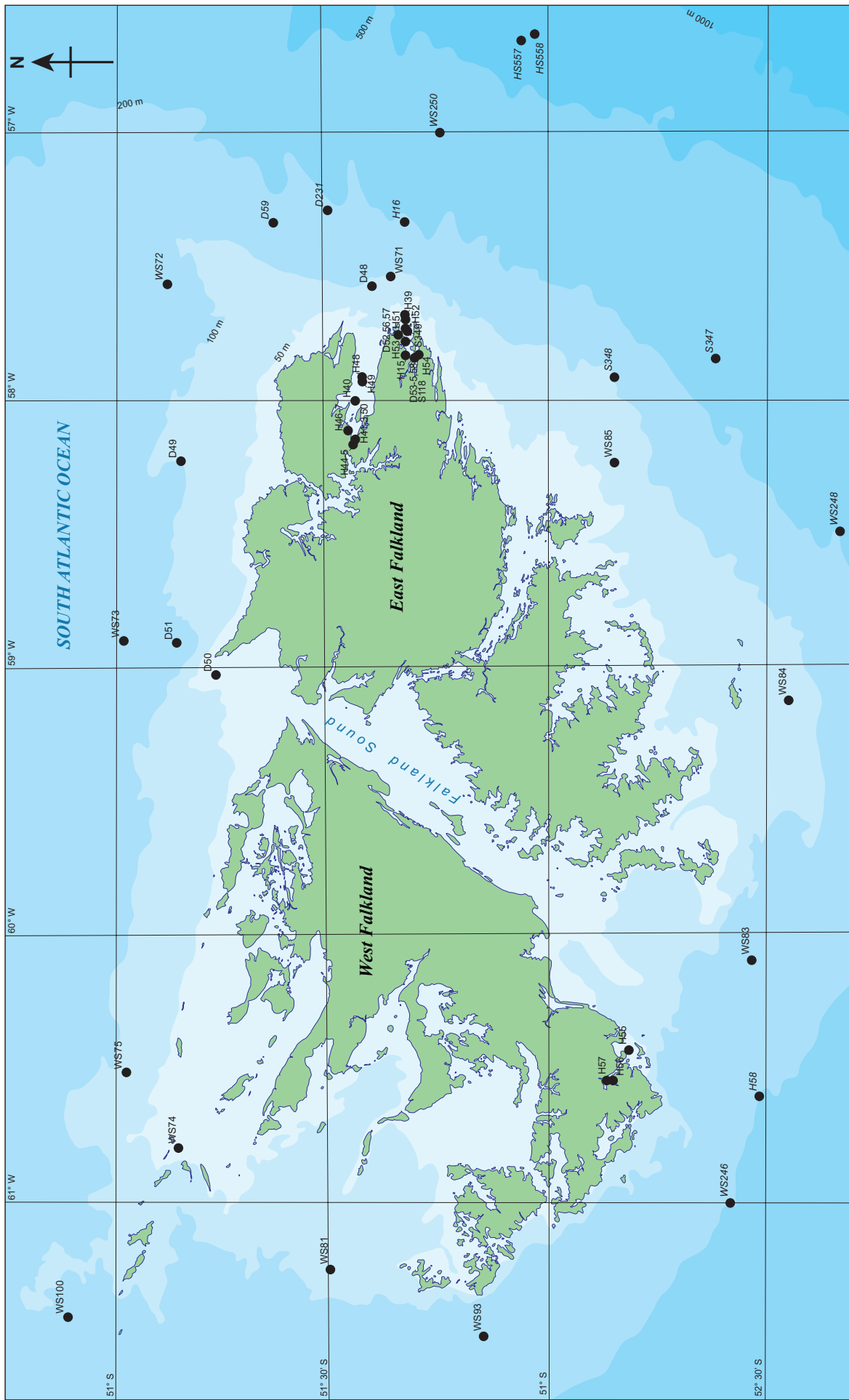


Figure 2. Location of historic sample stations taken within or just outside (in italics) Falkland Islands territorial waters. *D* = R.R.S. Discovery, 1926–27; *H* = Swedish Antarctic Expedition (Antarctic) 1902; *HS* = USNS Eltanin, 1963; *WS* = R.R.S. William Scoresby, 1927–28; *S* = S.Y. Scotia, 1903.

in a west-east direction. On reaching the Falkland Islands continental shelf, the flow splits in two, with a stronger eastern branch and weaker western one (Bianchi *et al.* 1982) (Figure 1). Northwestern parts of the Falkland Islands, however, are influenced by the Argentine Drift, a relatively warmer, fresher and more oxygen-rich water mass (Laptikhovskiy 2009) that represents the inflow of Patagonian Shelf water to the area (Arkhipkin *et al.* 2013).

1.2 Development of the Project

The investigation into the intertidal and nearshore polychaetes of the Falkland Islands was initiated in 2010 after discussion with local Falkland Islands scientists determined that there was both a need and support for such a project. A successful grant application (Shackleton Scholarship Fund, SSF) provided some funding for travel and Amgueddfa Cymru-National Museum Wales provided the remaining support. Fieldwork was planned for November-December 2011 to coincide with survey work being undertaken by the Shallow Marine Surveys Group (SMSG, a group of local divers carrying out volunteer marine surveys) that could contribute to the project. Fieldwork was concentrated around East Falkland and consisted mainly of shore collecting. Additional subtidal collecting by diving was included where possible and the total resulted in samples from 19 shores and 15 dive sites (Figure 3). A second fieldtrip in January 2013 (also supported by the SSF) extended the project to West Falkland, adding 20 new shores (10 in West Falkland) and 1 dive site to the inventory (Figure 3). A final visit in January 2015, sampled a further 9 shores and 3 dive sites (Figure 3), bringing the total number of shores sampled to 48 and dive sites to 19 (Appendix 5). Figures 4–11 depict a range of the different shore types sampled.

The range of shores (rocky, sandy, soft sediment, mixed sediment) and their spread around the Islands was planned to maximize the number of polychaete species likely to be encountered and also potentially indicate whether species distribution might be influenced by the differing maritime regimes affecting the shores. Final location of the sites was generally determined by access. Roads in the Falkland Islands are few (Figure 3) and much of the coastline is inaccessible except by boat or four wheel drive and a sound knowledge of the area. The majority of land is also privately owned and permission had to be sought for access to all but a small number of sites around Stanley.

1.3 Taxonomy of Falkland Islands Polychaeta

Despite the wealth of faunal data for the Antarctic and Magellan regions, very little data on Polychaeta actually exists specifically for Falkland Islands waters, with less for intertidal than

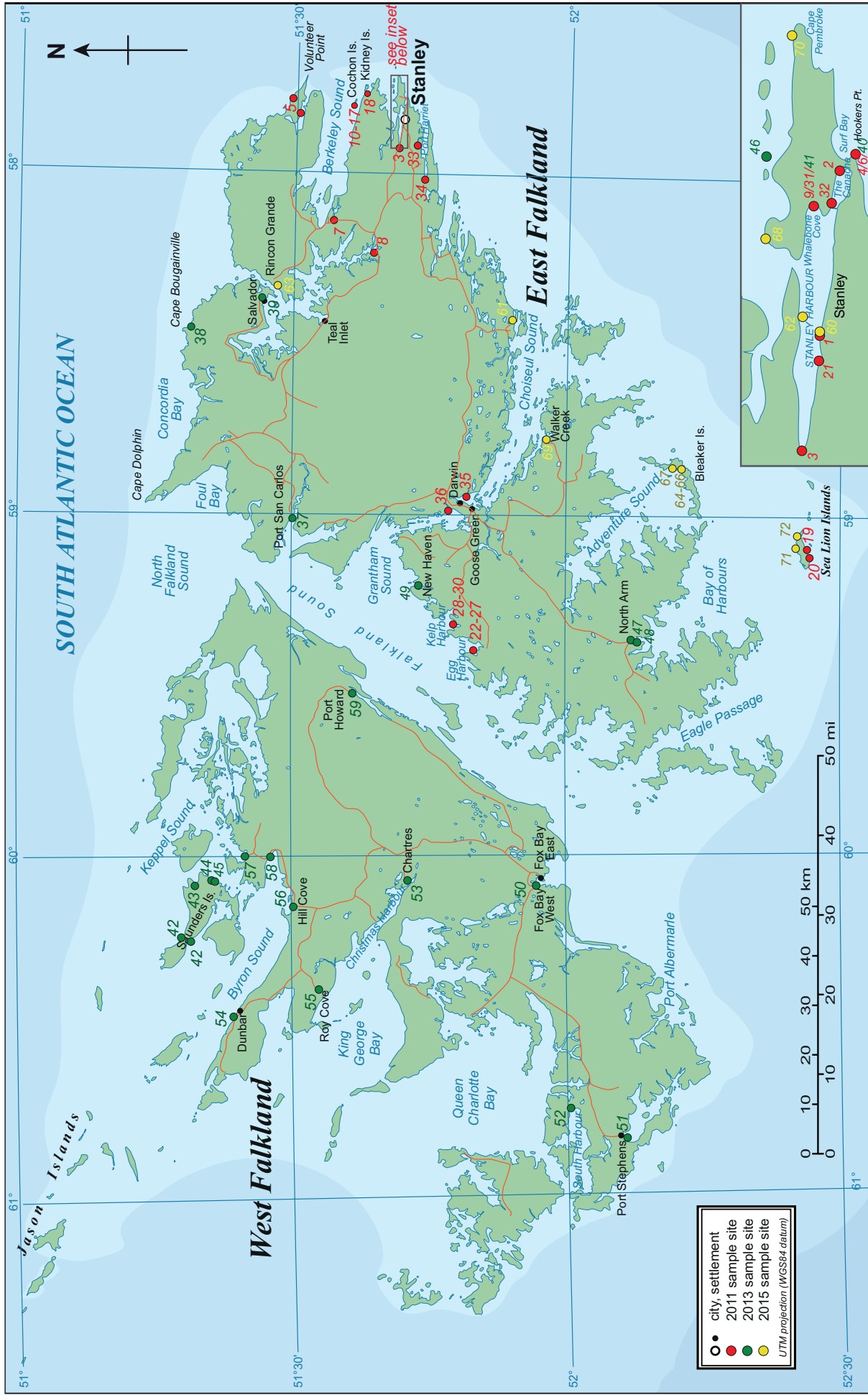


Figure 3. Map showing location of Falkland Islands sample sites 2011–2015 including enlarged inset map (bottom right) of Stanley area.

offshore species. A search for taxonomic literature on marine invertebrate groups, published between 1865–2010, using the electronic literature database Zoological Record, reveals only seven publications relating to Polychaeta from the Falkland Islands region in comparison to over 40 from nearby Chile and more than 20 for Argentina. Of those seven, only three specifically relate to intertidal fauna on the Islands themselves, while the rest relate to Falkland Islands ‘waters’. There are, of course, additional publications that report species from the occasional intertidal or nearshore sample taken as part of a much larger survey e.g. the *Discovery* and *Challenger* expeditions; however this illustrates the discrepancy in research outputs within the Magellan region. In terms of taxonomic effort specific to the intertidal or nearshore region of the Islands, the three publications on the Polychaeta contrast starkly to 12 and 13 publications on Crustacea and Mollusca respectively (1865–2010).

Some of the first polychaetes reported from the Falkland Islands, were collected by the German zoologist, W. Michaelsen, who visited Port Stanley in 1893 (after Ushuaia in 1892), and made two collections, both intertidal/shallow (results published by Ehlers 1897, 1901). Pratt (1898) reported on some shore polychaetes, collected by a Miss Blake of Hill Cove, West Falkland in 1896 along with several other groups. Further publications by Pratt (1901) and Fauvel (1916) were a result of intertidal and inshore collecting by Rupert Vallentin, a Cornish naturalist who conducted several expeditions to the Falkland Islands 1897–1911 (Oldfield 2015). However, after this time, very little intertidal collecting was done (at least for polychaetes).

Many of the national Antarctic expeditions that were mounted in the early part of the twentieth century, sailed past the Islands on their voyages, but most, including the *Challenger* and Australasian, British, French, Belgian and New Zealand Antarctic expeditions, took no samples from the region (see Hartman 1964 for a detailed review of Antarctic faunal expeditions). The Swedish Antarctic expedition (*Antarctic*: 1901–1904), Scottish National Antarctic expedition (*Scotia*: 1902–1904) and the *Discovery* Investigations (1926–1927 & 1931–1933: *Discovery Reports* v1–34) all visited the Islands and sampled there, including a small number of intertidal sites (Figure 2). Arwidsson (1911), Støp-Bowitz (1951) and Hartman (1953) reported species of Falkland Islands Polychaeta from the Swedish expedition, Pixell (1913) and Ramsay (1914) from the Scottish expedition and Monro (1930, 1936), Stephen (1941), Tebble (1960) and Harris (1969) from the *Discovery* Investigations, with new species being described in all of the publications. However, most stations were offshore and those that were inshore or intertidal were mostly located in the same easily accessed harbour

areas of Berkeley Sound and Port William/Stanley Harbour on the east coast of East Falkland. In 1963, a new subspecies of *Abarenicola* (*Abarenicola assimilis brevior* Wells, 1963) from the Falkland Islands and the Magellan region was published by Wells, one of the last publications based on those early collections. The Falkland Islands specimens he observed were those collected by Rupert Vallentin in the early 1900s. However, in **Paper 1**, new investigations of this and other subspecies of *Abarenicola assimilis*, using molecular techniques, determined that not only should all subspecies of *A. assimilis* be considered at species status but that there are, in fact, two species present on the Falkland Islands and not one. Re-examination of the original material that Wells (1963) used showed both species to have been present among the animals he observed.

Beyond the territorial limits, the USNS *Eltanin*'s extensive sampling programme brought it close to the Islands for a small handful (13) of stations. Only five of those were within the wider Falkland Islands EEZ, two to the east (Figure 2) and three to the south (south of Beauchêne Island), and two stations were located on Burdwood Bank. Results were reported on by Hartman (1967) and Fauchald (1982). Hartmann-Schröder (1983) detailed Polychaeta from the 1966, 1971 and 1978 cruises of the *Walther Herwig* which also visited the region.

In 1996, Tingley *et al.* (1996) carried out a shallow subtidal survey by diving around the Islands. However, as with most dive surveys, polychaetes were rarely recorded and then left mostly unidentified beyond family level. Since that time, investigations of the offshore seabed for potential oil extraction, by commercial companies, has resulted in several baseline surveys being undertaken (e.g. ERT Ltd. 1997; Perry 2005; Shah 2009; Williams *et al.* 2009). All of these surveys have concentrated on deep waters beyond 100 m depth and it has previously been noted that the faunal composition of polychaetes, along with other invertebrates, changes sharply between 100–300 m depth (Sanders & Hessler 1969; Grassle *et al.* 1979) as pressure and distance from the slope increases and temperature decreases. The Falkland Islands State of the Environment 2008 report (Otley *et al.* 2008) states that “*there is limited information on the intertidal and shallow marine environment (down to 30 m) in the Falkland Islands*” and also comments that most of the species recorded by Tingley *et al.* (1996) were echinoderms, molluscs and sea squirts.

Finally, in 2013, Neely & Brickle published the *Marine Life of the Falkland Islands* identification guide that contained a small number (10) of polychaete species. Of those entries, only five were identified to species level. Identifications were stated as being by members of the Shallow Marine

Surveys Group who had contributed to the guide, and did include two species that are not recorded by any of the previous surveys mentioned above (Table 2).

In short, there have been no direct investigations of Falkland Islands Polychaeta since the mid-20th century. A similar review of historic polychaete taxonomy in New Zealand by Glasby & Read (1998) found that up to 1950, 285 polychaete species had been either described (140 species) or reported (145 species) from New Zealand coastal and shelf depths. By the time of publication in 1998, the estimate was 471 species, more if historic reports of undescribed species were included. This illustrates one of the problems encountered in referring to historic species records, whereby the original researcher, observing animals not described at that time, incorrectly matches them to another available description, leading to records of species that do not actually inhabit that region. Glasby & Read (1998) estimated that out of the 145 taxa reported from but not described from New Zealand, most of those originally described from northern hemisphere localities would turn out to be mis-identifications. This is demonstrated in **Paper 2**, where the record from Pratt (1898) of *Perinereis atlantica*, described from the Cape Verde islands in the northern hemisphere, is considered doubtful and likely a case of mis-identification of the local species of *Perinereis*, not described until 16 years later. Elias *et al.* (2017) make a similar observation on the history of polychaete taxonomy in Argentina, whereby many of the early identifications were made by Europeans who gave them corresponding European names, thus leaving a legacy of ‘cosmopolitan’ species in the literature.

Modern collecting strategies and methods also enable collections from habitats possibly not accessible to earlier researchers, such as those sampled by divers. Animals that live in epifaunal turf for example, growing on walls and rock outcrops would not have been sampled by the grabs, trawls or dredges employed by the early surveyors, or even those relying on such techniques today. Nor would they be recorded by diver surveys that only record taxa visible without taking samples. A project to record polychaetes from the Isles of the Scilly in the UK utilising a combination of intertidal collecting, diver collecting and remote sampling by ship, found that 38% of intertidal species were not recorded subtidally, 17% of taxa recorded from diver collections were exclusive to those samples and 45% of taxa from ship samples were recorded exclusively by that method (Darbyshire 2011). The taxa described in **Papers 3 & 4** all inhabit such turf habitats, and the fact that they have not been discovered from continental South America, where recording has received greater effort, may suggest that they are endemic to the island region.

1.4 Biogeography of the Falkland Islands

1.4.1 Terminology

Biogeographical boundaries and names for regions and provinces have fluctuated over the years; however, the Falkland Islands have consistently been placed within a cold temperate ‘Magellan’ or ‘Magellanic’ province or region (e.g. Ekman 1935, 1953; Knox 1960; Hedgpeth 1969; Briggs 1974; Knox & Lowry 1977; Montiel *et al.* 2005a; Spalding *et al.* 2007). Depending on author, the actual area encompassed varied but generally included the southern part of South America, including Tierra del Fuego, and the Falkland Islands and extended out to Burdwood Bank. Briggs (1974) attempted to standardize terminology, so that provinces were defined as areas of 10% or more endemism located within larger biogeographic regions; however, this has not always been accepted with Camus (2001) referring to the Magellan area as a ‘province’ but Montiel *et al.* (2005a) using ‘region’. Knox and Lowry (1977) simply refer to a ‘Magellanic Area’. Faunal groups used in the different biogeographical analyses and attempts to define regions and provinces have also varied according to author. In Griffiths *et al.* (2009), an attempt was made to validate those regions previously proposed using faunal groups, but it was found that, at least in the Southern Ocean, they varied depending on the faunal group analysed.

Spalding *et al.* (2007) made a further attempt to standardize the system for defining coastal and shelf areas with Marine Ecoregions of the World (MEOW), based on 12 realms, 62 provinces and 232 ecoregions. Within this system, they tried to reconcile the differing boundary systems in place for South America, resulting in a Temperate South America realm containing five provinces. The Magellanic Province, one of those five, encompassed five ecoregions: ecoregion 186 was designated Malvinas/Falklands with a boundary similar to that of the current Exclusive Economic Zone boundary (UK claim) for the Islands and encompassing waters defined by the 200 m isobath.

Briggs & Bowen (2012) also split the Magellan Province into 4 separate provinces: southern Chile, Tierra del Fuego, southern Argentina and the Falkland Islands, all within a South American Region (the 5th province of Spalding *et al.* 2007, Chiloense, is beyond the northern limit of this region). This action was based on more detailed information on cold temperate faunas and levels of endemism than had been available to previous authors and applied the definition of ‘province’ to any area that showed levels of more than 10% endemism in at least 2 classes of benthic invertebrates. Divisions were, however, based primarily on fish distribution, although data on other marine groups were also employed.

1.4.2 *Polychaetes in Magellan biogeography*

Notably, the vast majority of studies on South American and Antarctic biogeography have not used polychaetes in their analyses even though they are known to be a major contributor to the benthos (Hutchings 1998). The first study to do so, along with data on Amphipoda, was that by Knox and Lowry (1977), who compiled a list of 677 species (119 not fully described) for the Subantarctic, Antarctic and Magellan areas. The analyses revealed relatively low levels of endemism in polychaetes from the Antarctic, Subantarctic and Magellan regions in comparison with the Amphipoda. The ‘Magellanic Area’, as they termed it, did however exhibit a level of 16% endemism for polychaete species, which would confirm the area as a ‘province’ as defined by Briggs (1974) earlier.

Nearly 30 years later, Montiel (2005) and Montiel *et al.* (2005a, b), conducted zoogeographical analyses of the Magellan ‘region’ using Polychaeta, the first studies to do so. In his thesis, Montiel (2005) concluded that the region could not be considered as a single zoogeographical entity and split the region into 3 sub-regions based on the zoogeographical patterns, one of which, FKLD, encompassed the southwest Atlantic area of the Magellan region. Despite these divisions though, endemism between the sub-regions was low with only 3% endemism within FKLD. In the first analysis of Montiel *et al.* (2005a), the Magellan region was investigated using an assembled list of 431 species, from 19 expeditions, although only 216 species were analysed due to omission of species without exact locations and those that only occurred once. In the second analysis (Montiel *et al.* 2005b), a comparison was made between the Magellan region and the Weddell Sea, this time using a total of 199 species for the Magellan region itself. Montiel *et al.* (2005a) split the region into two subregions, Pacific and Atlantic, as a result of the distribution data with levels of endemism for the two subregions reported as being less than 10%. Omission of the Polychaeta from previous biogeographical studies was theorized as being due to their wide geographical range and capability for wide dispersal. Häussermann & Försterra (2005), in a similar study on sea anemones, correlated the patterns of distribution they found with those shown by the Polychaeta (Montiel *et al.* 2005a).

De Broyer & Koubbi (2014) published a detailed summary of previous biogeographical systems and proposals as part of the Census for Marine Life’s *Biogeographic Atlas of the Southern Ocean*. The Atlas itself assembled an unprecedented inventory of 9064 validated species (including 588 polychaete species) representing planktonic species, macroalgae, zoobenthos, nekton, birds and mammals and produced more than 800 distribution maps. The area covered included the Southern

Ocean in its wider definition, south of the Sub-Tropical Front, however its main focus was the Southern Ocean *sensu stricto*, south of the Antarctic Polar Front. Koubbi *et al.* (2014), summing up at the end of the same publication, provided a summary map of Southern Ocean benthic biogeographic regions, once again including the Falkland Islands as part of a large-scale single Magellan region (see inset map, Figure 1).

1.5 General objectives of this thesis

The general objective of this thesis is to update and improve our knowledge of the systematics and distribution of Polychaeta around the Falkland Islands, with an emphasis on intertidal species. This emphasis is derived from a clear gap in our current knowledge about distribution of intertidal polychaeta as compared to those found offshore (see section 1.3). This objective is addressed through the following four specific objectives:

1. To update, improve and clarify the current knowledge of polychaete taxa in the Falkland Islands;
2. To indicate potential environmental drivers of polychaete distribution and composition around the Falkland Islands;
3. To determine the richness and taxonomic distinctness of the polychaete communities around the Falkland Islands;
4. To relate the current findings to the knowledge of the Polychaeta in the wider Magellan region.

1.6 Materials and Methods

Methods for field collection, preservation and laboratory work were the same for all fieldtrips with all samples collected by hand or by diving. The majority of specimens were relaxed in 7% magnesium chloride solution prior to fixation with either 4% formaldehyde in seawater or 100% ethanol, to maximize the quality of the preserved specimens. Shore collecting was undertaken from two hours prior to low water until the tide turned, following the tide down the shore as it receded, sampling as many different habitats as were present at different levels on the shore. Diving was conducted according to the safe diving rules followed by the Shallow Marine Surveys Group in the Falkland Islands, to depths no greater than 20 m. Full details of the sites and methods for the project are available as follows:

- detailed descriptions of all of the 2011 and 2013 sample sites, including sketches and photographs were published in the Interim Fieldwork Reports (Darbyshire 2012, 2013b)

provided to the Shackleton Scholarship Fund (SSF) after each fieldtrip. Methods used for the collection and analysis of samples were also included in the same reports with relevant details included in each of **Papers 1–4**;

- descriptions of sample sites from 2015 are unpublished, but the methods employed for collection, preservation and analysis were consistent with those used in 2011 and 2013;
- molecular sequencing methods and analyses of results were detailed in the 2016 progress report submitted to the SSF (Darbyshire 2016) as well as in **Paper 1**;
- a map of sample sites (Figure 3) and photographs of differing habitat types (Figures 4–11) are provided. A table listing location, co-ordinates and habitat types for each sample is given in Appendix 5;
- methods for statistical analyses are detailed in Chapter 6 along with the results.

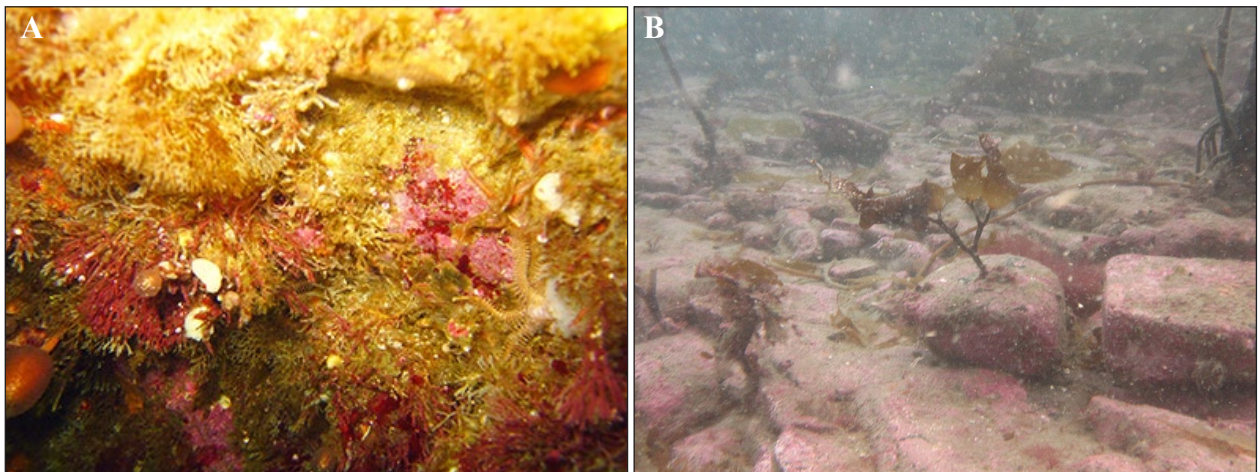


Figure 4. Subtidal habitats: *A. Hydroid-bryozoan epifaunal turf habitat, Cochon Island, east coast of East Falkland; B. rocky seabed, no turf, Shag Rookery Point, west coast of East Falkland.*

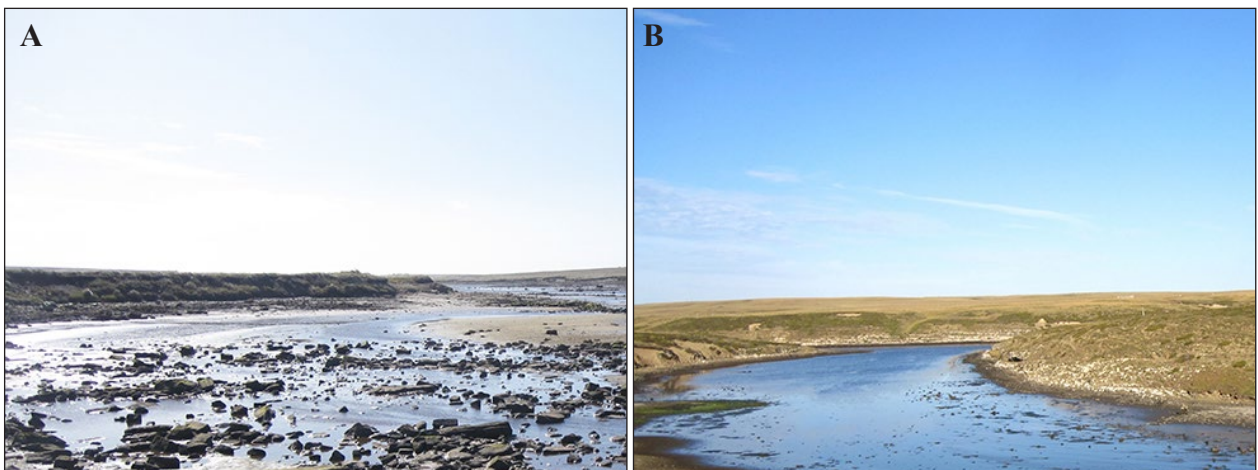


Figure 5. Typical creek environments: *A. Mullet Creek; B. North Arm*



Figure 6. Sandy bay: Fox Bay West



Figure 7. Rocky shore with rock pools, Cape Bougainville.



Figure 8. Mixed shore.



Figure 9. Mixed sediment type of loose sand and gravel.



Figure 10. Coarse sandy gravel.



Figure 11. Soft mud.

Chapter 2: Arenicolidae

The family Arenicolidae includes some of the most observed, studied and recognizable (at least remotely) taxa of the Polychaeta. The iconic sediment casts seen on the surface of many shores around the world are produced by members of *Arenicola* and *Abarenicola*, the lugworms, the largest of the four genera in the family. Of these two genera, only *Abarenicola* occurs in the ‘southern cold water zone’ (Wells 1963, 1980). Although present subtidally, all of the lugworm species occur mainly intertidally. Due to their accessibility on the shore, lugworms have been extensively studied and no new species had been described since Wells (1963) until 2017 (**Paper 1**).

In 1963, Wells described five subspecies of the South American *Abarenicola assimilis* (Ehlers, 1897), including one, *Abarenicola assimilis brevior*, which occurred in both the Magellan Strait and the Falkland Islands, although he noted some discrepancies among those specimens he observed from the Islands. As explained in Chapter 1, no further investigative work was then done on Falkland Islands Polychaeta, particularly intertidally, in the latter half of the 20th century, and *A. a. brevior* remained the only *Abarenicola* known from the Islands until 2017. Despite early molecular investigation confirming the presence of two *Abarenicola* taxa on the Islands (unpublished), the determination of consistent, defining characters was only facilitated once a large number of specimens had been sequenced and voucher specimens could be identified and compared. The defining characters on the animals are small, not always obvious to the naked eye and, in fact, had been noted by Wells in his publication but considered to be character variation within the species. Without the inclusion of genetics in this study, it is possible that the new species (*Abarenicola wellsi* Darbyshire, 2017a), which was not present among any of the South American specimens observed by Wells, would have remained undescribed for much longer. The ramifications of the sequencing results extended beyond the recognition of *A. wellsi*, with associated observations on the related *A. assimilis* subspecies providing evidence for elevating those subspecies to equal species status also.

Cryptic diversity (morphologically indistinguishable but genetically distinct taxa) in the Polychaeta has recently been reviewed by Nygren (2014) and is suggested to be common across all polychaete families, potentially contributing a significant portion of their biodiversity. More recent research by Nygren (pers. comm. 2017) has estimated that nearly half of the biodiversity in Norwegian waters is currently neglected by the use of morphology alone for identification, and that this increases to two thirds of the biodiversity on a northeast Atlantic scale. Similarly,

a recent molecular study by Brasier *et al.* (2016) on deep sea Antarctic polychaetes, uncovered not only unrecognized cryptic diversity in 50% of the species identified but also uncovered an additional 10 morphospecies (morphologically distinct, some described, some undescribed). The paper comments on how even experienced identifiers were missing the identification of some morphologically distinguishable species, resulting in lower reported diversity, but that the inclusion of molecular analysis provided confirmation of species presence enabling deeper investigation.

While the case of *Abarenicola* in the Falkland Islands is not one of cryptic diversity, it does illustrate a simple example of sequencing being used to confirm morphologically close taxa and thus prompting a deeper investigation of other species (the additional subspecies erected by Wells). The consideration of cryptic diversity, provides an important argument for further molecular investigation of the polychaete fauna in the Falkland Islands and the likelihood of additional, unrecognised species even amongst those collected during this study.

Chapter 3: Nereididae

Along with lugworms (Arenicolidae), the ragworms (Nereididae) are one of the most recognized families of polychaetes. Also utilized commercially for fishing bait as well as aquaculture, most intertidal members of the family are macro-sized and easily discovered on shores, under rocks or burrowing through the sediment. The family is much larger than the Arenicolidae with around 500 nominal species (Rouse & Pleijel 2001) in over 40 genera and is considered one of the largest in the Polychaeta (Hutchings *et al.* 2000).

Paper 2 provides a review of all of the intertidal and nearshore species of Nereididae that have been recorded from the Falkland Islands up to 2014. It does not include the deeper water species *Nicon maculata* Kinberg, 1866a, as that had only been recorded from the region in depths below 100 m, beyond the scope of this study. However, specimens sent to the author that were collected as a by-catch from bottom trawling by the Falkland Islands Government Fisheries Department confirmed the current presence of this species in the region. The paper has several additional aspects to it that contribute in different ways to the current understanding of Falkland Islands polychaete taxonomy:

- a new species, *Gymnonereis tenera* Darbyshire 2014 is described from the samples, the first record of this genus from the Islands and only the 7th to be described worldwide;
- the current status of recognition of both *Platynereis australis* (Schmarda, 1861) and *Platynereis magalhaensis* Kinberg, 1866b is reviewed;
- the records of *Nereis atlantica* McIntosh, 1885 are assessed for validity, the taxonomic description is updated and the taxon is transferred to a new genus;
- a key is provided for identification of all recorded species from the intertidal and nearshore environment of the Islands.

The new species, *G. tenera*, was only recorded from five stations, three in large numbers, around the Islands, and these were widely dispersed on eastern, central and north-western coasts. The lack of previous discovery is particularly surprising as one of the locations where it was found to be numerous, Roy Cove in the northwest of West Falkland, was one of the locations where Rupert Vallentin collected from. Possible reasons for the lack of previous discovery could be that the population (in Roy Cove) has only established relatively recently, that the population was previously very sparse in number such that the chance of discovery and collection was greatly

reduced but that it has since undergone a large increase or simply that, as the animals were not widespread across the entire shore, previous opportunistic sampling simply missed them.

Extremely difficult to separate morphologically from *P. australis*, the validity and status of *P. magalhaensis* has been debated historically, although it is currently considered valid. It was the most recorded nereid taxon subtidally and was widespread intertidally, living in tubes attached to the undersides of rocks. With parallels to the case of *A. brevior* and *A. wellsii* described in Chapter 2, *P. australis* and *P. magalhaensis* are also ideal candidates for molecular investigation. Unfortunately, sequencing of the Falkland Islands specimens was only partially successful and sequences of *P. australis* have proved difficult to access at this time. Read (2007) undertook a detailed study of the '*P. australis*' group, concluding that they could be separated morphologically at the epitoke stage. Following the methodology described by Read (2007), attempts were made to collect epitokes during the 2015 fieldwork, but this was unsuccessful. Although molecular results would be ideal to confirm or refute the distinctness of *P. magalhaensis* to *P. australis* and the other closely related taxa, a morphological analysis of *P. magalhaensis* epitokes is the final evidence required for comparison and will require dedicated sampling effort in the future.

One of the goals of this thesis is to review the taxonomy of Polychaeta from the Falkland Islands, updating and adding to the species list, but also correcting or highlighting where previous taxonomic errors might have been made. The case of *Nereis atlantica* is one of those. *Nereis atlantica*, now transferred to *Perinereis* (**Paper 2**), has not been recorded since its description from the Cape Verde Islands except for a record by Pratt (1898) from the Falkland Islands. *Perinereis falklandica* Ramsay, 1914, the only species of the genus believed to inhabit the Islands, was described from local specimens but not until 16 years after Pratt's record. If the description had been available, then it is believed likely that Pratt's record would have been of that species instead. Unfortunately, as is often the case with such old records, the original specimens could not be found and so the record can never truly be proven inaccurate. The record was, however, included in the published key for completeness. Conversely, *Neanthes kerguelensis* is the most widely recorded of all the nereids included in the review, being recorded across the southern hemisphere, demonstrating that species records can exist for the same species over long distances. This species too, has been recorded from both hemispheres although one of the northern hemisphere records could be discounted as being incorrect just by the morphological description of the specimens in question. The other northern records stand out as being inconsistent with the general distribution and were also highlighted as questionable.

The two remaining species considered valid for the region but not recorded by the modern surveys, *Nereis eugeniae* (Kinberg, 1866a) and *Eunereis patagonica* (McIntosh, 1885), were not recorded intertidally but there are several shallow subtidal records indicating that greater surveying effort offshore would be likely to reveal their presence. Both species show discrepancies in their descriptions by previous recorders and so the collection of new material from the Islands is extremely desirable in order to confirm the morphology of the local specimens.

Despite the wide range of specimens collected during the 2011–2015 surveys, enabling a detailed review of the family, **Paper 2** is not able to provide a complete picture of the taxonomy of Nereididae in the Falkland Islands. In order to do so, further collecting effort and both morphology and molecular work are required, demonstrating once again the importance of both techniques, in conjunction with one another, to provide answers.

Chapter 4: Chrysopetalidae

No members of the family Chrysopetalidae have previously been reported for the Falkland Islands or its waters. Species of the genus *Dysponetus* are all small and fragile and can be challenging to extract in good condition from samples unless handled with great care. Specimens collected from the Falkland Islands were all subtidal, inhabiting the hydroid/bryozoan turf that grew abundantly on many shallow rock faces (Figure 4A). The requirement for collection by divers in conjunction with careful handling and preservation is most likely the explanation as to why the species had not previously been detected.

Paper 3 describes the first two species of *Dysponetus* to be recorded from the southwest Atlantic, *Dysponetus bricklei* Darbyshire & Brewin 2015 and *D. ovalisetosus* Darbyshire & Brewin 2015. The closest previous records were from Antarctica to the south (an additional new species is described from there, *D. antarcticus* Darbyshire & Brewin 2015) or Tristan da Cunha and southwest Africa to the northeast. Of the new species described, only *D. antarcticus* had been recovered by remote sampling from sediment, the remaining two being both diver collected from rock scrapings.

The new species from the Falkland Islands was first incorrectly identified as *Dysponetus bulbosus* Hartmann-Schröder, 1993, the closest species in both geographical and morphological terms. However, in researching the previous descriptions of *D. bulbosus*, discrepancies were discovered that required more in-depth investigation into those historic specimens. This led to a re-description of *D. bulbosus*, the description of a new species (previously mis-identified as *D. bulbosus*), and enabled confirmation of the Falkland Islands specimens (and others from South Georgia) as distinct species. The size and fragility of the specimens meant that scanning electron microscopy (SEM) was the most appropriate technique for viewing the morphology and detailed observations could be made repeatedly without causing further damage to other specimens. Fortunately there was enough material available to allow both SEM and light microscopy.

As ever, molecular analysis is desirable, but no specimens collected in 2011 were preserved in ethanol as the turf samples collected were fixed straightaway and not sorted until later. On return in 2013, an attempt was made to collect more specimens from similar habitats but only a few were found with one preserved in ethanol. None were found in 2015 despite more diver collections. The sequencing of the single specimen preserved in ethanol failed

and no other specimens are currently available. Unlike the cases in Chapters 2 and 3, the case of *D. ovalisetosus* is not one where molecular answers are needed in order to confirm species distinction. The taxa can be distinguished readily on morphological characters alone, albeit needing careful, detailed observations under the microscope. Molecular work would, however, aid the wider systematics of the group by clarifying the relationships between taxa. Additionally, determining how closely related the taxa from the Falkland Islands, South Georgia and Antarctica are, including whether one taxon evolved from another, could shed light on the direction of distribution between these regions.

The case study of *Dysponetus* probably illustrates best how investigations to confirm one species can lead not only to the discovery of more but can also promote improved taxonomy of other taxa with wider implication for identification of polychaetes beyond the Falkland Islands region. It also further consolidates the expectation that many of those species identified from the region, particularly from groups that had not been recorded previously, are likely to be undescribed.

Chapter 5: Maldanidae

Maldanidae (bamboo worms) are an easily-recognised family of worms with distinctive cylindrical segments giving them an appearance much like bamboo. They are, however, fragile and can be difficult, if not impossible, to identify unless both anterior and posterior ends are present. A large family of over 200 nominal species worldwide (Rouse & Pleijel 2001), only three species had been recorded from Falkland Islands coastal waters previously. All are large animals, measuring several centimetres or more each. Fauvel (1916) reported all three of those species in his records of Rupert Vallentin's specimens, but only *Clymenella minor* Arwidsson, 1911 was reported by other recorders (Monro 1930, Hartman 1953). The latter species was, by far, the most abundant of the three species found on the shore in this study; at some sites, tubes dominated the substratum. All three species were rarely recorded from the subtidal samples although they were present in small numbers in some of the sediment samples collected.

In addition to the three known intertidal species, an additional subtidal, small maldanid was discovered in the samples and determined to be a new species, *Micromaldane shackletoni* Darbyshire, 2013a (**Paper 4**). Only eight members of the genus *Micromaldane* are known worldwide, all of which are small-bodied with none exceeding 12 mm in length. Animals build and reside within tubes that are generally attached to larger worm tubes (e.g. of Sabellidae or Terebellidae), bryozoans or hydroids, forming part of the epifaunal turf on rock. In parallel with the case of *Dysponetus* (Chapter 4), this type of habitat is generally inaccessible to remote sampling and would most likely explain why the species had remained undetected until now.

Importantly, observations on the specimens collected determined the animal to be a simultaneous hermaphrodite. Larvae in varying phases of development were discovered and imaged, using both light microscopy and SEM and all stages of the process from eggs and sperm through to sub-adults ready to leave the parental tube were described. Comparison of the stages of larval development was an important factor in determining the species to be distinct from others in the genus, particularly *M. androgyne* Rouse, 1990, the only other known *Micromaldane* to exhibit hermaphroditism. Together, *M. shackletoni* and *M. androgyne* provide evidence that the genus is valid and not a juvenile stage of another.

The current known distribution of *M. shackletoni* is restricted to a small area east and north of Stanley. However, all dive sites, and thus subtidal sampling, were either in that area a few miles

from Stanley or in the central region of Falkland Sound. No subtidal samples were taken to the west of the Islands. The lack of records from the central diving sites may reflect the habitats sampled, as boulders and rock walls were absent and the rocks encountered were mostly small and clean with no epifaunal turf (Figure 4B). The reproductive strategy of *M. shackletoni* though includes no inherent dispersal stage, providing a strong indication that the species could be endemic to the Islands and may be restricted to a small area. Other means of passive dispersal however, such as kelp rafting, could potentially transport such epifaunal species to other locations (see Section 7.3 for further discussion). Further sampling sites, particularly of subtidal epifaunal turf habitats, will be important in determining the actual distribution of the species, and, if truly restricted, could have conservation implications. At this time however, the main sites that the species is recorded from, around Cochon Island, are already part of a conservation area.

Chapter 6: Revised situation of the knowledge on Falkland Islands Polychaeta

6.1 Introduction

The following chapter considers the findings of the 2011–2015 fieldwork expeditions. The analyses of taxa highlight the relevant environmental factors affecting distribution and diversity, and correlations with fauna from both within and outside of the Magellan region are also made. The number and identification of taxa and their contribution to an updated species list for the area shows how deficient the knowledge of the group has been prior to now. A review of each polychaete family presented here details this change in knowledge and correlates with Objective 1 of this thesis, as outlined in Section 1.5 of Chapter 1: to update, improve and clarify the current knowledge of polychaete taxa in the Falkland Islands.

Objective 2, outlined in Section 1.5, to indicate potential environmental drivers of polychaete distribution and composition around the islands, is addressed using cluster analyses (Bray-Curtis similarity and multi-dimensional scaling (MDS)) to provide data on how the taxa are distributed in relation to shore height and sediment and habitat types. Analyses were conducted at three levels: all samples, all stations (where data was suitable for analysis) and all those samples where sediment was sieved to procure the smaller fauna. The latter samples provided the most comparable data in terms of the type of sampling, however as none of the samples were of specifically comparable size, all analyses were conducted on presence-absence data.

Finally, taxonomic distinctness indices enable a more detailed comparison of the samples in order to identify the focus of diversity around the Islands (Objective 3 of Section 1.5). Species richness (S , no. of species) is not a viable statistical method due to the lack of consistency across samples (Clarke & Warwick 2001a, b), although a few minor comments are made on how many taxa were present in samples or at sites. Taxonomic distinctness, however, has been shown to be independent of sample size (Clarke & Warwick 2001a, b) and therefore provides a viable insight into the contribution of taxa and habitats to each site's diversity. The measure of average taxonomic distinctness ($AvTD$, Δ^+) indicates whether a particular sample exhibits greater or lower than expected taxonomic spread for the number of species present (Sommerfield *et al.* 2008). Variation in taxonomic distinctness ($VarTD$, Λ^+), on the other hand, indicates how evenly distributed that spread is across the taxonomic groups. Finally, Objective 4, to relate the current findings of this thesis to the knowledge of Polychaeta in the wider Magellan region, is addressed in Chapter 7.

6.2 Taxonomy

Out of 72 stations sampled between 2011 and 2015, all but one station (stn 32), were sorted and identified for the results presented here. Station 32, a small *Macrocystis* holdfast was deemed too large and diverse a sample to be included at this stage of the project. From the remaining 71 stations, 218 polychaete taxa were identified (distinct taxa, not including any identified as indeterminate or juvenile), representing 124 genera from 37 families. Only 52 of those taxa are named at this time, four of which were described during the project (**Papers 1–4**). An additional three species (one additional family) are also reported from contract samples seen during the period of study. Of the taxa listed, 50 (23%) were exclusive to intertidal samples and 55 (25%) to subtidal samples. Species data for all samples is given in Appendix 6.

A complete list of nominal taxa recorded from the Falkland Islands, representing 149 taxa in 34 families, is provided in Table 2, combining all historic records with those presented here. Of these nominal taxa, 21 are new records for the Falkland Islands (includes two from contract samples), 4 are newly described taxa, and 124 were already known from the area (includes one from contract samples). Several other taxa are known to be new but may have been reported previously under other names. Out of the 149 identified taxa, 86% are also recorded from the wider Magellan region (15% exclusively), 48% are recorded from Antarctic waters and 45% from South Georgia. Species originally described from the northern hemisphere make up 14% of the taxa. ‘Endemic’ taxa make up 6% (9 taxa) of the list (see Section 7.3 for a more detailed discussion of endemism in the Falkland Islands and other regions). Of the latter, four are the species described from the current surveys and therefore distribution is naturally unknown outside of their recorded sites. The remaining five include four Spirorbinae species, three of which have had doubt cast on their identity by other authors and *Leitoscoloplos* nr. *kerгуelensis* which is believed to be a new species and has previously been highlighted as such by others, although *L. kerguelensis* itself is recorded from other localities in both the Magellan and Antarctic regions (see paragraph on Orbiniidae below).

The taxon list (current samples only) shows that Syllidae dominate the Falkland Islands fauna in terms of total number of taxa (20%), followed by Phyllodocidae (8%), Sabellidae (7%) and Polynoidae and Spionidae (6% each), with other families contributing 5% or less. When viewed according to the combined, identified taxa list, Syllidae remain the dominant family at 12%, followed by Sabellidae and Serpulidae (9%), Polynoidae (8%) and Terebellidae (7%). A short review of each family follows to summarise the taxonomic investigations. Family accounts here, and in all tables, are ordered according to the phylogeny of annelid taxa published by Struck (2011, 2012).

Table 2: Nominal species of Polychaeta recorded from the Falkland Islands up to present day. Records attributed to ‘Darbyshire’ (bold type, no date) are presented in this report for the first time. Names in green refer to holopelagic taxa. BB = specimens from Burdwood Bank only, south of the Falkland Islands. * denotes taxa that match the description in the published records but the correct identification is believed to be different. ** denotes taxa identified from contract samples, not the author’s fieldwork. ¹Ashworth (1903, 1912) changed this identification to *Arenicola assimilis* var. *affinis*, reiterated by Fauvel (1916) in his records; these identification were then further updated by Wells (1963) to *Abarenicola assimilis* brevior: all publications were referring to the same specimens. ²Re-identified by Orensanz (1990). ³Referred to *P. virgini* by Kirtley (1994).

Family	Species	Author	Recorded in Falkland Islands by:
Polynoidae	<i>Hermadion magalhaensi</i>	Kinberg, 1856	Pratt 1901; Fauvel 1916; Monro 1930, 1936; Hartman 1953; Darbyshire
	<i>Harmothoe magellanica</i>	(McIntosh, 1885)	Pratt 1898; Hartman 1953; Hartmann-Schröder 1983 (all as <i>Lagisca magellanica</i> (McIntosh, 1885)); Monro 1930 (as <i>Harmothoe impar</i> var. <i>notialis</i> Monro, 1930); Monro 1936; Hartman 1953 (as <i>Harmothoe brevipalpa</i> Bergström, 1916); Hartmann-Schröder 1983 (as <i>Harmothoe</i> cf. <i>brevipalpa</i> Bergström, 1916)
	<i>Lagisca vesiculosa</i>	(Grube, 1877)	Ehlers 1897
	<i>Harmothoe exanthema</i>	(Grube, 1856)	Monro 1930, 1936; Hartman 1953
	<i>Harmothoe spinosa</i>	Kinberg, 1856	Ehlers 1897; Fauvel 1916; Monro 1930; Hartman 1953
	<i>Neopolynoe antarctica</i>	(Kinberg, 1858)	Fauvel 1916; Monro 1930; Hartman 1953 (BB); Hartmann-Schröder 1983 (all as <i>Polynoe antarctica</i> Kinberg, 1858); Darbyshire
	<i>Polyeunoa laevis</i>	McIntosh, 1885	Monro 1930; Hartman 1953; Hartmann-Schröder 1983
	<i>Eunoe anderssoni</i>	(Bergstrom, 1916)	Hartman 1953
	<i>Eucranta mollis</i>	(McIntosh, 1876)	Hartman 1953 (BB)
	<i>Euphionella patagonica</i>	Monro, 1936	Hartmann-Schröder 1983
<i>Euphionella robusta</i>	Wesenberg-Lund, 1962	Darbyshire**	
<i>Halosydna patagonica</i>	Kinberg, 1856	Darbyshire	
Pholoidae	<i>Pholoe polymorpha</i>	(Hartmann-Schröder, 1962)	Darbyshire
Euphrosinidae	<i>Euphrosine ?armadilloides</i>	Ehlers, 1900	Hartman 1953
Orbiniidae	<i>Leitoscoloplos</i> nr. <i>kerguelensis</i>	(McIntosh, 1885)	Fauvel 1916 (as <i>Scoloplos kerguelensis</i> McIntosh, 1885); Darbyshire*
	<i>Leodamas cirratus</i>	(Ehlers, 1897)	Hartman 1953 (as <i>Scoloplos (Leodamas) cirratus</i> (Ehlers, 1897))

Family	Species	Author	Recorded in Falkland Islands by:
	<i>Leodamas marginatus</i>	(Ehlers, 1897)	Fauvel 1916 (as <i>Naineris marginata</i> Ehlers, 1897)
	<i>Scoloplos (Leodamas) cf. tribulosus</i>	(Ehlers, 1897)	Darbyshire
	<i>Phylo felix</i>	Kinberg, 1866b	Hartman 1953
	<i>Phylo felix asiaticus</i>	Wu, 1962	Monro 1930 (as <i>Aricia michaelseini</i> Ehlers, 1897); Darbyshire*
Chrysopetalidae	<i>Dysponetus ovalisetosus</i>	Darbyshire & Brewin, 2015	Darbyshire & Brewin 2015
Nereididae	<i>Gymnonereis tenera</i>	Darbyshire, 2014	Darbyshire 2014
	<i>Platynereis magalhaensis</i>	Kinberg, 1866b	Ehlers 1897; Pratt 1898 (as <i>Nereis eatoni</i> McIntosh, 1876), 1901; Fauvel 1916; Monro 1930, 1936; Hartman 1953; Darbyshire 2014
	<i>Platynereis australis</i>	(Schmarda, 1861)	Ramsay 1914 (as <i>Nereis australis</i> Schmarda, 1861)
	<i>Eunereis patagonica</i>	(McIntosh, 1885)	Pratt 1898; Hartman 1953 (BB) (all as <i>Nereis patagonica</i> McIntosh, 1885)
	<i>Neanthes kerguelensis</i>	(McIntosh, 1885)	Pratt 1898; Ramsay 1914; Fauvel 1916; Monro 1930, 1936; Hartman 1953 (all as <i>Nereis kerguelensis</i> Baird); Darbyshire 2014
	<i>Perinereis atlantica</i>	(McIntosh, 1885)	Pratt 1898 (as <i>Nereis atlantica</i>)
	<i>Nereis eugeniae</i>	(Kinberg, 1866a)	Ramsay 1914; Monro 1930; Darbyshire, 2014
	<i>Perinereis falklandica</i>	(Ramsay, 1914)	Ramsay 1914 (as <i>Nereis falklandica</i> Ramsay, 1914); Darbyshire, 2014
	<i>Nicon maculata</i>	Kinberg, 1866a	Hartman 1953 (BB) (as <i>Nicon ehlersi</i> Hartman, 1953); Darbyshire**
Syllidae	<i>Epigamia charcoti</i>	(Gravier, 1906)	Hartman 1953 (as <i>Autolytus charcoti</i> Gravier, 1906)
	<i>Autolytus maclearanus</i>	McIntosh, 1885	Hartman 1953 (as <i>Autolytus gibber</i> Ehlers, 1897)
	<i>Autolytus simplex</i>	Ehlers, 1900	Pratt 1901; Fauvel 1916; Monro 1930 1936; Hartman 1953
	<i>Pionosyllis kerguelensis</i>	(McIntosh, 1885)	Monro 1930, 1936; Hartman 1953 (BB) (all as <i>Eusyllis kerguelensis</i> (McIntosh, 1885))
	<i>Syllis valida</i>	Grube, 1857	Fauvel 1916; Monro 1930 (all as <i>Syllis brachycola</i> Ehlers, 1897); Hartman 1953 (as <i>Typosyllis brachycola</i> (Ehlers, 1897))
	<i>Syllis prolixa</i>	Ehlers, 1901	Monro 1930, 1936; Hartman 1953 (as <i>Typosyllis prolixa</i> (Ehlers, 1901))
	<i>Syllis sclerolaema</i>	Ehlers, 1901	Monro 1930, 1936; Hartman, 1953
	<i>Syllis variegata</i>	Grube, 1860	Monro 1930
	<i>Syllides articulosus</i>	Ehlers, 1897	Fauvel 1916; Hartman 1953
	<i>Exogone heterosetosa</i>	McIntosh, 1885	Fauvel 1916; Hartman 1953

Family	Species	Author	Recorded in Falkland Islands by:
	<i>Parexogone minuscula</i>	(Hartman, 1953)	Hartman 1953 (as <i>Exogone minuscula</i> Hartman, 1953)
	<i>Exogone verugera</i>	(Claparède, 1868)	Hartman 1953
	<i>Sphaerosyllis hirsuta</i>	Ehlers, 1897	Hartman 1953
	<i>Sphaerosyllis kerguelensis</i>	McIntosh, 1885	Fauvel 1916; Hartman 1953 (all as <i>Sphaerosyllis retrodens</i> Ehlers, 1897)
	<i>Brania rhopalophora</i>	(Ehlers, 1897)	Fauvel 1916; Hartman 1953 (all as <i>Grubea rhopalophora</i> Ehlers, 1897)
	<i>Procerastea nematodes</i>	Langerhans, 1884	Fauvel 1916 (as <i>Procerastea perrieri</i> Gravier, 1900)
	<i>Pionosyllis comosa</i>	Gravier, 1906	Hartman 1953
	<i>Trypanosyllis gigantea</i>	(McIntosh, 1885)	Monro 1930, 1936; Hartman 1953; Hartmann-Schröder 1983
Glyceridae	<i>Glycera capitata</i>	Ørsted, 1843	Ehlers 1897; Monro 1930; Darbyshire
	<i>Glycera lapidum</i>	Quatrefages, 1866	Darbyshire
	<i>Hemipodia simplex</i>	(Grube, 1857)	Darbyshire
Goniadidae	<i>Goniada gigantea</i>	(Verrill, 1885)	Pratt 1901 (as <i>Goniada norvegica</i> var. <i>falklandica</i> Pratt, 1901); Monro 1936 (as <i>Goniada eximia</i> (Ehlers, 1901)); Hartmann-Schröder 1983 (as <i>Ophioglycera eximia</i> (Ehlers, 1901))
	<i>Glycinde armata</i>	(Kinberg, 1866b)	Fauvel 1916; Darbyshire
Nephtyidae	<i>Aglaophamus virginis</i>	(Kinberg, 1865)	Hartman 1953
	<i>Aglaophamus macroura</i>	(Schmarda, 1861)	Fauvel 1916 (as <i>Nephtys macroura</i> Schmarda, 1861); Darbyshire*
	<i>Nephtys imbricata</i>	Grube, 1857	Monro 1930 (as <i>Nephtys serratifolia</i> Ehlers, 1897); Hartman 1953 (as <i>Nephtys serratus</i> Hartman, 1953)
Phyllodocidae	<i>Eteone aurantiaca</i>	Schmarda, 1861	Ehlers 1897; Pratt 1901; Hartman 1953 (all as <i>Eteone spathocephala</i> Ehlers, 1897)
	<i>Eteone sculpta</i>	Ehlers, 1897	Monro 1930; Hartmann-Schröder 1983; Darbyshire
	<i>Notalia picta</i>	(Kinberg, 1866b)	Ehlers 1897; Monro 1930; Hartman 1953 (all as <i>Eulalia picta</i> Kinberg, 1866b); Darbyshire
	<i>Eulalia subulifera</i>	Ehlers, 1897	Hartman 1953 (BB, as <i>Hypoeulalia subulifera</i> (Ehlers, 1897))
	<i>Phyllodoce patagonica</i>	(Kinberg, 1866b)	Hartman 1953 (BB, as <i>Anaitides patagonica</i> Kinberg, 1866b)
	<i>Eulalia magalaensis</i>	Kinberg, 1866c	Monro 1936; Hartman 1953 (BB, as ? <i>Steggoa magalaensis</i> (Kinberg, 1866c)); Darbyshire
	<i>Pelagobia longicirrata</i>	Greiff, 1879	Støp-Bowitz 1951

