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The Antarctic region as a marine biodiversity hotspot for echinoderms: Diversity and diversification of sea cucumbers

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ABSTRACT

The Antarctic region is renowned for its isolated, unusual, diverse, and disharmonic marine fauna. Holothuroids are especially diverse, with 187 species (including 51 that are undescribed) recorded south of the Antarctic Convergence. This represents ~4% of the documented Antarctic marine biota, and ~10% of the world's holothuroid diversity. We present evidence that both inter-regional speciation with southern cold-temperate regions and intra-regional diversification has contributed to species richness. The Antarctic fauna is isolated, with few shallow-water Antarctic species known from north of the Convergence, yet several species show recent transgression of this boundary followed by genetic divergence. Interchange at longer time scales is evidenced by the scarcity of endemic genera (10 of 55) and occurrence of all six holothuroid orders within the region. While most Antarctic holothuroid morphospecies have circum-polar distributions, mtDNA sequence data demonstrate substantial geographic differentiation in many of these. Thus, most of the 37 holothuroid species recorded from shelf/slope depths in the Weddell Sea have also been found in collections from Prydz Bay and the Ross Sea. Yet 17 of 28 morphospecies and complexes studied show allopatric differentiation around the continent, on average into three divergent lineages each, suggesting that morphological data fails to reflect the level of differentiation. Interchange and local radiation of colonizers appear to have rapidly built diversity in the Antarctic, despite the potential of cold temperatures (and associated long generation times) to slow the rate of evolution.

1. Introduction

Arguably the most conspicuous and general biogeographic trend on Earth is the latitudinal decrease in species diversity. This trend is evident on land and sea, in animals and plants, in shallow waters and even in the deep sea (Rex et al., 1993; Ricklefs and Schluter, 1993). Although there is substantial variation in the steepness of the latitudinal diversity cline as well as exceptions (Barnard, 1991; Clarke, 1992), the pervasiveness of this cline has led to considerable research exploring its causes and consequences (Pianka, 1966; Stehli et al., 1969; Jablonski et al., 2006). For most marine organisms the decline in diversity is steeper in the northern than southern hemisphere, and the Antarctic biota poses some of the most striking variations and exceptions (Clarke, 1992; Brandt et al., 2007a,b).

The Antarctic region is arguably the most faunistically distinct part of the world ocean. Isolated by the Antarctic Convergence, with temperatures hovering just above and below 0°C, the region poses great physiological challenges to marine life. As a result it has developed an endemic and disharmonic biota reminiscent of islands, with some parallel consequences. Noteworthy are the absence or low diversity of certain taxa (e.g., balanomorph barnacles, decapod crustaceans, cartilaginous and teleost fishes - with notable exception of the endemic radiation of notothenioids), that may be excluded by environmental conditions (Clarke and Johnston, 2003). Some of these, most notably teleosts and brachyuran crabs, include efficient durophagous predators that arose during the Mesozoic marine revolution, and have greatly influenced the evolution of the modern, shallow-water, tropical and temperate marine biota (Vermeij, 1977, 1987).

In contrast, other groups (e.g. echinoderms, polychaetes, pycnogonids, and peracarids) are able to handle the physiologically and ecologically challenging Antarctic environment and are strikingly diverse (Clarke and Johnston, 2003; Rogers, 2007). Echinoderms are especially abundant and conspicuous in the Antarctic, and represent ~10% of the recorded fauna (Clarke and Johnston, 2003: 4100 recorded benthic species). In comparison only 3.5% of 5640 marine species in the tropical Mariana Islands (Paulay, 2003), and 2.2% of the nearly 30,000 marine species in Europe are echinoderms

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(Costello et al., 2001). Even more strikingly, the Antarctic is home to ~20% of the world's known pycnogonid species (Child, 1995).

Such high diversity requires ecological and evolutionary explanations. The absence of many modern predators appears to have led to an ecological release of some of their prey in the Antarctic. Ecological release from durophagous predators may be responsible for the abundance and diversity of ophiuroids, crinoids, and brachiopods in the Antarctic benthos, that give the seascape a Paleozoic character (Aronson and Blake, 2001; Aronson et al., 2009). Brandt (1999) similarly argues that abundance and diversity of Antarctic peracarids results from ecological release associated with the virtual absence of decapods as both competitors and predators.

Ecological release does not directly drive diversity however, so more proximal causes need to be considered for high species richness. Species diversity arises from the balance between species origination and extinction. Origination can be through speciation or immigration, while extinction can be local or global. The time available, together with rate (and variation in the rate) of origination and extinction, determine species richness. High diversity can be the result of overall high origination rates, low extinction rates, or long time available with a balance in rates favoring origination.

A notable feature of Antarctic marine life is its relative homogeneity. Circum-Antarctic distributions and broad depth-ranges are noted characteristics of the fauna (Briggs, 1974; Pawson, 1994; Brey et al., 1996). Broad ranges have been attributed to environmental homogeneity, especially with depth, deep continental shelves, limited stratification and mixing by vigorous, circum-Antarctic circulation (Brandt et al., 2007a; Rogers, 2007). The main distributional boundary delineating the region, the Antarctic Convergence, is itself traversed by many species (Clarke et al., 2005).

The striking diversification that several Antarctic taxa have undergone contrasts with perceived lack of opportunities for isolation. High rates of origination also seem unlikely from a thermodynamic perspective, as mutation rates and speciation are temperature dependent and decrease markedly with latitude (Allen et al., 2006). However emerging data suggest that while some species show circum-polar genetic homogeneity (Jarman et al., 2002; Thornhill et al., 2008; Fraser et al., 2009), others have undergone geographic differentiation (Held and Wägele, 2005; Raupach and Wägele, 2006; Linse et al., 2007). The paucity of available geographically-extensive samples has limited exploration of circum-Antarctic differentiation.

A glacial diversity pump, caused by periodic isolation and reconnection of populations as ice sheets and their associated scour expand and retract with glacial cycles, has been proposed as a potential driver of speciation (Clarke and Crame, 1989). Low extinction rates may be favored by release from predation. Time available for speciation to act does not appear to be unusually long, as regional refrigeration is relatively recent, and its onset is correlated with the development of the modern Antarctic fauna, including the loss of temperature sensitive groups, like crabs, present during warmer geological epochs (Feldmann and Zinsmeister, 1984). The onset of glacial conditions and likely radiation of Antarctic fauna played out in roughly the same timeframe (Feldmann and Zinsmeister, 1984; Aronson and Blake, 2001) as the radiation of modern biota of coral reefs (Renema et al., 2008; Williams and Duda, 2008), i.e. ~Eocene to present, with acceleration toward present day conditions and biota in the Miocene.

Examination of large collections of Antarctic and Sub-Antarctic holothuroids from Prydz Bay, the Heard/Kerguelen Plateau, the Ross Sea, the Bellingshausen Sea, the Antarctic Peninsula and the South Atlantic (Fig. 1), together with genetic analyses of putative circum-Antarctic taxa across some of this range, allows us to assess diversity and distribution of Antarctic holothuroid species. How diverse are holothuroids in the Antarctic? Are circum-Antarctic species really genetically contiguous or do they represent cryptic, allopatric complexes?