Family	Species	Author	Recorded in Falkland Islands by:
Typhloscolecidae	<i>Sagitella kowalewskii</i>	Wagner, 1872	Monro 1930
	<i>Travisioopsis coniceps</i>	(Chamberlin, 1919)	Monro 1930 (as <i>Sagitella lobifera</i> (Chamberlin, 1919))
Sphaerodoridae	<i>Sphaerodoropsis parva</i>	(Ehlers, 1913)	Hartman 1953 (as <i>Sphaerodorum parvum</i> Ehlers, 1913)
Dorvilleidae	<i>Ophryotrocha claparedei</i>	Studer, 1878	Hartman 1953
Eunicidae	<i>Marphysa aenea</i>	(Blanchard in Gay, 1849)	Fauvel 1916 (as <i>Marphysa corallina</i> (Kinberg, 1865)); Darbyshire
	<i>Eunice pennata</i>	(Müller, 1776)	Monro 1930
Lumbrineridae	<i>Lumbrineris cingulata</i>	(Ehlers, 1897)	Monro 1930 (as ² <i>Lumbrineris magalhaensis</i>)
	<i>Lumbrineris magalhaensis</i>	Kinberg, 1865	Ehlers 1897 (as <i>Lumbriconereis magalhaensis</i> Kinberg, 1865); Monro 1930 (as ² <i>Lumbrineris tetraura</i> (Schmarda, 1861)); Hartman 1953
Oeonidae	<i>Arabella protomotans</i>	Orensanz, 1990	² Monro 1930 (as <i>Arabella iricolor</i> Montagu, 1804); Darbyshire
	<i>Notocirrus</i> cf. <i>virginis</i>	(Kinberg, 1865)	Darbyshire
Onuphidae	<i>Onuphis pseudoiridescens</i>	Averincev, 1972	Fauchald 1982 (as <i>Onuphis (Nothria) heterodentata</i> Fauchald, 1982 & <i>O. (N.) lithobiformis</i> Fauchald, 1982)
	<i>Paradiopatra quadricuspis</i>	(Sars, 1872)	Monro 1930 (as <i>Onuphis quadricuspis</i> M. Sars, 1872)
Acrocirridae	<i>Macrochaeta papillosa</i>	Ehlers, 1913	Hartman 1953 (BB)
Cirratulidae	<i>Cirratulus cirratus</i>	(O. F. Müller, 1776)	Fauvel 1916; Monro 1930; Hartman 1953
	<i>Cirriformia filigera</i>	(Delle Chiaje, 1828)	Fauvel 1916 (as <i>Audouinia filigera</i> (Delle Chiaje, 1828))
	<i>Cirriformia nasuta</i>	(Ehlers, 1897)	Hartman 1953
	<i>Promenia jucunda</i>	Kinberg, 1866d	Ehlers 1897; Pratt 1901
	<i>Protocirrinieris</i> cf. <i>antarcticus</i>	Monro, 1930	Darbyshire
	<i>Tharyx epitoca</i>	Monro, 1930	Hartman 1953
Flabelligeridae	<i>Flabelligera affinis</i>	Sars, 1829	Fauvel 1916; Monro 1930 (records referred to <i>F. induta</i> - Orensanz 1974)
	<i>Flabehlersia induta</i>	(Ehlers, 1897)	Ehlers 1897; Hartman 1953 (all as <i>Flabelligera induta</i> Ehlers, 1897)
	<i>Brada mammillata</i>	Grube, 1877	Hartman 1953
	<i>Pherusa swakopiana</i>	(Augener, 1918)	Hartman 1953 (as <i>Stylarioides swakopianus</i> Augener, 1918)
Capitellidae	<i>Notomastus latericeus</i>	Sars, 1851	Fauvel 1916
	<i>Capitella capitata</i>	(Fabricius, 1780)	Ehlers 1897; Hartman 1953

Family	Species	Author	Recorded in Falkland Islands by:
Opheliidae	<i>Ophelina gymnopyge</i>	(Ehlers, 1908)	Hartman 1953 (as <i>Ammotrypane gymnopyge</i> Ehlers, 1908)
Scalibregmatidae	<i>Scalibregmidex cf. chilensis</i>	Hartmann-Schröder, 1965	Darbyshire
Travisiidae	<i>Travisia olens</i>	Ehlers, 1897	Monro 1930; Darbyshire**
	<i>Travisia kerguelensis</i>	McIntosh, 1885	Hartman 1953; Darbyshire (as <i>Travisia cf. kerguelensis</i>)
Arenicolidae	<i>Abarenicola breviar</i>	(Wells, 1963)	¹ Pratt 1901 (as <i>Arenicola clapedii</i> Levensen, 1884); Fauvel 1916 (as <i>Arenicola assimilis</i> var. <i>affinis</i> Ashworth, 1912); Wells 1963 (as <i>Abarenicola assimilis breviar</i> Wells, 1963); Darbyshire 2017a
	<i>Abarenicola wellsi</i>	Darbyshire, 2017a	Darbyshire 2017a
Maldanidae	<i>Axiothella antarctica</i>	Monro, 1930	Monro 1930
	<i>Chymenella minor</i>	Arwidsson, 1911	Fauvel 1916; Monro 1930; Hartman 1953 (all as <i>Chymene minor</i> Arwidsson, 1911); Arwidsson 1911; Darbyshire
	<i>Lumbrichymenella robusta</i>	Arwidsson, 1911	Fauvel 1916; Darbyshire
	<i>Micromaldane shackletoni</i>	Darbyshire, 2013a	Darbyshire 2013a
	<i>Praxillella kerguelensis</i>	(McIntosh, 1885)	Fauvel 1916 (as <i>Chymene kerguelensis</i> (McIntosh, 1885); Darbyshire
Pectinariidae	<i>Cistenides ehlersi</i>	(Hessle, 1917)	Neely & Brickle 2013; Darbyshire (as <i>Cistenides cf. ehlersi</i>)
Terebellidae	<i>Hauchiella tribullata</i>	(McIntosh, 1869)	Hessle 1917
	<i>Neoamphitrite edwardsi</i>	(Quatrefages, 1866)	Monro 1930 (as <i>Amphitrite edwardsi</i> (Quatrefages, 1866))
	<i>Neoleprea streptochaeta</i>	(Ehlers, 1897)	Ehlers 1897; Fauvel 1916 (all as <i>Leprea streptochaeta</i> Ehlers, 1897); Hessle 1917; Monro 1930; Darbyshire
	<i>Nicolea chilensis</i>	(Schmarda, 1861)	Ehlers 1897 (as <i>Nicolea agassizi</i> (Kinberg, 1866d)); Fauvel 1916; Hessle 1917; Monro 1930; Hartmann-Schröder 1983; Darbyshire
	<i>Pista corrientis</i>	McIntosh, 1885	Monro 1930
	<i>Lysilla macintoshi</i>	Gravier, 1907	Darbyshire
	<i>Polycirrus hamiltoni</i>	Benham, 1921	Monro 1930
	<i>Polycirrus hesslei</i>	Monro, 1930	Monro 1930
	<i>Polycirrus macintoshi</i>	Glasby & Hutchings, 2014	Monro 1930 (as <i>Polycirrus kerguelensis</i> McIntosh, 1885)
	<i>Polycirrus multisetigerus</i>	Hartmann-Schröder, 1962	Darbyshire

Family	Species	Author	Recorded in Falkland Islands by:
	<i>Thelepus setosus</i>	(Quatrefages, 1866)	Ehlers 1897; Pratt 1901 (all as <i>Thelepus spectabilis</i> Ehlers, 1897); Hesse 1917 (as <i>Thelepus plagiotoma</i> (Schmarda, 1861)); Fauvel 1916; Monro 1930; Darbyshire*
Spionidae	<i>Boccardia chilensis</i>	Blake & Woodwick, 1971	Darbyshire
	<i>Boccardia polybranchia</i>	(Haswell, 1885)	Ehlers 1897; Pratt 1901; Fauvel 1916 (all as <i>Polydora polybranchia</i> Haswell, 1885); Darbyshire
	<i>Boccardia natrix</i>	(Söderström, 1920)	Hartman 1953 (BB)
	<i>Boccardiella</i> cf. <i>magniovata</i>	Read, 1975	Darbyshire
	<i>Dipolydora giardi</i>	(Mesnil, 1893)	Darbyshire
	<i>Polydora ciliata</i>	(Johnston, 1838)	Fauvel 1916
	<i>Rhynchospio</i> cf. <i>glutaea</i>	(Ehlers, 1897)	Darbyshire
	<i>Spiophanes bombyx</i>	(Claparède, 1870)	Fauvel 1916
Sabellariidae	<i>Idanthysus macropaleus</i>	(Schmarda, 1861)	Monro 1930 (as <i>Idanthysus armatus</i> Kinberg, 1866)
	<i>Phragmatopoma virgini</i>	Kinberg, 1866d	³ Pratt 1901 (as <i>Sabellaria macropalea</i> Schmarda, 1861); Neely & Brickle 2013; Darbyshire
Sabellidae	<i>Amphicorina alata</i>	(Ehlers, 1897)	Darbyshire
	<i>Amphicorina limbata</i>	(Ehlers, 1897)	Fauvel 1916; Hartman 1953 (all as <i>Oria limbata</i> Ehlers, 1897); Darbyshire
	<i>Amphicorina</i> cf. <i>magna</i>	Banse, 1957	Darbyshire
	<i>Bispira mariae?</i>	Lo Bianco, 1893	Pratt 1901
	<i>Bispira oatesiana</i>	Benham, 1927	Hartmann-Schroder 1983
	<i>Potamethus scotiae</i>	(Pixell, 1913)	Pixell 1913 (as <i>Potamis scotiae</i> Pixell, 1913)
	<i>Potamilla antarctica</i>	(Kinberg, 1866d)	Pixell 1913; Fauvel 1916; Monro 1930; Hartman 1953; Hartmann-Schröder 1983; Darbyshire
	<i>Potamilla neglecta</i>	(Sars, 1851)	Hartman 1953
	<i>Parasabella leucaspis</i>	(Kinberg, 1866d)	Fauvel 1916 (as <i>Bispira magalhaensis</i> (Kinberg, 1866d))
	<i>Perkinsiana antarctica</i>	(Kinberg, 1866d)	Neely & Brickle 2013; Darbyshire

Family	Species	Author	Recorded in Falkland Islands by:
	<i>Perkinsiana magalhaensis</i>	(Kinberg, 1866d)	Monro 1930 (as <i>Bispira magalhaensis</i> (Kinberg, 1866d)); Neely & Brickle 2013; Darbyshire
	<i>Perkinsiana pusilla</i>	(Johansson, 1922)	Johansson 1922 (as <i>Sabella pusilla</i> Johansson, 1922)
	<i>Pseudobranchiomma ceratodaula</i>	(Schmarda, 1861)	Pratt 1901 (as <i>Sabella ceratodaula</i> (Schmarda, 1861))
	<i>Sabella pusilla</i>	Johansson, 1922	Hartman 1953
Serpulidae	<i>Spirorbis spirorbis</i>	(Linnaeus, 1758)	Pratt 1901 (as <i>Spirorbis borealis</i> Daudin, 1800)
	<i>Protis brownii</i>	(Pixell, 1913)	Pixell 1913 (as <i>Apomatus brownii</i> Pixell, 1913)
	<i>Spirorbis (Paralaeospira) patagonicus</i>	Caullery & Mesnil, 1897	Pixell 1913 (as <i>Spirorbis patagonicus</i> Caullery & Mesnil, 1897)
	<i>Protolaeospira (Dextralia) falklandicus</i>	(Pixell, 1913)	Pixell 1913; Harris 1969 (all as <i>Spirorbis falklandicus</i> Pixell, 1913); Darbyshire
	<i>Paralaeospira claparedei</i>	(Caullery & Mesnil, 1897)	Fauvel 1916 (as <i>Spirorbis claparedei</i> Caullery & Mesnil, 1897); Darbyshire
	<i>Protolaeospira (Protolaeospira) tricostalis</i>	(Lamarck, 1818)	Fauvel 1916; Harris 1969 (as <i>Spirorbis lebruni</i> Caullery & Mesnil, 1897); Darbyshire
	<i>Paralaeospira aggregata</i>	Caullery & Mesnil, 1897	Hartman 1953 (as <i>Spirorbis aggregatus</i> Caullery & Mesnil, 1897)
	<i>Spirorbis auricularis</i>	Harris, 1969	Harris 1969 (referred to <i>P. lebruni</i> (= <i>P. tricostalis</i>) by Orensanz 1974)
	<i>Spirorbis flabellis</i>	Harris, 1969	Harris 1969 (Knight-Jones <i>et al.</i> 1973 throw doubt on the validity of these two species but do not attribute them to any other)
	<i>Spirorbis focalis</i>	Harris, 1969	Harris 1969
	<i>Romanchella perrieri</i>	Caullery & Mesnil, 1897	Harris 1969; Hartman 1953 (all as <i>Spirorbis perrieri</i> Caullery & Mesnil, 1897); Darbyshire
	<i>Serpula narconensis</i>	Baird, 1865	Hartman 1953 (BB); Hartmann-Schröder 1983 (all as <i>Serpula vermicularis narconensis</i> Baird, 1865)
	<i>Salmacina falklandica</i>	Monro, 1930	Monro 1930 (as <i>Salmacina dysteri</i> var. <i>falklandica</i> Monro, 1930)
Chaetopteridae	<i>Phyllochaetopterus socialis</i>	Claparède, 1869	Fauvel 1916
	<i>Chaetopterus variopedatus</i>	(Renier, 1804)	Monro 1930; Hartman 1953; Neely & Brickle 2013; Darbyshire (as <i>Chaetopterus</i> sp.)

- *Polynoidae*: 13 taxa recorded, three nominal species of which two (*Neopolynoe antarctica* (Kinberg, 1858) and *Hermadion magalhaensi* Kinberg, 1856) have previously been recorded. The third, *Halosydna patagonica* Kinberg, 1856, although not previously known from the Falkland Islands, is recorded from South America and was originally described from Magellan Sound, Chile. *Hermadion magalhaensi*, a large distinctive species, was the most common subtidal scaleworm identified and frequently found under rocks. An additional species, *Euphionella robusta* Wesenberg-Lund, 1962 was recorded from specimens collected by offshore trawlers in the region and constitutes not only a new record for the Islands but also the only other record of the species since its description from Chile by Wesenberg-Lund in 1962. A further eight previously recorded species were not found in these surveys.
- *Pholoidae*: No previous records of this family exist from the Falkland Islands. The single species identified, *Pholoe polymorpha*, was originally described from the Chilean south Pacific (Hartmann-Schröder 1962). Specimens were very small, uncommon and only identified from six stations.
- *Orbiniidae*: Eight taxa from three genera were recorded, although the identification of a small number of specimens as *Scoloplos* (*Scoloplos*) is tentative and the large-bodied *Phylo* specimens possibly represent two separate species requiring further investigation. Several species of *Scoloplos* (*Leodamas*) appear to be present, although it was not possible to definitively match them to those taxa previously recorded from surrounding and nearby waters. A species of *Leitoscoloplos* was also present, matching those reported by Fauvel (1916) as *L. kerguelensis* (McIntosh, 1885). However, more recent publications by Mackie (1987) and Blake (2017) have stated that Fauvel's specimens are not *L. kerguelensis* and instead are likely to be a new species although not enough material has been available to describe this species up to now. *Phylo felix asiaticus* Wu, 1962 was recorded previously by Monro (1930) although this species was described from the Yellow Sea and therefore this identification is also in doubt. Two other previously recorded species of *Scoloplos* (*Leodamas*) were not found.
- *Chrysopetalidae*: See **Chapter 4/Paper 3**. Only one species identified, no previous records of Chrysopetalidae for the area.

- *Hesionidae*: There are no previous records of Hesionidae from the Falkland Islands. Two taxa were identified, *Microphthalmus* sp. (potentially thought to constitute more than one species but consolidated here to one) and *Gyptis* sp.. *Microphthalmus* sp. were not uncommon members of the interstitial fauna as observed in sievings samples and were present at 21 stations. Only a single specimen of *Gyptis* sp. was collected.
- *Nereididae*: See **Chapter 3/Paper 2**. Four of the eight taxa previously recorded were identified from the surveys and one new species was described. Of the remaining taxa, the record of *Perinereis atlantica* was determined to be doubtful and those of *Platynereis australis* debatable and probably confused with *P. magalhaensis*. Records of *Eunereis patagonica* are valid although the species was not recorded here and *Nicon maculata* inhabits deeper water (>30 m) beyond the scope of this study, although it was recorded from specimens collected by offshore trawlers.
- *Syllidae*: The most diverse (taxonomically) and widespread family in the study by far, recorded from over 80% of the stations, with 19 genera and 44 taxa. None of those recorded have been identified to named species at this time although 18 species are recorded from the region.
- *Glyceridae*: Three species in two genera recorded, only one of which had been previously recorded. *Hemipodia simplex* Grube, 1857 is a new record. Taxa in this family were rare, only being recorded from seven stations.
- *Goniadidae*: In contrast to the closely-related Glyceridae, the single taxon recorded, *Glycinde armata* (Kinberg, 1866b) was common, found at 22 stations, often several at a time. The only other known taxon from the family, *Goniada gigantea* (Verrill, 1885), recorded several times by previous authors, was not found.
- *Nephtyidae*: Only a single taxon recorded from all samples, *Aglaophamus* cf. *macroura* (Schmarda, 1861), appears to be the same as that recorded by Fauvel (1916) from the Islands. However, the distinction between this species and *Aglaophamus virginis* (Kinberg, 1865), also recorded from the region by Hartman (1953) is not clear and requires further investigation. The only other taxon previously recorded, *Nephtys imbricata* Grube, 1857 was not found.

- *Phyllodoceidae*: 18 taxa recorded, four nominal species, all of which were known from the area previously. *Eulalia magalaensis* (Kinberg, 1866a), distinctively dark green, robust and long was the largest paddleworm found and common both subtidally and in intertidal crevices. Also common and distinctive was *Notalia picta* Kinberg, 1866b (dark green with yellow longitudinal lines), a much smaller species than *E. magalaensis* but more common intertidally. Two further species on the previously published list, *Eteone aurantiaca* Schmarda, 1861 and *Phyllodoce patagonica* (Kinberg, 1866c), were not found here.
- *Sphaerodoridae*: Four taxa recorded, all of the same genus, none named at this time. One species, of the same genus, has been previously recorded for the region: *Sphaerodoropsis parva* (Ehlers, 1913).
- *Dorvilleidae*: Represented by very small specimens, three taxa in two genera, all currently unnamed, were recorded. All were uncommon. Only a single taxon of the family, *Ophryotrocha claparedei* Studer, 1878, has been recorded from the area previously.
- *Eunicidae*: Another uncommon family, specimens were only collected from nine stations. Of the two taxa identified, one, *Lysidice* sp. 1 was only represented by a single specimen and is a new record for the genus in the Islands. The other, *Marphysa aenea* (Blanchard in Gay, 1849), although more common, was still only present at nine stations and was previously recorded by Fauvel (1916). *Eunice pennata* Müller, 1776, recorded by Monro (1930), was not found.
- *Lumbrineridae*: Only two taxa of the same genus were recorded in the samples, and neither are named at this time. *Lumbrineris* sp. 1 was the most common, being present at 33 stations, often very numerous in the samples, compared to *Lumbrineris* sp. 2, present only in small numbers and only at three stations. From other studies, *Lumbrineris cingulata* (Ehlers, 1897) and *Lumbrineris magalhaensis* Kinberg, 1865 (both originally described from the Magellan region), have been recorded for the Islands following Orensanz's re-identification (1990) of Monro's (1930) material. *Lumbrineris* sp. 2 has affinities with *L. magalhaensis* although further investigation is needed to determine if they are the same.
- *Oeonidae*: Three taxa in three genera were recorded, being some of the larger sized taxa recorded in the study. *Arabella protomutans* Orensanz, 1990, described from Antarctica, was

previously recorded from the area by Monro (1930) as *Arabella iricolor* Montagu, 1804. Monro's specimens were examined by Orensanz (1990) and re-identified as his new species *A. protomutans*. *Notocirrus* sp. 1 is most similar to *N. virginis* (Kinberg, 1865) although some small differences exist. This genus, as well as *Drilonereis* (unnamed), are new to the Islands.

- *Onuphidae*: The single taxon recorded, *Kinbergonuphis* sp., formed large dominant colonies at some sites both on- and offshore, with tubes visibly poking above the sand. The taxon is most similar to *Kinbergonuphis heterouncinata* (Hartmann-Schröder, 1965), however significant differences exist between the two. The only other members of the family known from the region are *Onuphis pseudoiridescens* Averincev, 1972, recorded by Fauchald (1982) from deeper offshore waters and *Paradiopatira quadricuspis* (Sars, 1872), recorded by Monro (1930) from 115 m.
- *Acrocirridae*: Three taxa in two genera were recorded in this family where previously only a single taxon had been reported from deeper water at Burdwood Bank. Each of the taxa, currently unnamed, were only recorded from 1–3 stations each, generally only as one or two specimens at a time, although *Macrochaeta* sp. 1 was particularly abundant (51 specimens) at one station. *Acrocirrus* sp. 1 appears closest to some species described from Japan although this seems unlikely and therefore requires further investigation. Neither *Macrochaeta* sp. 1 nor sp. 2 correspond to the description of *Macrochaeta papillosa* Ehlers, 1913, the only previously recorded taxon in this family.
- *Cirratulidae*: Eleven taxa in six genera are tentatively recorded. Differences between taxa were often subtle and difficult to quantify, resulting in several 'taxa' being amalgamated during the course of identification. Further study is still needed to definitively determine exactly how many taxa are present, particularly within *Cirratulus*. Only one of the taxa has a name at this time and has not been recorded previously. Five taxa from five genera have been recorded previously, with only two of those genera reported here.
- *Flabelligeridae*: Three taxa in three genera were recorded, all unnamed as yet. In comparison, four taxa in four genera (two of those the same as recorded here) are recorded previously. The taxon *Trophoniella* sp. 1 matches the general description, with some few differences, provided for *Therochaetella chilensis*, discovered and described from off the west coast of

Chile by Hartman (1967). The genus, not recorded since, was referred to *Trophoniella* as a junior synonym by Salazar-Vallejo (2012) and is a new record for the Islands. *Flabelligera* sp. 1 is distinct from both *Flabelligera affinis* Sars, 1829 and *Flabehlersia induta* (Ehlers, 1897) (previously *Flabelligera*) and cannot currently be assigned to any known species.

- *Cossuridae*: No specimens of Cossuridae were identified during the study and none have been recorded previously. However, contract work carried out (by the author) on fauna sampled from the Islands, revealed an abundant population of *Cossura* sp. from one site. The specimens were not in good enough condition, unfortunately, to identify to species level. The habitat was shallow, subtidal mud which was not one encountered as part of this study.
- *Paraonidae*: Three taxa from two genera were recorded, all currently unnamed. Abundance and frequency of occurrence were generally low although specimens of *Paradoneis* sp. 1 were locally abundant in some of the subtidal samples from Egg Harbour and Kelp Harbour in Falkland Sound (stns 22, 23, 26) and *Aricidea* sp. 1 was abundant in intertidal samples from Mullet Creek (stn 33). Both were numerous (*Paradoneis* sp. 1 particularly so with over 700 individuals in a small sample) at Chartres (stn 53). There are no previous records of the family from the Islands.
- *Capitellidae*: Two taxa from two genera have been recorded previously, both of which have been reported widely geographically in the literature. Potentially seven genera are recorded in this study, although three of those are tentative. Although unnamed at this time, this adds two previously unrecorded genera to those known from the area.
- *Opheliidae*: One species of *Ophelina* is recorded for the area previously and was not found during this study. Only a single taxon of *Ophelia*, represented by juvenile specimens that had not yet developed diagnostic adult characters, was represented in a small number (6) of samples. Although mostly found in small numbers, at one site (stn 49, New Haven), specimens were highly abundant with over 400 recorded. *Ophelia* has not been recorded from the Islands previously.
- *Scalibregmatidae*: The only previous records for this family were for the genus *Travisia*, now transferred to the new family Traviidae (Blake & Maciolek 2016). The remaining species

recorded, *Scalibregmides chilensis* Hartman-Schröder, 1965, one of only two taxa in the genus, was described from the Pacific coast of Chile but is not currently known from the Atlantic coast. Small differences between the new specimens and the description may prove to be significant. Additional specimens of *Scalibregmides* showed further variation and may represent another taxon again.

- *Travisiidae*: Two species of *Travisia* have previously been recorded from the area, both of which were recorded here either in the study samples or in contract samples. However, *Travisia* cf. *keruelensis* McIntosh, 1885, as recorded from the study samples, shows some differences from the original description that may prove it to be different with further study.
- *Arenicolidae*: See **Chapter 2/Paper 1** for details of the history and current findings in this family. Three taxa had been recorded previously, however those recorded by Pratt (1901) and Fauvel (1916) were all re-identified by Ashworth (1903, 1912) and Wells (1963) and attributed to *Abarenicola brevior* (Wells, 1963), leaving that species as the only one previously recorded. Both *A. brevior* and a new species, *Abarenicola wellsii* Darbyshire, 2017a, are recorded by this study.
- *Maldanidae*: Maldanidae were common in the samples, the most common taxon being *Clymenella minor* Arwidsson, 1911. With the exception of a single dive site (stn 62), *C. minor* was not recorded from any of the subtidal samples but was present in over 50% of the intertidal samples. In contrast, *Lumbriclymenella robusta* Arwidsson, 1911 and *Praxillella keruelensis* Arwidsson, 1911 were only recorded from one and seven sites respectively, two of the latter sites being subtidal. All three species were recorded from the area previously. The only other taxon previously recorded, *Axiothella antarctica* Monro, 1930 was not found. *Micromaldane shackletoni* Darbyshire, 2013a (see **Chapter 5/Paper 4**), was newly described during this study, and was recorded exclusively from subtidal samples.
- *Pectinariidae*: *Cistenides ehlersi* (Hessle, 1917), described from Argentina and the Magellan region and the only member of the genus known to inhabit nearby waters, was included by Neely & Brickle (2013) in their *Marine Life of the Falkland Islands* publication, although it was not recorded by any other previous survey. The single taxon recorded here from two subtidal sandy sites in Falkland Sound differs in several respects from the current description of *C. ehlersi*, and may represent a new species.

- *Ampharetidae*: Not previously recorded from the area, two taxa were identified but could not be attributed to any currently known genera at this time. All specimens are small, possibly juvenile, and exclusively subtidal. Further work is required to determine their identification.
- *Terebellidae*: Nine taxa from seven genera are reported previously of which three are also recorded here. The specimens of *Thelepus* sp. 1, the most abundant and largest terebellid recorded during the study, match the descriptions given by earlier authors who referred their specimens to *Thelepus setosus* (Quatrefages, 1866), a northern hemisphere species. However, comparison of *Thelepus* sp. 1 with a table of characters for all (at the time) known species of *Thelepus*, published by Hsueh & Li (2016), does not find a match and may indicate a new taxon. Further investigation will be required to determine this. Of the other taxa recorded by the study, *Lysilla macintoshi* Gravier, 1907 and *Polycirrus multisetigerus* Hartmann-Schröder, 1962 are both new records for the Islands. The other recorded species of *Polycirrus* were not found nor were any species of *Neoamphitrite* or *Pista*. *Hauchiella tribullata* (McIntosh, 1869) is, again, a northern hemisphere species, although Hesse did state that his species identification was uncertain. Hesse's description of his specimens from the Falkland Islands is brief and it is not clear at this time whether *Hauchiella* sp. 1 as identified here is the same as those specimens. It is clear, however, that *Hauchiella* sp. 1 does not conform to the published descriptions of any of the three known species of *Hauchiella* and is therefore likely to be a new species. Two other genera are tentatively identified from the samples and require further investigation, along with another taxon that could not be attributed to any of the currently known genera.
- *Spionidae*: Spionidae is a very diverse group of 39 genera, nine of which were recorded during the study, six for the first time, making it the next most generically diverse family recorded after the Syllidae. Fourteen taxa, five named at least tentatively, were recorded with *Dipolydora* and *Boccardia* being the only genera represented by more than one taxon. Only four taxa had been recorded previously, three of which were not found. Of those, one was only recorded from the deeper water of Burdwood Bank to the south, and the other two are both European species. It is expected that further investigation will find that *Spiophanes* sp. 1 and the *Spiophanes bombyx* (Claparède, 1870) recorded by Fauvel (1916) are the same but represent a different or undescribed species.
- *Sabellariidae*: A single taxon, *Phragmatopoma virginii* Kinberg, 1866d was recorded from both intertidal and subtidal sites and is known locally for forming subtidal reefs in some

areas (Neely & Brickle 2013). *Idanthyrsus macropaleus* (Schmarda, 1861), the only taxon in the family previously recorded from historical surveys of the area, was recorded by both Pratt (1901) and Monro (1930), although Pratt's records were referred to *P. virgini* by Kirtley (1994) in his taxonomic review of the family. *Idanthyrsus macropaleus* is also recorded from the Port Stanley area by Kirtley (1994) with reference to specimens in the Smithsonian collections collected by Waldo Schmitt on the R.R.S. *William Scoresby* in 1927. Strangely, the dates and station numbers in the Smithsonian catalogue records do not match the published station lists for the *William Scoresby* and so these records are not included in the compiled list given here. Kirtley's confirmation of Monro's identifications, however, provide confirmation that *I. macropaleus* should be present in the area.

- *Sabellidae*: Twelve taxa from eight genera have been recorded previously, only four of which were also recorded during this study. *Perkinsiana antarctica* (Kinberg, 1866d) was found to be the dominant large sabellid subtidally and was found intermixed with several other taxa, mostly unnamed at this time but believed to be species of *Parasabella*. *Perkinsiana magalhaensis* (Kinberg, 1866d), reported by Neely & Brickle (2013) as the species most likely to be found in rock encrustations, was only tentatively identified once. The two species are very difficult to separate and expert confirmation of these identifications is required. Of the smaller taxa, several species of both *Chone*, all currently unnamed, and *Amphicorina* were distinguished, only one species of which had been previously recorded.
- *Fabriciidae*: Previously a sub-family of Sabellidae (as Fabriciinae), no members of this family have previously been recorded from the area. Three distinct taxa of *Fabricia* were recorded from the samples as well as another taxon not currently attributed to a genus. Each taxon was individually abundant at different sites with *Fabricia* sp. 2 and *Fabricia* sp. 3 forming dense populations at some.
- *Serpulidae*: Thirteen taxa, all but two of the subfamily Spirorbinae, have been previously recorded from the Islands, of which four are also recorded here. No taxa outside of the Spirorbinae were recorded in this study. Knight-Jones *et al.* (1973) stated that in their investigations of *Spirorbis*, they were yet to find any taxa of *Spirorbis sensu stricto* in the Southern Atlantic and cast doubt on the validity of any records of the genus, with specific mention of both *Spirorbis flabellis* Harris, 1969 and *Spirorbis focalis* Harris, 1969, although there was no mention of what other taxa they might be referred to instead. Orensanz (1974)

listed *Spirorbis auricularis* Harris, 1969 as a synonym of *Protolaeospira lebruni* Caullery & Mesnil, 1897 (now *Protolaeospira tricostalis* (Lamarck, 1818)) but gave no details of his reasoning in doing so. Such doubts potentially reduce the known species list to nine. Those taxa that were collected were generally locally abundant and often specific to the habitat on which they were found. In total, 10 different taxa of Spirorbinae were distinguished of which only four are currently named. The complexity of Spirorbinae taxonomy is such that even generic identification of those unnamed taxa is uncertain at this time.

- *Chaetopteridae*: Two taxa from two genera were recorded. *Chaetopterus variopedatus* (Renier, 1804) has previously been reported from the Islands and is assumed there to be an introduced species (Neely & Brickle 2013), probably through shipping, as its type locality is Mediterranean. The taxon recorded here is not given this name until further investigation, possibly molecular, can deny or confirm the identification. The other species previously recorded, *Phyllochaetopterus socialis* Claparède, 1870, is also Mediterranean. *Phyllochaetopterus* was not recorded in this study, although a species of *Spiochaetopterus*, as yet unnamed, was. The animal, locally abundant, occurred in colonies, usually attached to subtidal rock.
- *Nerillidae*: Not previously recorded from the area, this family of small interstitial polychaetes was recorded from four sites, both intertidal and subtidal. Specimens are so small that it is possible that additional specimens from the same or other sites might easily have been lost through the sieve mesh thus leaving the family under-recorded. A single genus was identified although a more specific taxon name is lacking at this time.
- *Polygordiidae*: Not previously recorded from the area, none of these specimens were recovered whole with all but one fragment missing the essential posterior region. Identification is likely to remain generic only unless more, intact specimens can be collected.

6.3 Cluster Analyses

Cluster analyses of the results were carried out using PRIMER-E v6.1.18 (Clarke & Gorley 2006). Different levels of data were analysed to provide insight into how the results clustered together. Analyses were run on all of the separate samples, the stations (samples consolidated to stations) and those samples taken by sieving or washing off sediment through a 0.5 mm mesh sieve. Stations or samples (5c, 9b, 15b, 16a, 17, 18b, 24, 32, 43, 54g, 60, 65, 72) that existed only for a small

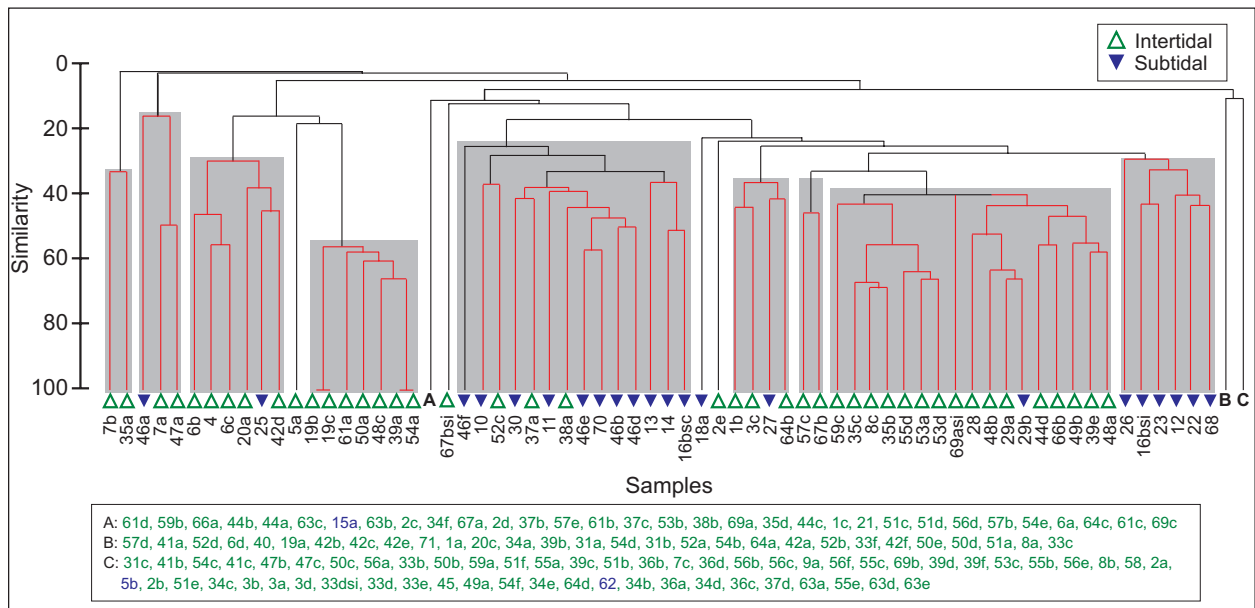


Figure 12. Bray-Curtis classification of all samples ($n=183$) used for analysis (presence-absence data; clusters of non-significantly different ($P<0.05$) samples coloured red. Samples in collapsed branches of non-significant clusters listed below dendrogram and coloured according to intertidal or subtidal position). Significant groups shaded grey.

number of specifically collected individuals (as opposed to a collection effort that only found a few specimens) were omitted. All data were transformed to presence/absence and Bray-Curtis similarity calculated. Dendrograms were constructed using the group-average method with additional factors representing shore height and sediment type overlaid. Significance of each branch ($p<0.05$) was calculated using the SIMPROF routine within PRIMER. Non-metric multidimensional scaling (MDS) plots were also produced, in both 2-d and 3-d, from the transformed data using 50 restarts but all other default settings.

Individual samples: 183 samples were used for the cluster analysis. Bray-Curtis similarity was plotted on a dendrogram with shore height (Appendix A7.1: subtidal, extreme low shore, low shore, mid-low shore, midshore and high shore), depth (Figure 12: intertidal or subtidal) and sediment types (Appendix A7.1: 19 types) overlaid. Assessments of shore height and sediment type were subjective and based on my assessment *in situ*. The basic assessment of subtidal versus intertidal heights (Figure 12) showed the best groupings with the majority of the subtidal samples (17/26) forming two discrete groups, one exclusively subtidal with 6 samples, and the other (formed of three sub-clusters and one outlier) forming a slightly mixed group of 11 subtidal and 3 intertidal (2 low shore and 1 midshore) samples. Whilst the rest of the shore height assessments seemed mostly intermixed, many of the low shore samples did form small groups within larger clusters (Appendix A7.1). Similarly, overlaying sediment types (Appendix A7.1) also produced mixed clusters with

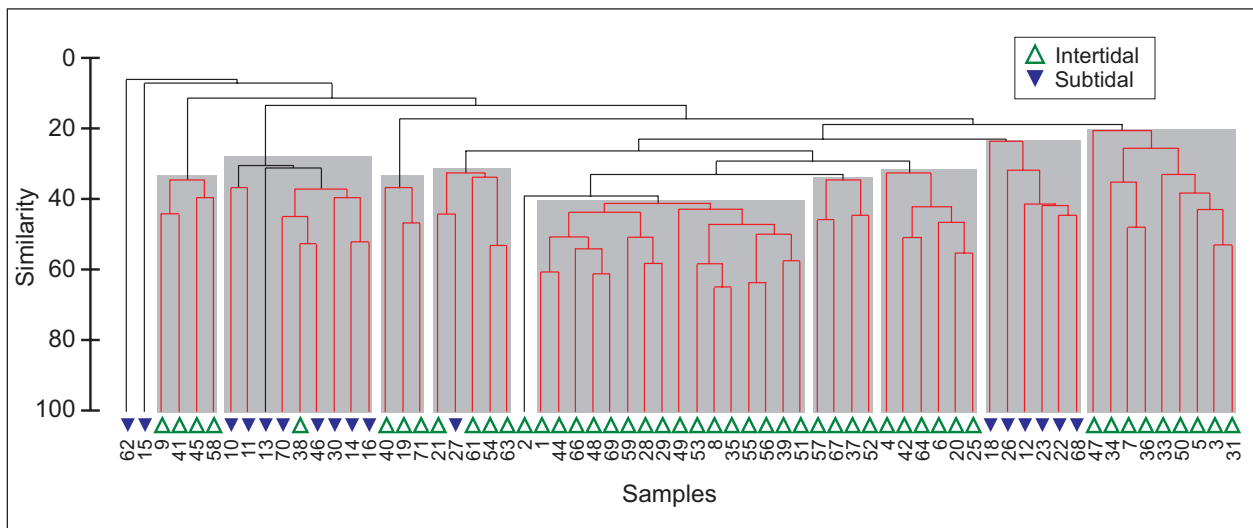


Figure 13. Bray-Curtis classification of all stations ($n=65$) used for analysis (presence-absence data; clusters of non-significantly different ($P<0.05$) samples coloured red). Significant groups shaded grey.

smaller, more discrete clusters within. In particular, those samples from scrapings, encrusting algae and crevices tended to form small clusters together and there was also a large cluster (86) consisting of more than two thirds of the ‘sand’ samples (66/89) along with a mix of other sediment types. Multi-dimensional scaling analyses (2-d and 3-d), relating samples to both sediment type and shore height, depict slightly more visual groupings (Appendix A7.2a–d). Stress levels are high for all MDS plots although the 3-d plots (Appendix A7.2c–d; stress=0.13) show some small improvement in interpretation over the 2-d plots (Appendix A7.2a–b; stress=0.18). The most visually apparent groupings depicted are those representing subtidal samples (Appendix A7.2a, c) and those from crevices, scrapings or encrusting algae, although the latter two are most apparent from the 3-d plot (Appendix A7.2b, d). In general, groups relating to specific factors such as depth, shore height, sediment type or geographic location were not clearly defined at this level.

Station analysis: Sixty-five stations were used for the station analysis with samples within each station consolidated to a single list of taxa. Significance, at the 5% level, was calculated with the SIMPROF routine. As shore height and sediment type could not be assessed at a general station level, only depth (subtidal/intertidal) and location were used to assess the results. Bray-Curtis similarity, combined with the SIMPROF results, highlighted 9 clusters and 3 outlying stations (Figure 13). Again, the majority of the subtidal stations were significantly different to the intertidal ones and formed two defined clusters. Stations 12, 18, 22, 23, 26 & 68 formed an exclusive subtidal cluster although neighbour to the majority of the intertidal stations. Stations 10, 11, 13, 14, 16, 30, 46 & 70 formed the other subtidal cluster with intertidal station 38, although

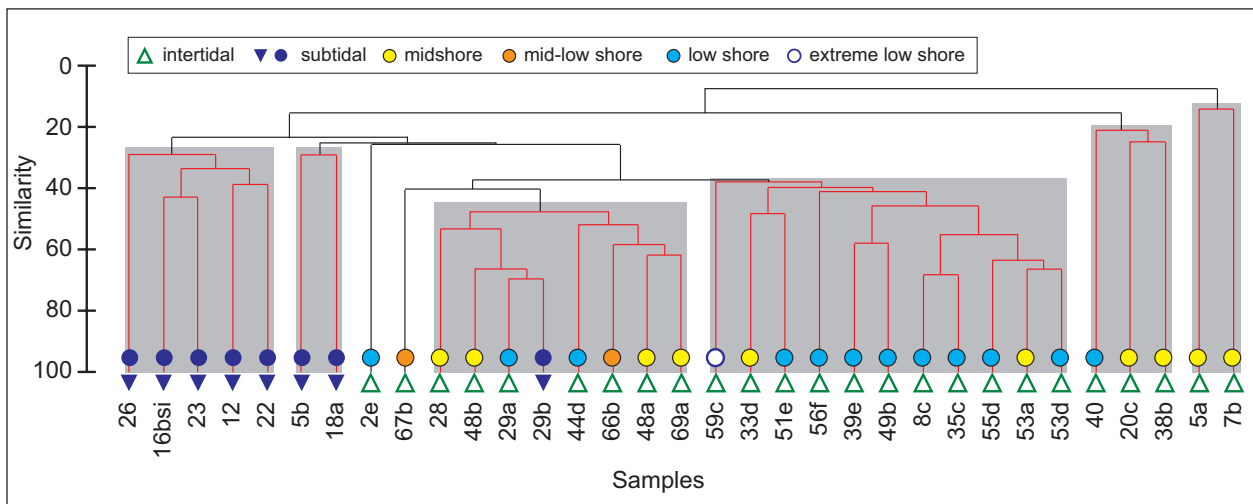


Figure 14. Bray-Curtis classification of sievings samples ($n=33$; presence-absence data; clusters of non-significantly different ($P<0.05$) samples coloured red). Significant groups shaded grey.

it could also be split into two closely-related clusters that included station 13 as an individual point. Of the remaining three subtidal stations, 15 & 62 were significantly different from all of the others and station 27 fell within an otherwise intertidal grouping. The MDS results depict the subtidal stations mostly clustering together although the stress value for the analysis was high (0.21; Appendix A7.3a) indicating that the depiction is not a reliable estimate of relatedness. The associated 3-d plot (Appendix A7.3b) returned a lower stress value of 0.15, indicating that although it was a more reliable assessment than the 2-d plot, it was still not a reliable assessment on its own and should only be interpreted in conjunction with the dendrogram. If an attempt is made to superimpose the clusters defined by the dendrogram onto the MDS, it becomes clearer that, despite the relative closeness of the subtidal stations, the significant groups are not, in fact, so easily delineated.

Sievings: Thirty-three samples, from both intertidal and subtidal sites, represented taxa from sediment that was sieved through a 0.5 mm sieve. These were analysed separately as the fauna comprised many more, smaller taxa that would be distinct from other samples but could show parity with each other. As before, a subtidal cluster was evident (Figure 14: samples 12, 16b, 22, 23 & 26), and included five of the eight subtidal samples. Of the remaining three, sample 5b (grouped with sample 18a), was defined as subtidal, although it was actually only taken from approximately 30 cm below low water, by wading. Sample 5a, from the same shore but intertidal, showed significant difference to the majority of the other samples, including 5b, but still grouped with another intertidal sample (7b). This can be contrasted with the final subtidal sample, 29b, sampled slightly further below low water (~0.5 m) by snorkelling but showing no significant

difference from its intertidal neighbour, and closest relation, 29a. If more detailed shore height assessments are overlain on the dendrogram (Figure 14), some small definition can be discerned with the majority of the low shore samples (8/12) forming a single cluster. Other clusters were more mixed. Assessments of sediment type (Appendix A7.4a), whether consolidated into more open categories or more detailed, showed small pockets of clustering within larger groups although they were not defined as significantly different overall. All of the 2-d MDS analyses (Appendix A7.4b-d) showed high stress values (0.19), with lower values of 0.14 returned by 3-d plots. The clusters, as defined by the dendrogram, were, for the most part, easily overlaid, highlighting the clustering together of subtidal samples in comparison to the more mixed shore heights evident within the other clusters. The exception to this was the 5b-18a cluster that, despite being highlighted as significantly different to other samples but not to each other, do not cluster together in the MDS plots (Figs A7.4b–f). There was no evidence of geographic bias within any of the clusters that was not better explained by the other factors.

6.4 Species richness & taxonomic distinctness

Species richness (S , no. of species) values are not directly comparable as the methods and level of sampling effort at each sample and station were not consistent (Clarke & Warwick 2001a, b) and are therefore not discussed. Unlike species richness though, taxonomic distinctness has been shown to be independent of sample size and applicable to presence/absence datasets providing a valid comparison between samples (Clarke & Warwick 2001a, b). All indeterminate taxa (including juveniles where only identified to genus level) were removed from the data and taxonomic distinctness was assessed using the *average taxonomic distinctness* (AvTD, Δ^+) and *variation in taxonomic distinctness* (VarTD, Λ^+) indices within PRIMER-E. A master species list was compiled as the taxonomic reference detailing species, genus and family affiliations for all taxa identified in the study. Funnel plots were produced (Figure 15), using the TAXDTEST function with 10000 random selections, to illustrate the spread of Δ^+ and Λ^+ values within simulated 95% probability limits (Clarke & Gorley 2006). The 95% probability curves indicate how closely the species list from each sample reflects the taxonomic distinctness structure of the master species list (all species identified across all samples). Values below the lower probability limit (AvTD, Δ^+) indicate that biodiversity is ‘below expectation’ (Clark & Gorley 2006) whereas values above the higher probability limit for VarTD (Λ^+) indicate significantly greater than expected values, i.e. a less even spread of diversity with dominance of the species list by one or a few species-rich groups. All values generated for both measures are listed in

Appendix 8, ranked by both average taxonomic distinctness (Tables A8.1a, A8.2a, A8.3a) and variation in taxonomic distinctness (Tables A8.1b, A8.2b, A8.3b).

Taxonomic distinctness: Values for average taxonomic distinctness (Δ^+) show little variation and most fall within the 95% probability limits on the funnel plot. When applied to the full suite of samples, the taxonomic distinctness indices show that, in comparison with the majority, the sievings samples tend to have decreased Δ^+ and increased Λ^+ values (Figure 15a–f; Tables A8.1) indicating depressed diversity with species lists dominated by one or a few species-rich groups. From the funnel plots, a narrow range of Δ^+ values (Figure 15a) is clear with the most significantly reduced Δ^+ values shown in samples 8c and 35b, but also to a lesser extent by other sievings samples and also sample 19a, where several capitellid taxa were identified but otherwise only one or two taxa from several other families. The funnel plots for Λ^+ (Figure 15b) show a much greater array of samples exceeding the 95% probability limits. Of those, the only ones not representing sievings samples are 19a, 31b and 38a, the latter being a pink encrusting algae scraping. The only western sample with significantly, albeit only slightly, elevated Λ^+ , was sample 44d although the corresponding Δ^+ was not significant. There was an even spread of intertidal and subtidal samples among the highlighted samples.

For the consolidated station measures, the funnel plots (Figure 15c-d) illustrate that stations 8, 14, 16, 19, 23, 27 and 35 all present lower than expected values for Δ^+ and of these, stations 8, 14, 16, 19 and 35, along with station 70 (borderline), also exhibit higher than ‘expected’ Λ^+ values. All of these stations included some form of niche habitat sample such as sievings, scrapings, algal turf or crevices. All of the stations were from eastern sites and were not dominated by either intertidal or subtidal stations.

When analysed as part of a stand-alone sievings group, samples 8c, 23, 35c, 49b and 53a all fall below ‘expected’ values of Δ^+ (Figure 15e) while the same samples, with the exception of sample 23 but the addition of sample 44d, show greater than expected values for Λ^+ (Figure 15f). Sievings samples were particularly rich in small Syllidae, Orbiniidae, Capitellidae and Sabellidae. When analysed together, it was notable that several sievings samples showed lower than expected Δ^+ values (Figure 15e) but greater than expected Λ^+ (Figure 15f). The most significant of these were samples 8c and 35c, also the only two samples whose station as a whole demonstrated significantly raised Λ^+ (Figure 15d). In relation to the all sample analysis (Figure 15b), 8c, 35c and 44d were all represented although 44d was only just above the 95% significance boundary. Sample 8c was

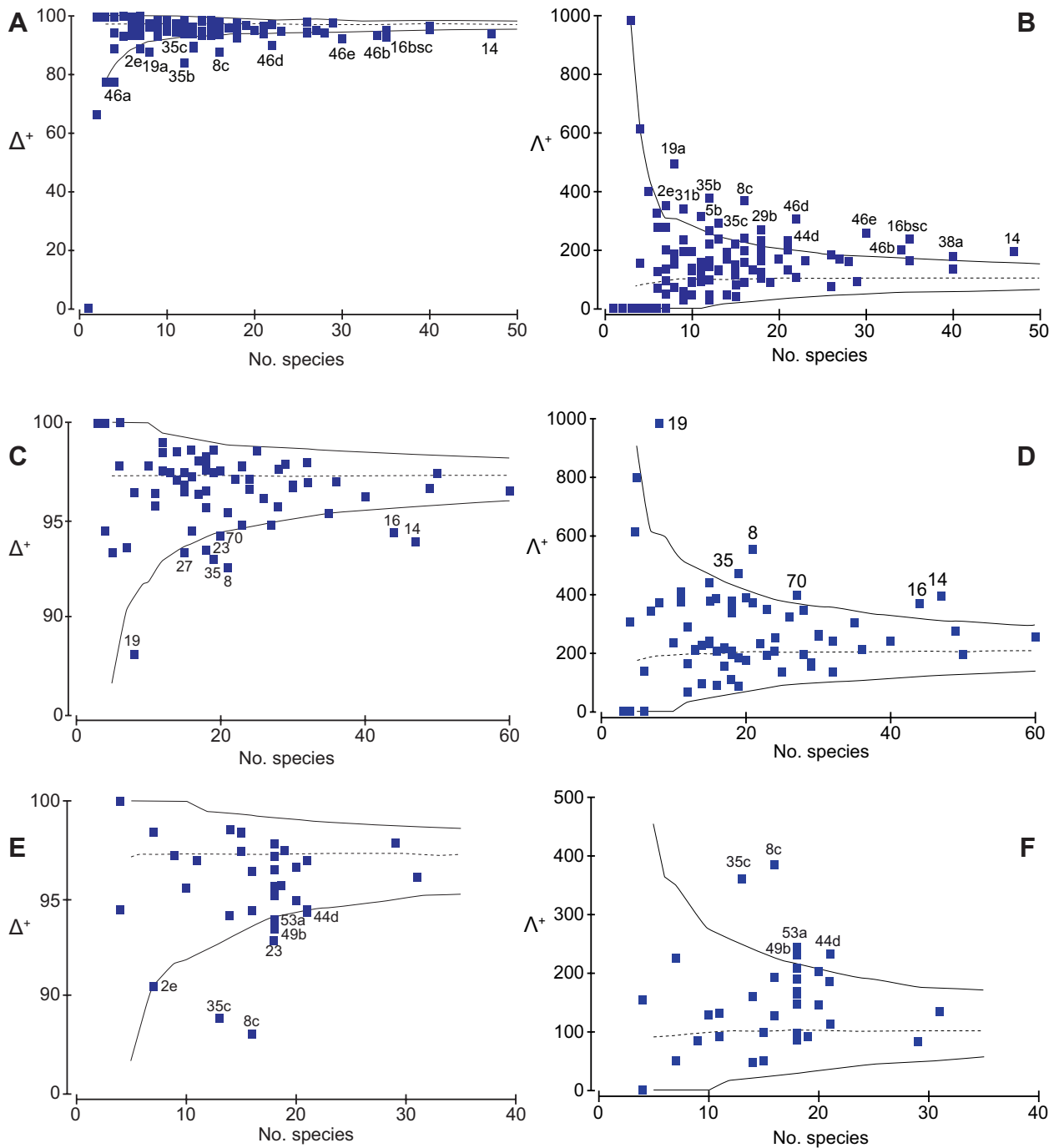


Figure 15. Funnel plots of average taxonomic distinctness (Δ^+) and variation in taxonomic distinctness (Λ^+) for all samples (A&B), stations (C&D) and sievings (E&F).

soft, fine sand containing a matrix of tubes of small Sabellidae and Maldanidae. The site was on a raised bank that only uncovered at low tide and nine out of the 17 taxa recorded there were Syllidae. Similarly, in sample 35c, a completely different habitat of mud and gravel, seven out of the 15 taxa were Syllidae. At station 46, where the highest number of taxa were recorded across all stations (60 taxa), a greater number of Syllidae taxa were recorded (16) but in addition to another 44 taxa spread across 23 families, thus this station fell within ‘expected’ values.

Overview: Those stations or samples that comprised particular microhabitats, such as epifaunal and pink encrusting algae scrapings and holdfasts, consistently returned high numbers of taxa per sample. Site 16, for example, consisted of several samples, including a sediment sieving (16bsi), but the scraping sample (16bsc) accounted for 80% of that site's taxa. Such sheltered microhabitats were all important sources for a range of taxa that were not found in more open habitats. The range in values of average taxonomic distinctness for most of the samples is narrow, indicating that taxonomically, the range of taxa present in each sample is comparable. In samples with significantly lower Δ^+ values but significantly raised Λ^+ , indicating a lower than expected taxonomic range with an associated dominance of the species lists by a small number of groups, this was invariably due to the Syllidae, and to a lesser extent Terebellidae and Sabellidae. Those samples or stations that exhibited reduced taxonomic diversity but no associated dominance were ones where only a very small number of taxa had been collected in the field. The range of taxa was therefore naturally low and the habitats were not of a specialized nature that encouraged single groups to dominate. Most samples/stations with reduced Δ^+ , however, showed a corresponding increase in Λ^+ and were typically those representing sievings or specialized habitat types with the latter generally also returning higher numbers of taxa.

6.4 Discussion

Syllidae, Terebellidae and Sabellidae represent some of the most speciose families of the Polychaeta, comprising around 700 (San Martín & Aguado 2014), 670 (Hutchings *et al.* 2017) and 400 (Capa *et al.* 2014) species respectively. Syllidae are often abundant and diverse in coastal samples (San Martín & Aguado 2014) and the diversity in morphology and mode of life enables them to exploit a diverse array of habitats including calcareous habitats, algal rhizomes and by attaching tubes to hydroid and bryozoan communities. Microhabitats such as biogenic encrustations, algal turf and epifaunal turf offer refuge from environmental stresses, particularly in rocky intertidal environments, but also in subtidal areas that can be exposed to strong waves and currents and are thus an important habitat for those animals that can exploit them. The three families dominate species lists from the subtidal epifaunal turf samples, with numerous tubes of Syllidae and Terebellidae attached to the hydroids and bryozoans that form the basis of the habitat and an array of Sabellidae embedded within the base turf, resulting in the elevated Λ^+ values returned. In particular though, a number of interstitial Syllidae genera (*Exogone*, *Prosphaerosyllis*, *Sphaerosyllis* and *Salvatoria*) were highly dominant in many of those samples that comprised sievings or epifaunal scrapings and particularly sampled small-

bodied taxa. These genera most likely contributed significantly to the elevated Λ^+ values for many of the microhabitat samples where diversity of other taxa was reduced, including 8c and 35c which were highlighted in all of the analyses. The findings reflect the contribution of these three families to the overall species list for the Falkland Islands whereby Syllidae contribute 12% of taxa and Sabellidae (9%) and Terebellidae (7%) also place among the top five families for number of taxa.

In addition to those generally dominating families, it was apparent from many of the taxa lists that the microhabitats also acted as ‘nursery’ areas for several polychaete families, with many juveniles being found in the samples. Nereididae, Orbiniidae and Terebellidae juveniles were notable in large numbers from some scrapings and, for Orbiniidae in particular, this was significant as adult orbiniid taxa were not found in the same habitats (e.g. stations 14, 16, 46). A study by Hernández-Guevara (2005) on juvenile and adult polychaete distribution in the Wadden Sea, found that some polychaetes did exhibit spatially-separated juveniles and adults and that juvenile abundance was significantly higher in ‘structured’ habitats (e.g. seagrass beds or fragmented shell patches) in comparison to non-structured sandy flats. Although the habitats studied were very different to those sampled here, the concept of juveniles favouring habitats that shelter from the environment and/or predation is the same. Use of the sheltered habitats as nursery grounds for some taxa may provide some explanation as to the richness of those habitats over the sedimentary ones, although taxonomic distinctness measures were more greatly affected by the dominating families discussed above, resulting in both a reduced diversity and unbalanced taxonomic structure.

In conclusion, three families dominate the species lists: Syllidae, Terebellidae and Sabellidae. These families have large numbers of taxa and are able to exploit a wide range of habitats through adaptation in morphology and life cycle, and take particular advantage of sheltered microhabitats. By contrast, some other families (e.g. Maldanidae, Phyllodocidae, Polynoidae), although widespread and diverse in the number of taxa recorded, did not monopolize the species lists in the same way, being more restricted in the type and number of habitats they occupied. Furthermore, some key microhabitats, such as encrusting algae, are used as nursery areas by a number of families, particularly the Nereididae, Orbiniidae and Terebellidae, often resulting in high numbers of juveniles in the samples.