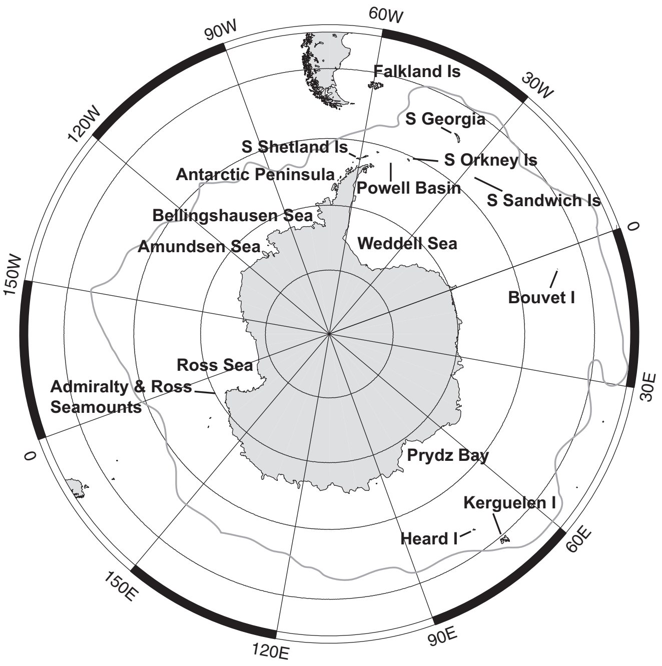

Fig. 1. Map of Antarctica, Antarctic Convergence (line), and sampling locations

This work results from the intersection of two large-scale projects. O'Loughlin and coworkers are actively revising the Antarctic holothuroid fauna by morpho-taxonomic means, and have also documented much of the temperate holothuroid fauna of Australia. Paulay and coworkers are generating sequence data on available holothuroids to understand species limits and phylogenetic relationships. Both projects are connected with a major revisionary effort on holothuroids, focused especially on the order Aspidochirotida (see: http://www.guammarinelab.com/peetcukes/index.html).

2. Methods

The Antarctic Convergence forms a major oceanographic boundary and delineates the Antarctic biogeographic region (Fig. 1). The South Shetland Islands, South Orkney Islands, South Sandwich Islands, South Georgia, Bouvet Island, Heard Island and McDonald Islands are considered to lie south of the Convergence. The Kerguelen Islands lie at the Convergence. The Falkland Islands, Prince Edward and Marion Islands, Crozet Islands, Amsterdam and Saint-Paul Islands, Tierra del Fuego, and Macquarie Island are north of the Convergence.

A comprehensive list of Antarctic holothuroid species from all depths south of the Antarctic Convergence was compiled from collections examined, and complemented from papers on Antarctic holothuroids by: Lampert (1886), Théel (1886), Hérouard (1901), Vaney (1906a, 1906b, 1906c, 1908, 1914), Ekman (1925, 1927), Mortensen (1925), Ludwig and Heding (1935), Heding and Panning (1954), Agatep (1967), Cherbonnier (1974), Belyaev (1975, 1989), Hansen (1975), Belyaev and Mironov (1982), Gebruk (1983, 1988, 1993), Gutt (1991), Massin (1992), Gebruk and Shirshov (1994), Smirnov and Bardsley (1997), Gebruk et al. (2003), O'Loughlin (2002, 2009), Massin and Hétérier (2004), O'Loughlin and Ahearn (2005, 2008), O'Loughlin (2009).

The following holothuroid collections have been determined using morpho-taxonomic methods. Collection abbreviations are as follows: NHM = Natural History Museum; NIWA = New Zealand National Institute of Water and Atmospheric Research;

NMV = Museum Victoria; NMNH = US National Museum of Natural History.

1. The southern Atlantic Ocean collections (at NHM) from The *Terra Nova* Expedition (1910–13), and the Discovery Investigations in the first decades of the last century by the RRS *Discovery* and RSS *William Scoresby*, are being determined by MO'L with volunteer assistants Melanie Mackenzie and Emily Whitfield.
2. The British, Australian and New Zealand Antarctic Research Expedition (BANZARE, 1929 and 1930) collections, principally off Kerguelen and eastern Antarctica (40°–180°E), were determined by MO'L (O'Loughlin, 2009).
3. The US Antarctic Research Program (USARP) collections (at NMNH) were determined by MO'L and the late Cynthia Ahearn (O'Loughlin and Ahearn, 2005, 2008).
4. The Australian National Antarctic Research Expedition (ANARE) collections from Prydz Bay (1985, 1987, 1991, 1993, 1997) and Heard I. (1985, 1992, 2003) (at NMV) were determined by MO'L with volunteer assistants Melanie Mackenzie and Emily Whitfield.
5. The BIOROSS *Tangaroa* 2004 expedition collection (at NIWA) from the Ross Sea was determined by MO'L and ND.
6. The Spanish Antarctic Benthos (BENTART) 2003 and 2006 collections (currently at University of Málaga) by R/V *Hesperides* from the Bellingshausen Sea and Antarctic Peninsula were determined by MO'L with Eugenia Manjón-Cabeza (O'Loughlin et al., 2009).
7. The collections by the BIOPEARL I and II British Antarctic Survey (BAS, 2006 and 2008, to be housed at NHM) expeditions to the Amundsen and Scotia Seas were determined by MO'L with volunteer assistants Melanie Mackenzie and Emily Whitfield.
8. The NIWA IPY Census of Antarctic Marine Life (CAML) 2008 collection from the Ross Sea and Scott and Admiralty Seamounts was determined by MO'L and ND.
9. The US Antarctic Marine Living Resources (US AMLR 2003, 2009) collections by R/V *Yuzhmorgeologiya*, and International Collaborative Expedition to collect and study Fish Indigenous to Sub-Antarctic Habitats (ICEFISH 2004) collection by the RV *Nathaniel B. Palmer*, donated to NMV by Susie Lockhart, and US AMLR 2006 collection lodged at NMNH by Susie Lockhart, all from the southern Atlantic Ocean, were determined by MO'L.