Chapter 7: Discussion

This thesis shows that the intertidal and shallow subtidal polychaetes of the Falkland Islands are far more diverse than has previously been apparent, with some described for the first time in the publications presented here. This diversity is centred on specific microhabitats such as epifaunal and algal turfs, algal holdfasts and biogenic encrustations that offer both shelter and a nursery environment to various families. The data set presented here is novel for the Magellan region as there are still few studies focusing on intertidal polychaetes across a wide range of habitats and locations in e.g. continental South America. However, this dissertation also points towards the potentially high, but yet uncovered diversity in the biogeographically close shores of the Scotia Arc (determined as Magellan-Antarctic transitional zones in Koubbi *et al.* 2014), where studies on polychaete infauna seem absent. Further information about intertidal polychaete species composition, as well as time, will reveal whether the new species described for the Falkland Islands are indeed endemic to these Islands. These points are discussed below, along with the perspectives for research on polychaetes of both the Falkland and Magellanic regions.

7.1 *Falkland Islands diversity*

The Polychaeta of intertidal and nearshore habitats around the Falkland Islands are understudied, with almost no research having been undertaken for more than 50 years. Waller (2008), in a survey of intertidal diversity in Antarctica and the Scotia Arc (the shallow water and island bridge linking Patagonia and the Antarctic), stated that “little is known about the intertidal fauna on Falkland Islands shores”. Recent overviews of the history and knowledge of benthic polychaetes in both Chile (Rozbaczylo *et al.* 2017) and Argentina (Elias *et al.* 2017), whose coasts and waters comprise the majority of the Magellan biogeographic zone in which the Falkland Islands sit, demonstrate how much research has been undertaken in those areas in comparison, not just in the past but also in more recent times. A similar picture of low numbers of studies covering the intertidal has also been reported for other less populated southern regions such as Antarctica itself (Waller 2008), South Georgia and the South Sandwich Islands (Barnes *et al.* 2006; Rogers *et al.* 2015) and other parts of the Scotia Arc (Waller 2008).

The results found in this study reflect those of some other intertidal studies around the Scotia Arc and Antarctic, whereby much of the diversity at intertidal sites was found to be concentrated in niche habitats such as crevices, under boulders, algal detritus and other protected habitats although

sediment diversity was not studied (Waller 2008; Brewin & Brickle 2010; Rogers *et al.* 2015). In the Falkland Islands, the richest samples (although generally dominated by small numbers of species-rich groups as indicated by the elevated variation in taxonomic distinctness, Λ^+) were also sheltered microhabitats such as epifaunal turf scrapings (e.g. stations 14 and 16), encrusting pink algae samples (e.g. sample 38a), crevices (sample 19a) and holdfasts (sample 37a). It is also notable that two of the four new species described so far (*Micromaldane shackletoni* and *Dysponetus ovalisetosus*) inhabited the diverse epifaunal turf present in samples 14 and 16. The contribution of sievings samples (sediment sieved through a 0.5 mm mesh), in terms of numbers and diversity of taxa, should not be underestimated and single samples often encompassed the majority of a station's taxa (e.g. 67b contained 31 of the 36 taxa for the station). They were also an important source of taxa, particularly small-bodied forms that could or would not be collected just by picking them out from the sediment.

The intertidal environments of shores further south than the Falkland Islands (such as those of the Scotia Arc) offer a lower variety of habitat types than are present in the Falkland Islands and diversity is correspondingly reduced there in relation to shallow water assemblages (Waller 2008; Rogers *et al.* 2015). In the warmer, and sometimes more sheltered, Falkland Islands shores, this may not necessarily be so expected. At the present time, sampling effort for infauna in the shallow subtidal (0–50 m) region of the Falkland Islands, in comparison to that undertaken here in the intertidal, is lacking and so how the diversity does vary between the two environments is unknown. However, the few subtidal sites included in the surveys, do give an indication that a much greater level of diversity may be present subtidally than is currently known, particularly in relation to epifaunal turf and other protecting habitats such as sabellariid reefs and holdfasts. A significant change in species composition from the intertidal to subtidal region was indicated by the level of apparent exclusiveness of taxa shown to each environment. Around 25% of the taxa identified were only recorded from the intertidal zone with a similar number then only recorded from the subtidal zone. Only 50% of the identified taxa were present in both regimes. Cluster analyses showed the intertidal and subtidal assemblages to generally be significantly different to each other with habitat type being of secondary importance. Shore height seemed to have limited influence, although the low and midshore samples showed some affinity to each other. Tidal range in the Falkland Islands is small (less than 2 m: Waller 2008) and in South Georgia, where tidal range is also low (~1.2 m, Husvik Harbour: Rogers *et al.* 2015), limited evidence of zonation within the macroalgae (John *et*

al. 1994) and some invertebrates (Barnes *et al.* 2006) was reported. There was no evidence in the clustering of the samples here that suggested any geographic influence on species composition in terms of location around the Islands. The differing regimes of the Argentine Drift and the Falklands Current therefore seem to have no influence on intertidal polychaete communities.

Faunal composition of the polychaetes followed that reported from other Magellan and Antarctic studies (Orensanz 1974; Knox & Lowry 1977; Gambi & Mariani 1999; Montiel 2005; Montiel *et al.* 2005a) with the Syllidae being the most diverse family recorded, both in terms of genera and taxa. Polynoidae and Terebellidae, reported as being the next most speciose families in the region by the same authors, were ranked 4th and 5th here after Sabellidae and Serpulidae. However, the list of Serpulidae contains several taxa that are considered doubtful and there are many more taxa in the Polynoidae and Terebellidae still to be identified than in Sabellidae or Serpulidae.

7.2 Magellan diversity

Studies on polychaete diversity within the Magellan region (Cañete *et al.* 1999; Gambi & Mariani 1999) or more widely on Chilean (Rozbaczylo & Simonetti 2000; Moreno *et al.* 2006, 2008) and Argentinean (Elias *et al.* 2017) shores, that are directly comparable with the work in the Falkland Islands, are few. Most investigate purely subtidal benthic communities, include both intertidal and offshore habitats or concentrate on specific environments such as estuaries or particular sediment types (Ríos & Mutschke 1999; Martin *et al.* 2004). Levels of around 400–500 polychaete taxa have been cited for the Magellan region although this has generally been reduced to around 200 taxa for analyses once those not identified to species level are removed (Knox & Lowry 1977; Montiel 2005; Montiel *et al.* 2005a, b). Data for these studies have been drawn from samples mostly collected from depths of 100 m or greater. Similar levels of polychaete diversity have been reported and used in analyses on nearby regions such as the Weddell Sea (163 species, Montiel *et al.* 2005b), Scotia Sea (190 taxa, Neal *et al.* 2017) and Scotia Arc (200 species, Montiel *et al.* 2016).

A study by Moreno *et al.* (2008), investigating polychaete diversity of the Chilean Pacific coast, looked at how diversity changed over a depth gradient from intertidal to abyssal (c. 4700 m) depths. The results showed that the highest diversity occurred in the intertidal zone, even compared to shallow waters, and declined steeply thereafter. The idea that polychaete diversity decreases with depth is not new and has been documented many times in the past for a range of deep-water

environments (e.g. Paterson & Lamshead 1995; Perez-Mendoza *et al.* 2003; Neal *et al.* 2017), however, studies extending this into the intertidal are scarce. The regional diversity cited earlier for depths of 100 m and greater would thus suggest that an estimate of over 220 taxa from the Falkland Islands intertidal/nearshore zone is not only a realistic one but possibly even on the low side. More than 150 taxa are still awaiting identification from the survey samples and, while many will undoubtedly match names already on the list, it is likely that others will significantly increase the species count for the region further.

In terms of biogeographic affinity, analysis of the identified species list shows the shallow water polychaete assemblage of the Falkland Islands to bear very high (>80%) similarity to the Magellan region, in comparison with South Georgia or Antarctica, with around twice as many shared taxa. This is to be expected and confirms its historic placement in the Magellan biogeographic region as well as reflecting the findings of others who have also examined the polychaete fauna from these regions (e.g. Knox & Lowry 1977; Montiel *et al.* 2005a, b). Knox & Lowry (1977) reported a high affinity between Falkland Islands and South Georgia Polychaeta although they did not put a figure on this. In relation to Antarctic polychaetes, Montiel (2005) estimated 35% overlap of taxa for the Magellan region while a study just of Magellan Strait soft bottom polychaetes found a much higher level of 62% shared taxa (Gambi & Mariani 1999). Comparisons of Magellan fauna with those from nearby Antarctica and South Georgia have varied greatly by faunal group as illustrated in Table 3 and can and do change following new survey work, discovery of new species and updated species lists. Until recently, there were almost no published figures specific to the Falkland Islands fauna detailing levels of endemism and overlap with fauna from nearby regions. A recent study on Bryozoa (Figuerola *et al.* 2017) reported an overlap with Magellan fauna of 90% and with those of South Georgia and Antarctica at 33% and 49% respectively, similar levels to those reported here (Table 3) for the polychaetes although with a lower affinity with South Georgia. A study on Cumacea (Mühlenhardt-Siegel 1999) though, found that despite a high Magellan-Antarctic connection (52%), that there was only a 10% overlap between Magellan and Falkland Islands taxa and only a 2% overlap of Falkland Islands and Antarctic taxa. The study by Waller (2008) on shores around the Scotia Arc found the Falkland Islands fauna to be significantly different to that at the other survey sites, but it was not clear how much overlap there was or what taxa were represented.

Table 3. Comparison of levels of endemism and overlap with South Georgia and Antarctic faunas for both the Magellan region (top figures) and Falkland Islands (bottom figures) for different faunal groups. *indicates updated figure following new survey work.

Faunal group	% Endemic	% Overlap South Georgia	% Overlap Antarctica	References
Polychaeta	15–16	–	35	Knox & Lowry 1977; Montiel 2005 (this thesis)
	6	45	48	
Amphipoda	53–55	6	16	Knox & Lowry 1977; De Broyer & Rauschert 1999
	–	–	–	
Cumacea	52	–	10	Mühlenhardt-Siegel 1999
	–	–	2	
Bryozoa	55	71	17	Moyano 1999
	4 (18*)	33	49	Figuerola <i>et al.</i> 2017
Nudibranchia	31	14	8	Schrödl 1999
	20	30	20	

7.3 Endemism

Estimates of endemism for Magellan fauna have varied greatly by faunal group although those reported for the Polychaeta are low in comparison (Table 3). Knox and Lowry (1977) and Montiel (2005) both returned similar estimates (15–16%) for the Polychaeta even though Montiel (2005) used nearly twice as many taxa. Other faunal groups (Amphipoda, Cumacea, Bryozoa and Nudibranchia) have returned figures ranging from 31–55% endemism for the region (Table 3). In relation to the Falkland Islands, Schrödl (1999) reported 20% endemism in nudibranchs although this only reflected two endemic species from a list of 10, whereas recent work on Bryozoa (Figuerola *et al.* 2017), from comprehensive species lists covering South American and Antarctic waters, indicated a level of 4% endemic Bryozoa to the Falkland Islands (Table 3), a more comparable level to the Polychaeta. The discovery of 19 new species from the Islands during their work however, then boosted that figure instantly to 18%.

At the current time, only the newly described species from this work, along with a few other historical records of doubtful identification, are ‘endemic’ to the Falkland Islands. All new species are, by the very nature of their discovery, endemic at the time of publication. Recent surveys in Falkland Islands waters such as those reported here for the Polychaeta, Goodwin

et al. (2011, sponges) and Figuerola *et al.* (2017, Bryozoa), demonstrate how many taxa are still undiscovered in the region, and this is undoubtedly the case for other invertebrate groups also, such that realistic levels of endemism are difficult to estimate. More detailed survey work around the Falkland Islands, with corresponding work by taxonomists, is likely to cause spikes in estimates of endemism for all invertebrate groups such as that seen in Figuerola *et al.* (2017). It may be that in time, those new species described from the Islands will be discovered elsewhere, however it is believed that some of these at least will prove to be truly endemic, such as the epifaunal hermaphrodite *Micromaldane shackletoni*, which has no apparent dispersal phase to promote distribution (**Paper 4**). The number of new species still waiting to be described from these surveys, suggest that more endemism may be identified, particularly if such taxa are determined to have been previously mis-identified as other Magellan species that are not, in fact, present in the Falkland Islands fauna.

The form of reproduction and dispersal employed by taxa is undoubtedly a key factor in their ability for dispersal. Goodwin *et al.* (2011) in their study of shallow water sponges from the Falkland Islands, found a large number of new species (12 out of 20) and stated that, as most sponges had limited dispersal capability, restricted distributions were likely. Brood protection in Cumacea was similarly suggested as a reason for limited dispersal and overlap of those taxa between regions (Mühlenhardt-Siegel 1999). While colonization into the Falkland Islands from the Magellan region, less than 300 miles away, is likely, species originating in the Falkland Islands seem less likely to be transported westwards back toward South America. The prevailing oceanographic currents affecting the Falkland Islands flow either north (Falkland Current) or east (Antarctic Circumpolar Current), thus transporting planktonic larvae out of the Magellan region and not back towards it. Looking eastwards, colonization of South Georgia by Falkland Islands taxa seems theoretically plausible except that nearly 1000 miles separate the land masses. Knox (1994) estimated mean current speeds within the Antarctic Circumpolar Current to reach 0.04–0.25 ms⁻¹ meaning that transport of larvae from the Falkland Islands to South Georgia could take at least 69 days, too long for Nereididae or Arenicolidae larvae as discussed below. Several potential pathways for transport and survival of fauna have been proposed however. Benthic migration north and eastwards along the Scotia Arc was theorized by Knox & Lowry (1977) and a recent study by Sands *et al.* (2015) also suggested this as one possibility explaining the movement of brittlestars from Antarctica to South America several times in recent (Pleistocene) history.

Kelp/debris rafting has also been proposed as potentially facilitating travel both eastwards and westwards (via storms that counter the prevailing current) by providing a platform for extended survival of both larvae and adults (Helmuth *et al.* 1994; Glasby & Alvarez 1999; Moyano 1999; Barnes *et al.* 2006; Nikula *et al.* 2010). The Polar Front is also considered a barrier to faunal exchange between those regions above and below it, however mesoscale eddies within both the Antarctic Circumpolar Current and the Falklands Current (Glorioso *et al.* 2005) may also present a possible means of larval transport back towards the Magellan region (Arntz 2005). Arntz *et al.* (2005) found that the northern branch of the Scotia Arc showed a more Magellan faunal composition while the southern branch was more Antarctic although Montiel *et al.* (2016) found faunal exchange to be greater between islands of the Scotia Arc and Antarctica than between the Magellan region and the Scotia Arc.

Of those new species described during the course of this study, one has no known dispersal capability and two may be limited. *Micromaldane shackletoni*, as discussed previously, utilizes direct development and juveniles attach their tubes to the parent thereby limiting dispersal (**Paper 4**). Reproduction in *Gymnonereis* is undescribed although eggs were found in some specimens collected here (**Paper 2**) and most current members of the family are gonochoric with lecithotrophic larvae (Rouse & Pleijel 2001; Pleijel & Rouse 2006). Lugworms (Arenicolidae) are also gonochoric and those species studied have been described with non-feeding larvae that have a ‘brief’ pelagic phase of a few days at the most (Darbyshire 2017b). Nothing is known of the reproduction in either *Abarenicola brevior* or *Abarenicola wellsi* (**Paper 1**) although it is unlikely that they would vary significantly from other lugworms. The species of *Dysponetus* discussed here are most likely to be able to disperse furthest. Although details of reproduction are poorly known in the genus, species are reported as gonochoric and planktonic development has been recorded for the family as a whole along with long dispersal capability (Watson-Russell 2000). Despite this, **Paper 3** describes different species for the Falkland Islands, South Georgia and Antarctica with no overlap currently known and no others described for the Magellan region. Of these species, kelp/debris rafting could be a potential vector for dispersal of *M. shackletoni*, as it has been documented in dispersal of Bryozoa (Moyano 1999; Figuerola *et al.* 2017) on which the species could attach, as well as *D. ovalisetosus* as part of a holdfast community. *Abarenicola brevior*, *A. wellsi* and *G. tenera* all inhabit soft sediments and no larvae or juveniles were documented from habitats that might suggest that kelp holdfasts or debris could potentially aid transport.

In order to properly compare the polychaete fauna for these related regions, the most important step now is to complete the current species list with accurate identifications. Only then will a more realistic picture of endemism and overlap with other faunas be available. The ideal situation would also be one where molecular information was available for all taxa, in order to definitively identify new species and assess the potential for cryptic species.

7.4 Final Conclusions & Future Directions

- Intertidal and nearshore diversity of the Falkland Islands polychaetes is understudied. The current findings go some way to remedy this and indicate a hitherto unrecognized diversity around the Islands. Further work is needed to continue the identification of unnamed taxa, and describe new species where relevant, to further bolster the information known about the fauna;
- Knowledge of the nearshore region (to 50 m) is still poor but initial indications are of high diversity and a distinct suite of species not present in the intertidal region or deeper waters. Further survey work in the nearshore region, ideally utilizing both ship sampling (grab/dredge) and diving is strongly recommended;
- The polychaete fauna of the Falkland Islands shows a high affinity with that of the Magellan region with very little endemism, although this is possibly due to lack of knowledge and modern work on the fauna, so that many species are incorrectly identified or unknown completely. To a lesser extent, there is also a strong affinity with the polychaete fauna of both South Georgia and Antarctica;
- Faunal composition of the intertidal and nearshore communities are most strongly influenced by whether they are intertidal or subtidal followed by sediment/habitat type; shore height has a minor influence in the intertidal region; location around the Islands appears to have no influence at the intertidal level.

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Appendices

Appendix 1

Paper 1

Darbyshire, T. 2017. A re-evaluation of the *Abarenicola assimilis* group with a new species from the Falkland Islands and key to species. *Proceedings of the 12th International Polychaete Conference, Cardiff, Wales 2016. Journal of the Marine Biological Association of the U.K.* **97(5)**: 897–910.

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A re-evaluation of the *Abarenicola assimilis* group with a new species from the Falkland Islands and key to species

TERESA DARBYSHIRE

Department of Natural Sciences, Amgueddfa Cymru–National Museum Wales, Cathays Park, Cardiff CF10 3NP, Wales, UK

The new species *Abarenicola wellsi* n. sp. from the Falkland Islands is described along with a re-description of *Abarenicola brevior* n. stat. with which it had previously been confused. The two species are distinguished using both morphological and molecular techniques, new characters are described and previously recognized characters are clarified, all of which support the assignment of species status as opposed to subspecies. Both species are part of the *Abarenicola assimilis* 'group' within which all taxa were originally described as subspecies. The group as a whole is re-evaluated and all members are elevated from subspecies to species status based mainly on the new characters of shape, distribution and pigmentation of the proboscoidal papillae. The group now consists of six species: *Abarenicola assimilis* n. stat., *A. brevior* n. stat., *Abarenicola devia* n. stat., *Abarenicola haswelli* n. stat., *Abarenicola insularum* n. stat. and *A. wellsi* n. sp.

Keywords: Cytochrome oxidase I, 16S, taxonomy, Polychaeta, *devia*, *haswelli*, *insularum*, *brevior*, *wellsi*

Zoobank identifier: LSID urn:lsid:zoobank.org:pub:BB3C6D30-DE58-4A08-924D-0E0E80304D45

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INTRODUCTION

Family Arenicolidae Johnston, 1835 contains some of the most well-known polychaete species due to their commercial value and exploitation worldwide. There are four genera, *Arenicola* Lamarck, 1801, *Abarenicola* Wells, 1959, *Arenicolides* Mesnil, 1898 and *Branchiomaldane* Langerhans, 1881, between them containing nearly 30 species. *Arenicola* and *Abarenicola* are the largest, and most widely recognized, genera with seven species in the former group and eight species, three of which are further split into two, four and five subspecies each, in the latter. Few phylogenetic studies have concentrated on the relationships within the family and its genera, the most significant being Bartolomaeus & Meyer (1999), a morphological study using chaetal morphology and development along with other literature and, most recently, a molecular study by Bleidorn *et al.* (2005) in which monophyly of the family as a whole, as well as the genera *Branchiomaldane* and *Abarenicola*, were supported.

Due to their large size and economic importance, species of *Arenicola* and *Abarenicola* have been well-studied historically and therefore few new species of *Abarenicola* have been described since two comprehensive studies in 1959 (Healy & Wells) and 1963 (Wells). Just prior to the former publication, Wells (1959) erected the genus *Abarenicola* for five species: *Abarenicola assimilis* (Ehlers, 1897), *Abarenicola claparedii* Levinsen, 1884, *Abarenicola pacifica* Healy & Wells, 1959, *Abarenicola pusilla* (de Quatrefages, 1866) and *Abarenicola*

vagabunda Healy & Wells, 1959. Included within *A. assimilis* was the variety *affinis*, described by Ashworth in 1903. Healy & Wells (1959) then split *A. vagabunda* into two subspecies, *A. v. oceanica* and *A. v. vagabunda*. In 1963, Wells raised *Abarenicola affinis* to a separate species and further split both *A. affinis* and *A. assimilis* into four and five subspecies respectively: *A. affinis affinis*, *A. affinis africana*, *A. affinis clarki*, *A. affinis chiliensis*, *A. assimilis assimilis*, *A. assimilis brevior*, *A. assimilis devia*, *A. assimilis haswelli* and *A. assimilis insularum*. In reference to his reasons for erecting subspecies rather than full species, Wells stated in the paper 'In the circumstances, it has not been difficult to show that various populations differ consistently in their morphological characters, but my estimate of the grade of taxonomic separation between any two forms is necessarily arbitrary, resting largely on analogy with those other Arenicolidae which I have studied in the field'. Indeed, the distinctions between the subspecies of *assimilis* were based primarily on a single internal characteristic, the number of oesophageal caeca, and the geographic separation of the populations. Since that time, no author has challenged the status of these subspecies as to whether they should remain as such or be elevated to full species status.

In 2011, a survey of intertidal polychaetes in the Falkland Islands was initiated. At that time, only a single subspecies of *Abarenicola*, *A. a. brevior*, was known from the islands. During the survey, specimens of *Abarenicola* were collected from a shore close to Stanley where local people thought that more than one species may be present. Samples of the lugworms were taken for molecular analysis which proved, using both 16S and COI genes, that two distinct species were indeed present. A more comprehensive survey of the lugworm populations was then undertaken in 2013, with specimens collected

Corresponding author:

T. Darbyshire

Email: Teresa.Darbyshire@museumwales.ac.uk

from shores around both East and West Falkland and preserved for both morphological and molecular analysis.

In his 1963 paper, Wells used material from the Falkland Islands (some of which had previously been utilized by Ashworth (1903) in his description of *Arenicola assimilis* var. *affinis*), as well as from the Magellan Strait and Beagle Channel, as part of his description of the new subspecies *A. a. brevior*. The specimens he had come from two populations, one on each of the islands of East and West Falkland although he found some differences between the two populations. The specimens from West Falkland were much like those from South America but those from East Falkland differed in some respects such as the occurrence of the first gill and the structure of the nephridiopores. In the paper, he commented on the differences stating that 'it may be that they represent genetically distinct forms'. The differences however did not constitute enough evidence for the establishment of another subspecies, probably because the number of oesophageal caeca in all of the worms were the same and this was the defining character he used in describing all of the different subspecies.

The new collection of specimens from stations all around both East and West Falkland (Figure 1) enabled more detailed observations to be made and additional characters to be brought to light. In conjunction with the molecular analyses, the resulting evidence is hereby used to raise *Abarenicola brevior* n. stat. to full species status and describe *Abarenicola wellsi* n. sp. at species level also.

The holotype and as many paratypes as possible of *A. brevior* were inspected as it was clear that, at least in respect to the

Falkland Islands, both species were present within the specimens used by Wells (1963) in his descriptions. However, except for the specimens from the East Falkland population, all of the other type specimens obtained belonged to *A. brevior*.

Additional observations were also made of the other species within the 'assimilis group', providing new characters on which to separate them and thereby warranting the elevation of these also to species status as *A. assimilis* n. stat., *A. devia* n. stat., *A. haswelli* n. stat. and *A. insularum* n. stat.

MATERIALS AND METHODS

Specimen collection and examination

Specimens were collected by hand from the shore by digging with a fork or spade. Some juvenile specimens were collected by sieving sediment through a 0.5 mm sieve. Most samples were relaxed with 7% magnesium chloride solution and then fixed with 4% formaldehyde in seawater. Prior to fixing, a small sample of tissue was removed from a wide selection of specimens and preserved in 100% ethanol for molecular analysis with the remainder of the animal fixed in formaldehyde. After a period of at least 2 days, fixed animals were rinsed with fresh water and preserved in 80% industrial methylated spirits with 2% propylene glycol added.

Morphological examinations, measurements and drawings were made using a Nikon Eclipse E400 binocular microscope and a Nikon Labophot-2 compound microscope. Microscope photographs were taken using AutoMontage™ software.

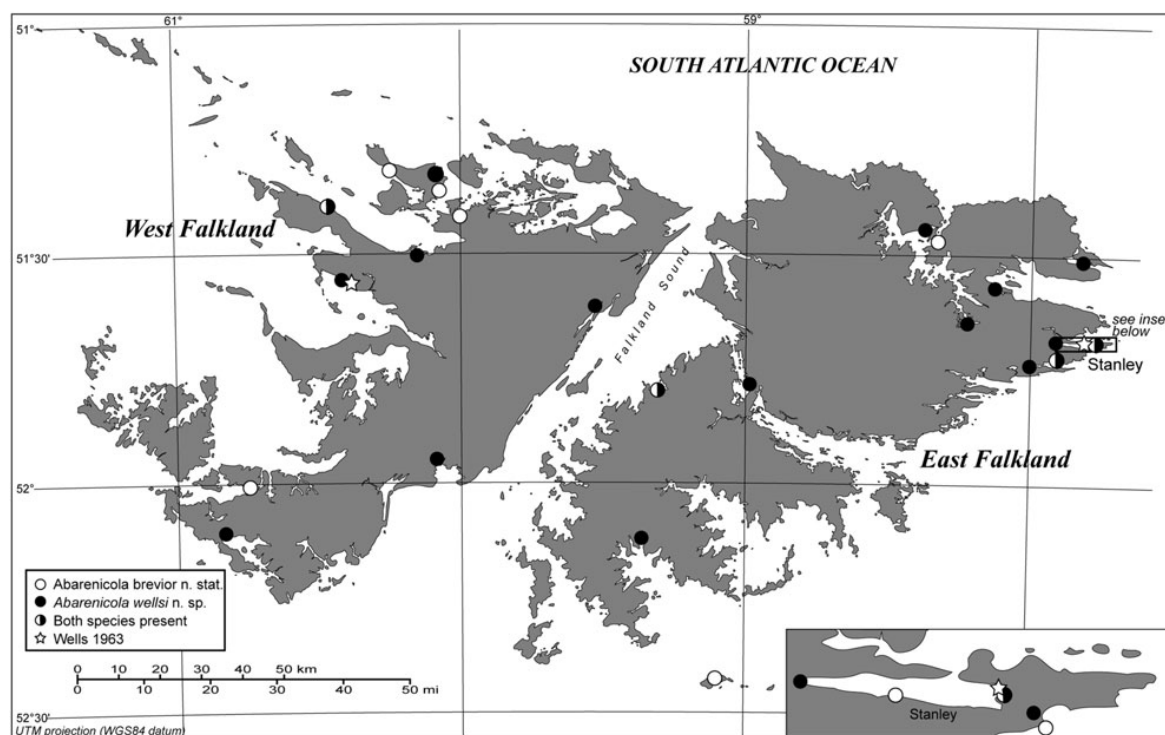


Fig. 1. Map showing the occurrence of *Abarenicola brevior* n. stat. and *Abarenicola wellsi* n. sp. around the Falkland Islands at the different sites sampled. Locations of specimens described by Wells in 1963 are also marked.

The holotype and most paratypes of *Abarenicola wellsi* n. sp. are accessioned in the zoological collections of National Museum Wales (NMW.Z). Paratypes are also deposited in the Natural History Museum, London (NHMUK), National Museum of Natural History, Smithsonian Institution, Washington DC (USNM) and the Zoological Museum, Hamburg (ZMH). All other specimens of *A. wellsi* n. sp. are accessioned in the National Museum Wales collections.

The holotypes of *Abarenicola brevior* n. stat. and *Abarenicola assimilis* n. stat. were borrowed for comparison from ZMH. Most of the remaining paratypes of *A. brevior* (NHMUK, ZMH, Swedish Museum of Natural History SMNH, Museum für Naturkunde Berlin ZMB) were also inspected to confirm their identification. The paratypes from USNM could not be confirmed. Holotypes of *Abarenicola devia* n. stat., *Abarenicola haswelli* n. stat. and *Abarenicola insularum* n. stat. were borrowed from NHMUK for observation as well as additional syntypes of *A. assimilis* from NHMUK and ZMB.

DNA extraction and sequencing

Universal cytochrome oxidase subunit I (COI) primers (Folmer *et al.*, 1994) were used to amplify an ~675 bp region of the COI 'barcoding' gene of 44 *Abarenicola* specimens (seven *A. brevior* n. stat., 37 *A. wellsi* n.sp.). In addition to COI, an ~544 bp region of the 16S large subunit mitochondrial ribosomal DNA was also sequenced for three specimens (one *A. brevior*, two *A. wellsi*), using the Palumbi (1996) primers 16SarL and 16SbrH.

For 16S, DNA was extracted using a Qiagen DNeasy kit. Between 1–5 µl of extract was used as a template in PCRs using GE Healthcare Illustra PuReTaq PCR beads with 0.25 µl of each primer (10 µM). Each reaction was then made up to 25 µl using ultra-pure water. 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. For COI, the process was carried out in its entirety by Central Biotechnology Services (CBS), Cardiff University using the same extraction kit and protocols and PCR beads. Cycling conditions were either that published by Pleijel *et al.* (2012): 95°C for 180 s, 5 cycles of 95°C for 40 s, 45°C for 40 s and 72°C for 50 s, 40 cycles of 95°C for 40 s, 51°C for 40 s and 72°C for 50 s, followed by 72°C for 300 s; or 95°C for 120 s, 35 cycles of 95°C for 40 s, 40°C for 45 s and 72°C for 90 s, and finally 72°C for 7 min. Some reactions that failed were re-run successfully with the addition of magnesium chloride to a final concentration of 2 mM. Products were cleaned using Sigma Aldrich GenElute PCR clean up kit, quantified on agarose gels and sequenced by CBS, Cardiff University. Sequences were edited and compiled in ApE v.2.0.38 and all identified haplotypes were submitted to GenBank (Table 1). Edited and aligned sequences were 573 and 463 bp in length for COI and 16S respectively.

DNA datasets and analysis

For 16S, all of the Arenicolidae sequences published by Bleidorn *et al.* (2005), except for *Arenicola marina* Linnaeus, 1758 and *Arenicola defodiens* Cadman & Nelson-Smith, 1993, were downloaded for comparison from GenBank along with two of the outgroup sequences (*Scalibregma*

inflatum (Rathke, 1843) and *Clymenura clypeata* (de Saint-Joseph, 1894)) also used by the author. Five sequences of *A. marina* and two of *A. defodiens* were available from the author's personal datasets. For COI, five sequences each of *A. marina* and *A. defodiens* were available from the author's personal datasets but no sequences from any other Arenicolidae species were available on GenBank. The same outgroups were used as for 16S (*S. inflatum*, *C. clypeata*). For those species where sequences from multiple specimens were available (*A. defodiens*, *A. marina*, *A. wellsi* and *A. brevior*), inter- and intraspecific distances were also calculated. For the phylogenetic analyses, a single reference sequence, for both COI and 16S, from each of the latter species was used. Sequences were aligned by CLUSTALW in MEGA v7.0.18 (Kumar *et al.*, 2016) using the default parameters and uncorrected pairwise differences (p-distance) were calculated. Maximum parsimony (MP) analysis with branch and bound search was carried out in MEGA v7.0.18 with clade support assessed via bootstrap values (1000 replicates). Maximum likelihood (ML) analyses were carried out using MEGA v7.0.18. Bootstrap values were calculated from 1000 replicates to provide a measure of clade support. Bayesian Inference (BI) was conducted using MrBayes 3.2 (Ronquist *et al.*, 2012). FindModel v2 (www.hiv.lanl.gov/content/sequence/findmodel/findmodel.html) was used to estimate the appropriate model of sequence evolution (GTR + Γ in each case). Two parallel runs of 1,000,000 generations, sampling trees every 1000 generations with the first 25% of trees discarded as burn-in were implemented in each case. Convergence was reached for both analyses before the burn-in period. The majority-rule consensus tree with posterior probabilities was determined from 751 trees.

RESULTS

SYSTEMATICS

Family ARENICOLIDAE Johnston, 1835

Genus *Abarenicola* Wells, 1959

Type species *Arenicola claparedii* Levinsen, 1884

DIAGNOSIS (Wells, 1959)

Arenicolidae with an achaetous tail. Prostomium non-retractile, in the form of a triangle with lateral extensions of its (anterior) base; with a shallow groove marking the attachment of the brain. Statocysts either present, with a tube to the exterior, or absent. Chaetigers (except the first two or three) subdivided into five annuli. Gills branched, the first (which may be reduced or absent) on chaetiger 7 or 8. None of the neuropodia approaches close to the mid-ventral line. Oesophageal caeca more than one pair. Gular membrane very thin; septal pouches absent. Nephridia five or six pairs, the first opening on chaetiger 4 or 5. Dioecious; gonads on the nephridia.

Abarenicola assimilis (Ehlers, 1897) n. stat.

(Table 2)

Arenicola assimilis Ehlers, 1897: 103–104. – Ehlers, 1900, 1901; Ashworth, 1903: 737–785, Pl. 36–37; *Abarenicola assimilis* Wells, 1959: 307, Pl. 2; *Abarenicola assimilis assimilis* Wells, 1963: 121–159, fig. 2, 3, Pl. 3, Table 1

Table 1. List of taxa used in this study with source and GenBank accession numbers (newly sequenced taxa in bold).

Taxa	Source	Accession numbers	
		16S	COI
<i>Scalibregma inflatum</i> (Rathke, 1843) (Scalibregmatidae)	GenBank	AY532331	KT307695
<i>Clymenura clypeata</i> (de Saint-Joseph, 1894) (Maldanidae)	GenBank	AY340449	KJ183005
Arenicolidae			
<i>Arenicola cristata</i> Stimpson, 1856	GenBank	AY569682	–
<i>Arenicola loveni</i> Kinberg, 1866	GenBank	AY569683	–
<i>Arenicola marina</i> (Linnaeus, 1758)	West Aberthaw, Wales, UK	KY652591	KY652595
<i>Arenicola defodiens</i> Cadman & Nelson-Smith, 1993	Porthcawl & Whiteford Burrows, Wales, UK	KY652590	KY652594
<i>Arenicola defodiens</i> (additional haplotypes)	Whiteford Burrows, Wales, UK	–	KY661884–5
<i>Arenicolides ecaudata</i> (Johnston, 1835)	GenBank	AY569688	–
<i>Branchiomaldane vincenti</i> Langerhans, 1881	GenBank	AY569690	–
<i>Branchiomaldane</i> sp.	GenBank	AY569689	–
<i>Abarenicola claparedi</i> (Levinsen, 1884)	GenBank	AY569684	–
<i>Abarenicola pacifica</i> Healy & Wells, 1959	GenBank	AY569685	–
<i>Abarenicola gilchristi</i> Wells, 1963	GenBank	AY569686	–
<i>Abarenicola affinis affinis</i> (Ashworth, 1903)	GenBank	AY568687	–
<i>Abarenicola brevior</i> (Wells, 1963) n. stat.	Falkland Islands	KY652592	KY652596
<i>Abarenicola brevior</i> (additional haplotypes)	Falkland Islands	–	KY661886–7
<i>Abarenicola wellsii</i> n. sp.	Falkland Islands	KY652593	KY652597
<i>Abarenicola wellsii</i> n. sp. (additional haplotypes)	Falkland Islands	KY661883	KY661888–98

TYPE MATERIAL EXAMINED

Lectotype: Ushuaia, Beagle Channel (ZMH V 4872a), low shore, coll. W. Michaelsen, 07.12.1892.

Syntypes: Ushuaia, Beagle Channel (NHMUK 1912.5.25.1–2), coll. W. Michaelsen; Stewart Island, Beagle Channel (NHMUK 1912.5.25.3), coll. W. Michaelsen; Ushuaia, Beagle Channel (ZMB 6762), coll. W. Michaelsen, 27.10.1892.

ADDITIONAL OBSERVATIONS

Eversible proboscis covered in papillae with some pigmentation. Proximal section with large, low, rounded, darkly pigmented papillae; median section initially with large, wide, conical and small, narrow, conical papillae, then small papillae only. Small papillae with some pigmentation.

REMARKS

General observations on the holotype and syntypes agreed with the original description of Ehlers (1897), supplemented by Wells (1963). New observations are based on the syntypes from NHMUK, two of which had been dissected to reveal the oesophageal caeca and one of which had an everted proboscis. The holotype (ZMH) also had a partially everted proboscis.

Abarenicola brevior (Wells, 1963) n. stat.
(Figures 1, 2 & 4; Tables 1 & 2)

Arenicola assimilis Ehlers, 1897: 103–104. – Ehlers, 1900, 1901. – Ashworth, 1910, 1912. – *Abarenicola assimilis brevior* Wells, 1963: 133–140, Table 1, Pl. 3.

TYPE MATERIAL EXAMINED

Holotype: Lapataia Nueva, Beagle Channel (V. 4871a).

Paratypes: (ZMH V.4871), 11.1892; Ushuaia, Beagle Channel, paratype (ZMH V.4874), 10.1892; Ushuaia, Beagle Channel, paratype (ZMH V.4872), 12.1892; Ushuaia, Beagle Channel, paratype (SMNH 1414), 05.1896; Puerto Robalo, Beagle Channel, 6 paratypes (NHMUK 1961.12.11–16), 01.1959; Susanna Cove, Magellan Strait, 2 paratypes

(ZMB 3629), 1893/5; Roy Cove, West Falkland, Falkland Islands, 2 paratypes (NHMUK 1912.4.9.3–4), 05.09.1910.

COMPARATIVE MATERIAL EXAMINED

East Falkland. Stanley foreshore, station 1a (51°41.454'S 057°51.870'W), under rocks in coarse sand, midshore, 1 specimen (NMW.Z.2011.039.0189), 15.11.2011; Hookers Point, station 6d (51°41.994'S 057°46.747'W), gravel in rock pool, low shore, 1 specimen (NMW.Z.2011.039.0178), 21.11.2011; Whalebone Cove, station 9a (51°41.330'S 057°48.092'W), medium-coarse sand, low shore, 4 specimens (NMW.Z.2011.039.0179–0181), 23.11.2011; Whalebone Cove, station 9b (51°41.318'S 057°48.011'W), medium-coarse sand, midshore, 5 specimens (4–NMW.Z.2011.039.0182; 1–ZMH P-27826), 23.11.2011; Kelp Harbour, by stone corral, station 28 (51°48.597'S 059°19.433'W), muddy sand, midshore, 2 specimens (NMW.Z.2011.039.0183), 04.12.2011; Kelp Harbour, off causeway, station 29a (51°47.715'S 059°18.400'W), coralline coarse sand, mid-low shore, 2 specimens (NMW.Z.2011.039.0184), 04.12.2011; Whalebone Cove, station 31a (51°41.307'S 057°47.985'W), in sand under rocks, high-midshore, 1 specimen (NMW.Z.2011.039.0185), 05.12.2011; Whalebone Cove, station 31b (51°41.308'S 057°48.005'W), medium-fine sand, mid-low shore, 6 specimens (NMW.Z.2011.039.0186), 05.12.2011; Whalebone Cove, station 31c (51°41.325'S 057°48.037'W), medium-fine sand, low shore, 1 specimen (NMW.Z.2011.039.0187), 05.12.2011; Mullet Creek, station 33b (51°43.121'S 057°54.833'W), rocks with coarse gravelly sand, high-mid shore, 1 specimen (NMW.Z.2011.039.0188), 07.12.2011; Hookers Point, station 40 (51°41.994'S 057°46.747'W), rock pool sediment, midshore, 8 specimens (NMW.Z.2012.082.0070–72), 05.12.2011; Whalebone Cove, station 41a (51°41.324'S 057°48.000'W), medium-coarse sand, high shore, 2 specimens (NMW.Z. 2012.082.0073–74), 15.01.2013; Whalebone Cove, station 41b (51°41.322'S 057°48.030'W), medium-coarse sand, midshore, 2 specimens (NMW.Z. 2012.082.0075–76), 15.01.2013; Rincon Grande, station 63a (51°28.241'S

Table 2. Comparison of morphological characters across all *Abarenicola* species.

Species and type locality	No. of chaetigers	Max. stems per gill	Statocysts (present/absent)	Chaetiger of 1st gill	Nephridia	Oesophageal caeca	Proboscoidal papillae
<i>Abarenicola assimilis</i> (Ehlers, 1897) n. stat. Ushuaia, Beagle Channel	20	9-12	P	viii	iv-ix, naked	1 + (4-7)	Some pigmentation, sizes intermix at transition; large - wide, conical; small - narrow, conical
<i>Abarenicola breviar</i> (Wells, 1963) n. stat. Lapataia Nueva, Beagle Channel	19	10-14	P	viii	iv-ix, naked	1 + (9-14)	Unpigmented, sizes intermix at transition; large - triangular, small - conical
<i>Abarenicola insularum</i> (Wells, 1963) n. stat. Campbell Island, New Zealand	19	10-14	P	viii	iv-ix, naked	1 + (4-6)	Some pigmentation, sizes intermix at transition; large - mushroom-like; small - conical
<i>Abarenicola devia</i> (Wells, 1963) n. stat. Shoreham, Victoria, Australia	19	13-18	P	vii	iv-ix, hooded	1 + (4-6)	Some pigmentation, transition between sizes abrupt, no intermixing; large - triangular; small - rounded
<i>Abarenicola haswelli</i> (Wells, 1963) n. stat. Burnie, Tasmania	19	10-13	P	ix	iv-ix, naked	1 + (7-9)	Some pigmentation, transition between sizes abrupt, no intermixing; large - trapezoidal, wider at base, arranged on ridges; small - conical
<i>Abarenicola wellsi</i> n. sp. Falkland Islands	19	12-17	P	vii	iv-ix, hooded	1 + (11-15)	Some pigmentation, sizes intermix at transition; large - triangular; small - conical
<i>Abarenicola affinis affinis</i> (Ashworth, 1963) Otago Harbour, New Zealand	19	No information	P	vii	iv-ix, hooded	1 + (6-9)	No information
<i>Abarenicola affinis clarki</i> Wells, 1963 Ralph's Bay, Hobart, Tasmania	19	-	P	vii	iv-ix, hooded	1 + 4	-
<i>Abarenicola affinis africana</i> Wells, 1963 Luderitz Bay, Southwest Africa	19	-	P	vii	v-ix, hooded	1 + (7-9)	-
<i>Abarenicola affinis chilensis</i> Wells, 1963 West Chiloe, Chile	19	-	P	vii	iv-ix, hooded	1 + (8-11)	-
<i>Abarenicola glichristi</i> Wells, 1963 Buffels Bay, Cape Peninsula, South Africa	19	-	P	viii	v-ix, hooded	1 + (16-20)	-
<i>Abarenicola pusilla</i> (de Quatrefages, 1866) Coquimbo, Chile	19	No information	A	viii	iv-ix, naked	1 + 8	No information
<i>Abarenicola claparedii claparedii</i> (Levinsen, 1884) Naples, Mediterranean Sea	19	-	A	vii	v-ix, hooded	1 + (3-4)	-
<i>Abarenicola claparedii vagabunda</i> (Healy & Wells, 1959) False Bay, Washington, USA	19	-	A	vii	v-ix, hooded	1 + (11-18)	-
<i>Abarenicola claparedii oceanica</i> (Healy & Wells, 1959) Dutch Harbour, Alaska, USA	19	-	A	vii	v-ix, hooded	1 + (7-9)	-
<i>Abarenicola pacifica</i> Healy & Wells, 1959 False Bay, Washington, USA	19	-	A	vii	v-ix, naked	1 + (3-6)	-

058°19.943'W), muddy with some gravel, midshore, 1 specimen (NMW.Z.2015.002.0001), 19.01.2015; *Saunders Island*. The Neck south, station 42a (51°18.515'S 060°14.396'W), sand, midshore, 5 specimens (NMW.Z.2012.082.0077), 17.01.2013; The Neck south, station 42b (51°18.473'S 060°14.481'W), sand, midshore, 6 specimens (NMW.Z.2012.082.0078), 17.01.2013; The Neck south, station 42c (51°18.472'S 060°14.492'W), sand under stones, midshore, 1 specimen (NMW.Z.2012.082.0079), 17.01.2013; The Neck south, station 42e (51°18.485'S 060°14.488'W), sand, low shore, 6 specimens (NMW.Z.2012.082.0080–81), 17.01.2013; Sealer Cove harbour, station 44a (51°21.739'S 060°04.910'W), mud & rocks, midshore, 1 specimen (NMW.Z.2012.082.0082), 18.01.2013; bay below settlement, station 45 (51°21.923'S 060°04.964'W), sand, low shore, 5 specimens (NMW.Z.2012.082.0083–84), 18.01.2013; *Sea Lion Island*. Cow Point, station 71 (52°25.287'S 059°04.596'W), fine sand in rock pool, low shore, 1 specimen (NMW.Z.2015.002.0002), 26.01.2015; *West Falkland*. South

Harbour, station 52a (52°00.201'S 060°44.791'W), sand under rocks, high-mid shore, 2 specimens (NMW.Z.2012.082.0085–86), 27.01.2013; South Harbour, station 52b (52°00.201'S 060°44.791'W), sand, midshore, 4 specimens (NMW.Z.2012.0087–88), 27.01.2013; South Harbour, station 52d (52°00.201'S 060°44.791'W), silty sand, low shore, 1 specimen (NMW.Z.2012.082.0089), 27.01.2013; Hot Stone Cove Creek, Dunbar, station 54b (51°23.078'S 060°30.919'W), sand, high shore, 1 specimen (NMW.Z.2012.082.0090), 29.01.2013; Hot Stone Cove Creek, Dunbar, station 54c (51°22.999'S 060°30.909'W), fine sand, midshore, 2 specimens (NMW.Z.2012.082.0091), 29.01.2013; Hot Stone Cove Creek, Dunbar, station 54d (51°22.895'S 060°30.892'W), under stones in fine sand, low shore, 1 specimen (NMW.Z.2012.082.0092), 29.01.2013; Hot Stone Cove Creek, Dunbar, station 54f (51°22.883'S 060°30.886'W), fine sand, low shore, 5 specimens (3– NMW.Z.2012.082.0093; 1– NHMUK 2017.87; 1– USNM 1422117), 29.01.2013; Shallow Bay, station 57d (51°25.255'S 059°59.857'W), shell/

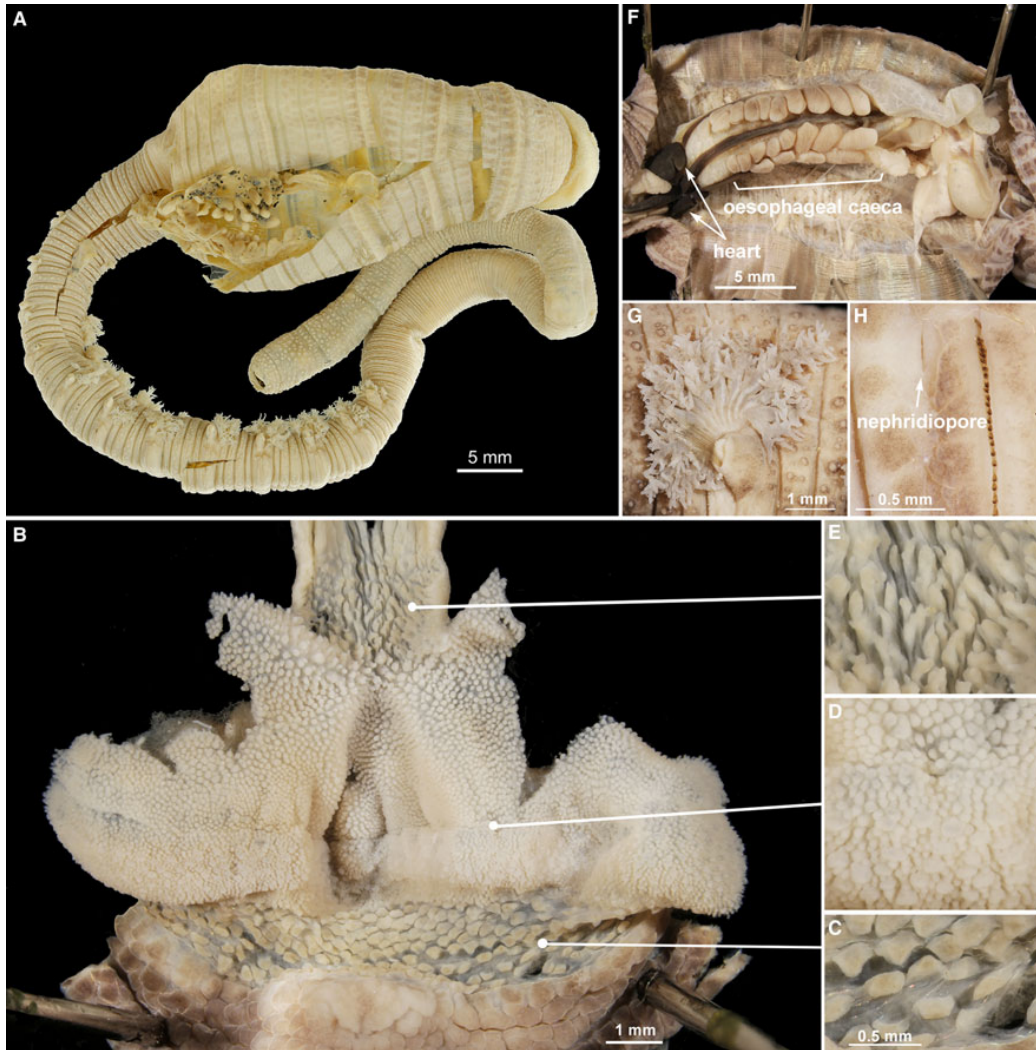


Fig. 2. *Abarenicola brevior* (Wells, 1963) n. stat. (A: HZM V.4871a; B–H: NMW.Z.2011.039.0181). A. holotype, whole body, dorsal view; B. everted proboscis, dorsal view; C. proximal papillae; D. median papillae; E. distal papillae; F. oesophageal caeca; G. chaetiger 14 gill, notopodium and notochoetae; H. chaetiger 7, nephridiopore and neurochaetae.

gravel/stones, midshore, 3 specimens (NMW.Z.2012.082.0094–95), 01.02.2013.

DESCRIPTION (incorporating Wells, 1963)

Holotype complete (Figure 2A), 85 mm long (tip of prostomium to end of final chaetiger), 9 mm wide at 1st chaetiger, 19 chaetigers. Paratypes 28–63 mm long, additional non-type specimens 3.5–184 mm long. Description based on holotype except for statolith form.

Body cylindrical, divided externally into three distinct regions: anterior ('head'), thorax ('body') and posterior caudal region ('tail'). Body widest over first few anterior chaetigers, tapering towards end of chaetigers, tail narrow, tubular. Colour pale brown (preserved). Epidermis tessellate to chaetiger 6, papillate from chaetiger 6 onward. All segments with distinct annulation. First 3 chaetigerous annuli slightly swollen, intervening annuli not reduced; number of annuli between first 4 chaetigers 2–3–4, thereafter 4.

Anterior region consisting of prostomium and 2 achaetigerous segments. Prostomium trilobate, non-retractile. Nuchal groove and statocyst with open-ended duct on either side. Statoliths small, numerous, evenly shaped, amber. Eyes absent. Eversible proboscis covered in unpigmented papillae (Figure 2A–E). Proximal section with large, flat, triangular papillae, more sparsely distributed than in following sections (Figure 2B, C). Median section densely covered initially with large, rounded and small conical papillae, then small papillae only (Figure 2B, D). Distal section papillae elongate, conical, irregular in size (Figure 2B, E).

Oesophageal caeca with 1 elongate and 10 or 11 smaller caeca (Figure 2F).

Thorax with 19 chaetigers (Figure 2A). Each segment with one enlarged annulation bearing noto- and neuropodia and, on chaetigers 8–19, branchiae (Figure 2A).

Notopodium trapezoidal outer torus with inner retractile, rounded lobe (Figure 2G) bearing 2 parallel rows of up to 25 simple capillaries. Neuropodia raised, elliptically shaped tori containing single row of 22–49 unidentate hooks, minutely serrated on the upper edge.

Branchiae large, branched, highly vascularized, 12 pairs (Figure 2G). First 2 pairs reduced in size. Median branchiae with 13 gill stems with multiple lateral branches and gill filaments off each stem. Gill stems fused together over lower third portion of length.

Six pairs of nephridia on chaetigers 4–9. Nephridiopores naked dorsi-ventral clefts located posterior to dorsal end of neuropodium (Figure 2H).

Achaetous tail papillate tube (Figure 2A), easily lost. Anus terminal.

REMARKS

Abarenicola brevior n. stat. is part of the 'cysted' group of *Abarenicola* species that possess statocysts with ducts to the exterior. This group comprises *Abarenicola assimilis* n. stat., *Abarenicola devia* n. stat., *Abarenicola haswelli* n. stat., *Abarenicola insularum* n. stat., *Abarenicola wellsii* n. sp., *Abarenicola affinis affinis*, *Abarenicola affinis africana*, *Abarenicola affinis clarki*, *Abarenicola affinis chiliensis* and *Abarenicola gilchristi*. Of these species, *A. brevior* is most similar to *A. assimilis*, *A. gilchristi* and *A. insularum* in having the first gill occurring on chaetiger 8 as opposed to chaetiger 7 (this is a correction to Wells' original description in which he stated that the first gill could occur on either

chaetiger 7 or 8). However, *A. brevior* is easily distinguished from *A. assimilis*, which has 20 chaetigers instead of the usual 19 possessed by *A. brevior* and the rest of the genus, and from *A. gilchristi* which has only 5 pairs of nephridia, from chaetigers 5–9, and hooded nephridiopores as opposed to 6 pairs of nephridia, on chaetigers 4–9, and naked nephridiopores. *Abarenicola brevior* can finally be distinguished from *A. insularum* using both the oesophageal caeca count and the appearance of the proboscidial papillae. In *A. brevior* the oesophageal caeca formula is 1 + (9–12) while in *A. insularum* the formula is 1 + (4–6). Additionally, the proboscidial papillae in the two species are quite different in form. *Abarenicola brevior* has a short sparse region of large, flat, triangular papillae followed by a densely papillated median region that initially has a small number of larger papillae intermixed with smaller conical papillae transitioning to small papillae only. *Abarenicola insularum*, however, has a long region of large, mushroom-shaped papillae (short but wide 'stalk' with rounded 'head'). Small numbers of small conical papillae gradually intermix with the larger papillae before increasing in number.

HABITAT

Sand of most grades from high to low shore and occasionally in the sand of rock pools.

DISTRIBUTION

Beagle Channel & Magellan Strait; Falkland Islands

Abarenicola devia (Wells, 1963) n. stat.
(Table 2)

Arenicola assimilis var. *affinis* Ashworth, 1911: 22–23. – Stach, 1944: 272.

Abarenicola assimilis devia Wells, 1963: 134, 140–141, fig. 3, Pl. 4, Table 1.

TYPE MATERIAL EXAMINED

Holotype: Shoreham, Victoria, Australia (NHMUK 1961.12.2); coll. F.H. Drummond, 1954.

ADDITIONAL OBSERVATIONS

Eversible proboscis covered in papillae with some pigmentation. Proximal section long with large, triangular, widely distributed papillae, slight pigmentation only; median section densely populated with very small, unpigmented, rounded papillae; distal section with larger, conical papillae. Abrupt transition from proximal to median section with distinct narrow division between.

Abarenicola haswelli (Wells, 1963) n. stat.
(Table 2)

Arenicola assimilis var. *affinis* Ashworth, 1911: 22–23. – *Abarenicola assimilis haswelli* Wells, 1963: 134, 141, fig. 3, Table 1.

TYPE MATERIAL EXAMINED

Holotype: Burnie, Tasmania (NHMUK 1912.4.9.31); coll. W.A. Haswell.

ADDITIONAL OBSERVATIONS

Eversible proboscis covered in papillae with some pigmentation. Proximal section with dense, large, trapezoidal papillae,

appearing to be arranged on transverse 'ridges'; median section densely populated with small, conical papillae. Abrupt transition from proximal to median section with distinct narrow division between.

Abarenicola insularum (Wells, 1963) n. stat.
(Table 2)

Arenicola assimilis var. *affinis* Ashworth, 1903: 754–764, 777–780, Pl. 36, figs 2, 7, 8, 11, 15, 20, Pl. 37, fig. 23. – Ashworth, 1911. – Ehlers, 1912. – Benham, 1921: 108. – Monroe, 1939: 133. – Fauvel, 1952.

Abarenicola assimilis insularum Wells, 1963: 134, 140, figs 3, 10e, Pl. 4, Table 1.

TYPE MATERIAL EXAMINED

Holotype: Tucker Cove, Campbell Island, New Zealand (NHMUK 1961.12.1); coll. P.M. Johns, 01.1960

ADDITIONAL OBSERVATIONS

Eversible proboscis covered in papillae with some pigmentation. Proximal section long with large, unpigmented, 'mushroom-shaped' papillae; median section initially with mostly large papillae intermixed with some small, conical papillae, transitioning gradually to denser, small papillae only.

Abarenicola wellsii n. sp.
(Figures 1, 3 & 4; Tables 1 & 2)

Arenicola assimilis var. *affinis* Ashworth, 1903: 768–772. – *Abarenicola assimilis brevior* Wells, 1963 (in part): 133–140, figs 2, 3, Table 1.

TYPE MATERIAL. Holotype: *East Falkland*. Whalebone Cove, station 9a (51°41.330'S 057°48.092'W), medium-coarse sand, low shore (NMW.Z.2011.039.0190), 23.11.2011.

Paratypes: *East Falkland*. (previously identified as *A. a. brevior*) Whale Sound, Stanley Harbour, 5 specimens (NHMUK 1961.12.17–21), Spring 1902; Whalebone Cove, station 9a (51°41.330'S 057°48.092'W), medium-coarse sand, low shore, 5 specimens (2– NMW.Z.2011.039.191–192; 1– NHMUK 2017.85; 1– ZMH P-27824; 1– USNM 1422115), 23.11.2011; Whalebone Cove, station 41a (51°41.324'S 057°48.000'W), medium-coarse sand, high shore, 1 specimen (NMW.Z. 2012.082.0096), 15.01.2013; Whalebone Cove, station 41c (51°41.327'S 057°48.081'W), medium-coarse sand, low shore, 1 specimen (NMW.Z. 2012.082.0097), 15.01.2013; *West Falkland*. Fox Bay West, station 50c (51°56.199'S 060°04.725'W), fine sand, mid-low shore, 2 specimens (NMW.Z.2012.082.0098–99), 25.01.2013; The Creek, Hill Cove, station 56a (51°30.094'S 060°07.447'W), medium sand, high shore, 2 specimens (NMW.Z.2012.082.0100–0101), 31.01.2013; The Creek, Hill Cove, station 56b (51°30.067'S 060°07.520'W), medium sand, midshore, 1 specimen (NMW.Z.2012.082.0102), 31.01.2013; Port Howard, station 59a (51°36.983'S 059°31.250'W), medium sand & shell, midshore, 2 specimens (NMW.Z.2012.082.0103–104), 03.02.2013.

COMPARATIVE MATERIAL EXAMINED.

East Falkland. The Canache, station 2a (51°41.680'S 057°46.967'W), medium sand, high shore, 5 specimens

(NMW.Z.2011.039.0193), 16.11.2011; The Canache, station 2b (51°41.708'S 057°46.996'W), medium sand, midshore, 1 specimen (NMW.Z.2011.039.0194), 16.11.2011; Moody Brook, station 3b (51°41.201'S 057°55.099'W), filamentous algae over muddy fine sand, low shore, 1 specimen (NMW.Z.2011.039.0195), 17.11.2011; Volunteer Point lagoon, station 5b (51°28.752'S 057°50.437'W), fine sand, just below low water, 4 specimens (NMW.Z.2011.039.0196), 20.11.2011; Mount Kent, station 7c (51°34.069'S 058°08.615'W), sandy mud, midshore, 4 specimens (NMW.Z.2011.039.0197), 22.11.2011; Coral Creek, Estancia, station 8a (51°39.036'S 058°13.036'W), soft sand over gravel, high shore, 1 specimen (NMW.Z.2011.039.0198), 22.11.2011; Whalebone Cove, station 9a (51°41.330'S 057°48.092'W), medium-coarse sand, low shore, 1 specimen (NMW.Z.2011.039.0199), 23.11.2011; Kelp Harbour, by stone corral, station 28 (51°48.597'S 059°19.433'W), muddy sand, midshore, 1 specimen (NMW.Z.2011.039.0200), 04.12.2011; Whalebone Cove, station 31c (51°41.325'S 057°48.037'W), medium-fine sand, low shore, 2 specimens (NMW.Z.2011.039.0201), 05.12.2011; Mullet Creek, station 33b (51°43.121'S 057°54.833'W), coarse gravelly/pebbly sand, high-midshore, 6 specimens (NMW.Z.2011.039.0202), 07.12.2011; Mullet Creek, station 33c (51°43.150'S 057°54.545'W), medium sand, mid-low shore, 4 specimens (NMW.Z.2011.039.0203), 07.12.2011; Sand Bay, Port Harriet, station 34c (51°44.169'S 058°00.610'W), fine sand over clay, high-midshore, 1 specimen (NMW.Z.2011.039.0204), 08.12.2011; Camilla Creek, station 36b (51°46.668'S 058°57.760'W), soft mud, midshore, 2 specimens (NMW.Z.2011.039.0205), 09.12.2011; Camilla Creek, station 36d (51°46.680'S 058°57.760'W), muddy sand, midshore, 1 specimen (NMW.Z.2011.039.0206), 09.12.2011; Port Salvador, station 39c (51°26.509'S 058°22.230'W), fine sand, high-midshore, 4 specimens (NMW.Z. 2012.082.0105–108), 14.01.2013; Whalebone Cove, station 41b (51°41.322'S 057°48.030'W), medium-coarse sand, midshore, 4 specimens (NMW.Z. 2012.082.0109–112), 15.01.2013; Whalebone Cove, station 41c (51°41.327'S 057°48.081'W), medium-coarse sand, low shore, 16 specimens (NMW.Z. 2012.082.0113–124), 15.01.2013; North Arm, station 47b (52°06.835'S 059°22.224'W), soft mud over sand and gravel, midshore, 1 specimen (NMW.Z. 2012.082.0126), 21.01.2013; North Arm, station 47c (52°06.835'S 059°22.224'W), soft mud over sand and gravel, low shore, 3 specimens (1– NMW.Z. 2012.082.0127; 1– ZMH P-27825; 1– NHMUK 2017.86), 21.01.2013; *Saunders Island*. above East Point, station 43 (51°19.679'S 060°05.527'W), muddy sand, midshore, 1 specimen (NMW.Z.2012.082.0125), 18.01.2013; *West Falkland*. Fox Bay West, station 50b (51°56.182'S 060°04.746'W), fine sand, midshore, 3 specimens (2– NMW.Z.2012.082.0128; 1– USNM 1422116), 25.01.2013; Fox Bay West, station 50d (51°56.238'S 060°04.612'W), fine sand, low shore, 7 specimens (NMW.Z.2012.082.0129–132), 25.01.2013; Fox Bay West, station 50e (51°56.235'S 060°04.673'W), fine sand, low shore, 42 specimens (NMW.Z.2012.082.0133–134), 25.01.2013; Moonlight Bay, station 51a (52°06.211'S 060°50.364'W), coarse sand, high-midshore, 2 specimens (NMW.Z.2012.082.0135), 26.01.2013; Moonlight Bay, station 51b (52°06.227'S 060°50.361'W), coarse sand, midshore, 1 specimen (NMW.Z.2012.082.0136), 26.01.2013; Moonlight Bay, station 51f (52°06.269'S 060°50.305'W), medium-coarse sand, extreme low shore, 3 specimens (NMW.Z.2012.

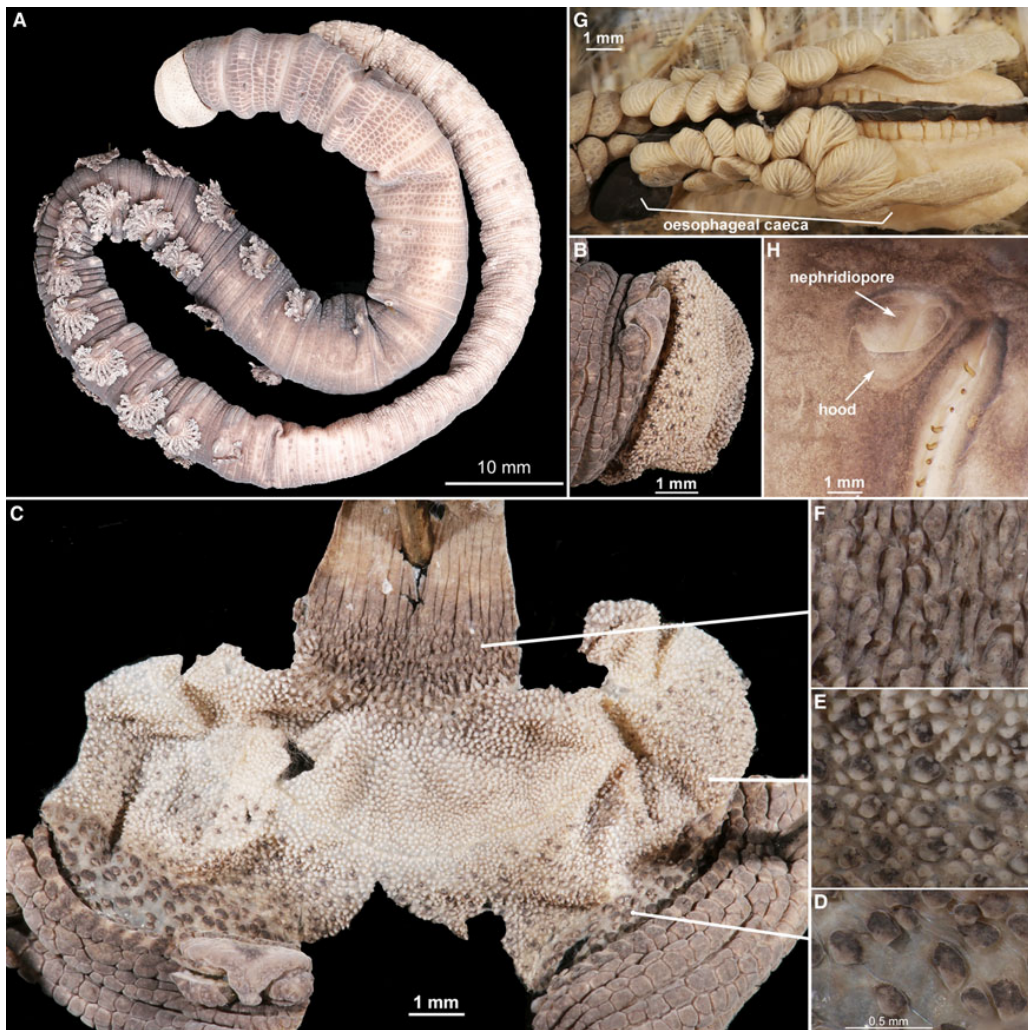


Fig. 3. *Abarenicola wellsi* n. sp. (A: NMW.Z.2011.039.0190; B: NMW.Z.2011.039.0192, paratype). A. holotype, whole body, dorsal/lateral view; B. prostomium & everted proboscis, dorsolateral view; C. everted proboscis, dorsal view; D. proximal papillae; E. median papillae; F. distal papillae; G. oesophageal caeca; H. chaetiger 7, nephridiopore and neurochaetae.

082.0143–144), 26.01.2013; Hot Stone Cove Creek, Dunbar, station 54c ($51^{\circ}22.999'S$ $060^{\circ}30.909'W$), fine sand, midshore, 3 specimens (NMW.Z.2012.082.0137), 29.01.2013; Crooked Inlet, Roy Cove, station 55a ($51^{\circ}32.521'S$ $060^{\circ}20.810'W$), soft black fine sand, high shore, 1 specimen (NMW.Z.2012.082.0138), 30.01.2013; The Creek, Hill Cove, station 56c ($51^{\circ}30.058'S$ $060^{\circ}07.568'W$), medium sand, midshore, 2 specimens (NMW.Z.2012.082.0139), 31.01.2013; The Creek, Hill Cove, station 56f ($51^{\circ}30.040'S$ $060^{\circ}07.726'W$), fine sand, low shore, 1 specimen (NMW.Z.2012.082.0140), 31.01.2013; Port Howard, station 59a ($51^{\circ}36.983'S$ $059^{\circ}31.250'W$), medium sand & shell, midshore, 2 specimens (NMW.Z.2012.082.0141), 03.02.2013.

DESCRIPTION. Holotype complete (Figure 3A), 90 mm long (tip of prostomium to end of final chaetiger), 19 chaetigers. Paratypes 15–130 mm long, additional non-type specimens 2–225 mm long. Description based on holotype except for internal characters.

Body cylindrical (Figure 3A), divided externally into three distinct regions: anterior ('head'), thorax ('body') and posterior caudal region ('tail'). Body widest over first few anterior chaetigers, tapering toward end of chaetigers, tail narrow. Colour both alive and fixed dark brown (paratypes and non-types vary in shade from brown to black). Epidermis tessellated up to chaetiger 7, thereafter more papillated. First 3 chaetigerous annuli slightly swollen, intervening annuli not reduced; number of annuli between first 4 chaetigers 2–3–4, thereafter 4.

Anterior region consisting of prostomium and 2 achaetigerous segments. Prostomium trilobate (Figure 3B), non-retractile. Nuchal groove and statocyst with open-ended duct on either side. Statoliths small, numerous, evenly shaped, amber. Eyes absent. Eversible proboscis covered in papillae (Figure 3A–F). Proximal section with widely distributed large, flat, triangular papillae (Figure 3C, D); darkly pigmented on the body, pale tips. Median section with large, pigmented and small, conical, unpigmented papillae intermixed initially (Figure 3C, E), transitioning to small papillae

only (Figure 3C). Distal section more darkly pigmented, papillae conical, irregular in size (Figure 3C, F).

Oesophageal caeca with one elongate and 11–15 smaller caeca (Figure 3G) on either side of midline. Elongate pair less than twice length of other caeca.

Thorax with 19 chaetigers (Figure 3A). Each segment with one enlarged annulation bearing noto- and neuropodia and, on chaetigers 7–19, branchiae (Figure 3A).

Notopodia rounded, retractable lobes within oval torus. Lobe darkly pigmented, outer edge pale. Notochaetae up to 25 capillaries, single line.

Neuropodia elliptically shaped tori containing a single row of unidentate hooks, minutely serrated on the upper edge, up to 37.

Branchiae large, branched, highly vascularized, 13 pairs (Figure 3A). First pair reduced in size. Up to 13 main gill stems; multiple lateral branches and gill filaments off each stem. Gill stems fused together over lower third portion of length.

Six pairs of nephridia on chaetigers 4–9. Nephridiopores partially hooded dorsio-ventral clefts located posterior to dorsal end of neuropodium (Figure 3H).

Achaetous tail papillate tube (Figure 3A), easily lost. Anus terminal.

ETYMOLOGY. *Abarenicola wellsii* is named after G.P. Wells, who contributed to our knowledge of both the anatomy and taxonomy of the Arenicolidae so significantly, and to whom most of the knowledge of the genus *Abarenicola* can be attributed.

HABITAT. Mostly from midshore down, in sand.

DISTRIBUTION. Falkland Islands

REMARKS. *Abarenicola wellsii* n. sp. is most similar to *Abarenicola devia* n. stat. as both species are the only members of the 'assimilis group' with both the first gill on chaetiger 7 and hooded nephridiopores (*Abarenicola brevior* n. stat., *Abarenicola haswelli* n. stat. and *Abarenicola insularum* n. stat. all have the first gill on chaetiger 8 and naked nephridiopores). However, the two species can be distinguished using the oesophageal caeca formula and the form of the proboscis papillae. The formula for *A. wellsii* is 1 + (11–15) and that for *A. devia* is 1 + (4–6). In *A. wellsii*, the proboscis has a short, proximal section of large, triangular, flap-like and widely spaced pigmented papillae followed by a median section of dense, intermixed, small, conical, unpigmented and large pigmented papillae transitioning to small papillae only, and finally a distal section of slightly larger, conical papillae. In *A. devia* the proximal section of large papillae forms a region approximately twice the length of that in *A. wellsii* and the papillae are only slightly pigmented. Additionally, the median region is densely covered with unpigmented small, rounded papillae only before a final distal section of larger conical papillae.

Variation

Body colour of both *Abarenicola brevior* n. stat. and *Abarenicola wellsii* n. sp. varied in life from pale to dark brown, occasionally nearly black, although *A. wellsii* tended to be darker in colour more often. Branchiae may be variably pigmented and extended following preservation. The number

of gill stems is generally largest on the median branchiae (chaetigers 12–14). Across the paratypes and non-type specimens of both species, this number varied from 9–17 and roughly correlated to size.

Although levels of pigmentation relating to both the epidermis and branchiae are variable, the pigmentation of the proboscis papillae appeared to be consistent. The larger proximal papillae of *A. wellsii* are always darkly pigmented along with those larger papillae intermixed with the smaller conical papillae of the median section, resulting in a 'spotted' appearance of the proboscis (Figure 3A–E). In contrast, all of the proboscis papillae of *A. brevior* are unpigmented (Figure 2B–E). This character appears to remain consistent even after preservation and can be identified on those specimens in the type series of *A. brevior* collected as far back as 1892.

Healy & Wells (1959) introduced the practice of describing the number of oesophageal caeca using the formula 1 + n/m , where 1 indicated the first pair of long caeca and n the number of subsequent smaller caeca on each side (or n/m where the number on each side differed). Within *A. brevior* the formula for oesophageal caeca is 1 + (9–14) and for *A. wellsii* 1 + (11–15). This does not vary significantly with size. The long caeca are generally less than twice the length of the other caeca, however they can be up to three times the length.

DNA results

For the 16S dataset, maximum parsimony returned two most parsimonious trees (tree length = 521; CI = 0.5208), the single difference between them being whether or not the two pairs of *Arenicola* species (*Arenicola defodiens*–*Arenicola marina* and *Arenicola cristata*–*Arenicola loveni*) grouped together as a clade. Both maximum likelihood and Bayesian inference yielded the same tree topology as the MP tree with the *Arenicola* clade (Figure 4), although this clade itself had no substantial bootstrap support and only weak support from Bayesian posterior probabilities (0.73). An *Arenicola*–*Abarenicola* clade was also unsupported despite it being recovered by all analyses. *Branchiomaldane* was recovered as monophyletic, well supported by maximum parsimony and Bayesian inference but not by maximum likelihood and *Arenicolides* was recovered as sister to *Arenicola*–*Abarenicola*, although again with only poor support. Monophyly of *Abarenicola* gained high support from all analyses (>85% bootstrap support, 0.97 Bayesian posterior probability) and within that, the clades representing both the cysted and cyst-less *Abarenicola* species were also strongly supported by all analyses (>95% bootstrap support and >0.99 posterior probabilities). The two Falkland Islands species formed a strongly supported group in themselves. The short branch lengths indicate how closely related *Abarenicola brevior* n. stat. and *Abarenicola wellsii* n. sp. are, more so than to the other *Abarenicola* species represented. This is also borne out by the pairwise differences which show a difference of only 0.02 between the two species. Between all of the *Abarenicola* species analysed, the remaining pairwise differences ranged from 0.032 (*A. brevior*–*Abarenicola affinis affinis*) to 0.1 (*Abarenicola gilchristi*–*Abarenicola pacifica*). In comparison, pairwise differences within the four *Arenicola* species analysed ranged from 0.035 (*A. marina*–*A. defodiens*, sympatric species in the UK) to 0.109 (*A. loveni*–*A. defodiens*).

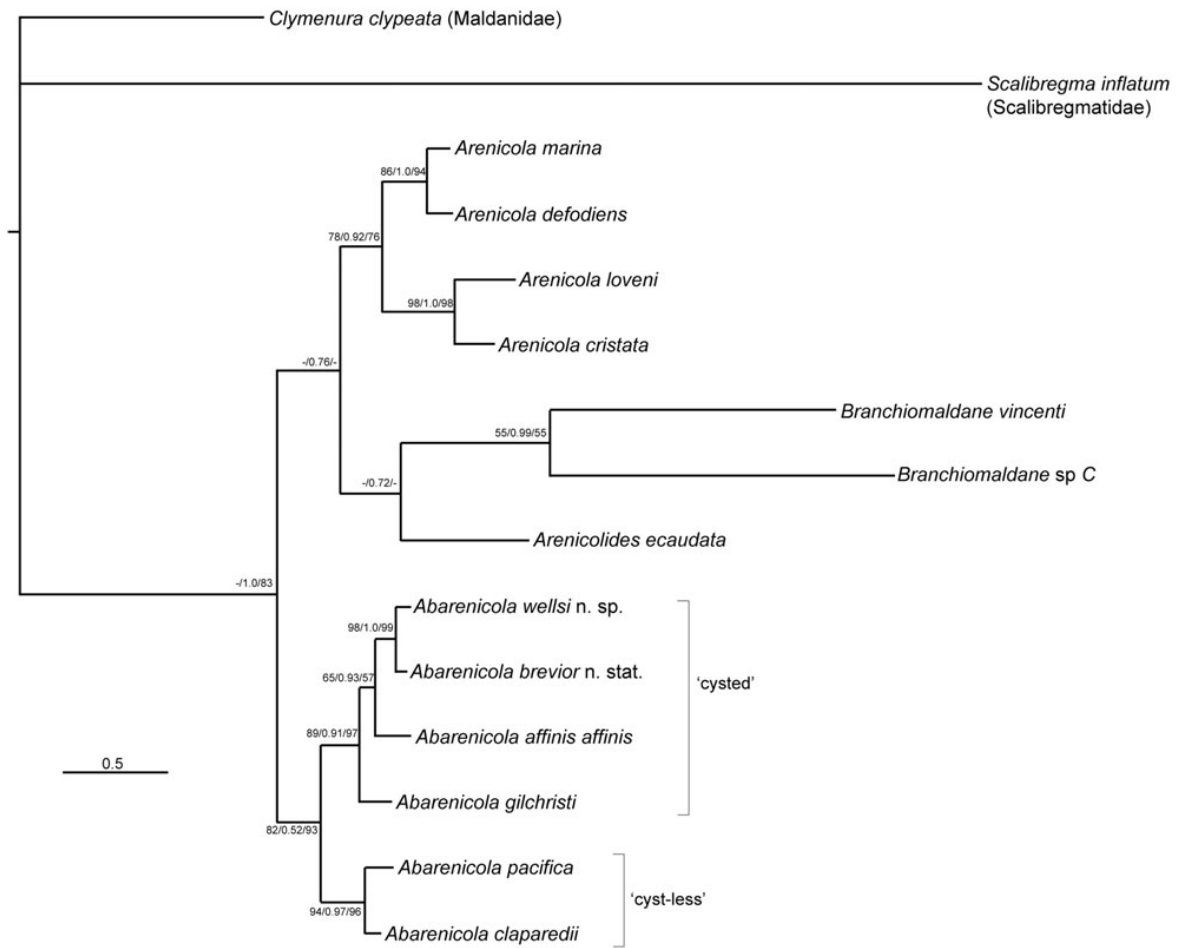


Fig. 4. Bayesian inference tree of the 16S rRNA gene dataset. The first value at each node represents the ML bootstrap support, the second the Bayesian posterior probabilities and the third the MP bootstrap support.

In the COI dataset, the only comparison available to the two Falkland Islands species was with the two UK species of *Arenicola*. All analyses recovered both *Abarenicola* and *Arenicola* as monophyletic clades but although, as with the 16S analysis, the *Abarenicola* clade gained strong support (99% bootstrap support; 0.99 posterior probability) there was once again no significant support for the *Arenicola* clade. Pairwise differences between congeners were higher than for 16S at 0.1 between *A. brevior* and *A. wellsii* compared with 0.14 between *A. marina* and *A. defodiens*. Intraspecific distances were 0.006 (*A. defodiens*), 0 (*A. marina*), 0.002 (*A. brevior*) and 0.002 (*A. wellsii*).

DISCUSSION

At the current time, there are six species described within the genus *Abarenicola*, of which three (*assimilis*, *affinis*, *claparedii*) are further split into multiple subspecies (Wells, 1963, 1964). In general, the subspecies are separated only on the internal character of the number of oesophageal caeca even though Wells did note differences in other morphological characters such as the form of the nephridiopores, position

of the first gill and ecological variations in habitat and geographic location. In a much later paper, Wells stated that 'in retrospect I am no longer so sure about my division of *Abarenicola assimilis* into four subspecies' (Wells, 1980). However, he still felt that there were not enough clear morphological characters available in these taxa in order to describe them at anything higher than subspecies level.

In 1963, Wells summarized many of the different characters that he felt existed for lugworms and rated them as to how useful he believed them to be in distinguishing species. The first of these, serial differentiations, included the number of chaetigers, the position of the first gill and the number of nephridia as well as details of the septa and septal vessels. Based on his observations of *Arenicola marina*, showing that considerable anomalies could occur in these differentiations (Wells, 1957), Wells stated that it was 'best not to separate species on the basis of such characters unless their variation was accompanied by differences of other kinds'. In the present study, observations on *Abarenicola brevior* and *Abarenicola wellsii* were made on 81 and 142 individuals respectively from sites located across both East and West Falkland (Figure 1). Although there was some variation in the size and occurrence of the first gill,

there was always at least one gill of some size present on chaetiger 7 for *A. wellsi*, but never for *A. brevior* on which the first gill always occurred on chaetiger 8. This was true even for juveniles once the branchiae had developed. One aberrant specimen did occur in the paratypes from Puerto Robalo (Chile) whereby the gills started from chaetiger 7 (not 8), however there were also only 18 chaetigers on that specimen instead of 19. It is therefore believed that for these species, the characters of occurrence of the first gill and number of chaetigers are valid in distinguishing them.

In describing the gills and nephridiopores, Wells did not state how useful he felt them to be as characters. In the two species *Arenicola marina* and *Arenicola defodiens*, that are sympatric in the UK, the gills have been shown to be useful characters in respect to the branching pattern (Cadman & Nelson-Smith, 1993; Brind & Darbyshire, 2015). However, in the *Abarenicola* species investigated here, the branching pattern and number of main gill stems do not show significant differences. The nephridiopores however, are consistent characters as to whether they are hooded (to any degree) or naked.

The oesophageal caeca were the main character that Wells used to distinguish his subspecies and the formula for the caeca, as defined by Healy & Wells (1959), is consistent within each species. Between *A. brevior* and *A. wellsi* however, there is no significant difference in the caecal count and other characters must be used. Observations on the other species in the *assimilis* group show that the relative size of the elongate caeca may also be an important character. For example, in *A. assimilis*, the elongate caeca were over three times longer than those of *A. brevior*, and in *Abarenicola insularum* around twice as long. However, at this time only the holotypes of the other species have been inspected and to be considered as a potential character many more individuals need to be investigated in order to determine how relevant this character may be.

The statocysts and statoliths are useful characters to distinguish the larger groups of *Abarenicola* e.g. the *assimilis* group, *affinis* group and *Abarenicola gilchristi*, but within the groups they are generally not distinct enough for use.

Other characters such as length, position of the nerve cord and the chaetae were not considered useful and indeed, between *A. brevior* and *A. wellsi* no discernible difference was found between either the notochaetae or neurochaetae. In general, *A. wellsi* tended to be larger and darker than *A. brevior*, something also noted by Wells (1963), however neither of these characters differed significantly enough to be useful.

Finally, one character that was not considered by Wells that has proven to be relevant in this work is that of the proboscival papillae. These have been found to differ in their pigmentation, shape and arrangement between the species and remain consistent both with size and, of particular relevance to pigmentation, the length of preservation.

The molecular results add additional detail to the analysis published by Bleidorn *et al.* in 2005, in which no species from the *A. assimilis* group were included. The topology of the tree recovered here is similar to that from the latter study based on their combined dataset of three genes, the main difference being the position of the acaudate genera, *Arenicolides* and *Branchiomaldane*, with respect to *Arenicola*. In both analyses, *Abarenicola* is well-supported as a monophyletic genus, and, within that, both the cysted and cyst-less species are also well-supported as sister-groups. The results do, however, reflect those of Bartolomaeus &

Meyer (1999) although this must be viewed with caution as some groups, despite being consistently recovered, did not receive support. The latter analysis, based on chaetal morphology and literature, hypothesized *Arenicola* and *Abarenicola* forming the taxon Caudata (despite being recovered in this analysis there was no support), with *Arenicolides* as sister taxon (as Arenicolinae; also present here but weakly supported) and finally, with *Branchiomaldane*, forming Arenicolidae.

It is unfortunate that only the 16S results are comparable with other sequences and that no other Arenicolidae species, other than *A. marina* and *A. defodiens* (Pires *et al.*, 2015 and this study), have been sequenced for the COI gene at this time. However, using the 16S results, the two Falkland Islands species are shown to be more closely related to each other than to the other *Abarenicola* species analysed and there is strong support for the formation of a clade with the other cysted species (*A. a. affinis*, *A. gilchristi*). The resulting tree also shows them to be grouped with *A. a. affinis*, although this has limited support. The results do, however, agree with those from the morphological analyses whereby greater differences are apparent between *A. gilchristi* and both the *A. assimilis* and *A. affinis* groups than between the latter two groups. The pairwise differences are lower between *A. brevior* and *A. wellsi* than between any of the other Arenicolidae species. The next lowest scores are found between *A. marina* and *A. defodiens*, two other species that show several parallels to the Falkland Islands species in their geographic closeness and taxonomic history but that are universally accepted as being distinct species. Indeed, *A. marina* and *A. defodiens* were also historically only distinguished as separate varieties of *A. marina* (Gamble & Ashworth, 1898; Ashworth, 1912), a distinction that Wells (1957) investigated and refuted, attributing the differences to minor genetic separation between populations. It was only in the 1990s that the two varieties were shown to be distinct both genetically and morphologically (Cadman & Nelson-Smith, 1990, 1993; Cadman, 1992). The intra- and interspecific distances for the Falkland Islands specimens also demonstrate that there is minimal genetic variation within each species compared with between them.

Despite Wells' doubts about the validity of some of the morphological characters, they have been shown to remain consistent within a species from juvenile through to adult and across numerous specimens from multiple populations. Although supporting molecular data are currently lacking for the other *assimilis* subspecies, the morphological characters are clear enough to also warrant the elevation of these taxa to species level as *Abarenicola assimilis* n. stat., *Abarenicola devia* n. stat., *Abarenicola haswelli* n. stat. and *Abarenicola insularum* n. stat. Additional molecular data for these species would however be useful to fully clarify the relationships between them and the other *Abarenicola* species. It is also likely that new investigations of the *affinis* subspecies may well bring to light new morphological characters to distinguish these in the same way as has been found for the *A. assimilis* group and, again, molecular analyses would be highly desirable for comparative purposes.

KEY FOR THE ABARENICOLA 'ASSIMILIS' GROUP SPECIES

- 1 Statocysts present (otic grooves absent)...
 - 2 (southern hemisphere cold temperate species)
 - Statocysts absent (otic grooves present)... northern hemisphere and *A. pusilla*

- 2 First 3 chaetigers strongly developed with reduction of intervening ordinary annuli... *Abarenicola affinis* group (4 subspecies)
 – First 3 chaetigers normally developed or only slightly thickened with no corresponding reduction of intervening annuli 3
- 3 20 chaetigers. *Abarenicola assimilis* n. stat.
 – 19 chaetigers 4
- 4 Nephridiopores naked. 5
 – Nephridiopores hooded 7
- 5 Branchiae from chaetiger 8 6
 – Branchiae from chaetiger 9 *Abarenicola haswelli* n. stat
- 6 Oesophageal caeca formula 1 + (4–6); long proximal section of ‘mushroom-shaped’ proboscoidal papillae, median section initially with more large than small papillae *Abarenicola insularum* n. stat.
 – Oesophageal caeca formula 1 + (9–14); short proximal section of wide, triangular proboscoidal papillae, median section initially with more small than large papillae *Abarenicola brevior* n. stat.
- 7 5 pairs of nephridia (chaetigers 5–9); branchiae from chaetiger 8; more than 16 oesophageal caeca *Abarenicola gilchristi*
 – 6 pairs of nephridia (chaetigers 4–9); branchiae from chaetiger 7; less than 16 oesophageal caeca 8
- 8 Oesophageal caeca formula 1 + (4–6); large and small proboscoidal papillae clearly divided on proboscis. *Abarenicola devia* n. stat.
 – Oesophageal caeca formula 1 + (11–15); large and small proboscoidal papillae intermix at beginning of median section *Abarenicola wellsii* n. sp.

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Correspondence should be addressed to:

T. Darbyshire
 Department of Natural Sciences,
 Amgueddfa Cymru – National Museum Wales,
 Cathays Park, Cardiff CF10 3NP, Wales, UK
 email: Teresa.Darbyshire@museumwales.ac.uk

Appendix 2

Paper 2

Darbyshire, T. 2014. Intertidal and nearshore Nereididae (Annelida) of the Falkland Islands, southwestern Atlantic, including a new species of *Gymnonereis*. *ZooKeys* **427**: 75–108.

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Intertidal and nearshore Nereididae (Annelida) of the Falkland Islands, southwestern Atlantic, including a new species of *Gymnonereis*

Teresa Darbyshire¹

¹ *Amgueddfa Cymru—National Museum Wales, Department of Natural Sciences, Cathays Park, Cardiff CF10 3NP, Wales, U.K.*

Corresponding author: *Teresa Darbyshire* (Teresa.Darbyshire@museumwales.ac.uk)

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Abstract

The intertidal and nearshore Nereididae of the Falkland Islands are detailed and a new species of *Gymnonereis* described. The new species, *Gymnonereis tenera* **sp. n.**, is the first record of the genus for the Falkland Islands. It is, so far, only known from a few intertidal locations in fine and muddy sands. Main distinguishing characters are: jaw teeth absent (in adults), 3 papillae in Area V–VI, falcigers absent, second ventral cirrus present throughout. *Nereis atlantica* McIntosh, 1885, known only from the description of a single specimen and one doubtful record from the Falkland Islands, is reviewed and transferred to *Perinereis* on the basis of the presence of shield-shaped bars in Area VI of the proboscis and the absence of notopodial falcigers. A key to all seven species discussed is provided.

Keywords

Taxonomy, paragnaths, Polychaeta, *Eunereis*, *Neanthes*, *Perinereis*, *Platynereis*

Introduction

The Nereididae is one of the largest polychaete families (Hutchings et al. 2000) and, intertidally, one of the most widespread and frequently encountered (Wilson 2000). Although not much literature exists on the intertidal polychaetes of the Falkland Islands, at least one species of Nereididae is recorded in each of the three papers (Pratt 1898, 1901; Fauvel 1916) published. Other records of Falkland Islands Nereididae have been from Antarctic/Southern Ocean research cruises that have also taken samples among and around the islands (Ramsay 1914; Monro 1930, 1936; Hartman 1953, 1967).

In all, eight species of nereidid, in six genera, have previously been recorded from stations listed as being within the Falkland Islands region. However, two of these species, *Platynereis australis* (Schmarda, 1861) and *P. magalhaensis* Kinberg, 1865 have been controversially synonymized (e.g. Benham 1909, 1921; Hutchings and Reid 1990) or kept separate (e.g. Fauvel 1916; Augener 1932; Hartman 1953, 1964) many times historically. Most recently, Read (2007) maintained both names pending investigation of the epitokous stage of *P. magalhaensis* to help resolve the issue. All but one record (Ramsay 1914) of *Platynereis* for the islands are as *P. magalhaensis* and this name is therefore retained in this paper with a discussion of the current situation. *Platynereis australis* is considered unlikely to occur around the islands, hence a description is not included.

Only species that have previously been recorded from Falkland Islands samples taken in less than 30 m (where diving and shallow survey work are most likely to take place) are considered in this paper. For this reason, *Nicon maculata* Kinberg, 1865 is also excluded as it has not been recorded from less than 129 m in the area (Monro 1936; Hartman 1953, 1967). *Eunereis patagonica* (McIntosh, 1885), *Nereis atlantica* McIntosh, 1885 and *Nereis eugeniae* (Kinberg, 1865) were not collected by the survey but are included because they have previously been recorded from shallow depths and could feasibly be recorded from shallow samples taken in the area. The descriptions and reports of each species are considered and details specific to the Falkland Islands reported. *Nereis atlantica* McIntosh, 1885 is reviewed and newly transferred to *Perinereis* Kinberg, 1865.

Most of the nereidids collected were found in mainly coarse or hard habitats, however, a new species of *Gymnonereis* Horst, 1919, a genus not previously recorded from Falkland Island waters, was identified from a small number of localities where it was almost entirely confined to intertidal, fine and muddy sands. *Gymnonereis* is a small genus of only six recognized species: *G. sibogae* Horst, 1918 (type locality: Strait of Makassar, Indonesia), *G. crosslandi* Monro, 1933 (type locality: Gorgona Island, Colombian Pacific), *G. fauveli* Hartmann-Schröder, 1962 (type locality: San Julián, Argentina), *G. phuketensis* Hylleberg & Nateewathana, 1988 (type locality: Andaman Sea, Thailand), *G. minyami* Hutchings & Reid, 1990 (type locality: Victoria, South Australia) and *G. yurieli* Hutchings & Reid, 1990 (type locality: Queensland, Australia). All members of the genus lack paragnaths, having only soft papillae on the oral ring and all, except *G. crosslandi*, exhibit highly vascularized dorsal cirrophores on median chaetigers. The new species is distinguishable from the other members of the genus using combinations of characters detailing the presence or absence of jaw teeth, falcigers and enlarged dorsal

cirrophores, the number and distribution of the oral ring papillae, the occurrence of accessory dorsal cirri and the relative lengths of the neuropodial lobes.

A key to the seven species of Nereididae recognized from the near shore (< 30 m) waters of the Falkland Islands is provided.

Terminology

The parapodia of the Gymnonereidinae are more complex than those of the Nereidinae and a diagram is provided in Figure 1 to compare and standardize the terminology used in this paper when describing the different species. In reference to *Gymnonereis*, the terminology used by Hutchings and Reid (1990) has been mostly adopted, with some modification according to Santos et al. (2005), and is detailed further in the Remarks for that section.

The terminology used to describe paragnath forms was reviewed by Bakken et al. in 2009 and has been applied here also. Where necessary, generic diagnoses have been emended to reflect this, with changes highlighted in italics.

Methods

In 2011 and 2013, intertidal and diving survey work was undertaken around the Falkland Islands, covering the two main islands, East and West Falkland, as well as some of the smaller outer islands. Specimens were collected by a variety of methods on the shore and by SCUBA diving. Intertidal habitats were investigated by digging and collecting specimens by hand, by sieving sediment through a 0.5 mm sieve, turning over rocks and removing attached tubes, splitting open rock crevices and by inspecting algal holdfasts. Sampling while diving involved scraping epifaunal turf off rocks, turning over rocks and removing attached tubes, and taking sediment samples that would later be sieved as above.

Specimens were relaxed with a 7% magnesium chloride solution where possible and then fixed with 4% formaldehyde in seawater. After a period of at least 2 days, animals were rinsed with freshwater and preserved in 80% industrial methylated spirits with 2% propylene glycol added.

Morphological examinations and measurements were made using a Nikon Eclipse E400 binocular microscope and a Nikon Labophot-2 compound microscope. Microscope photographs were taken using AutoMontage™ software.

The holotype and most paratypes of *Gymnonereis tenera* sp. n. are accessioned in the zoological collections of National Museum Wales (NMW.Z). Paratypes are also deposited in the Australian Museum (AM), Natural History Museum, London (NHMUK), National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM) and the Zoological Museum, Hamburg (ZMH). All other specimens are accessioned in the National Museum Wales collections.

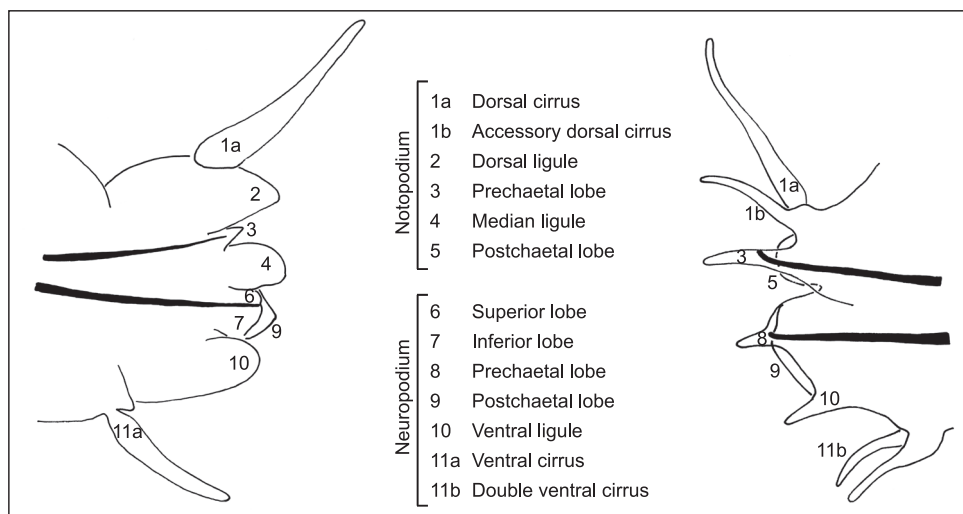


Figure 1. Terminology and diagrammatic representation of **A** a Nereidinae parapodium (modified from Hutchings and Reid 1990) and **B** a Gymnonereidinae parapodium (modified from Hylleberg and Nateewathana 1988), anterior view.

Taxonomy

Family Nereididae Blainville, 1818

Subfamily Gymnonereidinae Banse, 1977

Genus *Gymnonereis* Horst, 1919

Gymnorhynchus Horst, 1918: 247. — Pre-occupied by *Gymnorhynchus* Rudolphi, 1819; Cestoda (paper cited from Pettibone 1970).

Gymnonereis Horst, 1919: 64. — Pettibone 1970: 234. — Banse 1977: 621–622 (in part).

Type species. *Gymnonereis sibogae* (Horst, 1918) by monotypy

Diagnosis (after Hutchings and Reid 1990). Body elongate, depressed, attenuated posteriorly. Prostomium with frontal margin deeply incised between bases of frontal antennae.

Eversible pharynx with jaws having cutting edge smooth or serrated, with papillae on the oral ring. Notopodia with accessory dorsal cirri attached to dorsal cirrophores in anterior region only, with prechaetal lobes and short, rounded postchaetal lobes. Median segments with dorsal cirrophores greatly elongated and highly vascularized (except in *G. crosslandi*) and lacking accessory cirri. Dorsal transverse ridges present or absent. Chaetae homogomph or sesquigomph spinigers and homogomph or sesquigomph falcigers may be present. Chaetae very numerous in anterior chaetigers.

Remarks. Hutchings and Reid (1990) used the term 'sesquigomph', in a review of Australian Gymnonereidinae, to describe those chaetae that have a 3:2 ratio between the

boss and opposing prong of the shaft. Such chaetae were referred to as 'slightly hemigomph' by Fauchald (1977) or 'slightly heterogomph' by Hylleberg and Nateewathana (1988) in their descriptions of *Gymnonereis*. Terminology referring to the additional dorsal (=accessory dorsal) cirrus and ventral (=double ventral) cirri follow that of both Hutchings and Reid (1990) and Santos et al. (2005) in the first instance but only Santos et al. (2005) in the second. Finally, the parapodial projections referred to as 'prechaetal ligules' in both Hylleberg and Nateewathana (1988) and Hutchings and Reid (1990) are here termed prechaetal lobes, after Santos et al. (2005), who defined notopodial projections supported by aciculae as lobes and those without aciculae as ligules and found notopodial ligulae to be absent in *Gymnonereis*. This definition has also been applied here to the previously-termed 'neuropodial prechaetal ligules', referred to here as neuropodial prechaetal lobes (Fig. 1).

***Gymnonereis tenera* sp. n.**

<http://zoobank.org/66F36C23-ECF2-4F01-A2CF-BB12F84D1894>

Figures 2A–I, 9A–B

Material examined. East Falkland: Teal Creek, Stn 35d (51°49.248'S, 058°55.561'W), muddy sand, midshore, holotype (NMW.Z.2011.039.0102), 09.12.2011; Sand Bay, Port Harriet, Stn 34d (51°44.231'S, 058°00.585'W), fine sand, mid–low shore, 11 paratypes (9–NMW.Z.2011.039.0093–0095; 1–USNM 1231433; 1–ZMH p-27694), 08.12.2011; Teal Creek, Stn 35b (51°49.231'S, 058°55.573'W), sandy mud, midshore, 18 paratypes (NMW.Z.2011.039.0096), 09.12.2011; Teal Creek, Stn 35c (51°49.236'S, 058°55.563'W), mud, low shore, 22 paratypes (NMW.Z.2011.039.0097–0101), 09.12.2011; West Falkland: Crooked Inlet, Roy Cove, Stn 55b (51°32.546'S, 060°20.562'W), fine sand, high-midshore, 4 paratypes (1–AM W.46477; 1–NHMUK ANEA2014.31; 2–NMW.Z.2012.082.0001), 30.01.2013; Crooked Inlet, Roy Cove, Stn 55c (51°32.595'S, 060°20.367'W), fine sand, midshore, 2 paratypes (NMW.Z.2012.082.0002), 30.01.2013; Crooked Inlet, Roy Cove, Stn 55d (51°32.664'S, 060°20.255'W), fine sand, low shore, 3 paratypes (NMW.Z.2012.082.0003–0004), 30.01.2013; Crooked Inlet, Roy Cove, Stn 55e (51°32.688'S, 060°20.244'W), fine sand, low shore, 2 paratypes (NMW.Z.2012.082.0005), 30.01.2013.

Description. Holotype complete, 98 mm long, 1.5 mm wide (excluding parapodia; measured at widest part of anterior – approximately chaetiger 8), for 160 chaetigers. Complete paratypes 3–143 mm long, 0.15–2.53 mm wide (excluding parapodia) for 28–166 chaetigers. Description based on observations of the holotype and a dissected paratype (NMW.Z.2011.039.0098) used for illustrations. Variation shown by other paratypes described in later section.

Body depressed dorso-ventrally, widest anteriorly on chaetigers 8–10 (more pronounced in smaller specimens), then mostly uniform in width before tapering posteriorly. Colour pink/orange or grey/white in alcohol with black aciculae. Neurochaetae and subacicular notochaetae dark golden in anterior chaetigers, supracicular chaetae

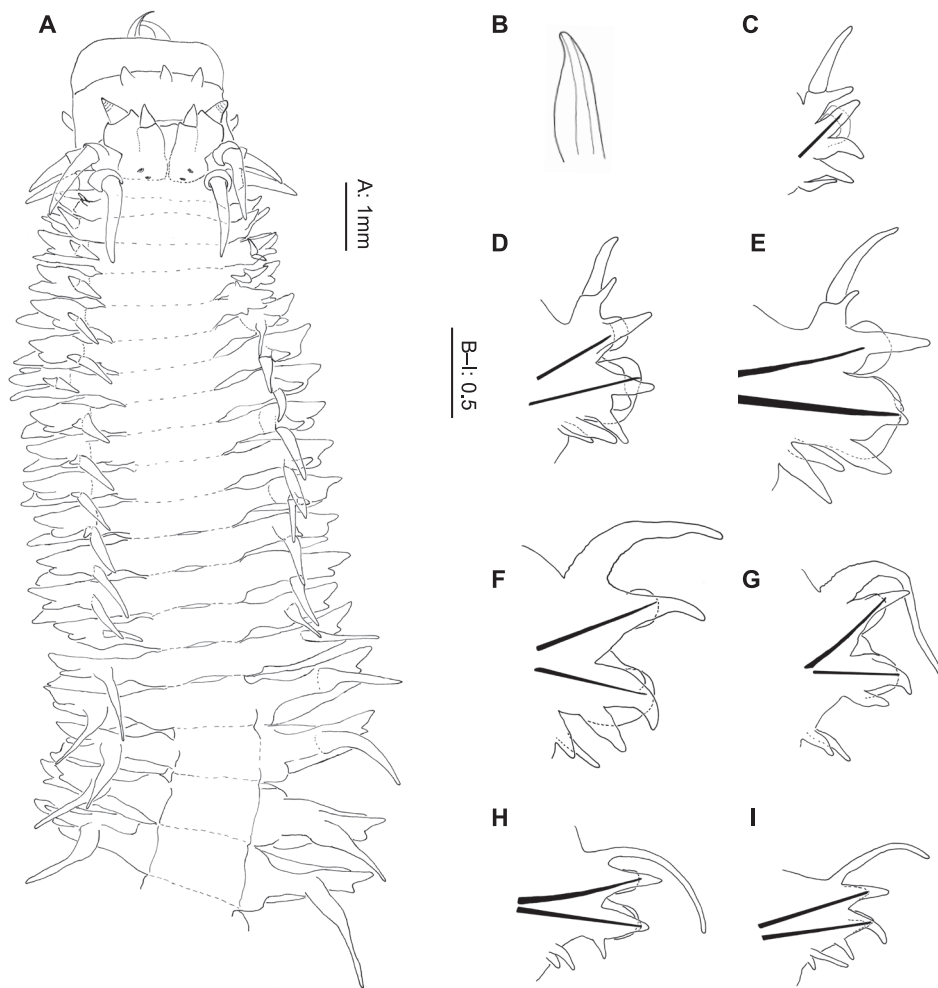


Figure 2. *Gymnonereis tenera* sp. n. (**A** NMW.Z.2011.039.0102 **B–I** NMW.Z.2011.039.0098): **A** holotype, anterior end, dorsal view (right chaetiger 4 aberrant) **B** jaw; **C**: left parapodium, chaetiger 1, anterior view **D** left parapodium, chaetiger 3, anterior view **E** left parapodium, chaetiger 9, anterior view **F** left parapodium, chaetiger 20, anterior view **G** left parapodium, chaetiger 30, anterior view **H** left parapodium, chaetiger 50, anterior view **I** left parapodium, chaetiger 100, anterior view.

pale amber; all chaetae pale amber from chaetiger 14. Live animals bright red on each side of body, including the parapodia, in region of vascularized, enlarged cirrophores; rest of body often with bright white dorsal bands centrally either side of central blood vessel from end of vascularized cirrophore region, fading in posterior. Where white colouration absent, body transparent, coloured only by visible gut and blood vessels. Methyl green staining of preserved animals shows glandular areas on tips of cirri and parapodial lobes but not on cirrophores or main body. Cuticle very soft when animals alive as well as post-fixation, body breaks easily when handled.

Prostomium with 2 pairs small, black (dark red when alive) eyes, often difficult to discern when preserved (Figs 2A, 9A). Anterior pair smaller, more laterally placed than posterior pair; crescent-shaped with additional small spot in far corners. Posterior pair darker, rounded. Prostomium subrectangular with deep cleft between antennae (Fig. 2A). Palps with large squat palpophores and short triangular palpostyles (0.4 mm long, 0.27 mm wide). Antennae equal length to or slightly longer than palps, more slender in form. Four pairs tentacular cirri, ventral pairs of equal length, 2/3 to 1/2 length of dorsal pairs; 2nd pair dorsal tentacular cirri marginally longer than 1st pair, reaching to chaetiger 4.

Peristomium dorsally more narrow than following segments. Jaws with smooth edges, teeth absent (Fig. 2A–B). Oral ring with triangular papillae arranged as follows (Figs 2A; 9A, B): Area V–VI = 3, VII–VIII = 7; maxillary ring bare.

Chaetigers 1–2 uniramous (Fig. 2C), single black acicula, tip curved, just emergent. Subsequent chaetigers all biramous (Fig. 2D–I), notoacicula not emergent, neuroacicula thicker, emergent anteriorly only up to around chaetiger 50. Dorsal cirri of chaetigers 1–12 with accessory dorsal cirrus (Fig. 2A, C–E), up to 1/3 length of main cirrus, appearing as extension to cirrophore rather than dorsal cirrus. From chaetigers 16–52 (Fig. 2F–G), dorsal cirrophores expanded and vascularized, although start and end of region difficult to define. Remaining chaetigers with dorsal cirrus long, narrow, tapering (Fig. 2H–I).

Double ventral cirri present throughout (Fig. 2C–I), branches unequal, ventral branch reducing in size posteriorly. Dorsal branch 1.5 times as long as ventral branch in anterior region, 4–5 times as long posteriorly.

Chaetiger 1 (Fig. 2C), neuroacicular papilla small, rounded, posterior and slightly dorsal to digitiform prechaetal lobe. Postchaetal lobe broad, rounded, approximately 2/3 length of prechaetal lobe. Acicular lobe similar shape to postchaetal lobe, approximately 1/2 length. Ventral neuropodial ligule of same size and shape as prechaetal lobe.

Chaetiger 3 (Fig. 2D) with basally swollen, digitiform notopodial prechaetal lobe twice as long as broadly rounded notopodial postchaetal lobe; acicular lobe 1/4 length of latter. Notochaetae in 2 unequal bundles, arranged as a smaller semicircle above and larger semicircle below the notopodial prechaetal lobe. Neuropodium as for chaetiger 1, ventral ligule of same size and shape as neuropodial prechaetal lobe. Neurochaetae in 2 semicircular fascicles of greater density than notochaetae. Superior fascicle arranged around neuroacicular papilla with larger, inferior bundle ventral and posterior to neuropodial prechaetal lobe. Arrangement continues to start of vascularized cirrophores then number of chaetae reduces posteriorly, becoming bundles rather than semicircles. Greatest density of chaetae occurs in chaetigers 6–8.

Posteriorly, neuropodial prechaetal lobe reducing in size, ventral ligule even more so. Neuropodial postchaetal lobes also decrease in size proportionately, becoming more conical.

Noto- and neurochaetae consist of both homogomph and sesquigomph spinigers throughout, no falcigers observed. Accurate numbers of chaetae and distribution of homogomph versus sesquigomph chaetae on anterior chaetigers difficult to identify due to density.

Table 1. Approximate chaetal counts of *Gymnonereis tenera* sp. n. (paratype, NMW.Z.2011.039.0098).

Chaetiger	Notochaetae	Neurochaetae
1	0	30
3	20	90
9	39	108
20	19	40
30	20	40
50	10	12
100	8	19

No dorsal flaps connecting chaetigers. Transverse, faintly defined ridges present from chaetiger 11–16.

Pygidium with anus terminal; 2 long cirri ventral to anus. Anal cirri of similar shape to dorsal cirri on body, 1.2 mm long.

Eggs found in 2 specimens, spherical, 120–130 µm diameter.

Variation. Most characters varied with number of chaetigers and continued to change as the number increased. Accessory dorsal cirri were not observed on animals with less than 95 chaetigers (unless regenerating) although they were absent in one specimen of 103 chaetigers (62 complete specimens examined; 27 with less than 95 chaetigers, 35 with 95 or more chaetigers). As chaetiger number increases, additional anterior dorsal cirri have accessory cirri, with animals of more than 160 chaetigers with accessory dorsal cirri as far as chaetigers 10–14. The variation in this character means that it should not be used as diagnostic for the species on its own but only in conjunction with other characters.

The faint transverse ridges connecting parapodia were mostly visible from chaetiger 11 to 15 or 16 but were occasionally observed as far back as chaetiger 20 on the largest specimens.

Determination of the start and end of the expanded cirrophores was difficult, particularly the former, as the transition was not as abrupt as described for some species. The region generally occurred from around chaetigers 11–18 and continued to chaetigers 22–51 over the range of body sizes observed.

Presence and number of the oral papillae did not vary with size although papillae were occasionally lost and a single specimen was identified with 4 papillae in Area V–VI. Relative length of tentacular cirri was also stable with the longest cirri always reaching to chaetiger 4 in all body sizes.

Although jaw teeth were absent in the majority of specimens, juveniles of less than 80 chaetigers (jaws of 26 specimens were examined including 12 juveniles of 33–80 chaetigers in size) were found to have 4–5 small teeth on each jaw with jaws in larger animals becoming more roughly crenated until the largest jaws appeared almost completely smooth.

Etymology. The specific name *tenera* is derived from the latin adjective *tener* meaning ‘soft, delicate’, referring to the very soft nature of the worm when alive and its fragility when handled.

Habitat. Found intertidally from mid to low shore in soft, fine, sand or mud sediments.

Remarks. With 3 papillae in Area V–VI of the oral ring and the absence of jaw teeth, *Gymnonereis tenera* sp. n. can be distinguished from all other *Gymnonereis* species except for *G. sibogae* and *G. phuketensis*. *Gymnonereis minyami* and *G. yurieli* both have jaw teeth and only 1 papilla in each of Areas V and VI. *Gymnonereis crosslandi* and *G. fauveli* both lack jaw teeth but *G. crosslandi* has only 1 papilla in each of Areas V and VI, accessory dorsal cirri in only chaetigers 1 and 2 (chaetiger 1 to 12 or further in *Gymnonereis tenera* sp. n.) and no enlarged dorsal cirrophores, whilst *G. fauveli* has 5 papillae in Area V–VI and accessory dorsal cirri from chaetiger 3 (as opposed to chaetiger 1 in the new species).

Gymnonereis tenera sp. n. is most similar to both *G. sibogae* and *G. phuketensis* and can only be distinguished from each of these through combinations of characters. Although Hutchings and Reid (1990) listed *G. sibogae* as having sesquigomph falcigers, Horst (1918), in his original description, actually stated that “the neuropodial fascicle does not contain true setae falcigerae, but instead of these some faintly heterogomph setigerous bristles, with a short, lanceolate terminal piece”, although his figures of the species (Horst 1924) did not illustrate this. Pettibone (1970) re-investigated and drew all of Horst’s specimens and in her detailed description of the first two chaetigerous segments stated that “a few lower neurosetae of some anterior setigers may have blades which end bluntly” and this was figured accordingly (Pettibone 1970, fig. 30c–e). No such short, blunt chaetae were observed on any specimens of *G. tenera* sp. n. A more consistent character is that of the length of the anterior, neuropodial prechaetal lobe. In *G. tenera* sp. n., this lobe is consistently longer than both the neuropodial acicular and postchaetal lobes and of a similar length to the ventral ligule. In *G. sibogae*, the neuropodial prechaetal lobe (termed the prechaetal ligule by Pettibone 1970) is as long as or shorter than the postchaetal lobe and shorter than the ventral ligule for at least the first nine chaetigers (Horst 1924, pl. XXX, fig. 1; Pettibone 1970, fig. 30c–d, fig. 31a,d,e,f, fig. 33b), thereafter becoming only slightly longer. Unfortunately, all of Horst’s specimens were incomplete with only 36–56 segments and the species does not appear to have been reported since, making further determination of differences between the two species difficult.

Apart from the character of presence or absence of jaw teeth, the new species is also very similar to *G. phuketensis*, although juveniles of the new species do have a small number of jaw teeth. Hutchings and Reid (1990) listed the character of jaw teeth as being present or absent for *G. phuketensis*, although the original description by Hylleberg and Nateewathana (1988) states only that they are present (adult specimens, no comments on the juvenile form) but that they can be weakly defined. Where jaw teeth are found in *G. tenera* sp. n., however, there are only up to 5 compared to 10 for *G. phuketensis*. Additionally, in *G. phuketensis* the dorsal cirrophores become “abruptly enlarged” from chaetiger 14 (Hylleberg and Nateewathana 1988) compared to a more gradual enlargement from chaetiger 12 for the new species and the second ventral cirrus is absent from around chaetiger 35 on *G. phuketensis* but present throughout on *G. tenera* sp. n.

Subfamily Nereidinae Blainville, 1818**Genus *Eunereis* Malmgren, 1865**

Eunereis Malmgren, 1865: 182–183

Type species. *Nereis longissima* Johnston, 1840

Diagnosis (after Bakken and Wilson 2005). Prostomium with entire anterior margin, one pair of antennae, one pair of biarticulated palps with conical palpostyles, four pairs of tentacular cirri with distinct cirrophores.

Two pairs of eyes. One apodous anterior segment, greater than length of chaetiger 1. Maxillary ring of pharynx without paragnaths. Oral ring, conical paragnaths: Area V, present or absent; VI, present or absent, smooth bars present or absent; VII–VIII, present or absent. Dorsal notopodial ligule present, similar in size or markedly reduced on posterior chaetigers. Prechaetal notopodial lobe present or absent; when present, restricted to a limited number of anterior chaetigers. Acicular process present or absent. Dorsal cirrus basally attached to dorsal notopodial ligule throughout all chaetigers, lacking basal cirrophore. Neuropodial postchaetal lobe absent or present. Notoaciculae absent from chaetigers 1 and 2. Notochaetae: homogomph spinigers present, homogomph falcigers present or absent. Neurochaetae, superior fascicle: homogomph spinigers and heterogomph falcigers present. Neurochaetae, inferior fascicle: heterogomph spinigers and heterogomph falcigers with long blades present.

***Eunereis patagonica* (McIntosh, 1885)**

Figure 3

Nereis patagonica McIntosh, 1885: 228–229, Pl. XXXV, figs 13–15, Pl. XVIIIA, figs 1–2. — Pratt 1898: 15.

Nereis (Eunereis) hardyi Monro, 1930: 109–111, fig. 39. — Monro 1936: 134–135.

Eunereis patagonica. — Hartman 1953: 29. — Hartman 1964: 97, Pl. XXX, figs 3–4. — Hartman 1967: 62–64, Pl. 15.

Material examined. Strait of Magellan, stn 313 (52°20'S, 067°39'W), sand, 100.6 m, 2 syntypes (NHMUK 1885.12.1.171) 20.01.1876; South America, off Uruguay, stn 1 (33°00'S, 051°10'W), blackish clay, 80 m, 2 specimens (SMNH 37888), 12.12.1901; south of West Falkland, Burdwood Bank, stn 59 (53°45'S, 061°10'W), gravel & stones, 137–150 m, 13 specimens (9–SMNH 37894; 4–SMNH 37902), 12.09.1902; off Falkland Islands, stn WS 86 (53°53'30"S, 060°34'30"W), 6 syntypes *Nereis (Eunereis) hardyi* (NHMUK 1930.10.8.841–844), 03.04.1927; Strait of Magellan, stn WS 834 (52°57'45"S, 068°08'15"W), 4 specimens *Nereis (Eunereis) hardyi* (NHMUK 1936.2.8.1463–1476), 02.02.1932.

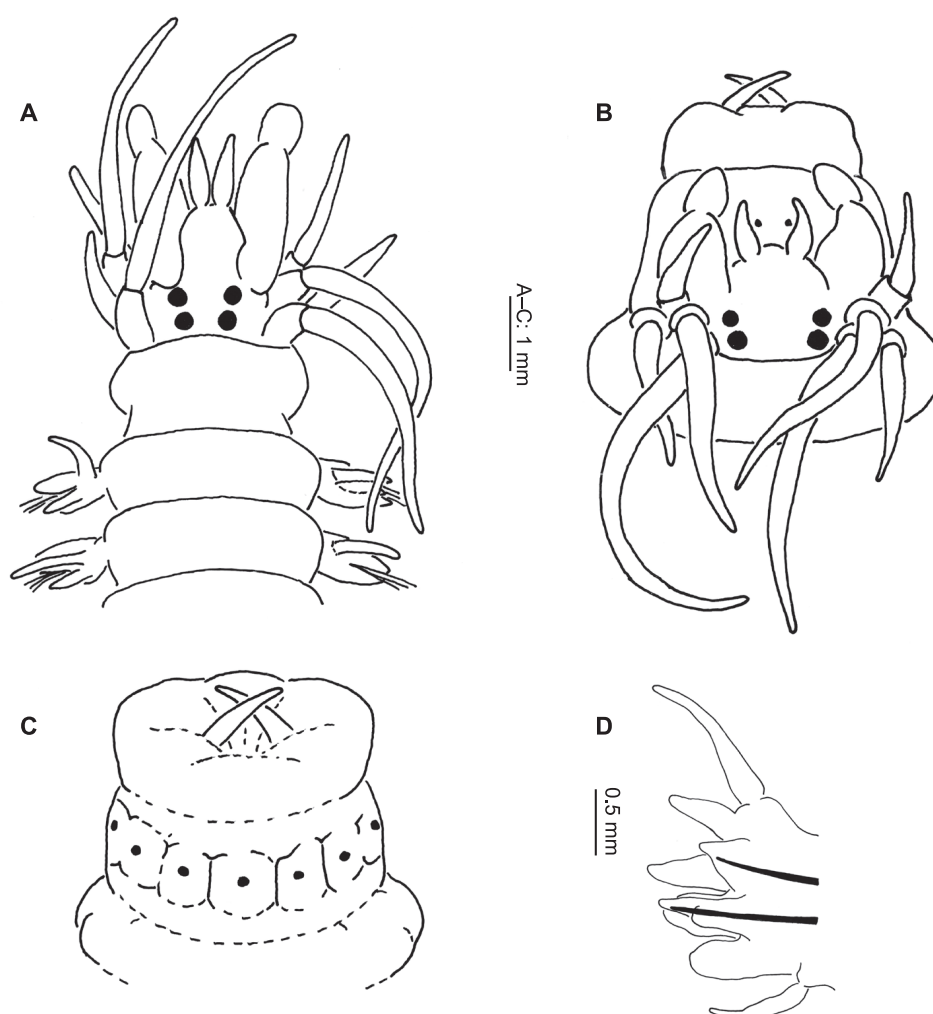


Figure 3. *Eunereis patagonica* (McIntosh, 1885) (after Monro, 1930, as *Nereis (Eunereis) hardyi*): **A** Anterior end, dorsal view **B** Prostomium and proboscis, dorsal view **C** Proboscis, ventral view **D** Parapodium.

Description. Length up to 130 mm, width to 5 mm (excluding parapodia) for up to 85 chaetigers. Eyes present (Fig. 3A–B). Tentacular cirri reaching to chaetiger 6–8 (postero-dorsal pair). Paragnaths absent from maxillary ring; arranged on oral ring as follows (Fig. 3B–C): Area V = 1–2; Area VI = 0; Areas VII–VIII = 7–8 in a row. Jaws dark, 5–10 teeth.

Dorsal cirrus longer than notopodia throughout (Fig. 3D), becoming more pronounced posteriorly. Anterior notopodia with dorsal and median ligules conical, median slightly more stout than dorsal. Small, notopodial prechaetal lobe present in anterior chaetigers.

Neuropodia with postchaetal lobe and ventral ligule equal-sized anteriorly; postchaetal lobe conical, reducing in size posteriorly, ventral ligule rounded in the anterior, conical posteriorly.

Notopodia with homogomph spinigers throughout, falcigers absent. Neuropodia with homogomph spinigers and heterogomph falcigers in superior fascicle, inferior fascicle with heterogomph spiniger and falcigers.

Species builds tough-walled tubes coated in sand grains and other coarse particles.

Remarks. The above description is based on McIntosh (1885), Monro (1930, 1936 as *N. hardyi*), and Hartman (1953, 1967). However, there is some discrepancy between the original descriptions that can now be clarified following examination of the specimens from those accounts. All three authors agree that paragnaths are absent in Areas I and II and that Area VII–VIII has a single row of 7–8. In Area III, paragnaths are absent on the specimens of both Monro (1930, 1936) and Hartman (1953, 1967), however there is a single conical paragnath present on McIntosh's specimen. Paragnaths are absent from Area IV on specimens of McIntosh and Monro as well as Hartman's (1953) Falkland Island specimens (SMNH 37894, 37902) but 3 conical paragnaths are present on her Uruguay specimens (SMNH 37888). The paragnaths described for Area V in Monro (1930, 1936) are present in identical form on Hartman's (1953) Falkland Island specimens, although she placed them in Area VI in her description, however her Uruguay specimens from the same survey have 3 conical paragnaths in the same position. A single paragnath is present in Area V of McIntosh's specimen and it is assumed that the second paragnath has been lost or is absent through aberration as McIntosh states in his description that the single paragnath is "nearly, but not quite median".

It is clear that Hartman's (1953) Uruguay specimens are a different, currently unidentified species but that her Falkland Island specimens are identical to those of Monro (1930, 1936). Hartman's 1967 description also agrees with Monro's and the modified description above reflects these specimens. The presence of the single paragnath in Area III of McIntosh's specimen requires further investigation as to whether this means that the species needs future re-assessment, as this would place the species in a different genus. Unfortunately, the specimen is in poor condition and a second, smaller specimen from the same location is even worse. However, a comparison of parapodia and what chaetae are available (the vast majority are broken on the McIntosh specimens) show them to be comparable. The paragnath arrangement above is therefore based on the specimens of Monro (1930, 1936) and Hartman (1953, 1967) that were actually collected from the Falkland Islands. The designation of McIntosh's specimen requires further investigation although as it only deviates from the others in the presence of that single paragnath in Area III it is possible it is aberrant.

Eunereis patagonica was first recorded from the Falkland Islands by Pratt (1898) from samples that were probably from intertidal or shallow water samples, however no actual habitat, depth or locality details were given. The only other records from

the Falkland Islands are those of Monro (as *Nereis hardyi*: 1930, 1936) and Hartman (1953, 1967) from offshore (106–150 m) samples, as well as an even deeper record at 1879–1886 m by Hartman (1967).

Outside of the region, the species was recorded by Hartman (1967) from 31 m (Cape Horn) to 300 m (South Shetland Islands) together with an additional record of a pelagic epitoke from the Pacific Antarctic Ridge at 3660 m considered to have been carried beyond its viable range.

The species is here believed unlikely to be found intertidally around the Falkland Islands but with potential to be found in the region's nearshore (< 30 m) waters; Pratt's 1898 record (if accurate), likely being from this region.

Habitat. Sand, shell, stones; 31–1886 m (?3660 m)

Distribution. Tierra del Fuego, Strait of Magellan, Cape Horn, Falkland Islands, South Shetland Islands, South Orkney Islands, ?Pacific Antarctic Ridge

Genus *Neanthes* Kinberg, 1865

Neanthes Kinberg, 1865: 171

Includes. *Nectoneanthes* Wilson, 1988: 5.

Type species. *Neanthes vaalii* Kinberg, 1865, by original designation

Diagnosis (after Bakken and Wilson 2005). Prostomium with entire anterior margin, one pair of antennae, one pair of biarticulated palps with conical palpostyles, four pairs of tentacular cirri with distinct cirrophores. Eyes present or absent. One apodous anterior segment, greater than length of chaetiger 1. Maxillary ring of pharynx, conical paragnaths: Areas I–IV, present or absent; IV, smooth bar-like paragnaths present or absent. Oral ring, conical paragnaths: Areas V and VI present as distinct groups or not separated; V–VIII, present or absent. Dorsal notopodial ligule present, similar in size on anterior and posterior chaetigers or markedly reduced on posterior chaetigers. Prechaetal notopodial lobe present or absent, smaller than dorsal notopodial ligule on anterior chaetigers, usually reduced or absent posteriorly, present throughout all chaetigers or restricted to a limited number of anterior chaetigers. Acicular process present or absent; present on anterior chaetigers, reducing in size posteriorly. Dorsal cirrus basally or mid-dorsally to subterminally attached to dorsal notopodial ligule on posterior chaetigers, lacking basal cirrophore. Neuropodial postchaetal lobe absent or present. Notoaciculae absent from chaetigers 1 and 2. Notochaetae: homogomph spinigers. Neurochaetae, superior fascicle: heterogomph spinigers present or absent, homogomph spinigers present, heterogomph falcigers on anterior chaetigers present, on posterior chaetigers present or absent. Neurochaetae, inferior fascicle: heterogomph spinigers present or absent, homogomph spinigers present or absent, heterogomph falcigers present.

***Neanthes kerguelensis* (McIntosh, 1885)**

Figures 4, 9C–D

Nereis kerguelensis McIntosh, 1885: 225–227, Pl. XXXV, figs 10–12, Pl. XVIA, figs 17–18. — Augener 1924: 330–333.

Neanthes kerguelensis. — Hartman 1954: 30. — Hartmann-Schröder 1962: 394–395. — Hartman 1967: 64. — Hutchings and Turvey 1982: 113. — Wilson 1984: 216–218. — Bakken and Wilson 2005: 528.

Material examined. East Falkland: Stanley foreshore, stn 1a (51°41.454'S, 057°51.870'W), under rocks in coarse sand, midshore, 3 specimens (NMW.Z.2011.039.0120), 15.11.2011; Stanley foreshore, stn 1b (51°41.459'S, 057°51.840'W), under rocks in coarse sand, midshore, 9 specimens (NMW.Z.2011.039.121), 15.1.2011; Stanley foreshore, stn 1c (51°41.459'S, 057°51.823'W), under rocks in coarse sand, low shore, 3 specimens (NMW.Z.2011.039.0122), 15.1.2011; The Canache, east of Stanley, stn 2c (51°41.716'S, 057°47.107'W), under rocks in gravel & coarse sand, mid-low shore, 6 specimens (NMW.Z.2011.039.0123), 16.1.2011; Hookers Point, stn 4 (51°41.994'S, 057°46.747'W), in & under pink encrusting algae, low shore, 3 specimens (NMW.Z.2011.039.0124), 15.1.2011; Hookers Point, stn 6b, (51°41.994'S, 057°46.747'W), algal holdfast scraping, low shore, 1 specimen (NMW.Z.2011.039.0125), 21.11.2011; Sea Lion Island: East Loafers Bay, stn 20a (52°26.306'S, 059°06.229'W), in & under pink encrusting algae, mid-low shore, 4 specimens (NMW.Z.2011.039.0126), 28.11.2011; East Falkland: west Stanley, stn 21 (51°41.402'S, 057°52.580'W), under small stones in coarse sand & gravel, 6 specimens (NMW.Z.2011.039.0127–0128), 01.12.2011; Egg Harbour, Shag Rookery Point, stn 27 (51°49.345'S, 059°26.719'W), under rocks in soft silty sand, 6 m, 2 specimens (NMW.Z.2011.039.0129), 03.12.2011; Kelp Harbour, stn 29a (51°47.715'S, 059°18.400'W), coralline coarse sand, mid-low shore, 15 specimens (NMW.Z.2011.039.0136), 04.12.2011; Stanley marina, stn 32 (51°41.600'S, 057°48.073'W), *Macrocystis* holdfast, 30 cm, 2 specimens (NMW.Z.2011.039.0132), 05.12.2011; Sand Bay, Port Harriet, stn 34f (51°44.130'S, 058°00.550'W), under rocks within mussel bed, midshore, 7 specimens (NMW.Z.2011.039.0130), 08.12.2011; Teal Creek, east of Darwin, stn 35d (51°49.248'S, 058°55.561'W), under rocks in sand, midshore, 4 specimens (NMW.Z.2011.039.0131), 09.12.2011; Cape Bougainville, stn 38b (51°18.727'S, 058°27.607'W), under rocks in gravel in rock pool, mid-low shore, 1 specimen (NMW.Z.2012.082.0019), 13.01.2013; North Arm, stn 48a (52°07.768'S, 059°22.131'W), mussel bed over silty coarse sand, midshore, 13 specimens (NMW.Z.2013.082.0020), 22.01.2013; West Falkland: Moonlight Bay, Port Stephens, stn 51c (52°06.232'S, 060°50.368'W), in crevices, midshore, 10 specimens (NMW.Z.2012.082.0021), 26.01.2013; The Creek, Hill Cove, stn 56d (51°30.061'S, 060°07.618'W), under algae-covered rocks in fine sand, midshore, 4 specimens (NMW.Z.2012.082.0022), 31.01.2013; Shallow Bay, stn 57e (51°30.032'S, 060°07.726'W), in crevices & under stones, low shore, 3 specimens (NMW.Z.2012.082.0023), 01.02.2013.

Description. Ninety-six entire specimens examined: length 5.9–61.3 mm, width 0.7–3.3 mm (excluding parapodia, measured at 8th chaetiger) for 29–70 chaetigers.

Colour pale cream in alcohol, some with dark brown, uniform shading remaining over anterior chaetigers.

Body depressed dorso-ventrally, of mostly uniform width, tapering in last few chaetigers. Prostomium longer than broad (Fig. 4A), antennae and palps about equal in length, with antennae 1/4 width of palpophores. Palpostyles very short, 1/5 length of palpophores. Four pairs tentacular cirri, postero-dorsal pair extending 2–7 chaetigers, usually 2–3. Two pairs small, equal-sized, black eyes, anterior pair more laterally placed.

Pharynx with conical paragnaths (Fig. 9C, D), variable in size, sometimes faint, not easily lost. Paragnaths arranged as follows: I = 1 (absent or too small to see in specimens of less than 45 chaetigers); II = 1–8; III = 1–9; IV = 6–17; V = 0; VI = 1 (2 on one specimen only); VII–VIII = 3–8. Jaws dark brown to black, 7–10 teeth.

Notopodia with dorsal and median ligule throughout. Of almost equal size, globular anteriorly (Fig. 4B), dorsal ligule becoming conical, median ligule becoming digitiform, in median chaetigers. Notopodial prechaetal lobe present from chaetigers 5–6 (Fig. 4B), increasingly fused to median ligule, absent posteriorly, difficult to determine more precisely due to the very gradual fusion, generally obvious for at least 10 chaetigers.

Dorsal cirrus 1–1.5 times length of dorsal ligule anteriorly (Fig. 4B), increasing to 2–2.5 times length posteriorly (Fig. 4C).

Neuropodia with postchaetal lobe and ventral ligule throughout; postchaetal lobe rounded anteriorly, reduced in size and digitiform posteriorly, ventral ligule globular anteriorly, conical posteriorly (Fig. 4B, C). Ventral cirrus approximately 3/4 length of ventral ligule, becoming equal in length posteriorly (Fig. 4B, C).

Parapodia biramous from chaetiger 3, sub-biramous on chaetigers 1–2. Notochaetae homogomph spinigers only. Neurochaetae with homogomph spinigers and heterogomph falcigers (Fig. 4D, E) in both superior and inferior (from 3) fascicles throughout. No heterogomph spinigers found.

Pygidium terminal; 2 long, tapering anal cirri inserted ventrally.

Remarks. In a detailed study of Australian and sub-Antarctic specimens of *N. kerguelensis*, Wilson (1984) described a wide variation in the numbers of paragnaths in Areas II, III and IV. This, combined with the apparent widespread occurrence across both hemispheres and from intertidal to 5000 m depths, would suggest that records of this species may, in fact, represent a species complex. Greater investigation in each area is required to properly resolve this.

The variation in paragnath numbers exhibited by the Falkland Islands specimens is within the boundaries of that described by Wilson (1984), although it falls consistently at the lower end of those ranges. In addition, the majority of specimens had tentacular cirri that extended only to chaetigers 2–4 (Wilson 1984: 4–8 chaetigers) although some did extend up to chaetiger 7, and the neuropodial postchaetal lobe was present throughout the body as opposed to only the anterior 20–30 chaetigers (Wilson 1984).

There are currently no published genetic sequences for *N. kerguelensis*. However, a comparison of some of these different populations using molecular techniques may help resolve these discrepancies.

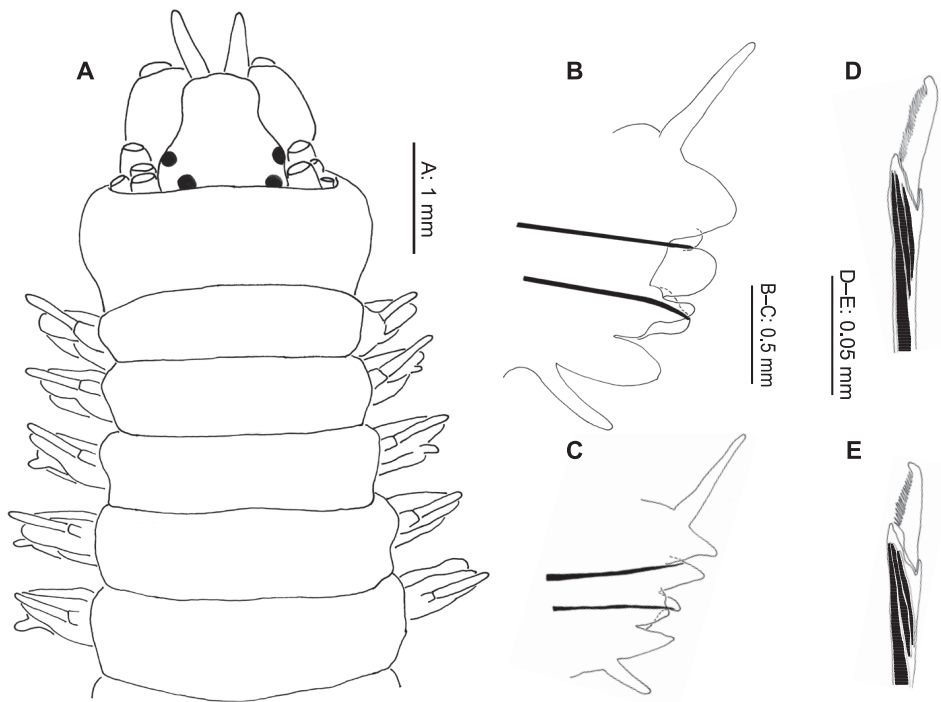


Figure 4. *Neanthes kerguelensis* (McIntosh, 1885) (NMW.Z.2011.039.0127): **A** anterior end (tentacular cirri removed), dorsal view **B** right parapodium, chaetiger 10, posterior view **C** right parapodium, chaetiger 47, posterior view **D** neuropodial heterogomph falciger, chaetiger 10 **E** neuropodial heterogomph falciger, chaetiger 47.

Habitat. Wilson (1984) describes the habitat as “associated with fouling communities, intertidal in rocks and sand on sheltered and exposed coasts, soft bottom benthos to 115 m deep”. Previous records from the Falkland Islands exist from intertidal to 197 m depth and from this survey from intertidal to 20 m depth in almost every habitat sampled (including algal holdfasts, epifaunal turf, coarse sand, gravel and under rocks), except for mud and fine-medium clean sands.

Distribution. Recorded widely across the southern hemisphere including Australia, New Zealand, Tasmania, Fiji, Taiwan, Antarctic Peninsula, sub-Antarctic Islands (incl. Kerguelen, Macquarie, South Shetlands, South Orkneys), Chile and the Falkland Islands. Previous records from the Falkland Islands exist from Pratt (1898), Fauvel (1916), Ramsay (1914), Monro (1930) and Hartman (1953) and the species was recorded from almost every location sampled during this survey.

Neanthes kerguelensis is also recorded from the Northern hemisphere from the Mediterranean and Azores (von Marenzeller 1902) and the UK (Comely 1973). The latter record, however, is discounted as the author describes his specimen as having 6–7 paragnaths in Area VI which would not identify it as this species.

Genus *Nereis* Linnaeus, 1758*Nereis* Linnaeus, 1758: 654.**Type species.** *Nereis pelagica* Linnaeus, 1758 (by original designation)

Diagnosis (after Bakken and Wilson 2005). Prostomium with entire anterior margin, one pair of antennae, one pair of biarticulated palps with conical palpostyles, four pairs of tentacular cirri with distinct cirrophores. Eyes present or absent. One apodous anterior segment, greater than length of chaetiger 1. Maxillary ring of pharynx, conical paragnaths: Areas I–III, present or absent; IV, present, smooth bar-like paragnaths present or absent. Oral ring: conical paragnaths present or absent. Dorsal notopodial ligule similar in size in anterior and posterior chaetigers or markedly reduced on posterior chaetigers. Prechaetal notopodial lobe present or absent, smaller than dorsal notopodial ligule on anterior chaetigers, usually reduced or absent posteriorly. Dorsal cirrus basally attached to dorsal notopodial ligule throughout all chaetigers, lacking basal cirrophore. Neuropodial postchaetal lobe absent. Notoaciculae absent from chaetigers 1 and 2. Notochaetae: homogomph spinigers, homogomph falcigers present. Neurochaetae, superior fascicle: homogomph spinigers present, heterogomph falcigers on anterior chaetigers present or absent, on posterior chaetigers present. Neurochaetae, inferior fascicle: heterogomph spinigers present or absent, heterogomph falcigers present or absent.

***Nereis eugeniae* (Kinberg, 1865)**

Figure 5

Nereis eugeniae Kinberg, 1865: 178.

Nereis eugeniae. — Ehlers 1897: 67–70, Pl. IV, figs 94–105. — Ehlers 1901: 105, Pl. XII, figs 18–22. — Ramsay 1914: 43. — Monro 1930: 104. — Hartman 1964: 100–101, Pl. XXX, figs 9–10. — Hartman 1967: 65.

Description. Length up to 170 mm, width up to 3 mm including parapodia for up to 125 chaetigers. Eyes absent or present. Paragnaths arranged as follows (Fig. 5A, B): Area I = 0; Area II = small group (up to 11); Area III = absent or sparse, irregular row (2–6); Area IV = absent or group (0–18); Area V = 0–1; Area VI = small group (3–6); Areas VII–VIII = sparse, irregular row (0–11). Jaws dark, 5–7 teeth.

Dorsal cirrus longer than notopodia throughout, becoming more pronounced posteriorly. Anterior notopodia (Fig. 5C) with dorsal and median ligules equal in size, dorsal ligule reducing in size posteriorly. Small notopodial prechaetal lobe present in anterior chaetigers.

Neuropodia with postchaetal lobe and ventral ligule conical; postchaetal lobe shorter than notopodial ligules and ventral ligule in anterior chaetigers, becoming more equal in size posteriorly (Fig. 5D).

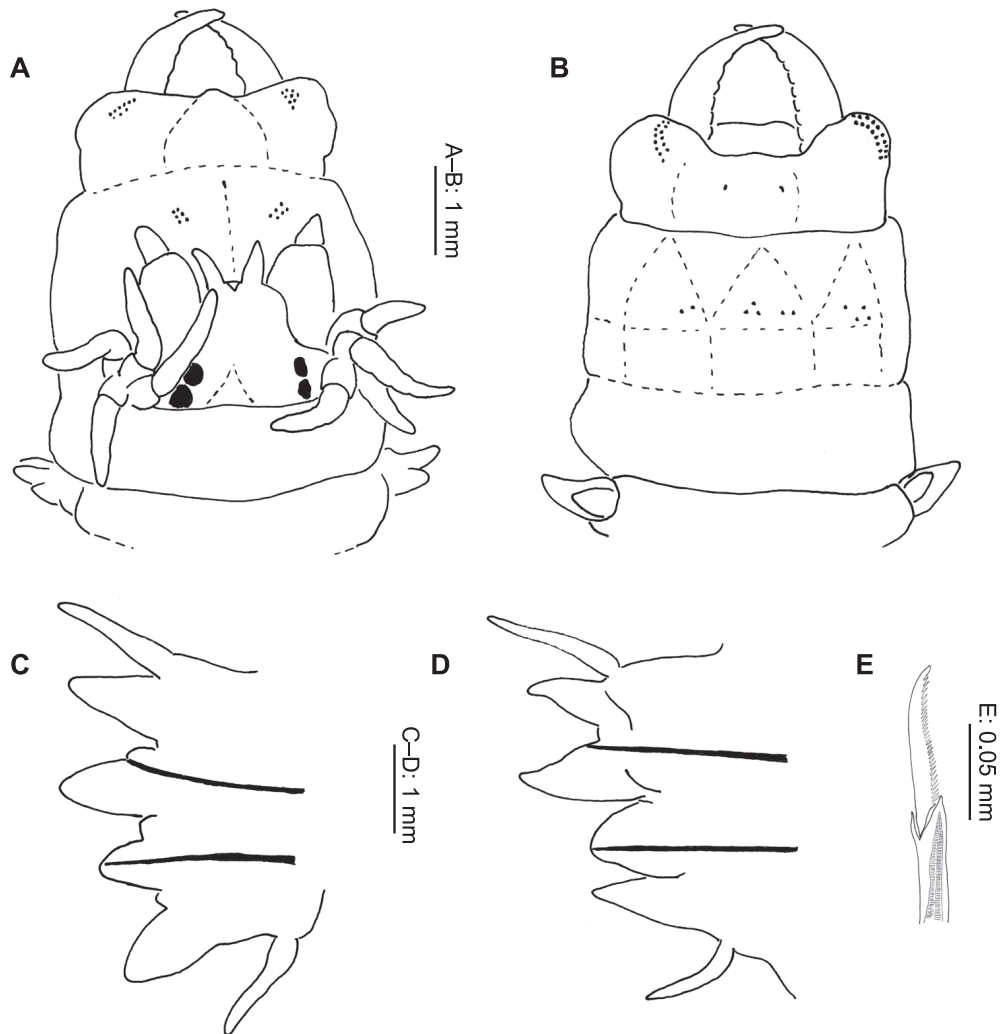


Figure 5. *Nereis eugeniae* Kinberg, 1865 (after Ehlers 1897): **A** anterior end, dorsal view **B** chaetiger 12 **C** chaetiger 37 **D** neuropodial heterogomph spiniger, posterior chaetiger **E** neuropodial heterogomph falciger, posterior chaetiger.

Anterior notopodia with homogomph spinigers only, 2–3 homogomph falcigers present from median chaetigers on. Neuropodia with homogomph spinigers and heterogomph falcigers in superior fascicle, inferior fascicle with heterogomph spinigers and falcigers (Fig. 5E).

Remarks. The above description is an amalgamation of the information provided by Ehlers (1897), Monro (1930) and Hartman (1964, 1967), although of these, only Monro published on specimens from the Falkland Islands. The type locality for the species is the Strait of Magellan, but Kinberg (1865) gave little detail about the animal

itself. The species was later comprehensively re-described and drawn by Ehlers (1897). Descriptions by different authors are quite variable, particularly regarding the paragnaths arrangements. Ramsay (1914) gave no details about his specimens except to say that they “agreed in all respects” with Ehlers’ description whereas Monro (1930) noted that, in contrast to Ehlers’ description, the paragnaths of Areas VII–VIII “form a single very sparse irregular row and in a number of the larger examples they appear to be altogether absent”

Nereis eugeniae was not collected by this survey, however it has been recorded from several offshore locations around the islands from 1–115 m (Ramsay 1914; Monro 1930) and Monro (1930) described the species as being “common off the Falkland Islands”. There are no intertidal records for the area, however *N. eugeniae* has been recorded intertidally from Chile (Ehlers 1901; Hartman 1967). Although not recorded here, the species is known to be present in shallow water around the islands and could potentially be found intertidally also.

Habitat. Sand, shell, stones, cobbles; intertidal–156 m.

Distribution. Strait of Magellan, Chile, Falkland Islands, Kerguelen Islands, Patagonia.

Genus *Perinereis* Kinberg, 1865

Perinereis Kinberg, 1865: 175–176. — Hutchings et al. 1991: 245.

Includes. *Arete* Kinberg, 1865; *Gnatholycastis* Ehlers, 1920.

Type species. *Perinereis novaehollandiae* Kinberg, 1865; by subsequent designation (Hartman 1948)

Diagnosis (after Bakken and Wilson 2005, emended). Prostomium with entire anterior margin, one pair of antennae, one pair of biarticulated palps with conical palpostyles, four pairs of tentacular cirri with distinct cirrophores. Two pairs of eyes. One apodous anterior segment, greater than length of chaetiger 1. Maxillary ring of pharynx, conical paragnaths: Area I, present or absent; II, present or absent; III, present; IV, present or absent, smooth bar-like paragnaths present or absent. Oral ring, conical paragnaths: Area V, present or absent; VI, present or absent, *smooth or shield-shaped* bars present; VII–VIII, present. Dorsal notopodial ligule similar in size in anterior and posterior chaetigers, or markedly elongate on posterior chaetigers. Prechaetal notopodial lobe present or absent, smaller than dorsal notopodial ligule on anterior chaetigers, usually reduced or absent posteriorly. Dorsal cirrus basally or mid-dorsally to subterminally attached to dorsal notopodial ligule on posterior chaetigers, lacking basal cirrophore. Neuropodial postchaetal lobe absent or present. Notoaciculae absent from chaetigers 1 and 2. Notochaetae: homogomph spinigers. Neurochaetae, superior fascicle: homogomph spinigers and heterogomph falcigers present. Neurochaetae, inferior fascicle: heterogomph spinigers present or absent, heterogomph falcigers present.

***Perinereis atlantica* (McIntosh, 1885), comb. n.**

Figure 6

Nereis atlantica McIntosh, 1885: 219–221, Pl. XXXV, figs 1–3, Pl. XVIa, figs 10–11. —

Pratt 1898: 16.

? *Nereis atlantica*. — Hartman 1964: 99, Pl. XXX, figs 7–8.**Material examined.** St Vincent, Cape Verde Islands (NHMUK.1885.12.1.161), holotype, July 1873.**Description.** Examination of the holotype (Fig. 6A–C), shows the description and illustrations by McIntosh to be quite accurate. The only refinements are as follows:

Body dorso-ventrally depressed, mostly of uniform width, gradually tapering in last 20–30 chaetigers to pygidium.

Paragnaths arranged as follows, all conical except for Area VI (Fig. 6B–C): Area I = 1 large, Area II = 6–8, Area III = 8, Area IV = 15–16 arranged in 3–4 rows, Area V = 1 small, Area VI = 1 shield-shaped bar with rounded apex, Area VII–VIII = 3 rows with 6 (distal row), 9 (middle row) & 4 (proximal row) evenly-spaced cones, middle and proximal cones more flattened and blunt than those of the distal row. Jaws robust, dark brown with 4 teeth (Fig. 6B).

Dorsal ligule expanded posteriorly to a greater extent than figured by McIntosh but not as much as *P. falklandica*.

Notochaetae all homogomph spinigers, neurochaetae homogomph and heterogomph spinigers and heterogomph falcigers (from observations of a limited number of chaetae, most broken so distribution between inferior and superior fascicles unknown). Falciger tips become shorter posteriorly but otherwise do not change in form along the body.

Pygidium terminal; 3 long, thin anal cirri of equivalent length to last 11 chaetigers (1 cirrus apparently lost as McIntosh's original description states 4 anal cirri, 2 each side of anus). Pygidium and last 3 chaetigers with appearance of regeneration.

Remarks. This species was described from a single specimen collected at Cape Verde Islands in the southeast Atlantic. McIntosh (1885) noted that the species appeared most closely related to *Perinereis*, however, the large, bar-shaped paragnaths characteristic of that genus were present in Area V not VI, Area VI being empty. He related the species most closely to *Nereis floridana* Ehlers, 1868, now *P. floridana* (Ehlers, 1868) and would most likely have also placed *N. atlantica* into *Perinereis* if *P. floridana* had already been placed there. The lack of notopodial falcigers would also now place it outside of *Nereis*. It is believed that the specimen is aberrant, with the large bars of Area VI here situated much closer together than would normally be expected and appearing to be in Area V instead (the aberration appears to be more than just an artifact of contraction). The additional cone behind one of the bars could be skewed out of position from Area V or may be an aberrant additional cone in Area VI (it is here assumed to be out of position from Area V due to an

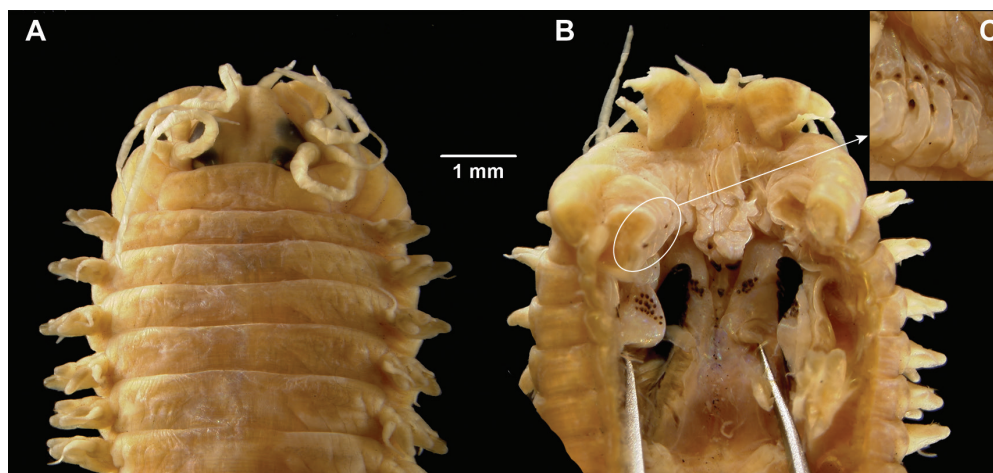


Figure 6. *Perinereis atlantica* (McIntosh, 1885) (NHMUK.1885.12.1.161): **A** anterior end, dorsal view **B** anterior end, ventral view **C** enlarged view of partial Area VII–VIII of proboscis.

aberration). An additional sign of possible aberration is that of the 4 (currently 3) anal cirri on a regenerating pygidium. More material will be required from the type locality to determine the true form and validity of the species. Until then, *Nereis atlantica* is transferred to *Perinereis* based on the large, bar-shaped paragnaths and the lack of notopodial falcigers.

Since its description, the only other record of the species has been by Pratt (1898) from Hill Cove on West Falkland (southwest Atlantic) although Hartman (1964) cast doubt on the validity of this record due to the distance from its original locality. Unfortunately, both McIntosh and Pratt gave only general locality details for their specimens and no details of habitat or depth. However, as Pratt's specimens generally came from shore or shallow water samples it is assumed that her *N. atlantica* were either intertidal or nearshore. Attempts to locate the specimens at Manchester (where she worked), Cambridge (where the other specimens she published on were loaned from) and the Natural History Museum, London have proved fruitless. The record from the Falkland Islands is therefore also considered doubtful in this paper. It is possible that, with *Perinereis falklandica* undescribed at that time and, as a student working on Bryozoa and not Annelida, Pratt mistakenly identified *P. falklandica* as *N. atlantica*. Unfortunately, without the specimens no confirmation of this is possible. Certainly, aside from Pratt's record, no other specimens like *P. atlantica* have ever been reported from the Falkland Islands.

With the shield-shaped bars now re-described into Area VI, the species would fall into 'Group 1A' of Hutchings et al. (1991) along with *P. floridana*: *Perinereis* species with 1 bar in Area VI and dorsal notopodial lobe not greatly expanded.

Habitat. Unknown.

Distribution. Cape Verde Islands, ?Falkland Islands.

***Perinereis falklandica* (Ramsay, 1914)**

Figure 7, 9E–F

Nereis (*Perinereis*) *falklandica* Ramsay, 1914: 44–46, pl. 3, figs 3–10.*Perinereis falklandica*. — Fauvel 1941: 280–281. — Hartman 1953: 29. — Day, 1954: 18. — Wesenberg-Lund 1962: 80–83, figs 30–31. — Hartmann-Schröder 1962: 410–411. — Hartmann-Schröder 1965: 298–299. — Rozbaczylo and Castilla 1973: 218–220, fig 2. — Rozbaczylo and Bolados 1980: 214–216. — Sampertegui et al. 2013: 30, fig. 1.

Material examined. East Falkland: The Canache, east of Stanley, stn 2c (51°41.716'S, 057°47.107'W), under rocks in gravel & coarse sand, mid-low shore, 9 specimens (NMW.Z.2011.039.0108–0109), 16.1.2011; Hookers Point, stn 6a, (51°41.994'S, 057°46.747'W), under pink encrusting algae, low shore, 3 specimens (NMW.Z.2011.039.0110), 21.11.2011; Hookers Point, stn 6c, (51°41.994'S, 057°46.747'W), under pink encrusting algae, low shore, 3 specimens (NMW.Z.2011.039.0111), 21.11.2011; Hookers Point, stn 6d, (51°41.994'S, 057°46.747'W), in silty gravel washings from rock pool, low shore, 1 specimen (NMW.Z.2011.039.0112), 21.11.2011; Egg Harbour, stn 25 (51°50.353'S, 059°27.351'W), rocks & mussel bed in silty coarse sand, mid-low tide, 12 specimens (NMW.Z.2011.039.0114), 03.12.2011; Sea Lion Island: East Loafers Bay, stn 20a (52°26.306'S, 059°06.229'W), in & under pink encrusting algae, mid-low shore, 1 specimen (NMW.Z.2011.039.0113), 28.11.2011; Saunders Island: The Neck, stn 42d (51°18.485'S, 060°14.504'W), under stones on rock ledges, mid-shore, 3 specimens (NMW.Z.2012.082.0011), 17.01.2013; West Falkland: Shallow Bay, stn 57b (51°30.032'S, 060°07.726'W), in crevices & under stones, high-mid shore, 2 specimens (NMW.Z.2012.082.0012), 01.02.2013; Shallow Bay, stn 57c (51°30.032'S, 060°07.726'W), in crevices & under stones, low shore, 5 specimens (NMW.Z.2012.082.0013), 01.02.2013.

Description. Thirty-nine entire specimens examined; length 19.5–73.6 mm, width (excluding parapodia) 1.5–4.3 mm for 65–89 chaetigers.

Colour in alcohol, dark brown body with pale parapodia, colour becoming paler more posteriorly, variably according to specimen. Head very dark green/brown with pale median line (Fig. 9E). Live colour green-brown with pale markings as described in alcohol.

Body dorso-ventrally depressed, uniform width for most of length, tapering slightly over last few chaetigers. Head with prostomium longer than broad (Fig. 7A), antennae short, stout, 2/3 length of broad palps. Four pairs short, tentacular cirri, pale with dark cirrophores, reaching to chaetiger 2–4. Two pairs small, black eyes, equal size, anterior pair more laterally placed (Fig. 7A). Eyes difficult to discern once preserved due to dark prostomial colour, particularly anterior pair.

Proboscis with conical (except for Area VI) paragnaths (Fig. 9E, F), variable in size and number, arranged as follows: Area I = 1 large, central surrounded by triangle of 32–150 small, faint, blunter cones; II = broad triangle of large and small cones, 9–28 each

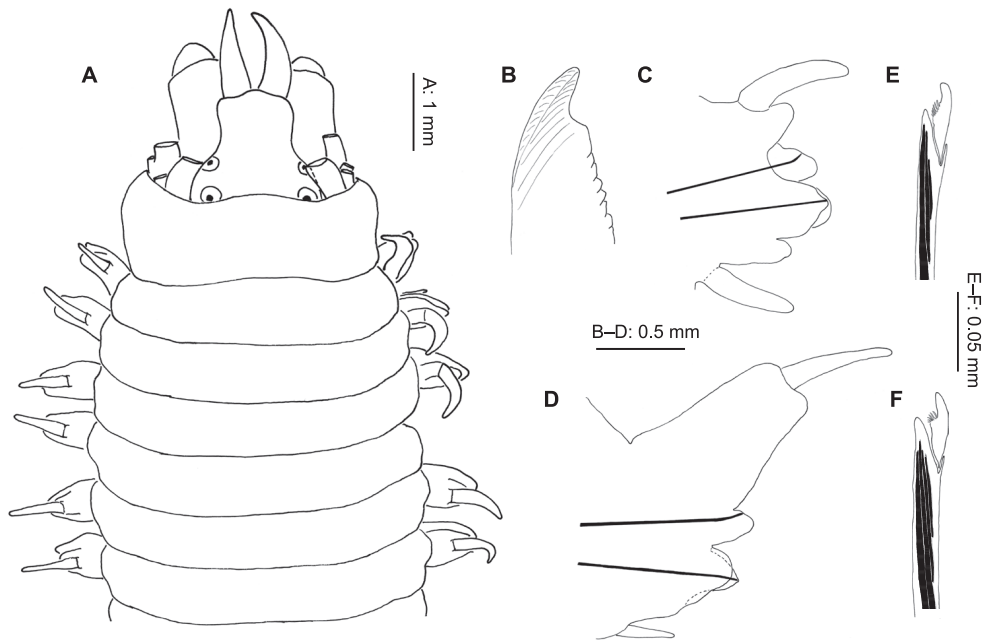


Figure 7. *Perinereis falklandica* Ramsay, 1914 (NMW.Z.2011.039.0108): **A** anterior end (tentacular cirri & right chaetiger 4 removed), dorsal view **B** jaw **C** right parapodium, chaetiger 4, posterior view **D** right parapodium, chaetiger 71, posterior view **E** neuropodial heterogomph falciger, chaetiger 4 **F** neuropodial heterogomph falciger, chaetiger 71.

side; III = oval patch of 11–20 medium-sized cones; IV = curved lines of 23–40 small–large cones; V = 1 large, blunt cone (1 aberrant specimen with 1 large & over 20 small cones); VI = 1 large, shield-shaped bar with pointed apex; VII–VIII = 2–3 single, large cones laterally, almost reaching Area VI, becoming a broad swath ventrally of 110–300 large and small blunt cones. Jaws dark black/brown with 5–10 teeth and large distal fang (Fig. 7B).

Anterior notopodia with dorsal and median ligules rounded anteriorly (Fig. 7C), becoming conical in median chaetigers; dorsal ligule swollen and elongated from around chaetiger 50 (Fig. 7D).

Neuropodia with conical postchaetal lobe and ventral ligule anteriorly, ventral ligule smaller, almost absent posteriorly.

Notochaetae homogomph spinigers throughout, figured specimen with 13 on chaetiger 4, reducing posteriorly to 6 on chaetiger 71 (of 89). Neurochaetae with homogomph spinigers in superior fascicle only (chaetiger 4: 5, chaetiger 71: 6), heterogomph falcigers present in both superior (chaetiger 4: 5; chaetiger 71: 3) and inferior (chaetiger 4: 15, chaetiger 71: 8) fascicles throughout, little change in form along body (Fig. 7E, F). Inferior fascicle with falcigers arranged in a C-shape on anterior chaetigers, thereafter in a transverse line.

Pygidium terminal; two short, anal cirri inserted ventrally.

Habitat. In this study, all specimens were from intertidal, mid-low shore locations, in hard substrates such as coarse sand/gravel, under rocks, in crevices and under pink encrusting algae.

Of the handful of other records in the literature, the species is mostly found intertidally in hard, often exposed habitats. Ramsay (1914) collected his specimens from 15 fathoms (27.4 m), the deepest record of this species.

Distribution. Falkland Islands, Magellan region (Orange Bay), Tristan da Cunha, Chile

Remarks. *Perinereis falklandica* has not been reported very widely in the literature since Ramsay described it from the Falkland Islands in 1914, although it was found to be quite common in coarse, intertidal habitats during this survey. Only one other record exists for the locality, being that of Hartman (1953), from a single intertidal sample at Port Louis. This is undoubtedly due to the fact that, other than Ramsay's original record, the species has rarely been identified from sublittoral samples and little intertidal work has been undertaken in the Falkland Islands. Outside of the Falkland Islands, with the exception of a single record from Tristan da Cunha (Day, 1954), it is mostly known from the coast of Chile (Fauvel 1941 (Magellan Strait); Wesenberg-Lund 1962; Hartmann-Schröder 1962, 1965; Rozbaczylo and Castilla 1973; Rozbaczylo and Bolados 1980; Sampertegui et al. 2013).

The validity of the species has not been questioned and it is easily distinguishable from other species. Type material was therefore not examined.

Descriptions of the specimens from the different localities are mostly uniform with the only variation being in the number of paragnaths found in Area V of the proboscis. Most authors have reported a single, large cone in this region with the exception of Day (1954; 1–3 cones), Rozbaczylo and Castilla (1973; 1–5 cones) and Sampertegui et al. (2013; 1–3 cones). All of the specimens in the current study exhibited only a single cone with the exception of one aberrant specimen with 1 large and 27 small cones. The latter specimen agrees with the usual description of *P. falklandica* in all other respects and is considered aberrant. The number of paragnaths in Areas I–IV and VII–VIII are highly variable and the range exhibited by the specimens in the current study fall within the larger range reported by Sampertegui et al. (2013).

Hutchings et al. (1991) placed *P. falklandica* into their 'Group 1B': *Perinereis* species with 1 bar in Area VI and dorsal notopodial lobe greatly expanded on posterior chaetigers.

Genus *Platynereis* Kinberg, 1865

Includes. *Iphinereis* Malmgren, 1865; *Pisenoë* Kinberg, 1865; *Leontis* Malmgren, 1867; *Nectonereis* Verrill, 1873; *Uncinereis* Chamberlin, 1919.

Type species. *Platynereis magalhaensis* Kinberg, 1865, by subsequent designation (Hartman 1948)

Diagnosis (after Read 2007, emended). Proboscis with chitinous paragnaths in form of parallel, *tight* rows of minute *rods* usually present on all areas except I, II and V. Pros-

tomium with 2 antennae, biarticulate palps and 2 pairs of eyes; 4 pairs of tentacular cirri. Peristomial segment apodous and first 2 parapodia sub-biramous. Chaetae include spinigers and falcigers. Homogomph notopodial falcigers usually present, in least in juveniles.

Remarks. The above description is emended with respect to the paragnath terminology introduced by Bakken et al. (2009). However, it should be noted that Bakken et al. (2009) only confirmed the form of paragnaths as tight rows of rods, as opposed to the previously described pectinate bars, for 3 species of *Platynereis* that did not include *P. magalhaensis*. This is now, however, confirmed for *P. magalhaensis* below.

***Platynereis magalhaensis* Kinberg, 1865**

Figures 8, 9G–I

Kinberg, 1865: 177. — 1910: 53, Pl. XX, fig. 6. — Pratt 1901: 2. — Fauvel 1916: 434–436, Pl. VIII, figs 21–22. — Monro 1930: 106–107, fig. 37. — Hartman 1948: 60–61.

Platynereis patagonica Kinberg, 1865: 177.

Platynereis antarctica Kinberg, 1865: 177.

Pisenoë maculata Kinberg, 1865: 176.

Nicon loxechini Kinberg, 1865: 178–179.

Nereis antarctica Verrill, 1876.

Nereis eatoni McIntosh, 1876: 320.

Nereis (Platynereis) eatoni McIntosh, 1885: 223–224, Pl. XXXV, figs 5–6.

Nereis magalhaensis. — Ehlers 1897: 63–65, Pl. V, figs 106–107.

Material examined. East Falkland: Stanley foreshore, stn 1c (51°41.459'S, 057°51.823'W), under rocks in coarse sand, low shore, 1 specimen (NMW.Z.2011.039.0145), 15.1.2011; The Canache, east of Stanley, stn 2e (51°41.731'S, 057°47.001'W), medium sand, low shore, 4 specimens (NMW.Z.2011.039.0146), 16.1.2011; Cochon Island: stn 10 (51°36.287'S, 057°47.684'W), under rocks, 9.5 m, 14 specimens (NMW.Z.2011.039.0147–0149), 24.11.2011; stn 11 (51°36.377'S, 057°48.9'W), under rocks, 9.6 m, 10 specimens (NMW.Z.2011.039.0150), 24.11.2011; stn 13 (51°36.322'S, 057°47.132'W) epi-faunal turf scraping, 13.6 m, 3 specimens (NMW.Z.2011.039.0141), 25.11.2011; stn 15a (51°36.449'S, 057°47.150'W), under rocks, 18.0 m, 1 specimen (NMW.Z.2011.039.0151), 26.11.2011; stn 16b (51°36.366'S, 057°47.082'W), epi-faunal turf scraping, 12.5 m, 1 specimen (NMW.Z.2011.039.0142), 26.11.2011; Kidney Island: stn 18b (51°37.517'S, 057°45.301'W), fine-medium sand, 4.6 m, 2 specimens (NMW.Z.2011.039.0152), 27.11.2011; East Falkland: west Stanley, stn 21 (51°41.402'S, 057°52.580'W), under small stones in coarse sand & gravel, 2 specimens (NMW.Z.2011.039.0153), 01.12.2011; Egg Harbour, stn 22 (51°47.471'S, 059°24.360'W), under rocks, 13.9 m, 4 specimens (NMW.Z.2011.039.0157), 02.12.2011; Egg Harbour, stn 23 (51°49.477'S, 059°23.926'W), under rocks,

11.6 m, 5 specimens (NMW.Z.2011.039.0143), 03.12.2011; Egg Harbour, Shag Rookery Point, stn 27 (51°49.345'S, 059°26.719'W), under rocks, 6 m, 1 specimen (NMW.Z.2011.039.0154), 03.12.2011; Kelp Harbour, stn 30 (51°47.021'S, 059°19.848'W), under rocks, 9.3 m, 4 specimens (NMW.Z.2011.039.0144), 04.12.2011; Sand Bay, Port Harriet, stn 34f (51°44.130'S, 058°00.550'W), under rocks within mussel bed, midshore, 4 specimens (NMW.Z.2011.039.0155), 08.12.2011; Teal Creek, east of Darwin, stn 35d (51°49.248'S, 058°55.561'W), under rocks in sand, midshore, 1 specimen (NMW.Z.2011.039.0156), 09.12.2011; Race Point Farm, Port San Carlos, stn 37a (51°30.276'S, 059°00.137'W), in crevices, mid-low shore, 3 specimens (NMW.Z.2012.082.0041–0042), 12.01.2013; Race Point Farm, Port San Carlos, stn 37b (51°30.277'S, 059°00.080'W), in crevices, low shore, 2 specimen (NMW.Z.2012.082.0043), 12.01.2013; Race Point Farm, Port San Carlos, stn 37c (51°30.276'S, 059°00.137'W), under stones, low shore, 1 specimen (NMW.Z.2012.082.0044), 12.01.2013; Race Point Farm, Port San Carlos, stn 37d (51°30.276'S, 059°00.137'W), among rocks & gravel in muddy sand, low shore, 1 specimen (NMW.Z.2012.082.0045), 12.01.2013; Cape Bougainville, stn 38a (51°18.720'S, 058°27.603'W), in pink encrusting algae in open crevices, low shore, 2 specimens (NMW.Z.2012.082.0047), 13.01.2013; Cape Bougainville, stn 38b (51°18.727'S, 058°27.607'W), under rocks in gravel in rock pool, mid-low shore, 2 specimens (NMW.Z.2012.082.0048), 13.01.2013; Saunders Island: Sealer Cove harbor, stn 44c (51°21.760'S, 060°04.896'W), under rocks in sandy gravel, low shore, 2 specimens (NMW.Z.2012.082.0049); 18.01.2013; Sealer Cove harbor, stn 44d (51°21.760'S, 060°04.896'W), under rocks in sandy gravel, low shore, 3 specimens (NMW.Z.2012.082.0050); 18.01.2013; East Falkland: North Arm, stn 48a (52°07.768'S, 059°22.131'W), mussel bed over silty coarse sand, midshore, 1 specimen (NMW.Z.2013.082.0051), 22.01.2013; North Arm, stn 48b (52°07.829'S, 059°22.079'W), coarse loose sand, mid-low shore, 1 specimen (NMW.Z.2013.082.0052), 22.01.2013; New Haven, stn 49b (51°43.855'S, 059°12.894'W), under rocks in sandy gravel, mid-low shore, 1 specimen (NMW.Z.2012.082.0054), 24.01.2013; West Falkland: Moonlight Bay, Port Stephens, stn 51d (52°06.266'S, 060°50.334'W), in crevices, mid-low shore, 1 specimen (NMW.Z.2012.082.0055), 26.01.2013; Hot Stone Cove Creek, Dunbar, stn 54g (51°22.883'S, 060°30.886'W), associated with large tunicate attached to rock, low shore, 1 specimen (NMW.Z.2012.082.0056), 29.01.2013; Shallow Bay, stn 57c (51°30.032'S, 060°07.726'W), in crevices & under stones, mid shore, 2 specimens (NMW.Z.2012.082.0057), 01.02.2013.

Description. Eighty-three entire specimens, juveniles to adults, were examined: length 1.9–105.1 mm, width 0.27–4.7 mm (excluding parapodia, measured at chaetiger 4–5) for 16–115 chaetigers. Description based on adult specimens only, defined by the absence of notopodial falcigers.

Colour pale in alcohol.

Body shape depressed dorso-ventrally, mostly of uniform width to posterior, then tapering in last few chaetigers.

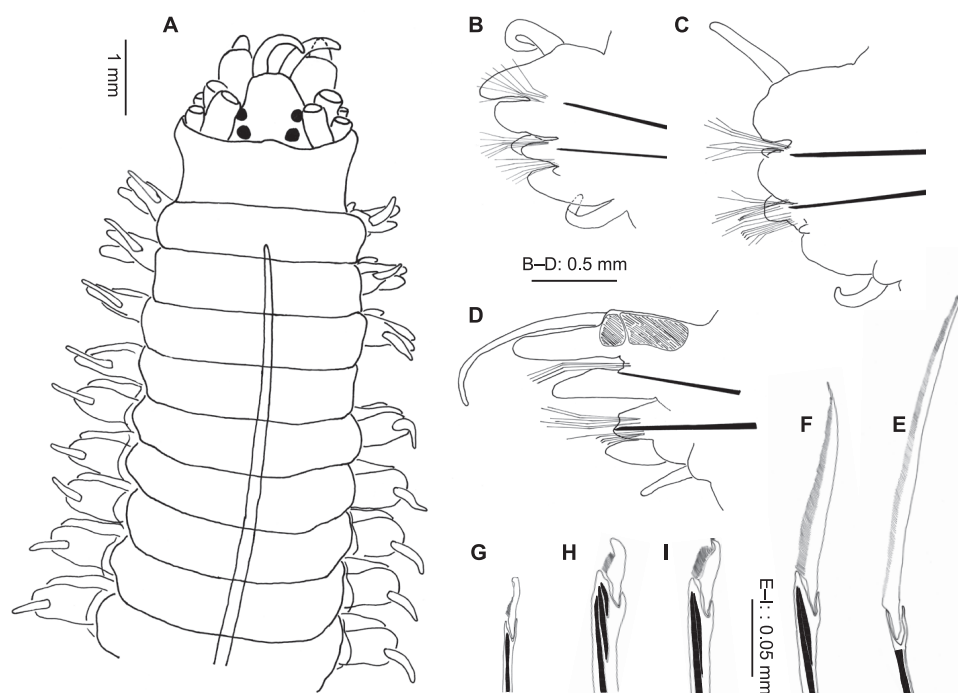


Figure 8. *Platynereis magalhaensis* Kinberg, 1865 (**A–F, H–I** NMW.Z.2011.039.0159 **G** NMW.Z.2011.039.0149): **A** anterior end (tentacular cirri & right chaetiger 4 removed), dorsal view **B** right parapodium, chaetiger 4, posterior view **C** right parapodium, chaetiger 10, posterior view **D** right parapodium, chaetiger 71, posterior view; right parapodium, chaetiger 4, posterior view **E** notopodial homogomph spiniger, chaetiger 10 **F** neuropodial heterogomph spiniger, chaetiger 10 **G** juvenile notopodial heterogomph falciger, chaetiger 20 **H** neuropodial heterogomph falciger, chaetiger 10 **I** neuropodial heterogomph falciger, chaetiger 71.

Prostomium longer than broad (Fig. 8A), antennae and palps about equal in length; antennae 1/2–1/3 width of palpophores. Four pairs tentacular cirri, postero-dorsal pair longest, reaching to chaetiger 11–14, rarely 16. Two pairs small, dark brown to black eyes, anterior pair marginally smaller, more laterally placed (Fig. 8A). Mid-dorsal nuchal cushion present, projecting forward slightly on to head from apodous peristomial segment (Fig. 8A). Peristomium approximately one third longer than following segments.

Proboscis with tight lines of rod-like paragnaths in Areas III, IV, VI, VII and VIII, absent in Areas I, II and V. Largest group in area IV with up to 9 long rows, innermost 3–4 rows incomplete. Area III with 3 small groups of up to 4 lines in each. Area VI, the smallest group, often faint, difficult to discern, with up to 3 short lines of rods (Fig. 9G, indicated by arrow). Area VII–VIII with 5 groups of up to 3 curved lines in each (Fig. 9I). Jaws dark brown with up to 12 teeth (Fig. 8G, I).

Parapodia subbiramous on chaetigers 1–2, biramous from chaetiger 3. Parapodial ligules thickened and rounded on chaetigers 5–11, sometimes, to a lesser extent, starting from chaetiger 4 and extending to chaetiger 12, occasionally 13, in larger animals (Fig. 8B, C).

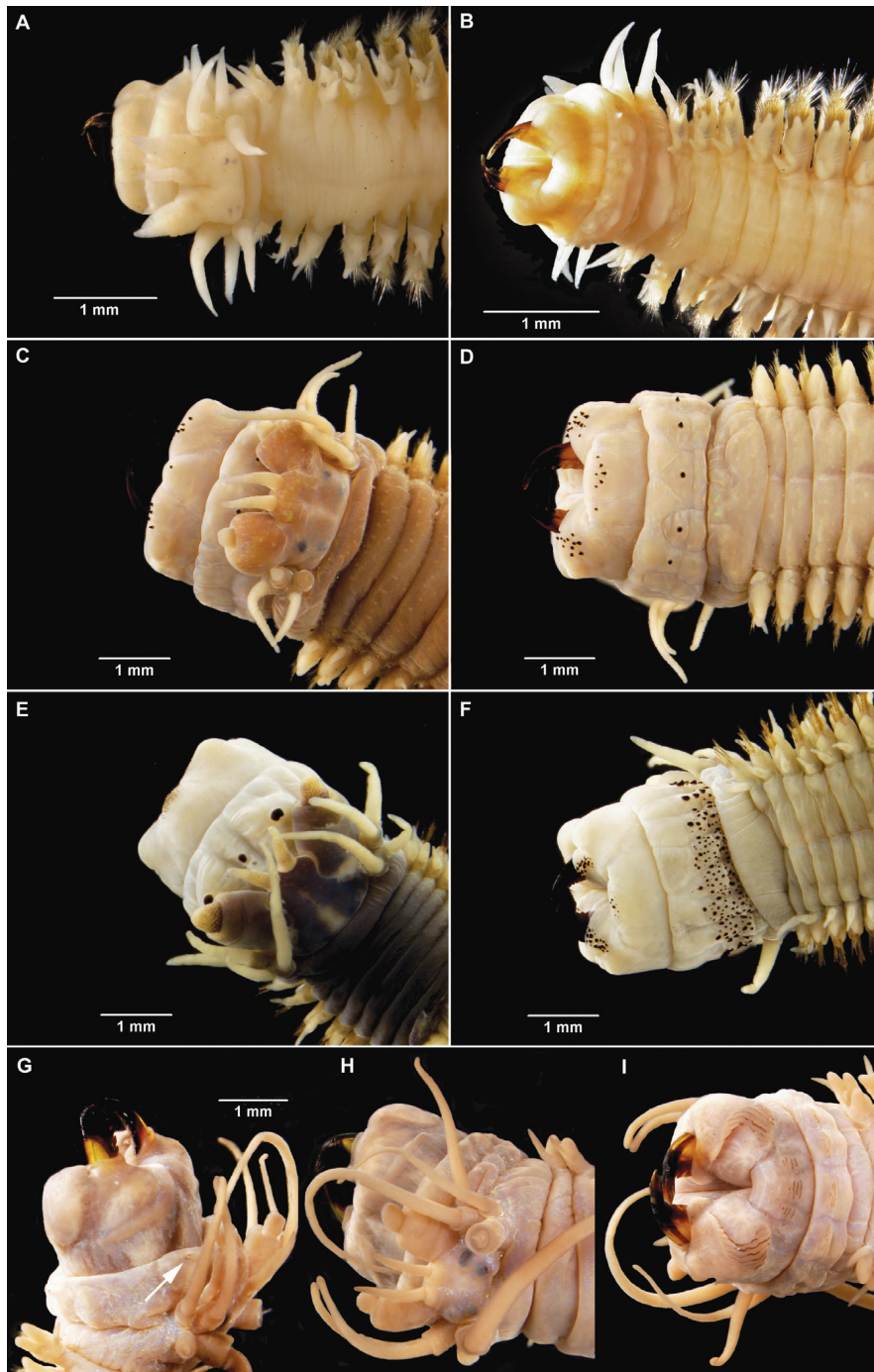


Figure 9. Images of the paragnaths of the species collected. *Gymmonereis tenera* sp. n. (NMW.Z.2011.039.0093): **A** dorsal view **B** ventral view; *Neanthes kerguelensis* (NMW.Z.2011.039.0129) **C** dorsal view **D** ventral view; *Perinereis falklandica* (NMW.Z.2011.039.0113) **E** dorsal view; **F** ventral view; *Platynereis magalhaensis* (NMW.Z.2011.039.0158) **G** lateral view (arrow indicating Area VI paragnaths) **H** dorsal view **I** ventral view.

From mid-body dorsal ligule lengthened and glandular (Fig. 8D). Dorsal cirrus longer than dorsal ligule throughout body, minorly so anteriorly, becoming more pronounced and elongate posteriorly (Fig. 8B–D).

Notochaetae homogomph spinigers (Fig. 8E), up to 25–30 per fascicle in mid-body, reduced to around 5 in last few chaetigers. Single heterogomph notopodial falciger, bifid with connecting tendon from tip (Fig. 8G), present in juveniles up to around 60–65 chaetiger stage, absent in adults. First occurrence of notopodial falciger retreats posteriorly as size increases, from around chaetiger 8 (of 16) to chaetiger 62 (of 64).

Neurochaetae homogomph and heterogomph spinigers (Fig. 8F) and heterogomph falcigers (Fig. 8H, I). Superior fascicle spinigers homogomph, up to 8, inferior fascicle spinigers heterogomph, up to 6 (usually 2–3). Falcigers heterogomph, from chaetiger 5 onwards; up to 7 above acicula, up to 17 below; greatest numbers mid-body reducing posteriorly.

Pygidium terminal; two long, thin anal cirri inserted ventrally.

Tube soft, with coarse grains of sand, shell and foraminifera adhered to it.

Remarks. *Platynereis magalhaensis* was the most common nereidid collected by diving with most rocks turned over having tubes attached to the underside. It was also widespread intertidally, again in tubes attached to rocks or algal holdfasts.

The original description of *P. magalhaensis* by Kinberg (1865) was brief with little detail except a general description of the head, and a statement that the tentacular cirri reached to the 15th segment and there were 12 teeth on the jaws. Several authors since then have expanded the description using either newly collected specimens (e.g. Ehlers 1897; Fauvel 1916) or by re-examining Kinberg's type material (Hartman 1948). The species can be distinguished from most other *Platynereis* species on a combination of the absence of paragnaths in Areas I, II and V and the absence of notopodial falcigers (in adults). However, *P. magalhaensis* remains difficult, if not impossible, to separate morphologically from the *P. australis* 'group' — *P. australis* (Schmarda, 1861), *P. karaka* Read, 2007, *P. kau* Read, 2007, *P. mahanga* Read, 2007 — resulting in a conflict of opinion with some authors synonymizing it with *P. australis* while others prefer to keep them separate.

Most recently, a detailed comparison of the *P. australis* group with *P. magalhaensis* was published by Read (2007), following which he concluded that while morphologically inseparable as atokes, as epitokes the species could be differentiated on the basis of characters such as number of pre-natatory segments and male pygidial form and thus *P. magalhaensis* should still be considered a valid species.

Unfortunately, no epitokous forms were among the specimens collected from the Falkland Islands so this aspect cannot be confirmed in this study. However, the few records of epitokes that do exist for this region (Ehlers 1897; Augener 1923; Monro 1930) indicate that the species is likely to be distinct from *P. australis* and Read (2007) additionally stated that records of *P. australis* outside of New Zealand should be re-assessed. The species collected from the Falkland Islands is therefore viewed as being appropriately placed under the name *P. magalhaensis*. However, further study of the epitokous form from the islands is necessary to help clarify the situation.

Key to intertidal and nearshore Nereididae in the Falkland Islands

- 1 Chitinous paragnaths present on pharynx; single ventral cirrus present throughout **2**
- Chitinous paragnaths absent from pharynx; double ventral cirri present
..... ***Gymnonereis tenera* sp. n.**
- 2 Paragnaths present as shield-shaped bars and /or variably-sized cones; chaetiger 5–10 parapodial lobes not noticeably different from lobes on remaining chaetigers **3**
- Paragnaths present as tight rows of rods; chaetigers 5–10 with globular parapodial lobes..... ***Platynereis magalhaensis* Kinberg, 1865**
- 3 Area VI with paragnaths as cones, shield-shaped bar with rounded apex or absent; posterior notopodial dorsal lobes not noticeably enlarged **4**
- Area VI with 1 large, shield-shaped bar with pointed apex; posterior dorsal notopodial lobes greatly enlarged ***Perinereis falklandica* Ramsay, 1914**
- 4 Falcigers absent in notopodia..... **5**
- Falcigers present in at least some notopodia..... **6**
- 5 Paragnaths absent on maxillary ring and Area VI; ventral fascicle of neuropodia includes heterogomph spinigers..... ***Eunereis patagonica* (McIntosh, 1885)**
- Paragnaths present on maxillary ring and Area VI; all spinigers homogomph, no heterogomph spinigers present..... ***Neanthes kerguelensis* (McIntosh, 1885)**
- 6 Conical paragnaths in Area VI, single sparse row of paragnaths in Area VII–VIII (sometimes absent); falcigers present in dorsal fascicle of neuropodia
..... ***Nereis eugeniae* (Kinberg, 1865)**
- Shield-shaped bar in Area VI, more than 1 row of paragnaths in Area VII–VIII; falcigers absent from dorsal fascicle of neuropodia.....
..... ***Perinereis atlantica* McIntosh, 1885, comb. n.***
- * The single record from the Falkland Islands (Pratt 1898) is considered doubtful

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Appendix 3

Paper 3

Authorship & Collaboration:

T. Darbyshire: Conception; author of most text; sole author of taxonomic work.

P.E. Brewin: Fieldwork and collection of specimens from South Georgia;
contribution of text to Introduction and Methods sections
regarding South Georgia project and fieldwork.

Darbyshire, T. & Brewin, P. 2015. Three new species of *Dysponetus* Levinsen, 1879 (Polychaeta: Chrysopetalidae) from the South Atlantic and Southern Ocean, with a re-description of *Dysponetus bulbosus* Hartmann-Schröder, 1982. *Zootaxa* **4040**: 359–370.

doi:10.11646/zootaxa.4040.3.7

RE: PhD thesis - brief response kindly requested - Inbox

Message

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RE: PhD thesis - brief response kindly requested

Paul Brewin

Sent: Wednesday, 9 May 2018 18:08
To: Teresa Darbyshire

You replied to this message on 09/05/2018 20:11.

Hi Teresa - good to hear from you and that you're nearing completion.

I can confirm that your description of our roles in the paper is correct.

Dr Paul Brewin
Director / Scientist
Shallow Marine Surveys Group
Falkland Islands, South Atlantic
+500 55346

<http://smsg-falklands.org>

Cheers
Paul

-----Original Message-----
From: Teresa Darbyshire <Teresa.Darbyshire@museumwales.ac.uk>
Sent: 09 May 2018 05:20
To: pbrewin@smsg-falklands.org
Subject: PhD thesis - brief response kindly requested

Hi Paul

How are you? I hope you and everyone else in the islands are well. I am finally nearing the end of a 12-month writing period to submit my thesis for a PhD by Published Works with Bangor University, based on my work on the Polychaetes of the Falkland Islands. As part of the submission, I need to supply a signed statement from any co-authors on joint publications in regards to the following regulation:

"Candidates may submit work(s) completed in collaboration with others in support of the candidature, but such work shall be accompanied by a detailed statement signed by each collaborator indicating the nature and amount of the work done by the candidate."

Below is my proposed text regarding the roles we each played in our publication.

Please can you reply by email, including your title and affiliation, stating whether you agree or disagree with the proposed text. If you disagree please detail your concerns. Please note that I will also be required to include your email correspondence as an Appendix to the thesis.

Many thanks for your help in this request.

Best wishes
Teresa

Publication

Darbyshire, T. & Brewin, P. E. 2015. Three new species of *Dysponetus* Levinsen, 1879 (Polychaeta: Chrysopetalidae) from the South Atlantic and Southern Ocean, with a re-description of *Dysponetus bulbosus* Hartmann-Schröder, 1982. *Zootaxa*, 4040 (3): 359-370.

Authorship

TD: Conception; author of most text; sole author of taxonomic work

PEB: Fieldwork and collection of specimens from South Georgia; contribution of text to Introduction and Methods sections regarding South Georgia project and fieldwork

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<http://zoobank.org/urn:lsid:zoobank.org:pub:C9FF307A-F3FD-4143-94BE-373E1C651A65>

Three new species of *Dysponetus* Levinsen, 1879 (Polychaeta: Chrysopetalidae) from the South Atlantic and Southern Ocean, with a re-description of *Dysponetus bulbosus* Hartmann-Schröder, 1982

TERESA DARBYSHIRE^{1,4} & PAUL E. BREWIN^{2,3}

¹Department of Natural Sciences, Amgueddfa Cymru—National Museum Wales, Cathays Park, Cardiff CF10 3NP, Wales, U.K.

²Shallow Marine Surveys Group, 2 Philomel Pl, Stanley, Falkland Islands, FIQQ 1ZZ, South Atlantic

³Government of South Georgia and South Sandwich Islands, Government House, Stanley, Falkland Islands, FIQQ 1ZZ, South Atlantic

⁴Corresponding author. E-mail: Teresa.Darbyshire@museumwales.ac.uk

Abstract

Three new species of *Dysponetus* (Polychaeta: Chrysopetalidae) are described from the South Atlantic and Southern Ocean: *Dysponetus ovalisetosus* n. sp. from the Falkland Islands, *Dysponetus bricklei* n. sp. from South Georgia and *Dysponetus antarcticus* n. sp. from Antarctica are all characterized by having notochaetae that are oval in cross-section in contrast to the D-shape described for seven of the other species of *Dysponetus*. *Dysponetus antarcticus* n. sp. is the most distinct due to the combination of both a ventral cirrus on segment 3 and four eyes. Formerly mis-identified as *Dysponetus bulbosus* Hartmann-Schröder, 1982, it was discovered while clarifying the contradictory descriptions of that species published by Hartmann-Schröder in 1982 and 1986. *Dysponetus bulbosus* is re-described and newly figured. *Dysponetus bricklei* n. sp. and *Dysponetus ovalisetosus* n. sp. can be determined by comparing several characters including position of the median antenna, shape of the palps and cirri, and the number and shape of both the noto- and neurochaetae.

Key words: taxonomy, notochaetae, Antarctica, South Georgia, Falkland Islands

Introduction

There are currently thirteen described species of the genus *Dysponetus* Levinsen, 1879 from around the world, with the most recent descriptions being from Europe (*Dysponetus joeli* Olivier *et al.*, 2012; Darbyshire 2012) and the Pacific coast of North America (*Dysponetus populonectens* Pleijel *et al.* 2012). Most species are described from shallow water although a small number have been reported from deep (> 400 m) to abyssal depths (*Dysponetus caecus* (Langerhans, 1880)—Böttgeman 2009, Watson *et al.* 2014; *Dysponetus gracilis* Hartman, 1965—Hartman & Fauchald 1971, Aguirrezabalaga *et al.* 1999; *Dysponetus hesionides* Böttgeman, 2009; *Dysponetus profundus* Böttgeman, 2009). All other species occur in shallow (less than 100 m) water, often 0–10 m, with the exception of *Dysponetus paleophorus* Hartmann-Schröder, 1974a which was described from 255 m off Norway. Most recently, Watson *et al.* (2014) listed an unidentified species of *Dysponetus*, from 133 m on a Northeast Atlantic seamount. Although not in good enough condition to identify definitively or describe separately, *Dysponetus* sp. 1 was described as being most like *D. joeli*, a shallow water European species currently known from water depths to 47 m.

A survey of the shallow subtidal and intertidal Falkland Islands Polychaeta was initiated in 2011 and several specimens of *Dysponetus* were collected in both 2011 and 2013. Subtidal sites were sampled both to the east and west of East Falkland, with *Dysponetus* collected only from the eastern sites. Additionally, two specimens of *Dysponetus* were collected as part of a large, quantitative intertidal and subtidal species and habitat survey of South Georgia (Shallow Marine Surveys Group, unpublished data). The survey spanned the entire north coast of South Georgia, but despite the scope of the survey, only a single specimen was collected at each of two sites.

There have been no previous records of this group from the southwest Atlantic and the only records from

Antarctica were of *D. bulbosus* Hartmann-Schröder, 1982 (Hartmann-Schröder 1993) and an unidentified specimen (*Dysponetus* sp., Hartman 1967). Comparisons are also made with *D. bidentatus* Day, 1954, the closest species geographically, recorded from the southeast Atlantic at Tristan da Cunha (Day 1954) and southwest Africa (Hartmann-Schröder 1974b).

The specimens from both the Falkland Islands and South Georgia are very similar to *D. bulbosus*, however contradictions between the different descriptions of *D. bulbosus* by Hartmann-Schröder (1982, 1986, 1993) necessitated examination of the type and non-type specimens. Hartmann-Schröder herself (1986) attributed the discrepancy in the descriptions to damage on the specimens or simply that she was unable to distinguish which cirri belonged to which segment and chaetae. The conflict between descriptions was commented on by Pleijel *et al.* (2012) who examined the type specimens and came to the same conclusions as presented here. This paper presents an expanded explanation of the resolution along with updated descriptions and figures.

Dysponetus bulbosus was first described from Eagle Bay in Western Australia (Hartmann-Schröder 1982). It was later recorded from South Australia (Hartmann-Schröder 1986) and then from Antarctica, south of King George Island (Hartmann-Schröder 1993), always in shallow water in sandy habitats with some algae or detritus. Re-examination of the 1993 non-type specimens of *D. bulbosus*, from Antarctica, were found to be a currently undescribed species of *Dysponetus*.

Dysponetus antarcticus **n. sp.** is therefore newly described from Antarctica, *D. ovalisetosus* **n. sp.** from the Falkland Islands and *D. bricklei* **n. sp.** from South Georgia. All three species have notochaetae that are oval in cross-section in contrast to all other species of *Dysponetus* which have D-shaped notochaetae, flattened paleae or shape is undescribed. The character is discussed in the Remarks sections for *D. ovalisetosus*.

Material and methods

Specimens of *Dysponetus ovalisetosus* **n. sp.** from the Falkland Islands were collected by diving (3–12 m depth) with substrate being scraped off rocks using a dive knife and placed in a sealable plastic bag until return to MV *Hans Hansson* (2011) or shore (diving via rigid inflatable boat, 2012). Samples were then relaxed in 7% magnesium chloride solution before being fixed in 4% formaldehyde in seawater. In 2012, samples were returned to the laboratory and sorted live under the microscope before either being fixed in formaldehyde or 96% ethanol.

The South Georgia *D. bricklei* **n. sp.** were diver collected by hand at 5–18 m depth. Depth stratified, quantitative (0.25m² quadrat) photographic surveys were conducted at 25 sites along 30 m transects. Samples from each quadrat were placed in individual small, fine mesh (3 mm) bags, which were in turn all placed in one large, coarse mesh (10 mm) bag by the diver. Specimens were sorted immediately and preserved in 96% ethanol.

Methods of collection for *D. bulbosus* and *D. antarcticus* **n. sp.** were not detailed in the respective publications. *Dysponetus* sp. (Hartman 1967) was collected from 4 fathoms by grapnel.

All drawings and measurements were made using a camera lucida attachment on a Nikon Labophot-2 compound microscope or a Nikon Eclipse E400 binocular microscope. Microscope photographs were taken using AutoMontage™ software and SEM images were obtained with a Neoscope SEM.

The holotype and paratype of *D. antarcticus* are from the Zoological Museum Hamburg (ZMH), as were Hartmann-Schröder's type and non-type specimens of *D. bulbosus*. Additional non-type specimens of *D. bulbosus* were borrowed from the Swedish Museum of Natural History (SMNH). *Dysponetus* sp. from Antarctica was kindly loaned from the Smithsonian Institute, Washington (USNM). Holotypes, paratypes and non-type material of *D. bricklei* and *D. ovalisetosus* are in the collections of National Museum Wales, Cardiff (NMWZ). Additional paratypes of *D. ovalisetosus* are deposited in the Natural History Museum, London (NHMUK) and the Zoological Museum Hamburg (ZMH).

Systematics

Family Chrysopetalidae Ehlers, 1864

Subfamily Dysponetinae Aguado, Nygren & Rouse, 2013

Genus *Dysponetus* Levinsen, 1879

Type species: *Dysponetus pygmaeus* Levinsen, 1879

Dysponetus bulbosus Hartmann-Schröder, 1982

Figure 1A–F, 2A–B

Hartmann-Schröder, 1982: p54, Figs 1–4.— Hartmann-Schröder 1986: p32, Figs 1–5.— Pleijel *et al.* 2012: p5.

Material examined. Cape Naturaliste, Eagle Bay, Western Australia, fine algal bed with sand, holotype (ZMH P-16752), 07.11.1975; Hallett Cove, Adelaide, south Australia, algae and encrustation in rockpools, 1 specimen (ZMH P-18720), 13.12.1975; Port MacDonnell, Cape Northumberland, 2 km west of town, lee side of abrasion zone with volcanic rock, algal bed & turf, 1 specimen (ZMH P-18764), 19.12.1975; Cowbowie Field Station, Yorke Peninsula, Gulf St Vincent, South Australia, Sta. 01 (35°05'N, 137°44'E), mixed sand & gravel, 3–5 m, 2 specimens (SMNH 83511), 28.02.2004.

Additional material examined. *Dysponetus* sp.: inlet by Bonaparte Point, Arthur Harbor, Anvers Island, Antarctica, Sta. 6-63 (64° 46'S, 064° 04'W), from fish trap crushed by small berg, 4 fathoms, 1 specimen (USNM 247268), 24.01.1963.

Morphological re-assessment. The detailed descriptions published by Hartmann-Schröder in each case are still essentially correct, the only amendments necessary being to the details of the first three segments together with some additional observations. The published descriptions for each specimen are slightly different to each other and, in fact, the description by Hartmann-Schröder 1993 is now known to be for a different species (see *D. antarcticus* n. sp.). However, re-examination, combined with details from larger, more recent specimens, shows that the 1982 and 1986 specimens all exhibit the same characteristics for the initial anterior segments as follows:

Segment 1: The original descriptions of *D. bulbosus* detail this segment as having either dorsal but no ventral cirri (Holotype—1982; 1993) or both dorsal and ventral cirri (1986). Additionally, either notochaetae but no neurochaetae were detailed (1982, 1993) or both cited as absent (1986). In all cases, even though appendages may have been lost, the cirrophores for the dorsal and ventral cirri are present and both notochaetae and neurochaetae are absent (Figs 1A, B, D–F; 2A).

Segment 2: The differences in the descriptions for this segment vary. The holotype is described as having a dorsal cirrus with the ventral cirrus described as 'not definitely absent', with both notochaetae and neurochaetae present (1982). The specimens from South Australia (1986) are cited with a dorsal but no ventral cirrus and notochaetae but no neurochaetae, and the Antarctic specimen (1993) as having both dorsal and ventral cirri and noto- but no neurochaetae. Examination of material illustrates that the latter case, despite being a different species is, in fact, correct for all specimens (Figs 1A, B, D–F; 2A); cirrophores indicate where missing appendages were originally present. The holotype and specimen from Adelaide both have obvious emergent acicula on segment 2 (Figs 1A, B, E, F), not visible on the specimen from Port McDonnell (Fig. 1C) or the more recent specimens from Yorke Peninsula (Fig. 2A). It is therefore believed that the emergence is either due to the very small size of the specimens or preservation, but is not a character.

Segment 3: In this case, all descriptions (1982, 1986, 1993) agree that both dorsal and ventral cirri as well as both noto- and neurochaetae are present. The first two, however, are both incorrect in the same respect—the ventral cirrus on this segment is absent (Figs 1B, D, F). Although clear under SEM (Fig. 2A), this character is difficult to confirm using normal light microscopy but can be detected at x1000 using oil immersion. At this magnification, it is possible to identify the cirrophores for lost ventral cirri below the neuropodium on any segment. Cirrophores are confirmed absent on the 3rd segment of all 1982 and 1986 material. Ventral cirri are present on segment 3 of the 1993 specimens, however, these specimens are now confirmed as a separate species and are described below as *D. antarcticus*.

Additional observations: single mouth appendage variable in size: barely visible on holotype (Fig. 1B), seemingly abnormally large on 1986 specimens (Figs 1D, F) but average size on more recent 2012 specimens (Fig. 2A). Notochaetae D-shaped in cross-section (Fig. 2B), two alternating rows of sharp denticles each side. Accessory chaetae (1–2) present (simple neurochaetae of same form as notochaetae), inserted dorsally and distally on neuropodial lobe.

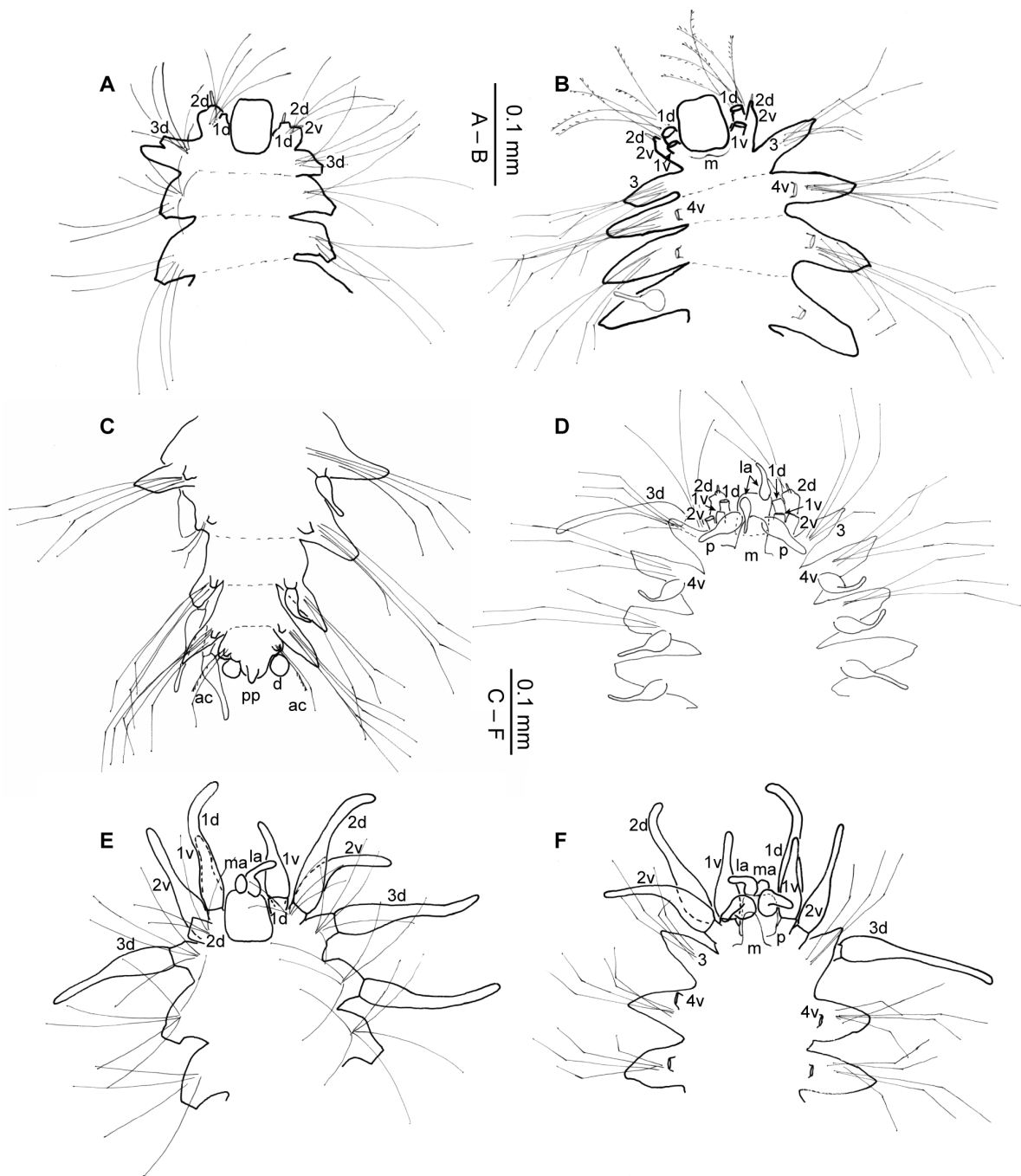


FIGURE 1. *Dysponetus bulbosus* Hartmann-Schröder, 1982: Holotype (HZM P-16752) A. anterior end, dorsal view; B. anterior end, ventral view; C. posterior end, ventral view; D. HZM P-18764, anterior end, ventral view; HZM P-18720 E. anterior end, dorsal view; F. anterior end, ventral view. Only a few chaetae drawn in each case for clarity. [ac=accessory chaeta, d=dorsal (cirrus/cirrophore), la=lateral antenna, ma=median antenna, m=mouth appendage, p=palp, pp = pygidial projection, v=ventral (cirrus/cirrophore); segment number indicated by numerals]

Final chaetiger (Fig. 1C) with few notochaetae, small rounded dorsal cirrus, neuropodium with single neurochaeta and accessory chaeta, no ventral cirrus. Pygidium slightly damaged, conical in appearance; single small projection, bluntly rounded, inserted posteroventrally (Fig. 1C)

Habitat. Algal beds, turf and encrustations in shallow water (0–5 m).

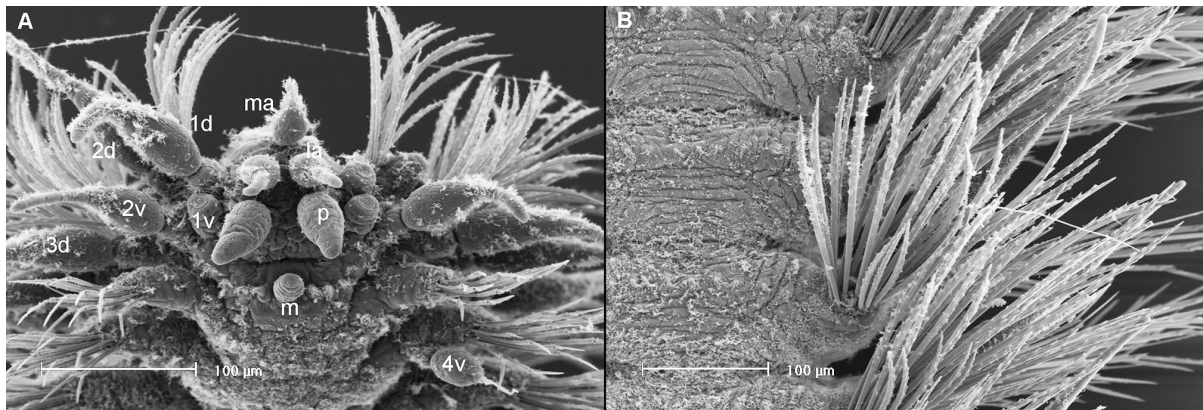


FIGURE 2. *Dysponetus bulbosus* Hartmann-Schröder, 1982: unaccessioned specimen A. anterior end, dorsal view; B. notochaetal fascicle, dorsal view. [d=dorsal (cirrus/cirrophore), la=lateral antenna, m=mouth appendage, p=palp, v=ventral (cirrus/cirrophore); segment number indicated by numerals]. Images: F. Pleijel.

Distribution. South and Western Australia.

Remarks. Prior to the 1993 publication, the only other record of *Dysponetus* from Antarctica was a damaged specimen identified by Hartman in 1967. The latter specimen is very small (12 segments) with a slightly damaged anterior end. It appears very like *D. bulbosus*, with possession of a single mouth appendage and a ventral cirrus absent on segment 3. However, it is not deemed in good enough condition to definitively confirm the species identification. The distribution of *D. bulbosus* is now restricted to Australia.

***Dysponetus antarcticus* n. sp.**

Figure 3A–D

1993: *Dysponetus bulbosus* Hartmann-Schröder: p128–9.

Material examined. South of King George Island, Antarctica, Sta. near O’Higgins (63° 00.49’S, 057° 09.45’W), very fine sand with Bryozoa, gorgonians, much detritus, 97 m, holotype (ZMH P-21914) paratype (ZMH P-27740), 22.12.1991.

Description. Holotype posteriorly incomplete, 2.7 mm long for 15 chaetigers (15th chaetiger removed for SEM). Paratype whole, juvenile, 1.29 mm for 14 chaetigers. Maximum width measured both between segments, 0.7 mm (holotype) and 0.26 mm (paratype), and including chaetae, 3.0 mm (holotype) and 1.07 mm (paratype). Description based on holotype except where specified. Measurements and counts of chaetae and cirri from holotype only.

Body shape cylindrical, ventrally flattened, tapered over last 2–3 segments at posterior. Colour pink-brown in alcohol.

Prostomium sub-rectangular (Fig. 3A), only slightly wider anteriorly. Eyes absent or degraded beyond visibility (see Remarks for comment on presence of eyes). Median antenna, present on paratype but not holotype, anterodorsally attached, same shape but slightly shorter than lateral antennae. Lateral antennae bottle-shaped (Fig. 3B), 1 remaining on holotype (150 µm long), arising immediately dorsal to palps. Palps (190 µm long) directed posteriorly (Fig. 3B), stouter than antennae or cirri, approximately 3 times as long as wide. Nuchal organs not observed. Single mouth appendage small, difficult to discern. Single pair of small jaws, barely visible through body even with methyl green staining. Proboscis not observed.

First two segments elevated dorsally with four pairs tentacular cirri, dorsal pairs lost, ventral pairs of similar shape and size as following ventral cirri. First segment achaetous, second segment with notochaetae only, situated anterior to dorsal tentacular cirrus, easily confused with first segment. Third and following segments all biramous, dorsal, ventral cirri, noto- and neurochaetae present. Cirrophores present.

Notopodial lobes reduced. Dorsal cirri long (307–373 µm, few remaining on holotype, only present mid-body

and posterior), slender, slightly shorter than notochaetae. Cirrophores present, styles slightly proximally swollen, distally tapering, tips blunt. Notochaetae very long, greater than body width, inserted slightly dorsal and anterior to dorsal cirrus, directed posteriorly and laterally, crossing dorsum by 10th chaetiger. Notochaetae oval in cross-section (Fig. 3C), with alternating, offset sharp denticles, up to 20. Notochaetal count, mid-body segments, up to 23.

Neuropodia well developed, with anterior ligule. Compound neurochaetae, with heterogomph shafts and bidentate falcigerous blades with short, robust teeth on the blade (Fig. 3D); longer than body width. Neurochaetal count, mid-body segments, at least 20–30. At least 1 accessory simple chaeta present, similar to but smaller than notochaetae, inserted distally and anteriorly on neuropodial lobe. Ventral cirri of similar shape to but smaller and shorter than dorsal cirri (length 67–227 μ m, longest on median chaetigers), arising ventral to neuropodial lobe, directed posteriorly.

Final segment (paratype) lacking chaetae. Pygidium with single large projection (35 μ m), cylindrical, distally tapering, inserted posteroventrally, anus terminal, some signs of damage. Posterior possibly regenerating.

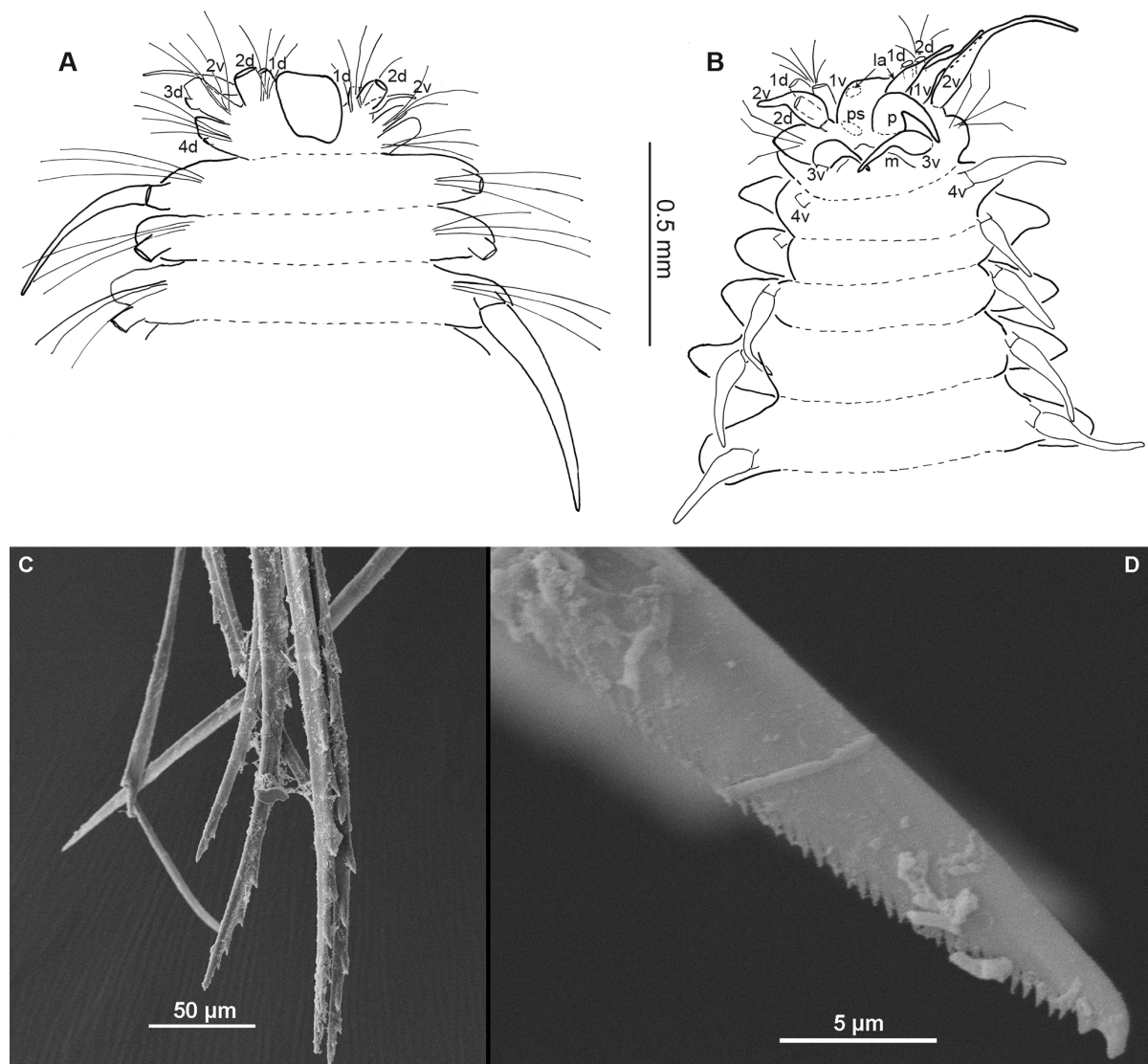


FIGURE 3. *Dysponetus antarcticus* n. sp.: Holotype (HZM P-21914) A. anterior end, dorsal view; B. anterior end, ventral view; C. Notochaetae; D. Neurochaeta tip. Only a few chaetae drawn in each case for clarity. [d=dorsal (cirrus/cirrophore), la=lateral antenna, ma=median antenna, m=mouth, p=palp, ps = palp scar, v=ventral (cirrus/cirrophore); segment number indicated by numerals]

Etymology. This species is named after Antarctica, the locality from which it was collected.

Habitat. Very fine sand with bryozoan, gorgonians and detritus; 97 m.

Distribution. South of King George Island, Antarctica

Remarks. *Dysponetus antarcticus* n. sp. has 4 eyes (described as present in Hartmann-Schröder's 1993 paper although now faded by time), ventral cirri on segment 3, elongated palps, single mouth appendage and an anterodorsally inserted median antenna.

The presence of ventral cirri on segment 3 places *Dysponetus antarcticus* initially closest to *D. caecus*, *D. paleophorus* and *D. pygmaeus* and, potentially, *D. hebes* Webster & Benedict, 1887 for which the character is undescribed. However, eyes are absent in all of these species except for *D. hebes* which has two. In addition, *Dysponetus hebes*, has sphaerical palps, an anteriorly inserted median antenna and a double mouth appendage, whereas *Dysponetus antarcticus* has elongated palps, an anterodorsally inserted median antenna and single mouth appendage.

***Dysponetus bricklei* n. sp.**

Figure 4A–D

Material examined. Cooper Bay, South Georgia, Sta. COOP 02 (54° 47.063'S, 035° 48.539'W), coralline encrusted bedrock/boulder with algal turf, 5–10 m, holotype (NMW.Z.2015.008.0001), 25.01.2010; Prion Island, South Georgia, Sta. PR002-6 (54° 1.862'S, 037° 15.032'W), coralline encrusted bedrock/boulder with algal turf, 15–18 m, 1 paratype (NMW.Z.2015.008.0002), 19.11.2010.

Description. Holotype posteriorly damaged, possibly incomplete, 1.47 mm long for 22 chaetigers. Paratype complete in 3 fragments, 2.04 mm for 14 chaetigers, possibly regenerating posteriorly; 1 segment removed for SEM, 1 segment removed for sequencing (failed). Maximum width measured both between segments, 0.57 mm (holotype) and 0.44 mm (paratype), and including chaetae, 1.2 mm (holotype) and 1.09 mm (paratype). Description based on both type specimens (head appendages more visible on paratype).

Body shape cylindrical, ventrally flattened, tapered over last 2–3 segments at posterior. Colour white-yellow in alcohol.

Prostomium (Fig. 4A) sub-rectangular, only slightly wider anteriorly. Four eyes present, red-brown. Median antenna dorsally attached, same shape as but slightly shorter (68 µm) than lateral antennae (77 µm). Lateral antennae bottle-shaped, arising immediately dorsal to palps (Fig. 4B). Palps (90–100 µm long) directed posteriorly, more stout than antennae or cirri, approximately twice as long as wide. Nuchal organs not observed. Single mouth appendage present (Fig. 4B). Single pair of jaws, visible with methyl green staining. Proboscis not observed.

First two segments slightly elevated dorsally with four pairs tentacular cirri (Fig. 4A), dorsal pairs of similar shape and size as following dorsal cirri, ventral pairs slightly longer but same shape as later ventral cirri. First segment achaetous, second segment with notochaetae only, situated anterior to dorsal tentacular cirrus. Third segment biramous; dorsal cirri present, ventral cirri absent (Fig. 4B). Following segments all biramous with both dorsal and ventral cirri. Single noto- and neuroacacula present in each parapodium.

Notopodial lobes reduced. Dorsal cirri long (170–380 µm), slender, similar in length to or just shorter than notochaetae, cirrophores present. Styles proximally swollen, distally tapering, tips blunt. Notochaetae long, inserted slightly dorsal and anterior to dorsal cirrus, directed posteriorly, not meeting over or crossing dorsum. Chaetae oval in cross-section, with alternating, offset sharp denticles, up to 17 (Fig. 4C). Notochaetal count, mid-body segments, 30–40.

Neuropodia well developed, with slightly longer dorsal lobe. Compound neurochaetae, with heterogomph shafts and bidentate falcigerous blades with long, fine teeth on the blade (Fig. 4D); not longer than body width. Neurochaetal count, mid-body segments, 28–33. No accessory simple chaetae observed. Ventral cirri of similar shape to but smaller and shorter than dorsal cirri, bulbous base more pronounced (length 90–170 µm, longer posteriorly), inserted posteroventrally to neuropodial lobe, directed posteriorly.

Final segment (paratype) lacking chaetae, single lobe present each side, no cirri or cirrophores apparent; pygidium without projection, rounded. Posterior possibly regenerating.

Etymology. *Dysponetus bricklei* n. sp. is named after Dr Paul Brickley, co-founder of the Shallow Marine Surveys Group, in recognition of his large contribution to subtidal ecology throughout the South Atlantic as well as his continued support of this work.

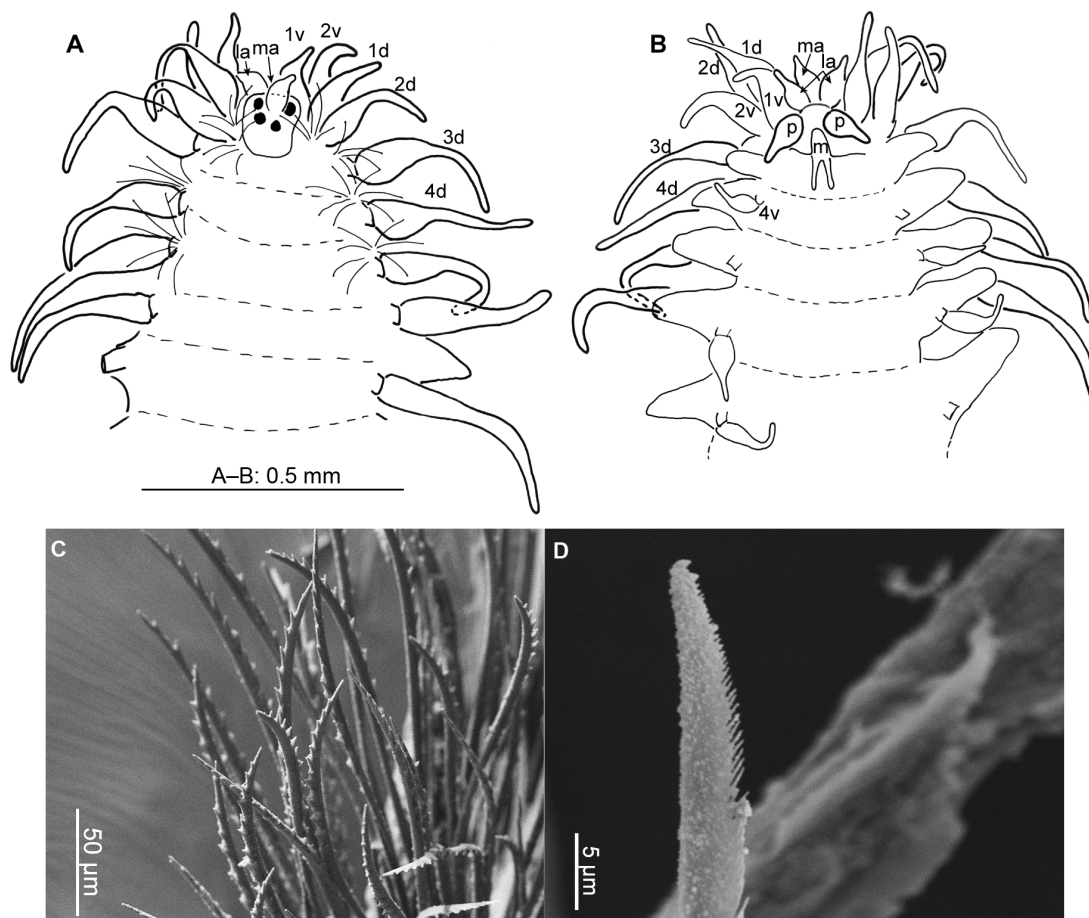


FIGURE 4. *Dysponetus bricklei* n. sp.: Holotype (NMW.Z.2015.008.0001) A. anterior end, dorsal view; B. anterior end, ventral view; Paratype (NMW.Z.2015.008.0002) C. Notochaetae; D. Neurochaeta tip. Only a few chaetae drawn in each case for clarity. [d=dorsal (cirrus/cirrophore), la=lateral antenna, ma=median antenna, m=mouth appendage, p=palp, v=ventral (cirrus/cirrophore); segment number indicated by numerals]

Habitat. Coralline encrusted bedrock/boulder with algal turf in shallow (5–18 m) water.

Distribution. South Georgia (Prion Island, Cooper Bay).

Remarks. *Dysponetus bricklei* n. sp. is similar to *D. bipapillatus*, *D. bidentatus*, *D. bulbosus*, *D. joeli*, *D. macroculatus*, *D. ovalisetosus* n. sp. & *D. populonectens* in having the combination of the following characters: 4 large eyes, elongated palps and ventral cirri absent on segment 3. The remaining species all have either 0 or 2 eyes, except for *D. antarcticus* which has 4 eyes but has a ventral cirrus on segment 3. Using SEM, *D. bricklei* can be separated from all of the above, except for *D. bidentatus* and *D. macroculatus* (for which the character is undocumented), and *D. ovalisetosus* on the shape of the notochaetae which are oval in *D. bricklei* but D-shaped in all of the rest (e.g. Dahlgren 1996, Fig. 2A for *D. bipapillatus*). This character, unfortunately, is not detectable with light microscopy, however there are several other characters which are. The palps of *D. populonectens* are elongated cylindrical whereas those of *D. bricklei* have a bulbous base, *D. bipapillatus* and *D. macroculatus* both have anterior insertion of the median antenna whereas *D. bricklei* has anterodorsal insertion, *D. joeli* has accessory neurochaetae and 20–26 neurochaetae as opposed to absent accessory chaetae and 28–33 neurochaetae, *D. bidentatus* has slender, tapering ventral cirri unlike the bulbous base and abruptly tapering tips of the ventral cirri on *D. bricklei* and *D. ovalisetosus* has neurochaetae with long, tapering hairs on the blade in contrast to the shorter spines on the neurochaetae of *D. bricklei*. Additionally, the ventral cirri of *D. ovalisetosus* have more bulbous bases than those of *D. bricklei* and the notochaetae and neurochaetae are more numerous.

Dysponetus bricklei is most similar to *D. bulbosus* in many characters. Both have the same arrangement of chaetae and cirri over the first 3 segments and similar-shaped dorsal and ventral cirri and head appendages.

Dysponetus bulbosus however has far fewer noto- and neurochaetae with only up to 16 notochaetae and 20 neurochaetae recorded compared to the average of 20–30 notochaetae and 28–33 neurochaetae counted on *D. bricklei*. Additionally, the final chaetiger of *D. bulbosus* has some chaetae and a pygidial projection compared to no chaetae or projection on *D. bricklei* (although the posterior of the latter may be regenerating).

***Dysponetus ovalisetosus* n. sp.**

Figure 5A–G

Material examined. East Falkland: near Yorke Point, west of Cape Pembroke, Sta. 46f (51° 40.4'S, 057° 45.9'W), section of *Phragmatopoma* colony, 3–4 m, holotype (NMW.Z.2012.082.0067), 1 paratype (NMW.Z.2012.082.0068) 20.01.2013; near Yorke Point, west of Cape Pembroke, Sta. 46e (51° 40.4'S, 057° 45.9'W), epifaunal scraping from rock, 3–4 m, 1 paratype (NMW.Z.2012.082.0069), 20.01.2013; west Cochon Island, Sta. 14 (51° 36.217'S, 057° 47.585'W), rock walls & gullies with epifaunal growth and pink encrusting algae, 10.4 m, 6 paratypes (NMW.Z.2011.039.0173), 25.11.2011; northeast Cochon Island, Sta. 16b (51° 36.366'S, 057° 47.082'W), epifaunal scraping, 12.5 m, 13 paratypes (2—NHMUK ANEA 2015.1116–7; 2—ZMH P-27763; 9—NMW.Z.2011.039.0174, NMW.Z.2011.039.0176–7 (SEM)), 26.11.2011; Kelp Harbour, Sta. 30 (51° 47.021'S, 059° 19.848'W), rocks in silty sand, 9.3 m, 1 paratype (NMW.Z.2011.039.0175), 04.12.2011.

Description. Holotype complete, slight posterior damage, 2.3 mm long for 19 chaetigers. Complete paratypes 1.12–1.93 mm for 12–19 chaetigers; 14 incomplete specimens, either anteriorly or posteriorly incomplete. Maximum width measured (holotype) both between segments, 0.29 mm and including chaetae, 0.83 mm. Description and measurements based mainly on holotype unless otherwise specified.

Body shape cylindrical, ventrally flattened, widest mid-body, tapering over last few segments. Colour white-yellow in alcohol.

Prostomium (Fig. 5A) oblong, only slightly wider anteriorly. Four eyes present, red-brown. Median antenna, anterodorsally attached, same shape as but half as long (36 µm) as lateral antennae (73–77 µm). Lateral antennae bottle-shaped, arising immediately dorsal to palps (Fig. 5A, C). Palps (68–77 µm long) directed posteriorly, stouter than antennae or cirri (Fig. 5C). Nuchal organs not observed. Single mouth appendage present (Fig. 5C). Single pair of jaws, visible with methyl green staining. Proboscis not observed.

First two segments slightly elevated dorsally with four pairs tentacular cirri, dorsal pairs of similar shape and size as following dorsal cirri, ventral pairs slightly longer but same shape as ventral cirri (Fig. 5A, C). First segment achaetous, second segment with notochaetae only, situated anterior to dorsal tentacular cirrus (Fig. 5A, C). Third segment biramous; dorsal cirri present, ventral cirri absent (Fig. 5C). Following segments all biramous with both dorsal and ventral cirri and noto- and neurochaetae (Fig. 5C). Cirrophores present, visible where any cirrus lost. Single noto- and neuroacicula present in each biramous parapodium.

Notopodial lobes reduced. Dorsal cirri long (160–230 µm), slender, slightly shorter than notochaetae, cirrophores present. Styles proximally swollen, distally tapering, tips blunt. Notochaetae long, inserted slightly dorsal and anterior to dorsal cirrus, directed posteriorly, not meeting over or crossing dorsum. Chaetae oval in cross-section, with alternating, offset sharp denticles (Fig. 5D, E), approximately 14. Notochaetal count, mid-body segments, over 40.

Neuropodia well developed, more curved ventrally, tip of aciculum emergent. Compound neurochaetae, with heterogomph shafts and bidentate falcigerous blades with long, tapering hairs on the blade (Fig. 5F); up to same length as notochaetae, not longer than body width. Neurochaetae inserted ventral to acicula, number over 30, mid-body segments. 1–2 accessory simple chaetae present, similar to but much smaller than notochaetae, inserted distally and anteriorly on neuropodial lobe. Ventral cirri smaller and shorter than dorsal cirri (length 30–140 µm, longest on median chaetigers), bulbous base more pronounced with more abruptly tapering and finer tips, inserted posteroventrally to neuropodial lobe, directed posteriorly. Single pair of digitiform appendages (possible external genital organs—see Remarks) inserted anteroventrally to ventral cirri (Fig. 5G) on segment 8 (length 100 µm).

Pygidium conical with single projection (0.27 µm), cylindrical, inserted posteroventrally (Fig. 5B). No eggs or sperm detected in any specimens.

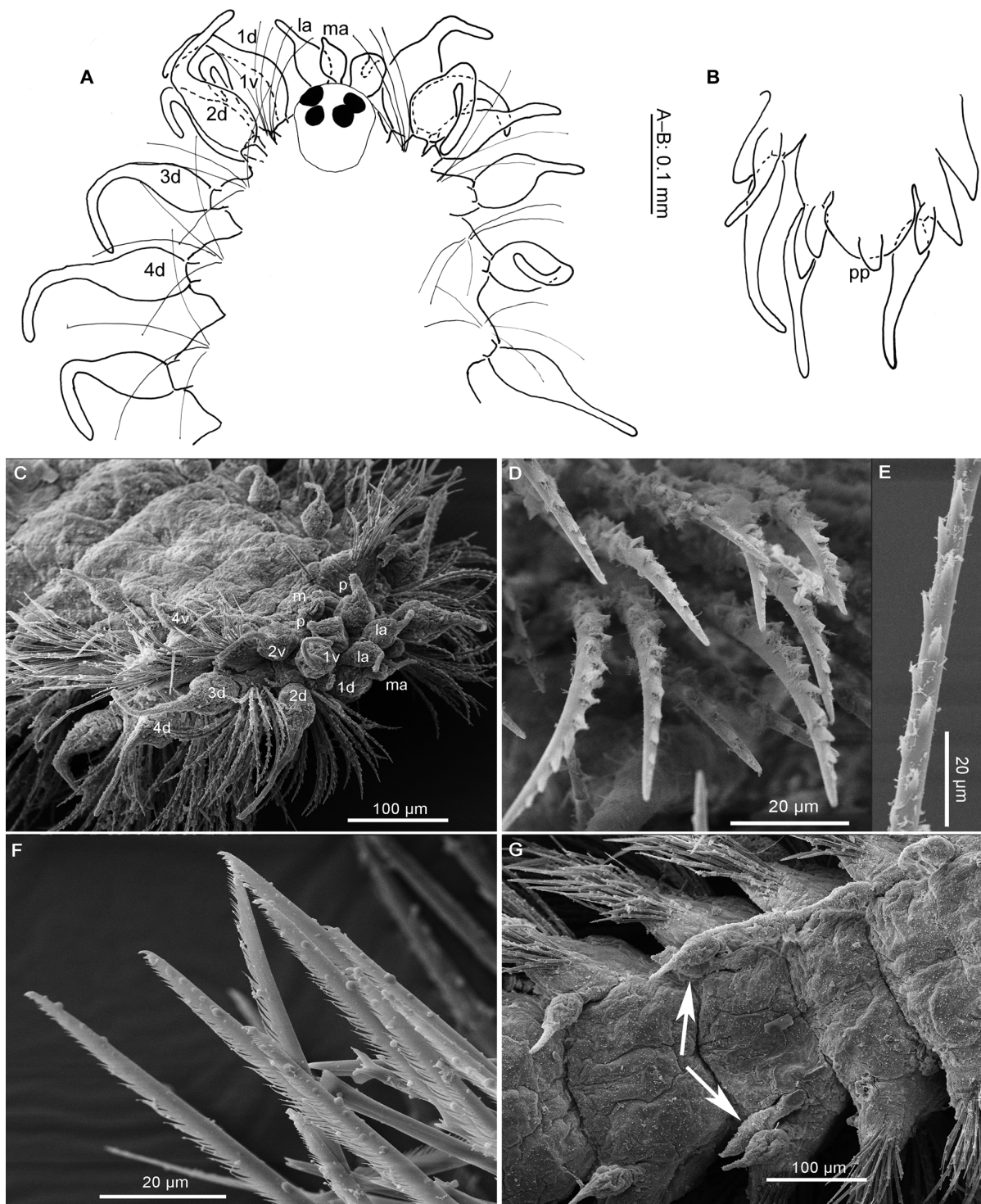


FIGURE 5. *Dysponetus ovalisetosus* n. sp.: Holotype (NMW.Z.2012.082.0067) A. anterior end, dorsal view; B. posterior end, ventral view; Paratype (NMW.Z.2011.039.0176) C. anterior end, ventral view; paratype (NMW.Z.2011.039.0177) D. notochaetae; E. magnified view of notochaeta; F. neurochaetae; paratype (NMW.Z.2011.039.0176) G. median section, ventral view—arrows indicate possible genital organs on segment 8. [d=dorsal (cirrus/cirrophore), la=lateral antenna, ma=median antenna, m=mouth appendage, p=palp, pp=pygidial projection, v=ventral (cirrus/cirrophore); segment number indicated by numerals]

Etymology. The specific name *ovalisetosus* is derived from the latin ‘ovali’ meaning ‘oval’ and ‘seta’ meaning ‘bristle’, referring to the shape of the notochaetae which are oval in cross-section in contrast to the D-shape reported for many other species of *Dysponetus*. Although the other species described herein also have oval notochaetae, the character was first detected in this species (see Remarks).

Habitat. Epifaunal turf on rocks, coarse sand; 3–13 m depth.

Distribution. Falkland Islands (East Falkland)

Remarks. *Dysponetus ovalisetosus* n. sp. belongs to the group of *Dysponetus* species with 4 eyes, a mouth appendage, elongated palps and ventral cirri absent on segment 3: *D. bidentatus*, *D. bipapillatus*, *D. bricklei* n. sp., *D. bulbosus*, *D. joeli*, *D. macroculatus* and *D. populonectens*. Of these species, the shape of the ventral cirri, with its bulbous base and abruptly tapered distal section, make it most similar in general appearance to *D. bulbosus*. However, it can be separated from most of these species by the shape of the notochaetae, which are oval in cross-section rather than D-shaped. The shape of the notochaetae has not yet been confirmed for either *D. bidentatus* or *D. macroculatus*. However, *D. ovalisetosus* has anterior insertion of the median antenna as opposed to dorsal insertion on *D. bidentatus* and the shape of the ventral cirri is much more abruptly tapering. In contrast to *D. macroculatus*, *D. ovalisetosus* has ventral cirri that taper far more abruptly and there are also far more noto- and neurochaetae present (for similar-sized animals) with fewer denticles present on the notochaetae. The remaining species, *D. bricklei*, also has oval notochaetae, however, as documented in the description for *D. bricklei*, *D. ovalisetosus* differs in the number of noto- and neurochaetae and the shape of the ventral cirri and neurochaetae. Dahlgren (1996; Fig. 2A) was the first to specifically describe the cross-sectional shape of *Dysponetus* notochaetae with his description of D-shaped notochaetae in *D. bipapillatus*. In the same paper, however, he also described *D. macroculatus* but did not state whether the notochaetae for that species also had the same appearance. In 2009, Böttgeman noted D-shaped notochaetae for *D. caecus*, *D. hesionides* and *D. profundus* and both Olivier *et al.* (2012) and Darbyshire (2012; Fig. 2C) figured the same for *D. joeli* in 2012. No mention is made of shape in the description for *D. populonectens* however it can be determined from the published SEM images. Additional unpublished SEM's of *D. bulbosus*, made during research for the same paper and figured earlier in this paper, confirm the D-shape for that species also. Cross-sectional shape is still unknown for *D. bidentatus*, *D. hebes*, *D. macroculatus*, *D. paleophorus* (which also has 1 or 2 flattened paleae in parapodia from segment 6) and *D. pygmaeus*. *Dysponetus gracilis* has notochaetae and paleae that are ‘broadly expanded instead of spinelike and curved’ (Hartman 1965). *Dysponetus ovalisetosus* was the first species on which oval notochaetae were observed although this character was later noted for both *D. bricklei* and *D. antarcticus* also. Further research is required to determine if these are the only *Dysponetus* species with this character or if any of the remaining species for which the character is unknown also exhibit it.

The additional pair of ventral digitiform appendages observed on chaetiger 8 of some specimens, were first described for *D. bipapillatus* (Dahlgren, 1996) but have not been reported from any other *Dysponetus* species until now. Dahlgren proposed that the appendages could be external genital organs, but no additional research has been done on their possible purpose. The appendages are not present on every specimen, being found on only 3 out of the 10 specimens of *D. bipapillatus* examined and 7 out of the 21 specimens of *D. ovalisetosus*, roughly the same ratio in each species. In neither case were gametes found at the same time that would indicate the sex of the specimen.

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Appendix 4

Paper 4

Darbyshire, T. 2013. A new species of *Micromaldane* (Polychaeta: Maldanidae) from the Falkland Islands, southwestern Atlantic, with notes on reproduction. *Zootaxa* **3683**: 439–446.
doi:10.11646/zootaxa.3683.4.7



A new species of *Micromaldane* (Polychaeta: Maldanidae) from the Falkland Islands, southwestern Atlantic, with notes on reproduction

TERESA DARBYSHIRE

Amgueddfa Cymru–National Museum Wales, Department of Biodiversity & Systematic Biology, Cathays Park, Cardiff CF10 3NP, Wales, U.K. E-mail: Teresa.Darbyshire@museumwales.ac.uk

Abstract

Micromaldane shackletoni n. sp. is described from the Falkland Islands in the southwest Atlantic. It is only the eighth species of *Micromaldane* to be recognized worldwide and is a new record of the genus for the Falkland Islands. The main characters of the new species are: up to 23 chaetigerous segments; nuchal organs as rounded ciliated pits with small central grooves anteriorly; two kinds of notochaetae: lancet-shaped chaetae and fine capillaries; neurochaetae as a single row of strongly curved, avicular uncini; a single pre-anal achaetigerous segment and anal plaque funnel-shaped with a crenated edge. This new species is a simultaneous hermaphrodite, only the second report of this reproductive mode in the genus along with *Micromaldane androgyne* Rouse, 1990. The stages of larval development from internal gametes to external in-tube development are also discussed.

Key words: taxonomy, simultaneous hermaphrodite, eggs, sperm, larvae

Introduction

Micromaldane is a small genus of only seven species worldwide. The genus was erected by Mesnil in 1897 for the European species *Micromaldane ornithochaeta*. Since then, other species have been described from the Red Sea (*M. bispinosa* Hartmann-Schröder, 1960), India (*M. jonesi* Kumaraswamy Achari, 1968) and Australia (*M. androgyne*, *M. nutricula*, *M. pamela* and *M. rubrospermatheca*: all by Rouse, 1990). Except for *M. ornithochaeta*, none of the species have been reported outside their original type locality (De Assis *et al.* 2007). The widely distributed European species has been recorded further afield from Mexico (Jiménez-Cueto & Salazar-Vallejo 1997), Antarctica (Fauvel 1951; Branch 1994) and British Columbia, Canada (Berkeley & Berkeley 1962). A catalogue of the Nicomachinae with taxonomic keys to species and a review of current literature, including *Micromaldane*, was published by De Assis *et al.* in 2007.

All species of this genus are small, the largest reported species being *M. jonesi* at around 12 mm in length. Historically there has been debate over the validity of the genus with several authors, including Fauvel (1927), Hartman (1959) and Day (1967) suggesting that specimens in fact represent a juvenile stage of *Nicomache* Malmgren, 1865 rather than a distinct species. However, several of the species were described with reproductive products inside the body (Mesnil 1897; Rouse 1990) indicating that they were mature adults. In addition, Rouse (1990) and this paper describe the presence of directly developing larvae inside tubes of specimens indicating that these specimens must indeed be adults and not still-developing juveniles of another species.

A large-scale study of the intertidal and nearshore polychaetes of the Falkland Islands began in 2011. Subtidal rock scrapings of hydroid and bryozoan turf were found to have many small tubes of *Micromaldane* embedded within and attached to the turf species (no specimens have so far been found from intertidal samples). The majority of the larger specimens were found to be in various stages of reproduction, enabling an investigation of development from presence of internal gametes to larval stages and fully developed adults. The new species is the first record of the genus from the Falkland Islands.

Materials and methods

Specimens of *Micromaldane shackletoni* n. sp. were collected by SCUBA diving at five stations off Cochon Island, a nature reserve in Berkeley Sound on the northeast coast of the Falkland Islands. Samples of a hydroid/bryozoan turf were scraped off rock and placed into small bags. On the surface, samples were bulk relaxed in a 7% magnesium chloride solution and fixed in 4% formaldehyde. They were later rinsed with fresh water and preserved in 80% industrial methylated spirits with 2% propylene glycol added.

Morphological examinations and measurements were made using a Nikon Eclipse E400 binocular microscope and a Nikon Labophot-2 compound microscope. Microscope photographs were taken using AutoMontage™ software and SEM images were obtained using a Neoscope SEM.

Holotype, most paratypes, and other non-type specimens are accessioned in the collections of the National Museum Wales (NMW.Z). Paratypes are also deposited in the Natural History Museum, London (NHMUK), the Australian Museum, Sydney (AM), Zoologisches Institut und Zoologisches Museum der Universität, Hamburg (ZMH) and the National Museum of Natural History, Smithsonian Institution, Washington D.C. (USMN).

Systematics

Class Polychaeta Grube, 1850

Family Maldanidae Malmgren, 1867

Subfamily Nicomachinae Arwidsson, 1906

Genus *Micromaldane* Mesnil, 1897

Type species: *Micromaldane ornithochaeta* Mesnil, 1897

Diagnosis (emended). No cephalic plate. Eyespots present or absent. Notopodia short and rounded, neuropodia with elongated tori; notochaetae and neurochaetae present on all chaetigers. Notochaetae of 2 or 3 kinds: stout, spatulate or straight lancet-type chaetae with striations, delicate geniculate chaetae with fine teeth along one margin and/or fine bordered capillary chaetae. Neurochaetae as strongly curved avicular, rostrate, uncini on all chaetigerous segments. Pre-anal achaetigerous segment present or absent. Anal plaque with central anus sunk inside funnel; edges evenly crenated without cirri.

Remarks. The above diagnosis is expanded from that of Rouse (1990). Table 1 compares morphological characters for all known species.

Micromaldane shackletoni n. sp.

Figures 1–3; Table 1

Material examined. SW Atlantic, Falkland Islands: Cochon Island, Stn 14 (51° 36.217' S, 057° 47.585' W), rock scraping, 10.4 m, holotype (NMW.Z.2011.039.0001), 27 paratypes (1—AM W.43557; 2—NHMUK 2013.416; 24—NMW.Z.2011.039.0002–0024; NMW.Z.2011.039.0025 on SEM stub), 25.11.2011; Cochon Island, Stn 10 (51° 36.287' S, 057° 47.684' W), rock scraping, 9.5 m, 1 paratype (NMW.Z.2011.039.0026), 24.11.2011; Cochon Island, Stn 11 (51° 36.377' S, 057° 47.489' W), from *Chaetopterus* tube, 9.6 m, 1 paratype (NMW.Z.2011.039.0027), 24.11.2011; Cochon Island, Stn 13 (51° 36.322' S, 057° 47.132' W), bryozoan scraping, 13.6 m, 3 paratypes (NMW.Z.2011.039.0028–0030), 25.11.2011; Cochon Island, Stn 16B (51° 36.366' S, 057° 47.082' W), hydroid/bryozoan turf scraping, 12.5 m, 62 paratypes (1—AM W.43558; 51—NMW.Z.2011.039.0031–0081; NMW.Z.2011.039.0082–0087 on SEM stubs; 2—USNM 1207943; 2—ZMH P-27462), 26.11.2011.

Description. Holotype (Fig. 1A) complete, 8.3 mm long, 0.3 mm wide for 21 chaetigers. Complete paratypes 3.6–11.0 mm long, 0.3 mm wide for 19–23 chaetigers. The following description is based on preserved specimens with 19 or more chaetigers.

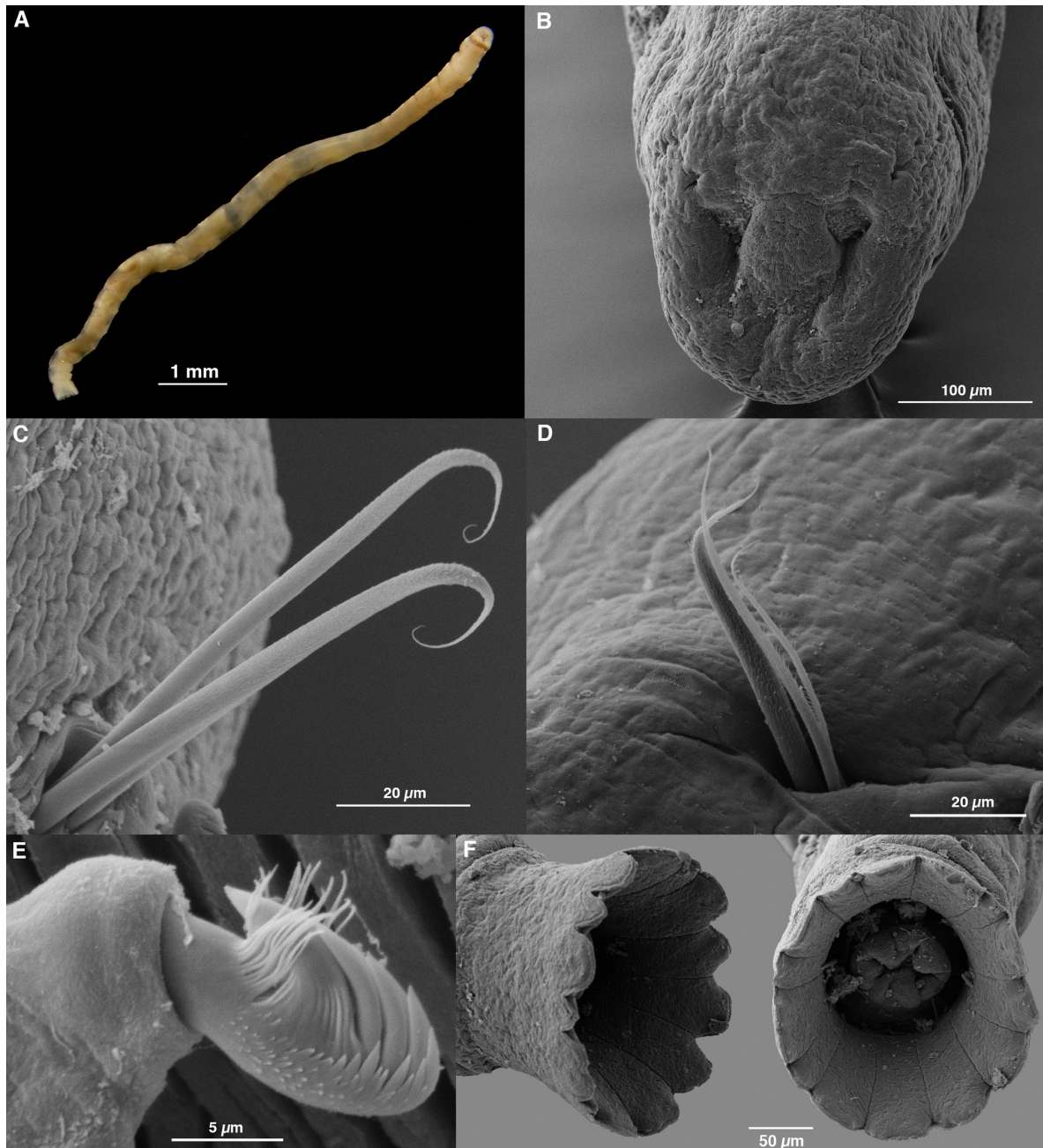


FIGURE 1. *Micromaldane shackletoni* n. sp. A. NMW.Z.2011.039.0001. Holotype, dorsal view; B. NMW.Z.2011.039.0082 (B&C). Dorsal view of prostomium showing ciliated nuchal organs; C. Lancet chaetae, chaetiger 4 (capillary chaeta/e broken); D. NMW.Z.2011.039.0025 (D&E). Single lancet chaeta with 2 capillary chaetae, chaetiger 6; E. Uncinus, chaetiger 8; F. NMW.Z.2011.039.0083. Anal plaque, oblique lateral (left) and posterior (right) views.

Body cylindrical, slightly wider on prostomial segment but uniform in width for rest of body. Body cream or yellowish in alcohol, some brown pigment visible on prostomial and anterior two segments; not observed alive.

Prostomium fused to peristomium, rounded anteriorly, forming a slight arched dorsal keel. Small cluster of black eyespots visible each side of prostomium anterior to buccal opening. Nuchal organs rounded ciliated pits with small, central groove anterior to each (Fig. 1B).

Notochaetae of two types: straight (under light microscopy, tips curved under SEM conditions), stout, lancet-shaped chaetae (Fig. 1C, D), distally tapering with covering of fine hairs, and fine capillary chaetae with similar haired covering (Fig. 1D). All chaetigers with 1–2 (rarely 3) lancet-shaped chaetae and 1–3 capillary chaetae.

Neuropodia of all chaetigers with uncini, up to 9 (rarely 10) in a single row. Chaetiger 1 with 1 or 2 uncini increasing to maximum number (4–10, number highly variable) on chaetigers 9–11, thereafter decreasing to 1 or 2 on final chaetiger (Fig. 2). Uncini strongly curved with long shafts, large main fang with 4 smaller teeth above and numerous additional teeth surrounding (Fig. 1E). To each side of main fang, subrostral barbules project upwards and forwards.

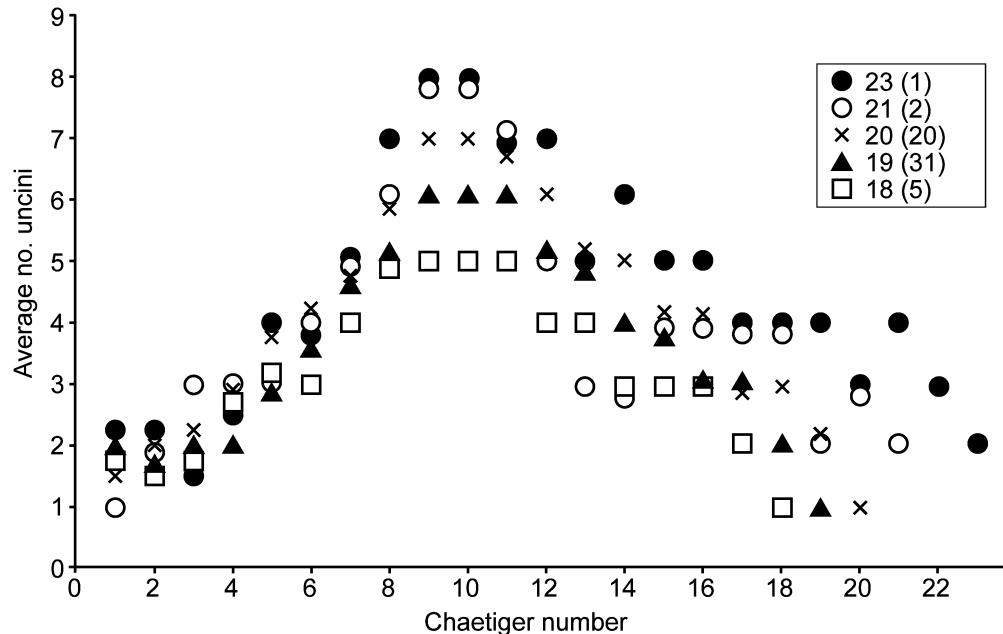


FIGURE 2. Comparison of average number of uncini per chaetiger for each size group. Number of specimens used for each size group is given in brackets after the total chaetiger number.

Chaetigers increase in length to median chaetigers then decrease progressively thereafter. Single pre-anal achaetigerous segment present. Anal plaque funnel-shaped, radially symmetrical, edge gently crenated (number variable); anus central (Fig. 1F).

Tube soft, composed of mucus and loosely bound sand grains. Numerous individuals identified with both eggs and sperm (Fig. 3A) floating free in the coelomic cavity and some tubes found with directly developing larvae (see below: Reproduction). Larvae were at different stages from pre-chaetigerous to 14 chaetigers (Fig. 3B–G). Spermathecae absent.

Methyl green staining produced ‘speckles’ over the entire body, more ventral than dorsal, with staining more concentrated on ventral side of anterior 6 chaetigers, prostomium (ventral and anterior dorsal) and pre-anal chaetiger (dorsal and ventral).

Variation. The number of chaetigers is very variable with independent (having their own tube) individuals ranging in size from 15 to 23 chaetigers. Most specimens with 19 chaetigers or more had internal reproductive products visible while only a small number of 18-chaetiger specimens, none smaller, were found containing eggs and sperm. The latter is therefore taken as the size of onset of maturity. Only a single individual was found with 23 chaetigers, with the majority of mature specimens identified having 19 or 20.

Length was extremely variable even among those specimens with the same number of chaetigers (none of those individuals measured showed obvious signs of regeneration). Body width showed little variation regardless of length.

The number of uncini on each chaetiger increased with the total number of segments but showed large variation even within the same size category. Fig. 2 compares the average number of uncini per segment for each of the mature adult size groups (18–23 chaetigers). Average chaetal counts are highest in the mid-body region (chaetigers 8–11) where a general increasing trend relative to total chaetiger number is evident.

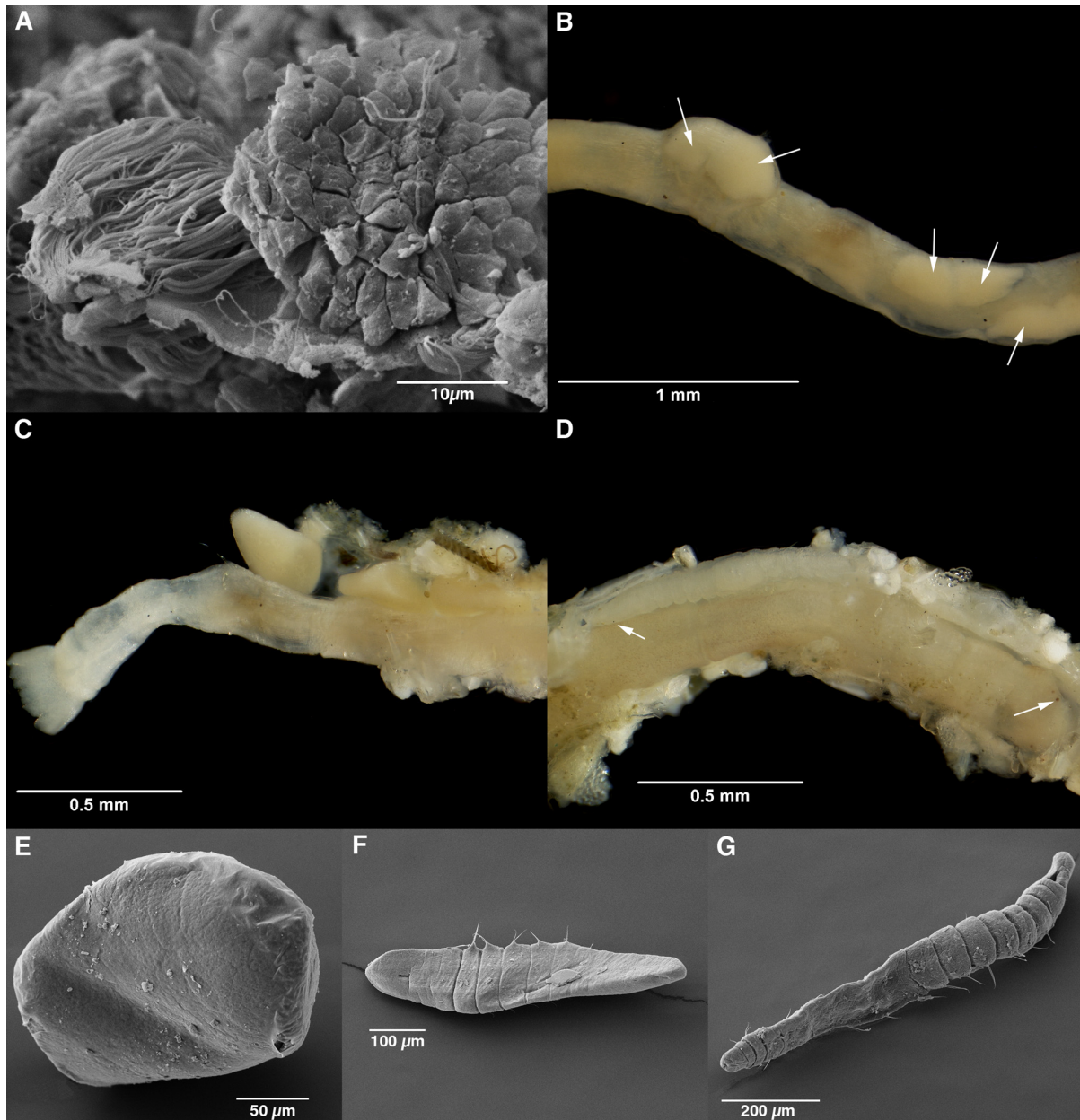


FIGURE 3. *Micromaldane shackletoni* n. sp. A. NMW.Z.2011.039.0025. Egg with sperm ‘packet’ adjacent from inside adult specimen; B. NMW.Z.2011.039.0024. Early undeveloped larva in process of extrusion from adult body, other embryos visible still inside body cavity (indicated by arrows); C. NMW.Z.2011.039.0080. External, undeveloped larvae between body wall and outer tube; D. NMW.Z.2011.039.0081. 14-chaetiger larva still developing inside tube (larva eyespot indicated by left arrow, adult by right arrow); E. NMW.Z.2011.039.0084 (E–G). Early stage larva, no cilia or differentiation visible; F. 7-chaetiger larva: buccal opening, segmentation and notochaetae present, no cilia, uncini or anal development visible at this stage; G. 14-chaetiger larva, uncini present on all chaetigers, anus visible but anal plaque still undeveloped.

Reproduction. Eggs and sperm were both visible within reproductive individuals and were confirmed as such using scanning electron microscopy (Fig. 3A: egg 30 μm diameter, sperm ‘packet’ 30x16 μm). As no specimens contained only sperm or only eggs, and no spermathecae were found, the species is presumed to be a simultaneous hermaphrodite as described previously for *M. androgyne* Rouse, 1990. More advanced individuals contained larger pre-chaetigerous embryos and a single animal was found with a large swelling on one side of the body that appeared to be the ‘budding-off’ of ripe embryos (Fig. 3B). Additional animals were found with the pre-

chaetigerous larvae (up to 12) inside the tube rather than the body (Fig. 3C). Further specimens were identified with 5–7 chaetiger or 13–14 chaetiger larvae still developing inside the parental tube (Fig. 3D). In each case, all larvae within a single tube were at a similar stage of development. The number of developing larvae reduced with increasing size from up to 12 pre-chaetigerous larvae in a tube to only three 13 or 14-chaetiger larvae. These observations, however, are only based on a very small number of specimens.

Larval development was investigated in those larvae found in parental tubes. No cilia were visible on any of the larvae at any stage (Fig. 3E–G). Early stage larvae, with no differentiation visible on the body, were approximately 210 μm by 160 μm in size (Fig. 3E). By the 7-chaetiger stage (Fig. 3F: 0.58 mm long, 0.1 mm wide) segmentation was visible with an identifiable prostomial segment and associated buccal opening. No eyespots were visible at this stage. Notochaetae of both types were present but uncini were absent and the posterior end was still undeveloped. At 14 chaetigers (Fig. 3G: 0.84 mm long, 0.1 mm wide), just prior to leaving the parental tube, eyespots were visible on the prostomium. Fig. 3D shows a 14-chaetiger larva positioned alongside but in the opposing direction to the parental body as indicated by the visible eyespots of both animals (see arrows on figure). Notochaetae had developed on all visible segments and uncini on all but the most posterior chaetiger. The anus was visible but the anal plaque was still undeveloped. Investigation of larger individuals showed that this character does not fully develop until around the 16-chaetiger stage. At 15 chaetigers in size, animals were independent and had constructed their own tube.

Etymology. This species is named after Sir Ernest Shackleton, Antarctic explorer, for whom the Shackleton Scholarship Fund is commemorated, in recognition of the Fund's support of this work.

Habitat. All specimens were collected subtidally (9–14 m) from rock scrapings of epifaunal 'turf'. Tubes were attached to any available structure within the 'turf' including hydroids, bryozoans and polychaete tubes (including those of other *Micromaldane*).

Remarks. *Micromaldane shackletoni* n. sp. is distinguishable from most other species of *Micromaldane* by having both a pre-anal achaetigerous segment and straight lancet chaetae (Table 1). This combination of characters is closest to *M. androgyne* and *M. bispinosa*. However, *M. androgyne* has only single or no capillary chaetae in each chaetiger, as opposed to 1–3 in *M. shackletoni* n. sp. and straight nuchal grooves as opposed to rounded, ciliated pits. For a smaller number of segments (maximum 23 as opposed to maximum 25), *M. shackletoni* n. sp. is also a much longer animal, almost twice the length, than *M. androgyne*. A comparison of larval development between the two species further confirms the distinction between them: larvae of *M. androgyne* remain in the parental tube until 19 chaetigers as opposed to 14 chaetigers for larvae of *M. shackletoni* n. sp.; uncini are present on most chaetigers by the 14-chaetiger stage in *M. shackletoni* n. sp. but not until 19 chaetigers in *M. androgyne* and development of the anal plaque is earlier in *M. androgyne* (visible from 11 chaetigers) than in *M. shackletoni* n. sp. where the anal plaque is still undeveloped at 14 chaetigers. *Micromaldane bispinosa* remains unique in the group in possessing two types of uncini whereas *M. shackletoni* n. sp., like the rest, has only one type.

Past suggestions that the genus *Micromaldane* represents only a post-larval stage of another maldanid have been shown to be incorrect by the taxonomic and reproductive studies carried out by Rouse (1990; 1992a–b), in which several different species of *Micromaldane* were shown to be fully mature, reproductive adults. Both gonochorism (*M. nutricula*, *M. pamela*, *M. rubrospermatheca*) and hermaphroditism (*M. androgyne*) are represented in the genus (Rouse 1990, 1992a), and all brood directly with larvae developing within the adult tube. No reproductive details were given for *M. jonesi* (Kumaraswamy Achari 1968) and there were only brief mentions of the presence of eggs in *M. ornithochaeta* (Mesnil 1897) and possible sperm in *M. bispinosa* by Hartmann-Schröder (1960).

Larval development of *Micromaldane* species was compared with that of other maldanid genera by Rouse (1992a). Within the Maldanidae, only *Euclymene oerstedii* (Claparède, 1863) has been reported to show hermaphroditism, although only a minority of the population exhibited this, the rest being gonochoristic (Pilgrim 1964). *Boguea enigmatica* Hartman, 1945 is the only other maldanid known to exhibit direct development similar to that of *Micromaldane* (Rouse 1992a). However, larvae of that species were found at several stages of development within a single tube and hermaphroditism was not evident (Wolf 1983).

Micromaldane shackletoni n. sp. represents only the second report of simultaneous hermaphroditism in the genus, third in the family as a whole, thereby providing further evidence for the validity of the genus.

TABLE 1. Comparison of morphological characters for all currently described species of *Micromaldane*.

Species	Type Locality	Max segments	Achaetous pre-anal segment?	No. capillaries	No. & form of lancet chaetae
<i>M. androgyne</i> Rouse, 1990	Australia	25	Y	0–1	1–2 straight
<i>M. bispinosa</i> Hartmann-Schröder, 1960	Red Sea	21	Y	1–3	1–2 straight
<i>M. jonesi</i> Kumaraswamy Achari, 1968	India	19	N	absent	? spatulate
<i>M. nutricula</i> Rouse, 1990	Australia	19	N	0–?	1–3 straight
<i>M. ornithochaeta</i> Mesnil, 1897	France	17	Y	2	1–2 spatulate
<i>M. pamela</i> Rouse, 1990	Australia	23	N	1–3	1–3 straight
<i>M. rubrospermatheca</i> Rouse, 1990	Australia	21	N	0–2	1 straight
<i>M. shackletoni</i> n. sp. Darbyshire, 2013	Falkland Islands	23	Y	1–3	1–2 straight

TABLE 1. (Ccontinued)

Species	No. geniculate chaetae	No. uncini	Length (mm)	Reproductive mode
<i>M. androgyne</i> Rouse, 1990	absent	2–9	5.5	simultaneous hermaphrodite
<i>M. bispinosa</i> Hartmann-Schröder, 1960	absent	2–8	8	unknown
<i>M. jonesi</i> Kumaraswamy Achari, 1968	?	2–8	12	unknown
<i>M. nutricula</i> Rouse, 1990	0–3	1–6	3.5	gonochoristic
<i>M. ornithochaeta</i> Mesnil, 1897	absent	?	4	unknown
<i>M. pamela</i> Rouse, 1990	0–6	1–15	8	gonochoristic
<i>M. rubrospermatheca</i> Rouse, 1990	0–2	1–5	3	gonochoristic
<i>M. shackletoni</i> n. sp. Darbyshire, 2013	absent	1–9	11	simultaneous hermaphrodite

Acknowledgements

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Appendix 5

*Localities and details of stations and
samples from fieldwork*

Table A5.1: 2011 sites

Table A5.2: 2013 sites

Table A5.3: 2015 sites

Site No.	Locality	Latitude	Longitude	Sediment Type Sampled
1a	Stanley foreshore, east of Government Jetty	51° 41.454' S	057° 51.870' W	under rocks in coarse sand
1b		51° 41.459' S	057° 51.840' W	"
1c		51° 41.459' S	057° 51.823' W	"
2a	The Canache	51° 41.680' S	057° 46.967' W	brown medium sand, grey beneath
2b		51° 41.708' S	057° 46.996' W	"
2c		51° 41.716' S	057° 47.107' W	under rocks in small ponds
2d		51° 41.708' S	057° 47.117' W	rocks & kelp holdfast
2e		51° 41.731' S	057° 47.001' W	brown medium sand
3a	Moody Brook, south of river entry point	51° 41.211' S	057° 55.189' W	soft filamentous algae over muddy fine sand
3b		51° 41.201' S	057° 55.099' W	as a but softer
3c		51° 41.204' S	057° 55.096' W	black coarse sand & gravel under rocks
3d		51° 41.179' S	057° 55.202' W	soft sandy mud with algal mat cover
4	north of Hookers Point	51° 41.994' S	057° 46.747' W	pink encrusting algae on rocks
5a	Volunteer Lagoon	51° 28.753' S	057° 50.432' W	rocks over gravel
5b		51° 28.752' S	057° 50.437' W	soft sand, some gravel
5c	Volunteer Beach	no position		<i>Macrocystis</i> bladders with spirorbidae/serpulidae from strandline
6a	north of Hookers Point, large rock pool (= site 4)	51° 41.994' S	057° 46.747' W	white (dead?) encrusting algae
6b				algal scraping
6c				pink encrusting algae
6d				gravel sievings from base of rock pool
7a	inlet from Uranic Bay, north Mount Kent boundary	51° 34.045' S	058° 08.896' W	soft muddy sand
7b		51° 34.053' S	058° 08.847' W	mud
7c		51° 34.069' S	058° 08.615' W	sandy mud
8a	Coral Creek, Estancia (2nd inlet west of Estancia farm)	51° 39.036' S	058° 13.036' W	soft sand over gravel
8b		51° 39.024' S	058° 13.067' W	medium-fine sand
8c		51° 38.946' S	058° 13.145' W	soft fine sand with many small tubes
9a	Whalebone Cove, in front of <i>Lady Elizabeth</i> wreck	51° 41.330' S	057° 48.092' W	fine sand, numerous lugworm casts
9b		51° 41.318' S	057° 48.011' W	
10	Cochon Island, west	51° 36.287' S	057° 47.684' W	rocks with pink encrusting algae & spirorbid tubes on coarse sand
11	Cochon Island, mid	51° 36.377' S	057° 47.489' W	large rocks & boulders over coarse sand; many <i>Chaetopterus</i> tubes
12	Cochon Island, southwest	51° 36.152' S	057° 47.773' W	embedded boulders/bedrock with large patches of coarse shell & sand. Boulders with <i>Chaetopterus</i> and thick crusts of pink encrusting algae
13	Cochon Island, mid	51° 36.322' S	057° 47.132' W	rocks walls & gullies with epifaunal growth and pink encrusting algae
14	Cochon Island, west	51° 36.217' S	057° 47.585' W	as 13, more shallow
15a	Cochon Island, east	51° 36.449' S	057° 47.150' W	rock wall to rocks/cobbles on coarse sand, no loose sediment on seabed
15b		51° 36.433' S	057° 47.123' W	
16a	Cochon Island, east	51° 36.369' S	057° 46.973' W	rock walls, pink encrusting algae; bryozoan/hydroid turf on sheltered overhangs
16b		51° 36.366' S	057° 47.082' W	
17	Cochon Island, mid	51° 36.403' S	057° 47.335' W	
18	Kidney Island, Kidney Cove	51° 37.517' S	057° 45.301' W	fine-medium sand, patches of visible tubes

Site No.	Locality	Latitude	Longitude	Sediment Type Sampled
19a	Sealion Island, southeast coast above Tussac Pond	52° 26.155' S	059° 05.270' W	silt-encrusted algal turf from rocks
19b				split rock crevices
19c				split rock crevices
20a	Sealion Island, south coast, East Loafers bay	52° 26.306' S	059° 06.229' W	pink encrusting algae from rock fissures
20b		52° 26.275' S	059° 06.341' W	under large clean stones
20c		52° 26.325' S	059° 06.090' W	coarse grey shale over medium sand/silt
21	Stanley west, in front of planet sculpture, east of <i>Jhelum</i> wreck	51° 41.402' S	057° 52.580' W	small stones over coarse sand & gravel
22	Egg Harbour, Parker Shoal	51° 47.471' S	059° 24.360' W	under small rocks on coarse sand & silt
23	Egg Harbour, off Long Point	51° 49.477' S	059° 23.926' W	stones on finer sediment than 22, more silt & organic debris
24	Egg Harbour, by jetty	51° 50.865' S	059° 23.168' W	algal mat in shallow water
25	Egg Harbour, bay east of Shag Rookery Point	51° 50.353' S	059° 27.351' W	rocks with seed mussels embedded in silty coarse sand & gravel
26	Egg Harbour, southwest side High Cliff Island	51° 48.578' S	059° 28.805' W	large rocks on medium sand
27	Egg Harbour, Shag Rookery Point	51° 49.345' S	059° 26.719' W	flat rocks embedded in soft silty sand
28	Kelp Harbour, by stone corral	51° 48.597' S	059° 19.433' W	muddy sand with tubes
29a	Kelp Harbour, off causeway	51° 47.715' S	059° 18.400' W	coralline coarse sand as a but further offshore
29b		no position		
30	Kelp Harbour	51° 47.021' S	059° 19.848' W	rocks in silty fine sand
31a	Whalebone Cove, in front of <i>Lady Elizabeth</i> wreck (= site 9)	51° 41.307' S	057° 47.985' W	under algae-covered rocks
31b		51° 41.308' S	057° 48.005' W	soft fine sand
31c		51° 41.325' S	057° 48.037' W	"
32	Stanley, by Marina bridge	51° 41.600' S	057° 48.073' W	<i>Macrocystis</i> holdfast
33a	Mullet Creek	51° 43.099' S	057° 54.951' W	rocks with coarse gravelly sand
33b		51° 43.121' S	057° 54.833' W	coarse gravelly/pebbly sand
33c		51° 43.150' S	057° 54.545' W	medium sand
33d		51° 43.155' S	057° 54.517' W	"
33e		51° 43.146' S	057° 54.333' W	medium-fine sand
33f		51° 43.138' S	057° 54.345' W	under rocks & in gravel
34a	Sand Bay, Port Harriet	51° 44.098' S	058° 00.626' W	gravelly coarse sand, many Maldanidae
34b		51° 44.105' S	058° 00.619' W	"
34c		51° 44.169' S	058° 00.610' W	fine sand over grey clay/coarse gravelly sand
34d		51° 44.231' S	058° 00.585' W	fine sand, no gravel, layers of brown plant detritus visible
34e		51° 44.152' S	058° 00.529' W	fine sand over small rocks, some clay
34f		51° 44.130' S	058° 00.550' W	rocks with mussel clumps
35a	Teal Creek, east of Darwin	51° 49.202' S	058° 55.615' W	soft mud over clay & coarse gravel
35b		51° 49.231' S	058° 55.573' W	soft mud over rocks, many tubes
35c		51° 49.236' S	058° 55.563' W	as b, deeper mud
35d		51° 49.248' S	058° 55.561' W	under rocks
36a	Camilla Creek, north of Darwin	51° 46.580' S	058° 57.704' W	soft mud over loose gravel
36b		51° 46.668' S	058° 57.760' W	deep mud
36c		as b		mud over rocks & gravel
36d		51° 46.680' S	058° 57.760' W	soft muddy sand

Table A5.1: Location and sampling details of sites visited in 2011 (dive sites indicated in green)

Site No.	Locality	Latitude	Longitude	Sediment Type Sampled
37a	Race Point Farm, Port San Carlos	51° 30.276' S	059° 00.137' W	large crevices and overturned rocks
37b		51° 30.277' S	059° 00.080' W	large split crevices
37c		51° 30.286' S	059° 00.021' W	under large stones, split crevices
37d		51° 30.268' S	058° 59.998' W	rocks & gravel in black muddy sand
38a	Cape Bougainville, Port Salvador	51° 18.720' S	058° 27.603' W	open, damp crevices with pink encrusting algae, sheltered by <i>Lessonia</i> kelp
38b		51° 18.727' S	058° 27.607' W	under rocks & in gravel sievings from rock pools
39a	beach below settlement, Port Salvador	51° 26.509' S	058° 22.230' W	gravelly sand
39b		just below a		medium sand, tubes visible
39c		just below b		medium sand, lugworm casts present
39d		just below c	soft black sandy mud	
39e		51° 26.455' S	058° 22.105' W	fine sand, firmer than site d
39f		51° 26.496' S	058° 22.113' W	medium sand, black under surface
39g		51° 26.442' S	058° 22.091' W	fine, soft sand with large bivalves
40	Hookers Point (=sites 4 & 6)			gravel sievings from bed of rock pool
41a	Whalebone Cove, in front of <i>Lady Elizabeth</i> wreck (= site 9&31)	51° 41.324' S	057° 43.000' W	medium-coarse sand
41b		51° 41.322' S	057° 48.030' W	"
41c		51° 41.327' S	057° 43.081' W	"
42a	The Neck (south), Saunders Island	51° 18.515' S	060° 14.396' W	fine grey-white sand
42b		51° 18.473' S	060° 14.481' W	"
42c		51° 18.472' S	060° 14.492' W	under stones in sand
42d		51° 18.485' S	060° 14.504' W	under stones on rock ledges
42e		51° 18.485' S	060° 14.488' W	fine grey-white sand
42f	The Neck (north)	51° 18.288' S	060° 14.144' W	"
43	bay above East Point, Saunders Island	51° 19.679' S	060° 05.527' W	muddy sand, dominated by maldanid tubes
44a	Sealer Cove harbour, Saunders Island	51° 21.739' S	060° 04.910' W	mud & rocks
44b		51° 21.751' S	060° 04.906' W	gravelly surface of feeder channel
44c		51° 21.760' S	060° 04.896' W	under rocks embedded in sandy gravel
44d		51° 21.765' S	060° 04.896' W	coarse sediment among mussel clumps
45	bay below settlement, Saunders Island	51° 21.923' S	060° 04.964' W	sand
46	near York Point, east of Cape Pembroke			rock ridges & pinnacle with <i>Macrocystis</i> & <i>Lessonia</i> kelp. Encrusting pink algae with <i>Phragmatopoma</i> and sabellids
47a	North Arm, creek before Main House	52° 06.828' S	059° 22.240' W	soft, shallow mud over rock/gravel
47b		52° 06.835' S	059° 22.224' W	
47c		between a&b		
48a	North Arm, around jetty & shearing sheds	52° 07.768' S	059° 22.131' W	mussel bed over silty coarse sand
48b		52° 07.829' S	059° 22.079' W	coarse loose sand
48c		52° 07.955' S	059° 22.111' W	split rock crevices on mussel beds
49a	New Haven	51° 43.862' S	059° 12.878' W	large rocks over loose sandy gravel
49b		51° 43.855' S	059° 12.894' W	
50a	Fox Bay West	51° 56.145' S	060° 04.764' W	fine sand
50b		51° 56.182' S	060° 04.746' W	"
50c		51° 56.199' S	060° 04.725' W	"
50d		51° 56.238' S	060° 04.612' W	"
50e		51° 56.235' S	060° 04.673' W	"

Site No.	Locality	Latitude	Longitude	Sediment Type Sampled
51a	Moonlight Bay, Port Stephens	52° 06.211' S	060° 50.364' W	coarse brown/grey sand
51b		52° 06.227' S	060° 50.361' W	"
51c		52° 06.232' S	060° 50.368' W	rock crevices split open & under rocks
51d		52° 06.266' S	060° 50.334' W	"
51e		52° 06.266' S	060° 50.336' W	soft sand
51f		52° 06.269' S	060° 50.305' W	"
52a	South Harbour	52° 00.201' S	060° 44.791' W	under rocks
52b		few m below a		fine sand, some tubes visible at surface
52c		52° 00.210' S	060° 44.841' W	rock ledges, overhangs, crevices
52d		few m below b		soft silty sand
53a	Chartres	51° 42.755' S	060° 04.710' W	shale & muddy gravel
53b		51° 42.761' S	060° 04.716' W	small ridges of rock split open
53c		51° 42.764' S	060° 04.705' W	soft black muddy sand
53d		51° 42.776' S	060° 04.717' W	"
53e		Chartres, Top Dip Shanty	51° 44.081' S	059° 59.209' W
54a	Dunbar, Hot Stone Cove Creek	51° 23.078' S	060° 30.919' W	soft sand
54b		as a		"
54c		51° 22.999' S	060° 30.909' W	soft fine grey sand
54d		51° 22.895' S	060° 30.892' W	under stones in fine sand
54e		51° 22.864' S	060° 30.891' W	exposed rock ledges & crevices with encrusting pink algae
54f		51° 22.883' S	060° 30.886' W	fine brown/grey sand, some tubes visible
54g		as f		fauna associated with large tunicate under rock
55a	Crooked Inlet, Roy Cove	51° 32.521' S	060° 20.810' W	soft black fine sand
55b		51° 32.546' S	060° 20.562' W	"
55c		51° 32.595' S	060° 20.367' W	"
55d		51° 32.664' S	060° 20.255' W	"
55e		51° 32.688' S	060° 20.244' W	"
56a	The Creek, Hill Cove	51° 30.094' S	060° 07.447' W	medium grey sand
56b		51° 30.067' S	060° 07.520' W	medium sand
56c		51° 30.058' S	060° 07.568' W	"
56d		51° 30.061' S	060° 07.618' W	under algae covered rocks in fine sand
56e		51° 30.053' S	060° 07.646' W	fine sand
56f		51° 30.040' S	060° 07.693' W	"
57a	Shallow Bay	51° 30.032' S	060° 07.726' W	seed mussel bed over fine sand & gravel
57b		as a		in crevices & under stones
57c		as a		"
57d		as a		shell/gravel/sand/stone
57e		as a		in crevices & under stones
58	West Lagoons	51° 28.012' S	060° 00.228' W	fine clean sand
59a	Port Howard	51° 36.983' S	059° 31.250' W	black, shelly medium sand & gravel
59b		51° 36.962' S	059° 31.252' W	as a with less gravel
59c		51° 36.958' S	059° 31.241' W	clean medium sand, many tubes

Table A5.2: Location and sampling details of sites visited in 2013 (dive site indicated in green)

Site No.	Locality	Latitude	Longitude	Sediment Type Sampled
60	Boathouse Jetty, Stanley	51° 41.498' S	057° 51.549' W	pelagic sample
61a	East Cove, Mare Harbour	51° 53.952' S	058° 26.134' W	thin sections of split rock
61b		51° 53.949' S	058° 25.827' W	large flat rocks, gravelly sediment below
61c		51° 53.955' S	058° 26.093' W	vertical ridges of layered rock
62	Wreck of the <i>Handel</i> , Stanley Harbour			kelp & soft, muddy seabed
63a	Rincon Grande	51° 28.241' S	058° 19.943' W	soft muddy sand, some gravel
63b		51° 28.238' S	058° 20.072' W	rocks & rocky ridges, little sediment
63c		51° 28.241' S	058° 19.943' W	small, flat rocks over coarse sandy gravel
63d		just below a		soft muddy sand, some gravel
63e		just below d		soft muddy sand, some gravel
64a	Settlement Bay (west), Bleaker Island	52° 12.388' S	058° 51.167' W	soft, muddy sand, black with some tubes
64b		few m from a		under rocks, organically rich with weed
64c		52° 12.396' S	058° 51.324' W	under rocks, in coarse gravelly sand
64d		few m from a		as a, more tubes consolidating sediment
65	harbour wall, Bleaker Island	52° 12.396' S	058° 51.324' W	pelagic sample
66a	southeast of larger Settlement Bay, Bleaker Island	52° 12.693' S	058° 52.002' W	under rocks in black, smelly sediment
66b		52° 12.742' S	058° 51.746' W	sand overlain by flaky calcareous alga
67a	north edge of Lafonia Point, Bleaker Island	52° 11.913' S	058° 51.424' W	under rocks & within calcareous algae
67b		as a		sievings from same as a
68	near Gypsy Cove, northeast of Stanley	51° 40.473' S	057° 49.001' W	ridges of bedrock with pink encrusting algae & kelp, silty sandy gravel in patches
69a	Walker Creek	51° 57.896' S	058° 46.618' W	muddy gravel, dead mussel shells, some algae
69b		51° 57.006' S	058° 46.538' W	coarse sand & gravel
69c		51° 58.011' S	058° 46.474' W	rocky mussel bed & flat rocks in sediment
70	Cape Pembroke	51° 40.878' S	057° 44.017' W	<i>Phragmatopoma</i> reef
71	Cow Point, Sea Lion Island	52° 25.287' S	059° 04.596' W	shallow sand from rock pool
72	North Beach, Sea Lion Island	52° 25.509' S	059° 03.526' W	<i>Macrocystis</i> bladders with <i>Spirorbinae</i>

Table A5.3: Location and sampling details of sites visited in 2015 (dive sites indicated in green)

Appendix 6

*Sample data from Falkland Islands fieldwork,
2011–2015*

Table A6.1: 2011 sites

Table A6.2: 2013 sites

Table A6.3: 2015 sites

Species	Station scrapping (sc) / sievings (si)	60	61a	61b	61c	61d	62	63a	63b	63c	63d	63e	64a	64b	64c	64d	65	66a	66b	67a	67b	67b	68	69a	69a	69b	69c	70	71	72	TOTAL	
		si										si										si										
<i>Capitella</i> sp. 2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	-	-	-	-	-	-	-	-	-	-	-	7	
<i>Capitella</i> sp. 3	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	1	-	-	-	-	3	-	-	-	-	3	-	-	-	7	16	
<i>Notomastus</i> sp. 1	-	-	-	-	-	-	-	-	-	6	1	-	-	-	-	2	-	-	-	1	-	-	-	-	-	-	-	-	-	-	10	
OPHELIIDAE																																
<i>Ophelia</i> sp. juv.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-	-	-	-	6	
ARENICOLIDAE																																
<i>Abarenicola wellsi</i>	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	
<i>Abarenicola brevior</i>	-	-	-	-	-	-	1	-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	5	
MALDANIDAE																																
<i>Euclymeninae</i> indet.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-	-	-	3	
<i>Clymenella minor</i>	-	-	-	-	-	5	4	2	-	3	6	-	-	-	3	-	1	3	1	-	2	-	7	2	5	-	-	-	-	-	44	
<i>Clymenella minor</i> ?	-	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	3	-	8	2	-	2	71	-	-	-	-	-	-	-	91	
<i>Praxillella kerguelensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	
<i>Micromaldane shackletoni</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-	-	2	
TEREBELLIDAE																																
<i>Terebellidae</i> sp. indet./juv.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	
<i>Neoleprea streptochaeta</i>	-	-	-	-	1	-	1	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	5	
<i>Nicolea chilensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	
<i>Thelepus</i> sp. 1	-	-	3	-	1	-	-	-	-	1	2	-	1	1	1	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	14	
? <i>Lanicola</i> sp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	
<i>Polycirrus multisetigerus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	2	
<i>Terebellidae</i> gen.1 sp.1	-	-	-	1	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	
SPIONIDAE																																
<i>Boccardia polybranchia</i> (=sp.1&3)	-	13	-	1	-	-	-	-	-	-	-	-	-	-	8	-	-	-	1	-	-	-	-	-	-	2	-	8	-	-	33	
<i>Prionospio</i> sp. 1	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	
<i>Rhynchospio</i> cf. <i>glutaea</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	23	1	4	-	-	-	-	-	11	-	-	40	
SABELLARIIDAE																																
<i>Phragmatopoma virgini</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	21	1	-	-	22	
SABELLIDAE																																
<i>Sabellidae</i> indet. Juv.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	
<i>Parasabella</i> sp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	
<i>Chone</i> sp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	3	-	-	-	4	
<i>Amphicorina alata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3	-	-	-	3	
<i>Amphicorina</i> cf. <i>limbata</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	12	12	-	-	-	-	-	-	-	24	
FABRICIIDAE																																
<i>Fabricia</i> sp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	2	
SERPULIDAE																																
<i>Spirorbinae</i> indet.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	P	
<i>Spirorbinae</i> sp.3 (=8)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	
<i>Paralaeospira claparedei</i> (=sp. 7)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	
<i>Spirorbinae</i> sp.11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	
NERILLIDAE																																
<i>Mesonerilla</i> sp. 1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	2	
POLYGORDIIDAE																																
<i>Polygordius</i> sp. indet.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	
TOTAL		4	16	38	6	6	14	8	22	7	17	11	13	24	21	17	16	5	1043	27	1314	104	101	228	228	28	38	79	34	P	3469	

Table A6.3: Raw data for all samples collected in 2015. P = species present in large numbers, greater than 100, but too difficult to count accurately; a nominal value of 100 was used in analyses for such samples. (Note: this is the raw data, not that used for analysis.)

Appendix 7

Dendrograms and MDS plots from statistical analyses

Figure A7.1a–b: Cluster analysis of all samples

Figure A7.2a–d: MDS plots for all samples

Figure A7.3a–b: MDS plot for stations

***Figure A7.4a–f: Cluster analysis and MDS
plots for sievings***

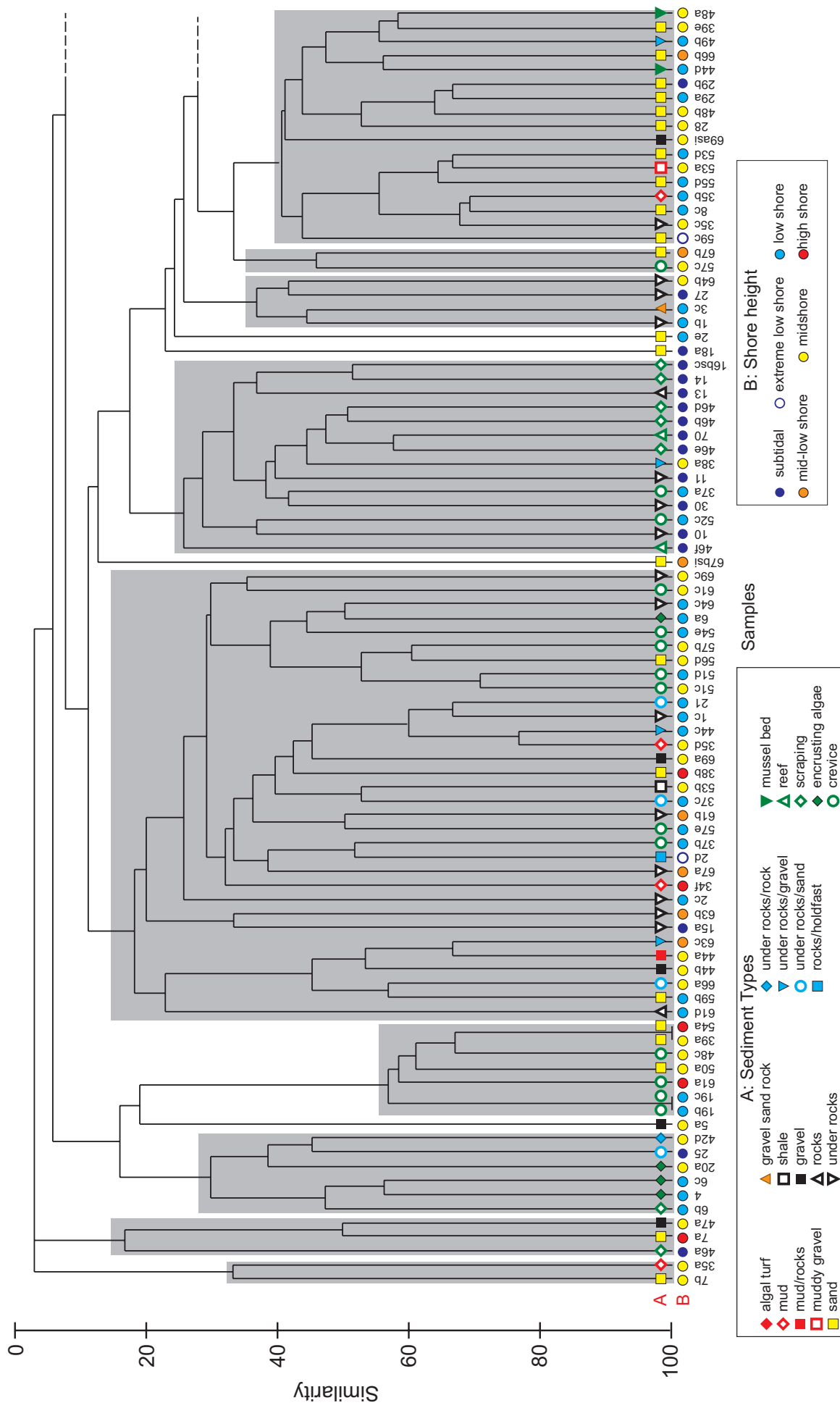


Figure A7.1a: Bray-Curtis classification of all samples used for analysis (presence-absence data). Significant clusters shaded grey and samples coded with shore height and sediment type information. Second half of dendrogram on next page.

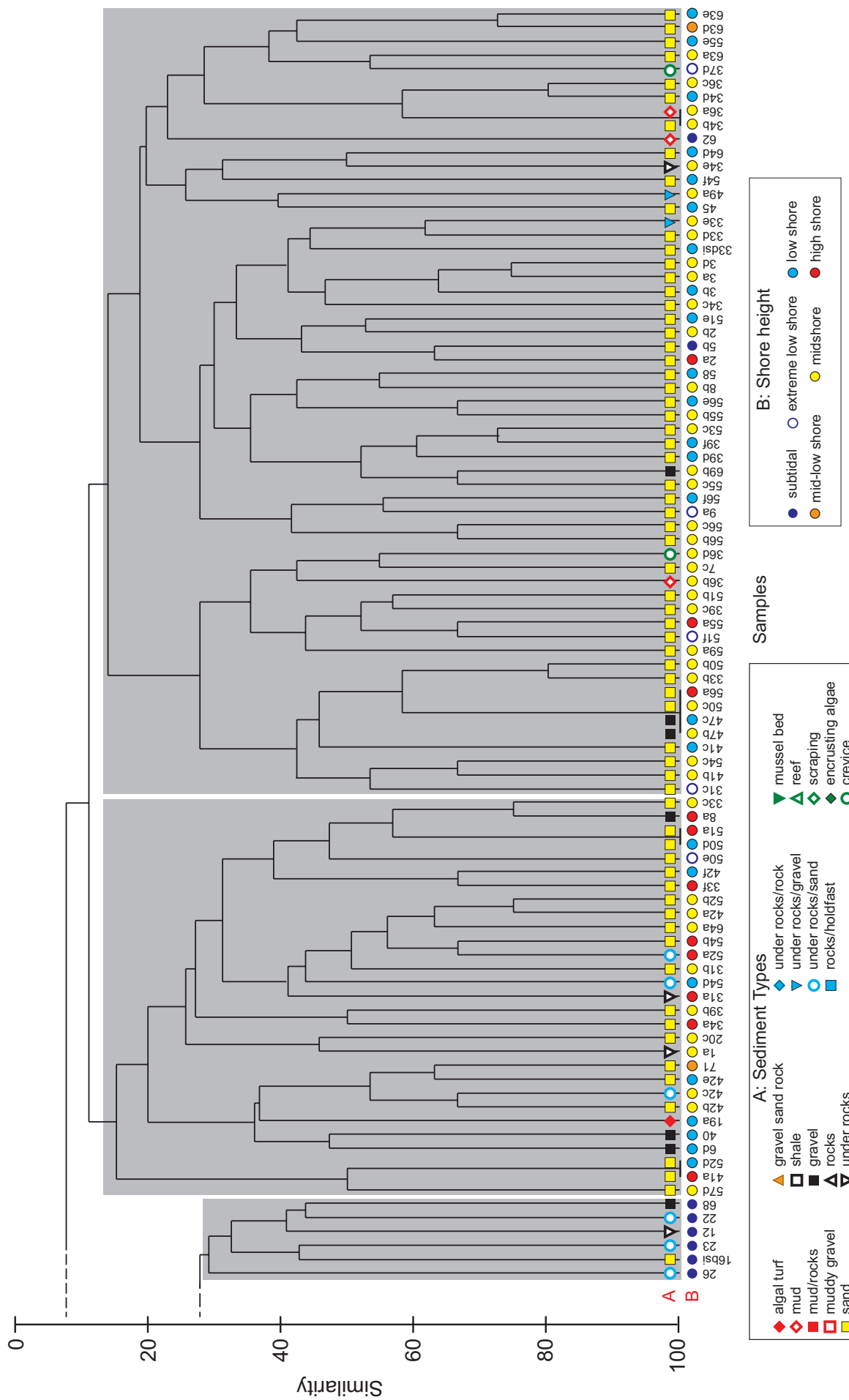


Figure A7.1b: Bray-Curtis classification of all samples used for analysis (presence-absence data). Significant clusters shaded grey and samples coded with shore height and sediment type information. First half of dendrogram on previous page.

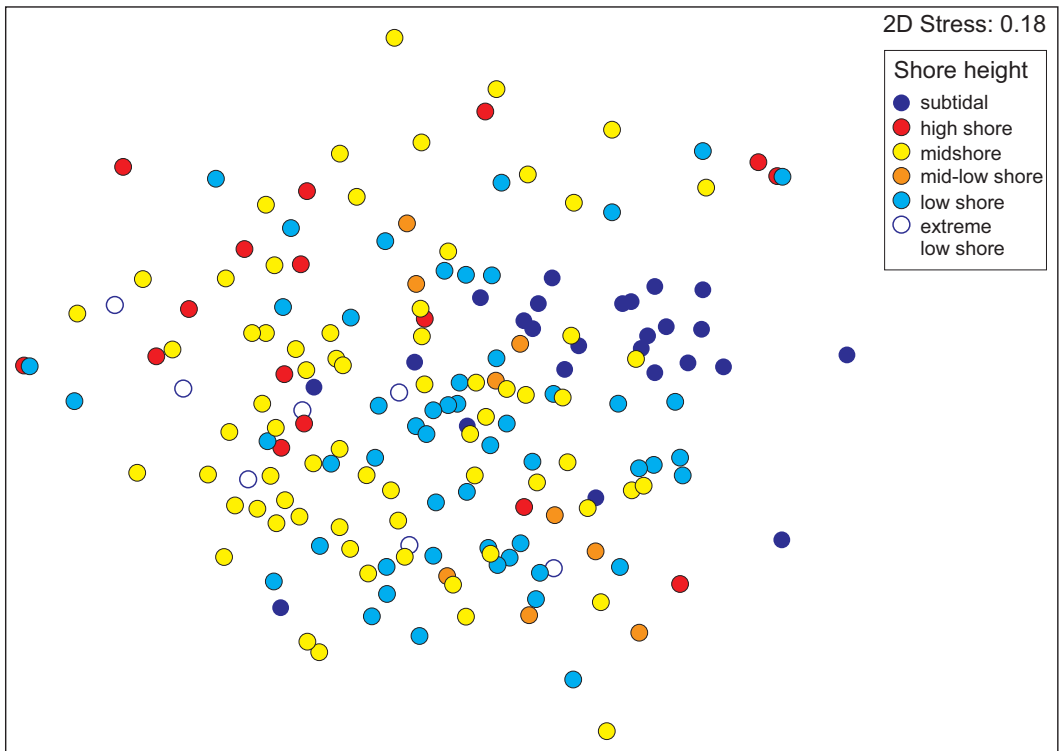
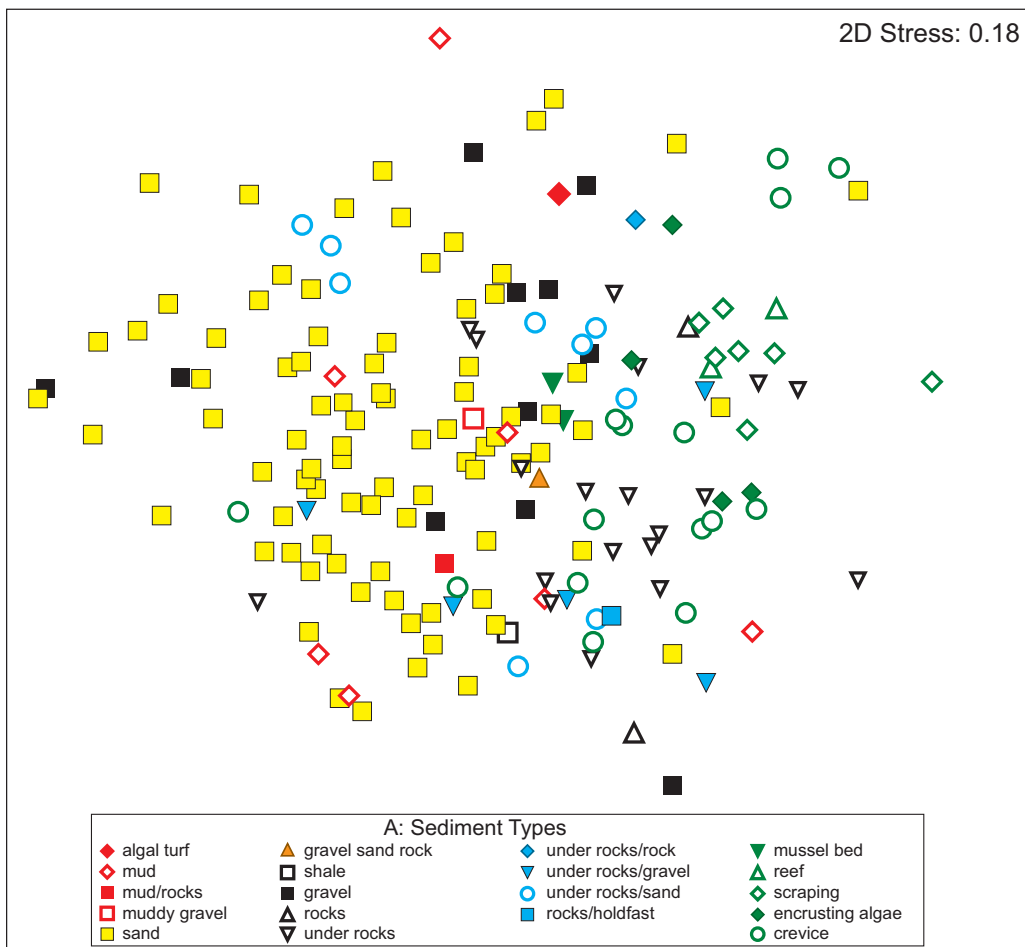


Figure A7.2a: Multi-dimensional scaling (MDS) ordination of samples with shore height plotted. Sample labels omitted for clarity.

Figure A7.2b: Multi-dimensional scaling (MDS) ordination of samples with sediment types plotted. Sample labels omitted for clarity.



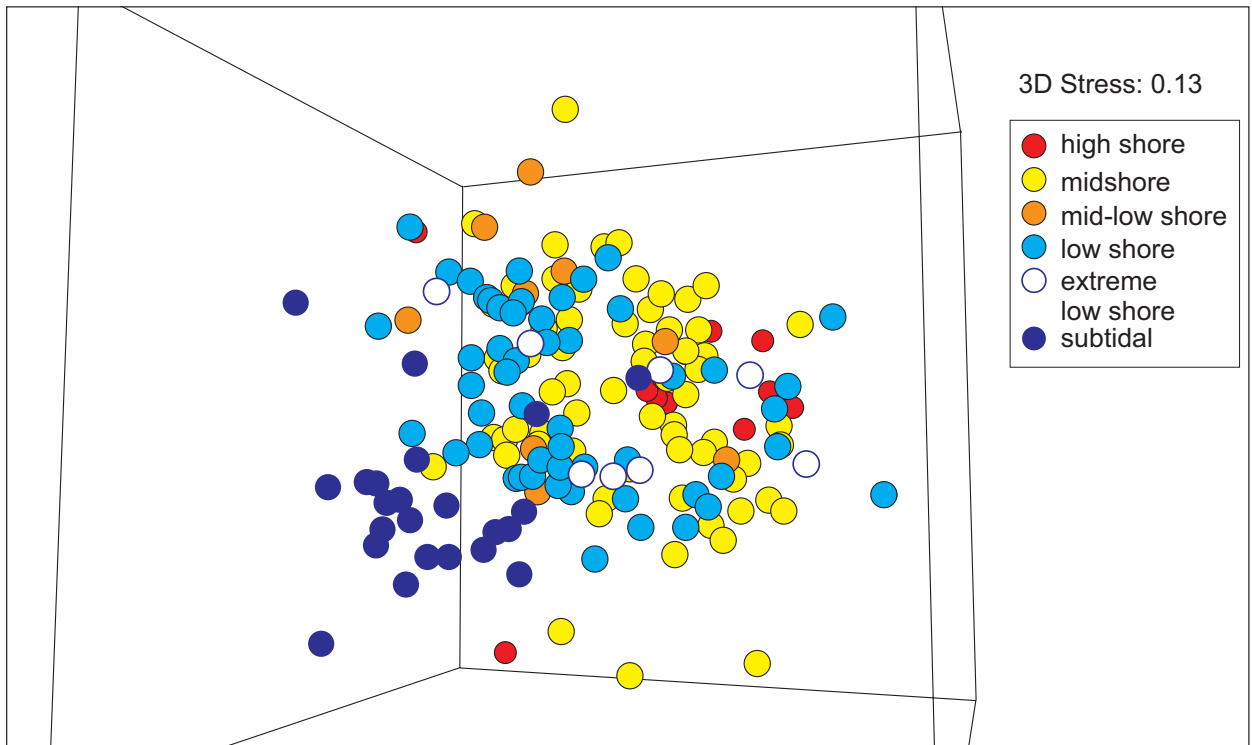
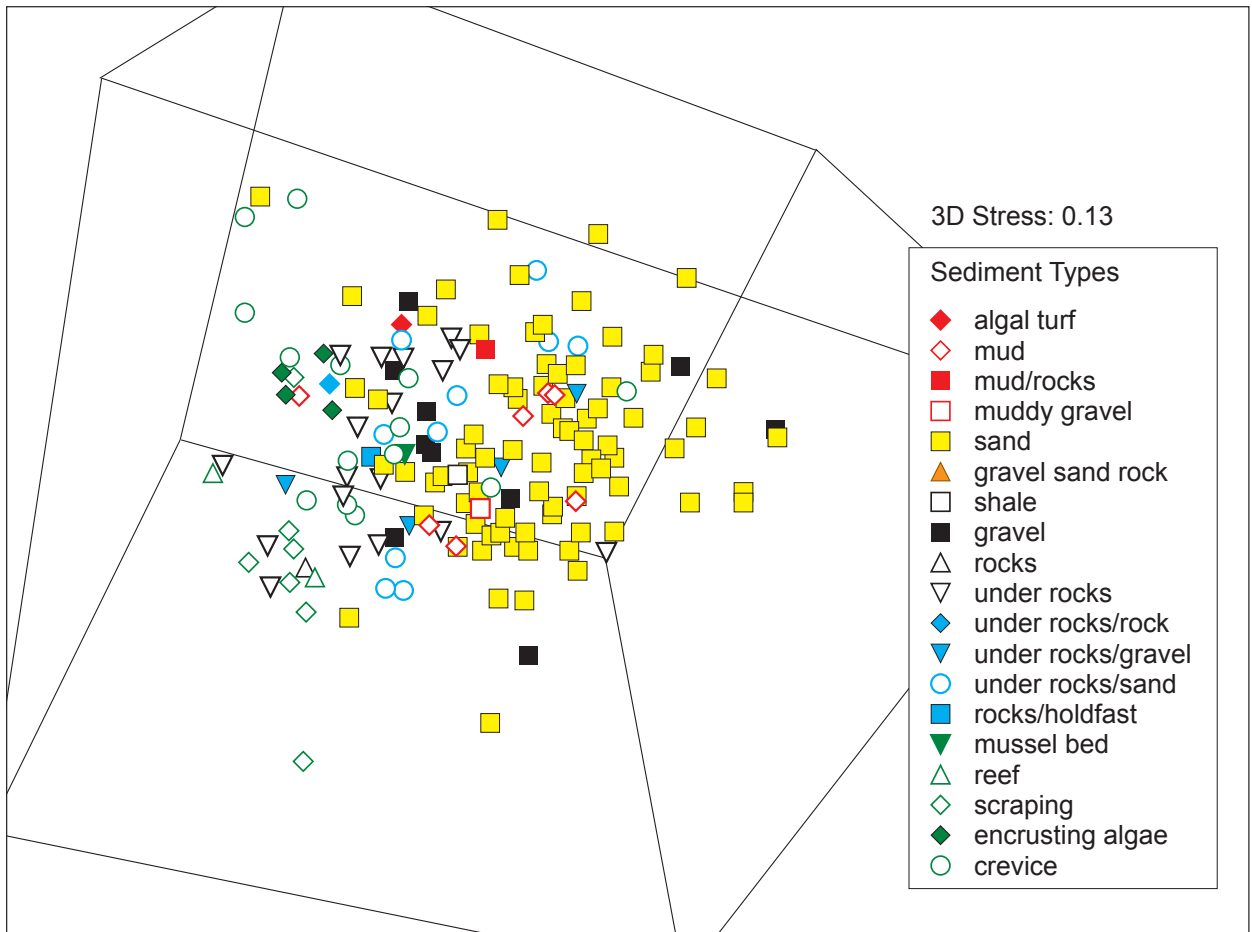


Figure A7.2c: Multi-dimensional scaling (MDS) ordination of samples with shore height plotted. Sample labels omitted for clarity.

Figure A7.2d: 3D Multi-dimensional scaling (MDS) ordination of samples with sediment types plotted. Sample labels omitted for clarity.



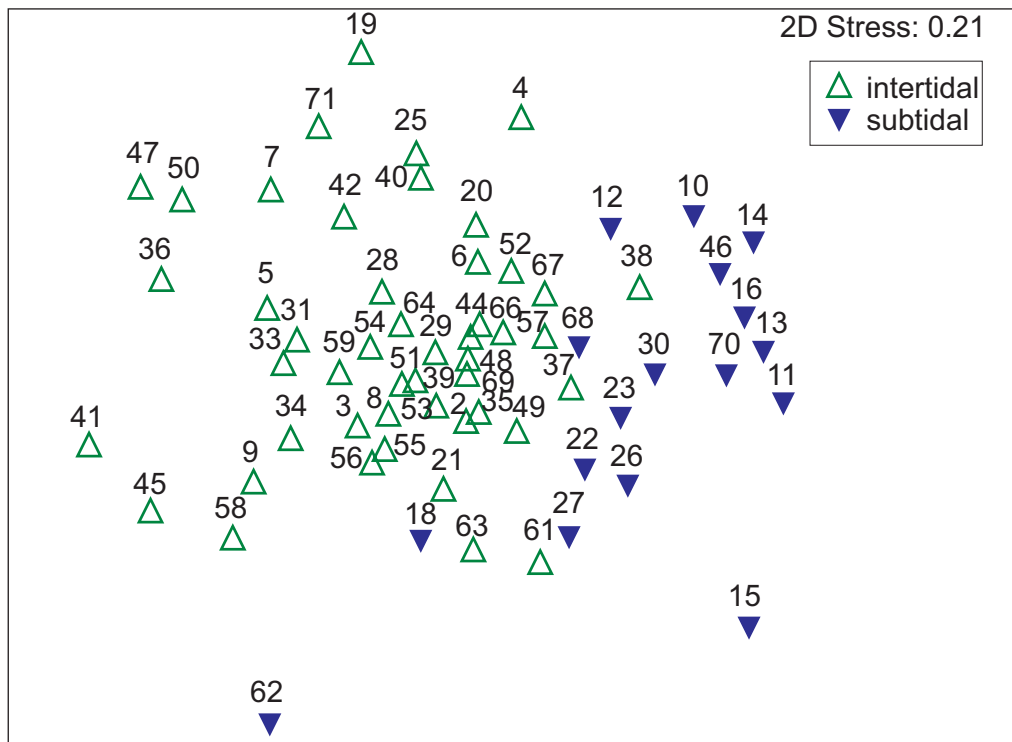
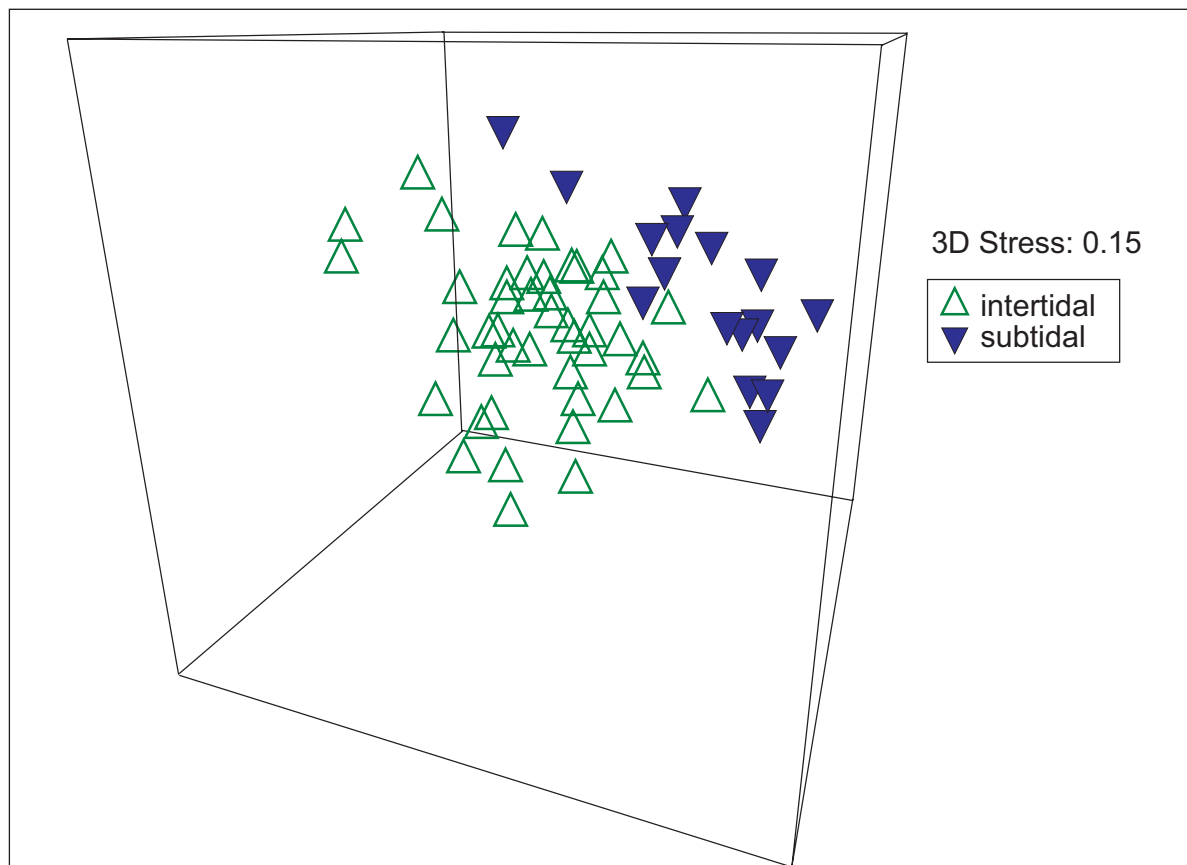


Figure A7.3a: Multi-dimensional scaling (MDS) ordination of stations with depth (intertidal/subtidal) plotted.

Figure A7.3b: 3D Multi-dimensional scaling (MDS) ordination of stations with depth (intertidal/subtidal) plotted. Labels omitted for clarity.



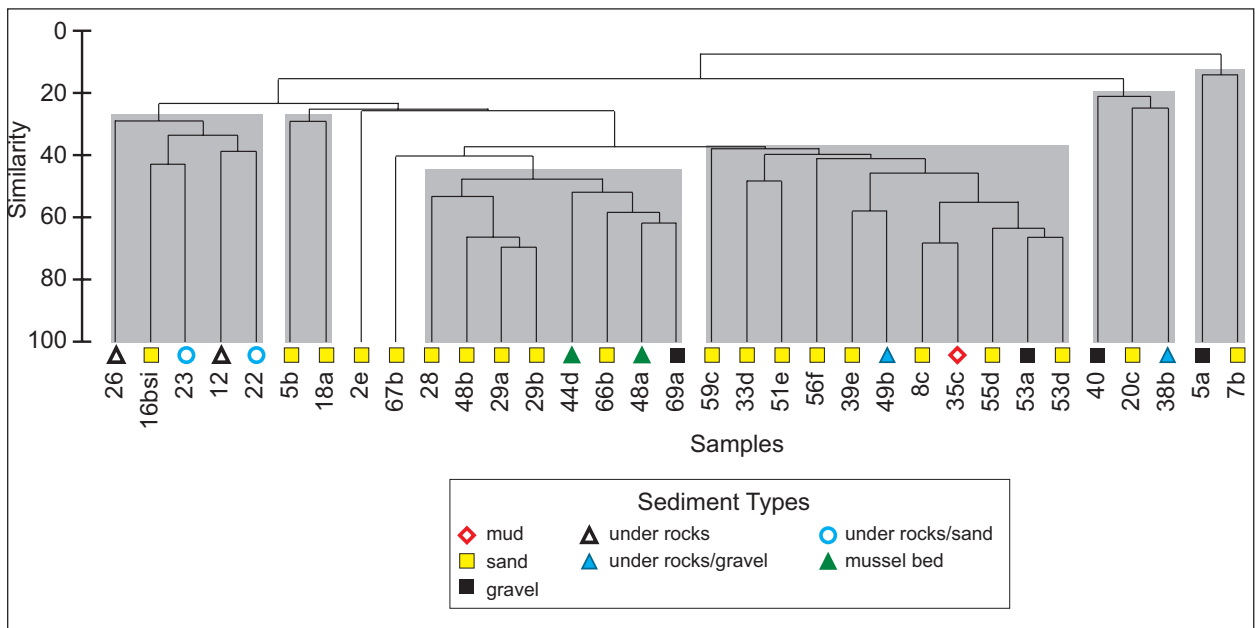


Figure A7.4a: Bray-Curtis classification of sievings samples (presence-absence data; clusters of non-significantly different ($P < 0.05$) samples shaded grey).

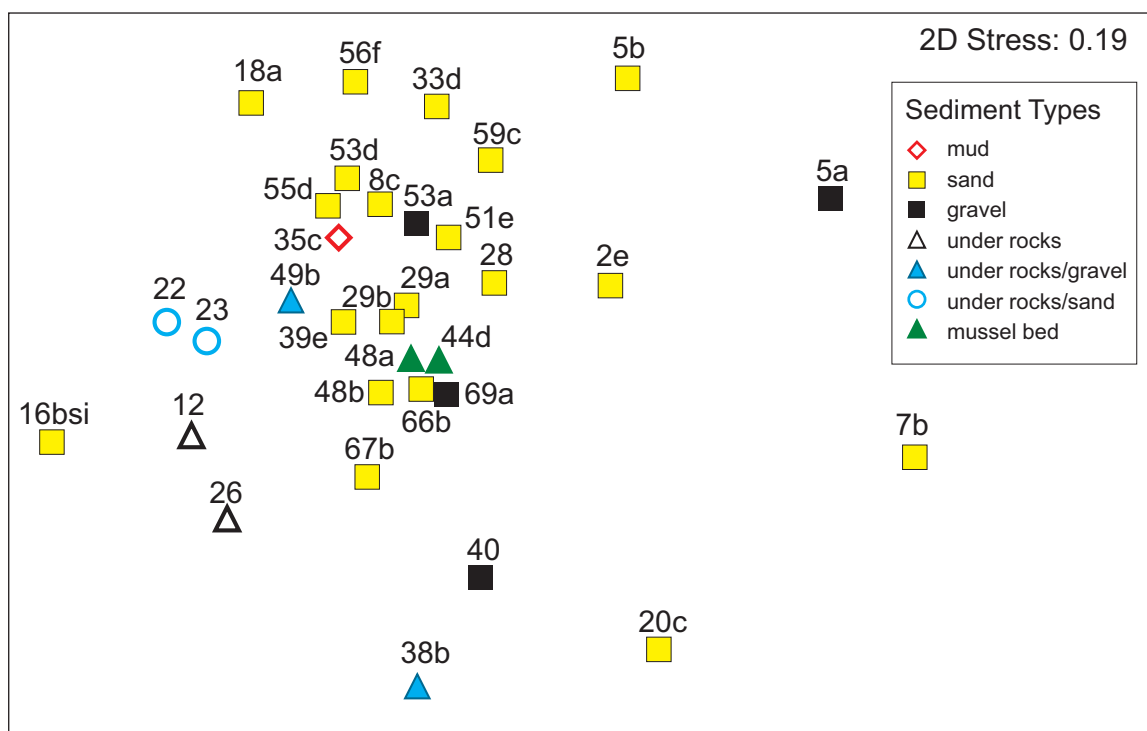


Figure A7.4b: Multi-dimensional scaling (MDS) ordination of sievings with sediment type plotted.

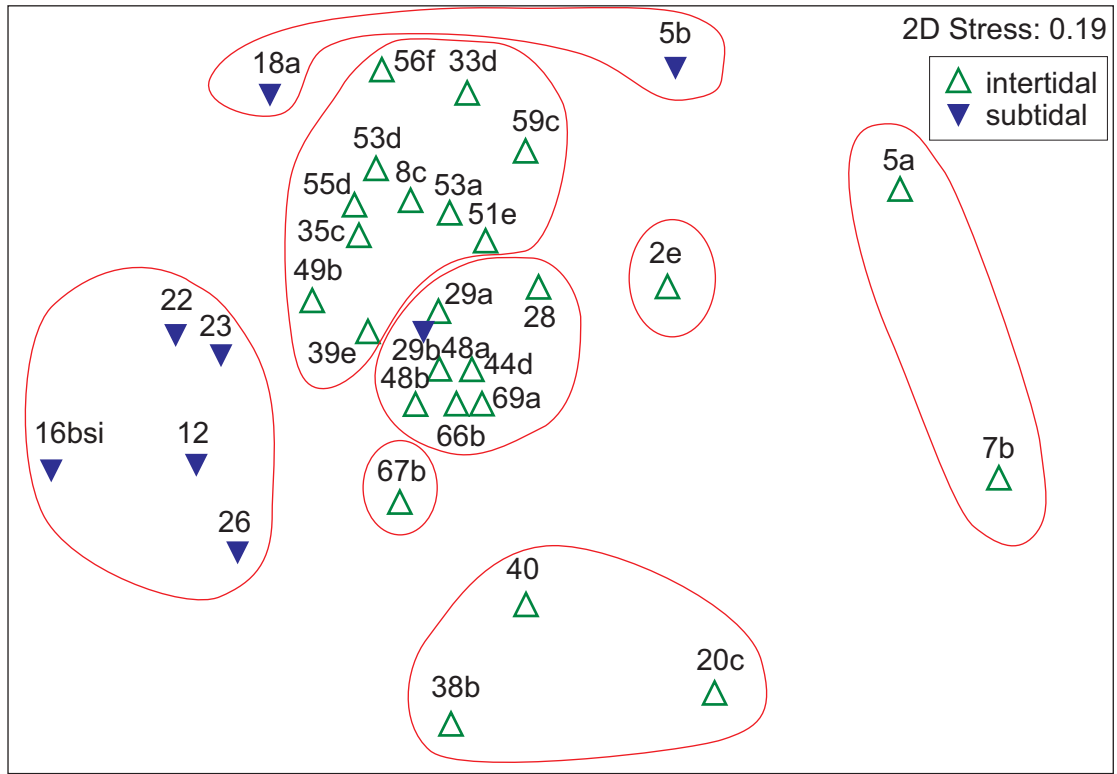
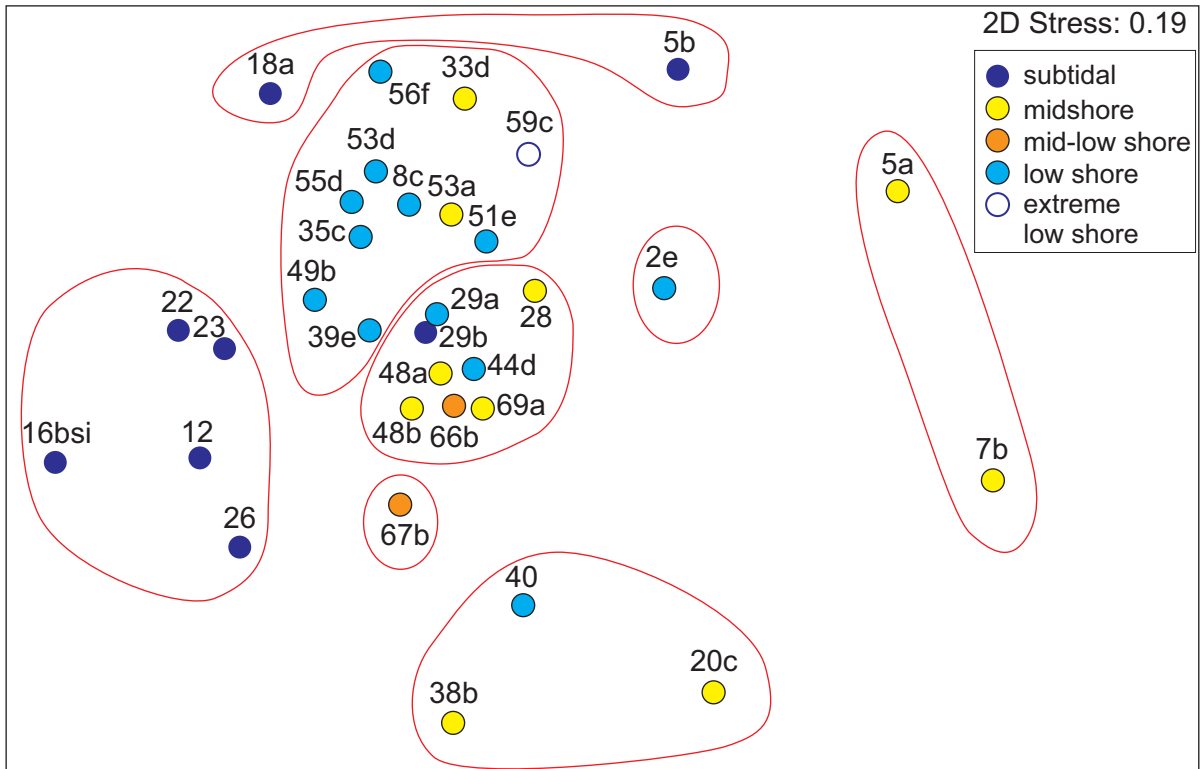


Figure A7.4c: Multi-dimensional scaling (MDS) ordination of sievings samples with depth (intertidal/subtidal) plotted and clusters overlain.

Figure A7.4d: Multi-dimensional scaling (MDS) ordination of sievings samples with shore height plotted and clusters overlain.



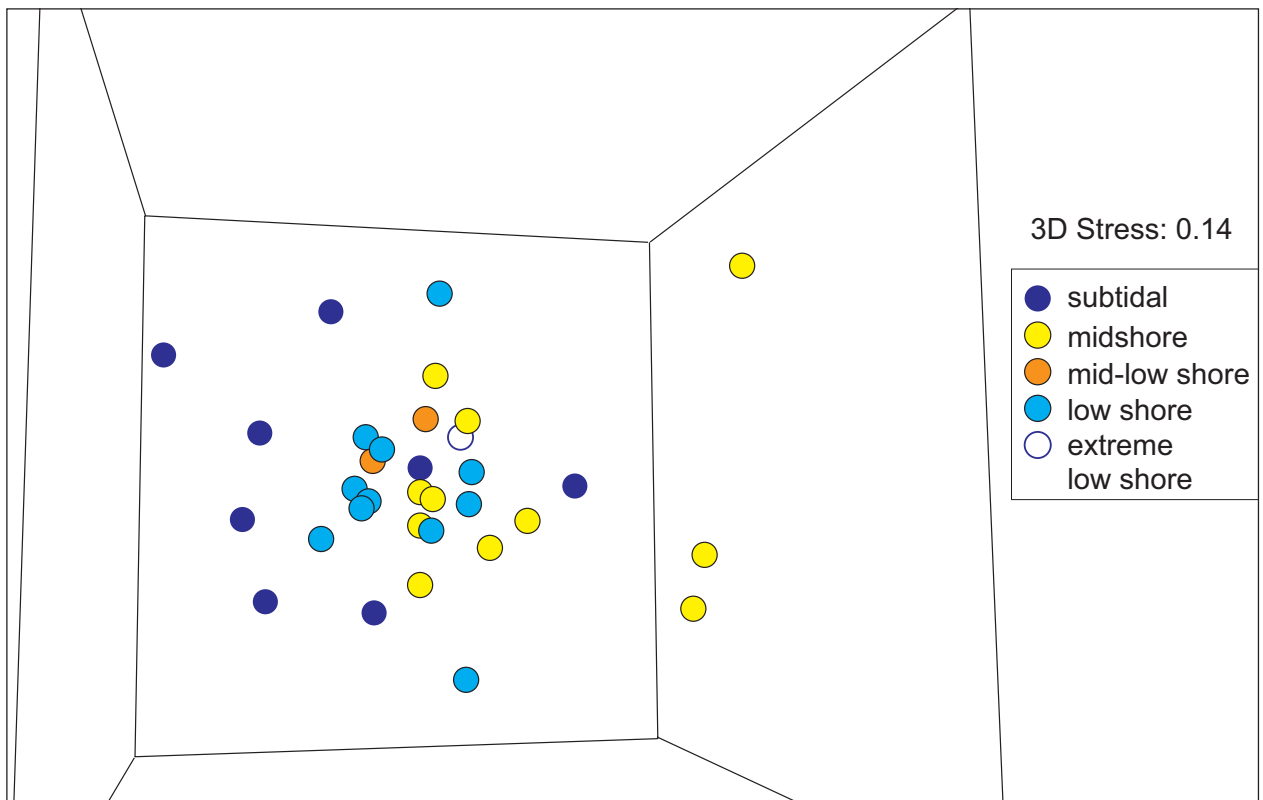
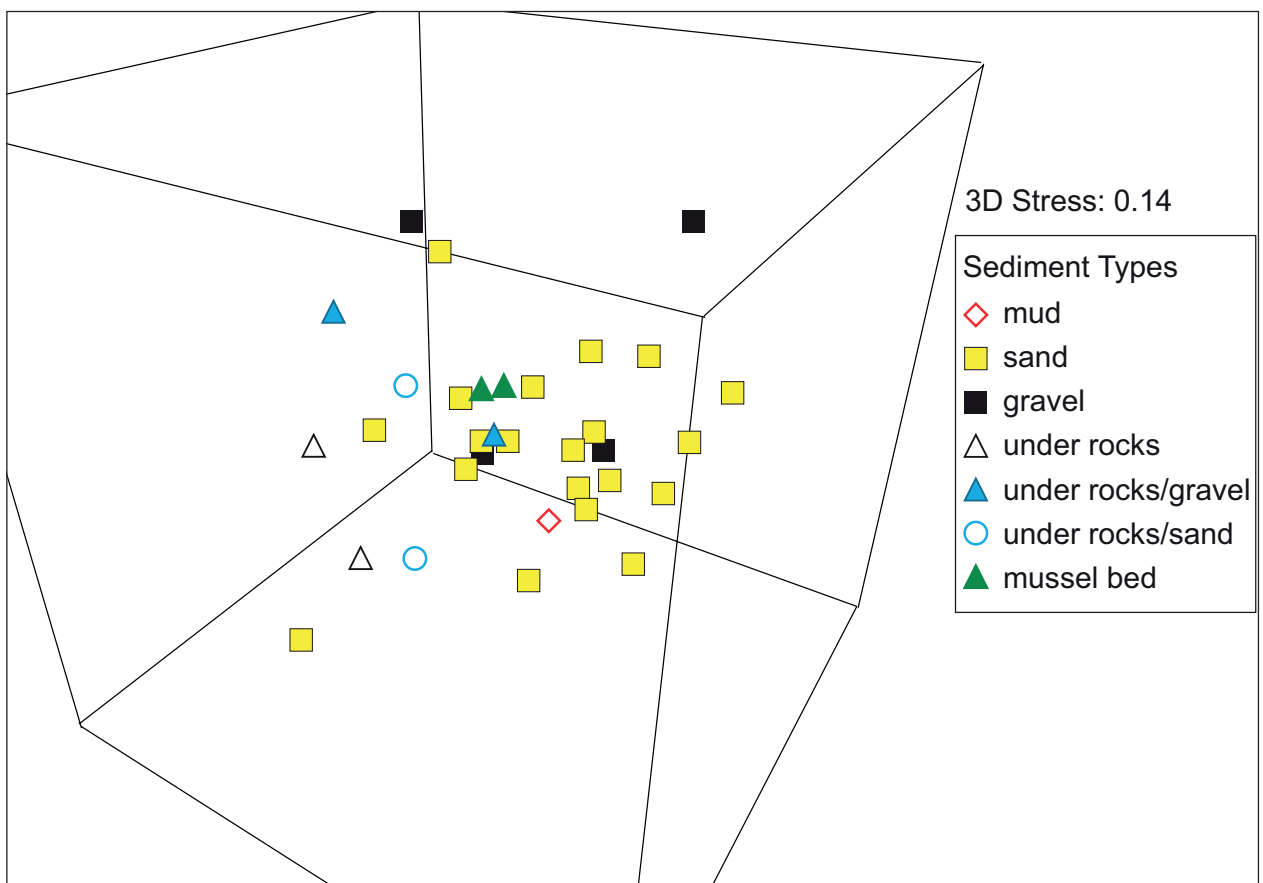


Figure A7.4e: 3D Multi-dimensional scaling (MDS) ordination of sievings samples with shore height plotted.

Figure A7.4f: 3D Multi-dimensional scaling (MDS) ordination of sievings samples with sediment type plotted.



Appendix 8

Taxonomic distinctness values

Table A8.1: All samples

a. ranked by average taxonomic distinctness (Δ^+)

b. ranked by variation in taxonomic distinctness (Δ^+)

Table A8.2: All stations

a. ranked by average taxonomic distinctness (Δ^+)

b. ranked by variation in taxonomic distinctness (Δ^+)

Table A8.3: Sievings samples

a. ranked by average taxonomic distinctness (Δ^+)

b. ranked by variation in taxonomic distinctness (Δ^+)

Rank	Sample	Δ^+	Λ^+	Rank	Sample	Δ^+	Λ^+	Rank	Sample	Δ^+	Λ^+	Rank	Sample	Δ^+	Λ^+
1	3a	100	0	48	63a	100	0	95	56f	96.83	138.07	142	16bsi	93.77	193.21
2	3d	100	0	49	63c	100	0	96	64c	96.83	95.74	143	46b	93.70	201.96
3	7a	100	0	50	63d	100	0	97	13	96.83	116.91	144	69b	93.65	277.15
4	7c	100	0	51	63e	100	0	98	29a	96.67	131.75	145	64b	93.52	235.77
5	15a	100	0	52	64a	100	0	99	6c	96.58	130.76	146	23	93.46	204.19
6	19b	100	0	53	66a	100	0	100	37a	96.45	134.14	147	27	93.33	220.11
7	19c	100	0	54	31a	99.07	30.01	101	71	96.43	185.66	148	39d	93.33	325.93
8	20c	100	0	55	67a	99.07	30.01	102	28	96.30	124.26	149	52b	93.33	400.00
9	31c	100	0	56	25	98.99	32.65	103	48b	96.30	167.84	150	55c	93.33	400.00
10	33b	100	0	57	57e	98.73	40.72	104	11	96.08	131.68	151	58	93.33	325.93
11	33c	100	0	58	40	98.53	46.69	105	69a	95.96	219.37	152	61d	93.33	325.93
12	33d	100	0	59	37d	98.52	47.19	106	51e	95.86	193.47	153	8b	93.33	400.00
13	33e	100	0	60	63b	98.48	48.21	107	55d	95.83	158.56	154	52a	93.33	400.00
14	33f	100	0	61	2c	98.41	50.39	108	39f	95.56	276.54	155	16bsc	93.11	238.23
15	34a	100	0	62	42d	98.41	50.39	109	51c	95.56	128.40	156	29b	93.03	270.93
16	34c	100	0	63	5a	98.41	50.39	110	56e	95.56	276.54	157	49b	92.81	231.53
17	34d	100	0	64	44c	98.41	50.39	111	3c	95.56	128.40	158	46e	92.34	258.01
18	34e	100	0	65	1c	98.15	58.30	112	2d	95.56	149.56	159	46d	90.33	305.76
19	36c	100	0	66	51d	98.15	58.30	113	38a	95.51	177.87	160	35c	89.74	293.67
20	39b	100	0	67	53b	98.15	58.30	114	6b	95.45	164.52	161	42b	88.89	617.28
21	39c	100	0	68	18a	98.10	81.03	115	42e	95.37	194.62	162	50e	88.89	617.28
22	41b	100	0	69	46f	98.05	74.83	116	53d	95.26	170.54	163	2e	88.89	352.73
23	41c	100	0	70	21	97.98	96.93	117	6a	95.24	136.05	164	19a	88.10	493.20
24	42a	100	0	71	22	97.78	90.87	118	33dsi	95.24	136.05	165	8c	88.06	366.59
25	44a	100	0	72	10	97.78	87.65	119	30	95.18	163.53	166	35b	84.34	377.77
26	45	100	0	73	35d	97.78	69.14	120	70	95.16	169.64	167	42c	77.78	987.65
27	47a	100	0	74	62	97.78	69.14	121	6d	95.00	197.22	168	46a	77.78	617.28
28	48c	100	0	75	51b	97.78	69.14	122	48a	94.99	185.49	169	34f	66.67	0
29	49a	100	0	76	57b	97.78	69.14	123	1b	94.87	169.06	170	46c	66.67	0
30	50b	100	0	77	1a	97.62	153.06	124	68	94.86	162.44	171	50a	66.67	0
31	50d	100	0	78	36b	97.62	153.06	125	59c	94.81	195.34	172	33a	0	0
32	51a	100	0	79	64d	97.62	73.70	126	57c	94.71	160.13	173	34b	0	0
33	51f	100	0	80	12	97.60	103.19	127	20a	94.55	195.46	174	35a	0	0
34	53c	100	0	81	61b	97.58	115.34	128	5b	94.55	313.68	175	36a	0	0
35	54b	100	0	82	2b	97.58	155.74	129	67b	94.46	181.29	176	39a	0	0
36	54c	100	0	83	67bsi	97.58	115.34	130	7b	94.44	154.32	177	41a	0	0
37	54d	100	0	84	9a	97.47	145.14	131	8a	94.44	154.32	178	42f	0	0
38	54f	100	0	85	52c	97.11	107.11	132	31b	94.44	339.51	179	44b	0	0
39	55a	100	0	86	26	97.08	88.92	133	36d	94.44	154.32	180	47b	0	0
40	56b	100	0	87	37c	97.04	89.99	134	55e	94.44	154.32	181	47c	0	0
41	56c	100	0	88	54e	97.04	139.37	135	69asi	94.44	239.79	182	50c	0	0
42	56d	100	0	89	38b	96.97	91.83	136	14	94.33	193.94	183	52d	0	0
43	57d	100	0	90	4	96.97	132.23	137	39e	94.29	200.15	184	53e	0	0
44	59a	100	0	91	2a	96.83	201.56	138	44d	94.29	231.90	185	54a	0	0
45	59b	100	0	92	37b	96.83	95.74	139	69c	93.94	266.30	186	56a	0	0
46	61a	100	0	93	55b	96.83	201.56	140	53a	93.90	224.23	187	57a	0	0
47	61c	100	0	94	3b	96.83	201.56	141	66b	93.89	240.43				

Table A8.1a: Taxonomic distinctness values for all samples used in statistical analysis, ranked by average taxonomic distinctness, Δ^+

Rank	Sample	Δ^+	Λ^+	Rank	Sample	Δ^+	Λ^+	Rank	Sample	Δ^+	Λ^+	Rank	Sample	Δ^+	Λ^+
1	42c	77.78	987.65	48	71	96.43	185.66	95	18a	98.10	81.03	142	39c	100	0
2	42b	88.89	617.28	49	48a	94.99	185.49	96	46f	98.05	74.83	143	41a	0	0
3	46a	77.78	617.28	50	67b	94.46	181.29	97	64d	97.62	73.70	144	41b	100	0
4	50e	88.89	617.28	51	38a	95.51	177.87	98	51b	97.78	69.14	145	41c	100	0
5	19a	88.10	493.20	52	53d	95.26	170.54	99	57b	97.78	69.14	146	42a	100	0
6	52b	93.33	400.00	53	70	95.16	169.64	100	62	97.78	69.14	147	42f	0	0
7	55c	93.33	400.00	54	1b	94.87	169.06	101	35d	97.78	69.14	148	44a	100	0
8	8b	93.33	400.00	55	48b	96.30	167.84	102	53b	98.15	58.30	149	44b	0	0
9	52a	93.33	400.00	56	6b	95.45	164.52	103	1c	98.15	58.30	150	45	100	0
10	35b	84.34	377.77	57	30	95.18	163.53	104	51d	98.15	58.30	151	46c	66.67	0
11	8c	88.06	366.59	58	68	94.86	162.44	105	5a	98.41	50.39	152	47a	100	0
12	2e	88.89	352.73	59	57c	94.71	160.13	106	44c	98.41	50.39	153	47b	0	0
13	31b	94.44	339.51	60	55d	95.83	158.56	107	42d	98.41	50.39	154	47c	0	0
14	39d	93.33	325.93	61	2b	97.58	155.74	108	2c	98.41	50.39	155	48c	100	0
15	58	93.33	325.93	62	7b	94.44	154.32	109	63b	98.48	48.21	156	49a	100	0
16	61d	93.33	325.93	63	8a	94.44	154.32	110	37d	98.52	47.19	157	50a	66.67	0
17	5b	94.55	313.68	64	36d	94.44	154.32	111	40	98.53	46.69	158	50b	100	0
18	46d	90.33	305.76	65	55e	94.44	154.32	112	57e	98.73	40.72	159	50c	0	0
19	35c	89.74	293.67	66	1a	97.62	153.06	113	25	98.99	32.65	160	50d	100	0
20	69b	93.65	277.15	67	36b	97.62	153.06	114	31a	99.07	30.01	161	51a	100	0
21	39f	95.56	276.54	68	2d	95.56	149.56	115	67a	99.07	30.01	162	51f	100	0
22	56e	95.56	276.54	69	9a	97.47	145.14	116	3a	100	0	163	52d	0	0
23	29b	93.03	270.93	70	54e	97.04	139.37	117	3d	100	0	164	53c	100	0
24	69c	93.94	266.30	71	56f	96.83	138.07	118	7a	100	0	165	53e	0	0
25	46e	92.34	258.01	72	33dsi	95.24	136.05	119	7c	100	0	166	54a	0	0
26	66b	93.89	240.43	73	6a	95.24	136.05	120	15a	100	0	167	54b	100	0
27	69asi	94.44	239.79	74	37a	96.45	134.14	121	19b	100	0	168	54c	100	0
28	16bsc	93.11	238.23	75	4	96.97	132.23	122	19c	100	0	169	54d	100	0
29	64b	93.52	235.77	76	29a	96.67	131.75	123	20c	100	0	170	54f	100	0
30	44d	94.29	231.90	77	11	96.08	131.68	124	31c	100	0	171	55a	100	0
31	49b	92.81	231.53	78	6c	96.58	130.76	125	33a	0	0	172	56a	0	0
32	53a	93.90	224.23	79	3c	95.56	128.40	126	33b	100	0	173	56b	100	0
33	27	93.33	220.11	80	51c	95.56	128.40	127	33c	100	0	174	56c	100	0
34	69a	95.96	219.37	81	28	96.30	124.26	128	33d	100	0	175	56d	100	0
35	23	93.46	204.19	82	13	96.83	116.91	129	33e	100	0	176	57a	0	0
36	46b	93.70	201.96	83	67bsi	97.58	115.34	130	33f	100	0	177	57d	100	0
37	2a	96.83	201.56	84	61b	97.58	115.34	131	34a	100	0	178	59a	100	0
38	55b	96.83	201.56	85	52c	97.11	107.11	132	34b	0	0	179	59b	100	0
39	3b	96.83	201.56	86	12	97.60	103.19	133	34c	100	0	180	61a	100	0
40	39e	94.29	200.15	87	21	97.98	96.93	134	34d	100	0	181	61c	100	0
41	6d	95.00	197.22	88	64c	96.83	95.74	135	34e	100	0	182	63a	100	0
42	20a	94.55	195.46	89	37b	96.83	95.74	136	34f	66.67	0	183	63c	100	0
43	59c	94.81	195.34	90	38b	96.97	91.83	137	35a	0	0	184	63d	100	0
44	42e	95.37	194.62	91	22	97.78	90.87	138	36a	0	0	185	63e	100	0
45	14	94.33	193.94	92	37c	97.04	89.99	139	36c	100	0	186	64a	100	0
46	51e	95.86	193.47	93	26	97.08	88.92	140	39a	0	0	187	66a	100	0
47	16bsi	93.77	193.21	94	10	97.78	87.65	141	39b	100	0				

Table A8.1b: Taxonomic distinctness values for all samples used in statistical analysis, ranked by variation in taxonomic distinctness, Λ^+

Rank	Sample	Δ^+	Λ^+	Rank	Sample	Δ^+	Λ^+	Rank	Sample	Δ^+	Λ^+	Rank	Sample	Δ^+	Λ^+
1	15	100	0	18	62	97.78	69.14	35	13	96.83	116.91	52	30	95.35	152.05
2	45	100	0	19	36	97.78	118.52	36	69	96.78	132.68	53	70	94.78	197.47
3	47	100	0	20	64	97.76	95.99	37	53	96.70	129.63	54	68	94.73	174.25
4	21	98.99	32.65	21	51	97.62	97.21	38	38	96.66	138.10	55	32	94.44	154.32
5	63	98.64	43.62	22	56	97.60	103.19	39	29	96.62	125.44	56	66	94.44	191.36
6	18	98.61	44.37	23	55	97.54	87.53	40	46	96.52	127.85	57	16	94.36	184.33
7	54	98.56	68.28	24	9	97.47	145.14	41	61	96.51	176.67	58	49	94.21	194.55
8	40	98.53	46.69	25	26	97.47	91.04	42	42	96.51	188.86	59	14	93.86	197.72
9	25	98.48	81.88	26	31	97.46	120.53	43	71	96.43	185.66	60	50	93.65	171.33
10	10	98.26	55.06	27	34	97.44	107.39	44	4	96.36	188.80	61	23	93.46	189.67
11	3	98.04	77.85	28	37	97.41	97.63	45	11	96.32	109.03	62	27	93.33	220.11
12	5	98.04	77.85	29	59	97.22	103.40	46	57	96.24	119.76	63	41	93.33	400.00
13	2	97.98	67.62	30	1	97.11	116.73	47	44	96.10	162.59	64	35	92.98	236.65
14	22	97.87	83.02	31	48	97.10	104.32	48	7	95.76	204.22	65	8	92.54	277.68
15	52	97.87	77.55	32	33	97.07	113.51	49	6	95.68	172.39	66	19	88.10	493.20
16	12	97.82	96.92	33	67	96.98	105.54	50	28	95.64	169.83				
17	58	97.78	69.14	34	39	96.91	120.37	51	20	95.40	185.16				

Table A8.2a: Taxonomic distinctness values for all stations used in statistical analysis, ranked by average taxonomic distinctness, Δ^+

Rank	Sample	Δ^+	Λ^+	Rank	Sample	Δ^+	Λ^+	Rank	Sample	Δ^+	Λ^+	Rank	Sample	Δ^+	Λ^+
1	19	88.10	493.20	18	68	94.73	174.25	35	13	96.83	116.91	52	3	98.04	77.85
2	41	93.33	400.00	19	6	95.68	172.39	36	1	97.11	116.73	53	5	98.04	77.85
3	8	92.54	277.68	20	50	93.65	171.33	37	33	97.07	113.51	54	52	97.87	77.55
4	35	92.98	236.65	21	28	95.64	169.83	38	11	96.32	109.03	55	62	97.78	69.14
5	27	93.33	220.11	22	44	96.10	162.59	39	34	97.44	107.39	56	58	97.78	69.14
6	7	95.76	204.22	23	32	94.44	154.32	40	67	96.98	105.54	57	54	98.56	68.28
7	14	93.86	197.72	24	30	95.35	152.05	41	48	97.10	104.32	58	2	97.98	67.62
8	70	94.78	197.47	25	9	97.47	145.14	42	59	97.22	103.40	59	10	98.26	55.06
9	49	94.21	194.55	26	38	96.66	138.10	43	56	97.60	103.19	60	40	98.53	46.69
10	66	94.44	191.36	27	69	96.78	132.68	44	37	97.41	97.63	61	18	98.61	44.37
11	23	93.46	189.67	28	53	96.70	129.63	45	51	97.62	97.21	62	63	98.64	43.62
12	42	96.51	188.86	29	46	96.52	127.85	46	12	97.82	96.92	63	21	98.99	32.65
13	4	96.36	188.80	30	29	96.62	125.44	47	64	97.76	95.99	64	15	100	0
14	71	96.43	185.66	31	31	97.46	120.53	48	26	97.47	91.04	65	45	100	0
15	20	95.40	185.16	32	39	96.91	120.37	49	55	97.54	87.53	66	47	100	0
16	16	94.36	184.33	33	57	96.24	119.76	50	22	97.87	83.02				
17	61	96.51	176.67	34	36	97.78	118.52	51	25	98.48	81.88				

Table A8.2b: Taxonomic distinctness values for all stations used in statistical analysis, ranked by variation in taxonomic distinctness, Λ^+

Rank	Sample	Δ^+	Λ^+	Rank	Sample	Δ^+	Λ^+
1	20c	100	0	18	28	95.64	169.83
2	40	98.53	46.69	19	59c	95.56	128.40
3	18a	98.41	50.39	20	48a	95.21	165.84
4	5a	98.41	50.39	21	53d	94.91	202.19
5	22	97.87	83.02	22	39e	94.44	186.07
6	12	97.82	96.92	23	7b	94.44	154.32
7	26	97.47	91.04	24	66b	94.44	191.36
8	56f	97.46	99.37	25	44d	94.29	231.90
9	33d	97.22	84.88	26	16bsi	94.14	161.01
10	48b	97.17	86.39	27	29b	93.90	209.70
11	29a	96.98	112.60	28	53a	93.68	243.31
12	38b	96.97	91.83	29	23	93.46	189.67
13	5b	96.97	132.23	30	49b	92.81	231.53
14	69a	96.67	146.78	31	2e	90.48	226.76
15	51e	96.51	147.62	32	35c	88.89	360.87
16	55d	96.39	125.85	33	8c	88.06	385.11
17	67b	96.13	133.16				

Table A8.3a: Taxonomic distinctness values for all sievings samples used in statistical analysis, ranked by average taxonomic distinctness, Δ^+

Rank	Sample	Δ^+	Λ^+	Rank	Sample	Δ^+	Λ^+
1	8c	88.06	385.11	18	67b	96.13	133.16
2	35c	88.89	360.87	19	5b	96.97	132.23
3	53a	93.68	243.31	20	59c	95.56	128.40
4	44d	94.29	231.90	21	55d	96.39	125.85
5	49b	92.81	231.53	22	29a	96.98	112.60
6	2e	90.48	226.76	23	56f	97.46	99.37
7	29b	93.90	209.70	24	12	97.82	96.92
8	53d	94.91	202.19	25	38b	96.97	91.83
9	66b	94.44	191.36	26	26	97.47	91.04
10	23	93.46	189.67	27	48b	97.17	86.39
11	39e	94.44	186.07	28	33d	97.22	84.88
12	28	95.64	169.83	29	22	97.87	83.02
13	48a	95.21	165.84	30	5a	98.41	50.39
14	16bsi	94.14	161.01	31	18a	98.41	50.39
15	7b	94.44	154.32	32	40	98.53	46.69
16	51e	96.51	147.62	33	20c	100	0
17	69a	96.67	146.78				

Table A8.3b: Taxonomic distinctness values for all sievings samples used in statistical analysis, ranked by variation in taxonomic distinctness, Λ^+