Although conditions of preservation vary among these collections, many were taken relatively recently (often as part of CAML efforts) and preserved in alcohol (sometimes after a period of freezing). This effort is leading to a complete systematic reassessment of the Antarctic sea cucumber fauna, and is being published in a series of revisions and subregional taxonomic reviews (O'Loughlin, 2002, 2009; O'Loughlin and Ahearn, 2005, 2008; O'Loughlin et al., 2009). Many species remain undescribed, but have been studied, but not yet published upon (see below).

Tissue samples from identified, vouchered specimens were sequenced for a portion of the mitochondrial Cytochrome C Oxidase subunit I gene. The sequencing effort we are pursuing on holothuroids is bottom up: i.e. evaluating within species variation and cryptic species first, followed by selection of representatives for broader phylogenetic study. COI is the first pass in this effort, and insufficient coverage at other loci precludes discussing these in this study. DNA extraction, primers, PCR conditions, and sequencing protocols used have been described previously (O'Loughlin et al., 2007). More recent samples were extracted and sequenced at the Smithsonian's LAB facility using robotic methods. For these, genomic DNA was extracted from up to ~20 mg minced preserved tissue via an automated phenol:chloroform extraction on an Autogenprep965 (Autogen, Holliston, MA), using the mouse tail tissue protocol, with a final elution volume of 50 μL. For newer samples we used the new echinoderm primers developed by Hoareau and Boissin (2010). Geneious® was used for sequence editing and alignment for recent samples. Sequences are deposited in GenBank under accession numbers HM196536-HM196705.

Of 467 specimens sequenced for COI from the Antarctic region and 290 specimens from various Subantarctic and southern temperate localities, we selected 352 Antarctic and 23 Subantarctic/southern temperate specimens for analysis. These represent all species or species complexes known from multiple localities separated by 1000 km, excluding the taxonomically challenging genus *Pseudostichopus* (characterized by an almost complete lack of ossicles). The selected Subantarctic samples were included because they fell within Antarctic species complexes, resulting in a total of 375 OTUs. Voucher information for all sequenced specimens are given in Online Supplementary Materials.

We analyzed the sequence data with RAxML (Stamatakis, 2006) using the GTRGAMMA model of molecular evolution. We selected the tree with the highest likelihood score based on 20 independent runs. We ran 200 bootstrap replicates and estimated the frequency of the edges for the tree selected in this set of replicates. We extracted each species-group from the tree and prepared the figures using the packages ape 2.5-1 (Paradis et al., 2004) and phylobase (Bolker et al., 2010) in R 2.10.1 (R Development Core Team, 2009).

The resulting phylogeny was examined for differentiation of Evolutionary Significant Units (ESUs; Moritz, 1994). We define ESUs as taxa that are reciprocally monophyletic in at least one genetic marker and have a second, independent genetic marker, morphological character, color, or distribution that is differentiated in a congruent manner with the first marker (Meyer and Paulay, 2005; Malay and Paulay, 2010). ESUs thus meet the criteria for the phylogenetic species concept. When ESUs are sympatric, they also conform to the biological species concept.

3. Results

3.1. Diversity based on morpho-taxonomic study

Examination of collections and literature reveals 187 species of holothuroids (51 undescribed) currently known from all depths in the Antarctic region (Tables 1 and 2). The suspension feeding dendrochirotids (83 species) are most diverse, followed by the deep water, deposit feeding elasipodids (47 species). Several areas within Antarctica have received focused attention as follows.

Gutt (1991) listed Weddell Sea holothuroids to a depth of 1180 m, and this depth limit is used in this work when comparing distributions. The Weddell Sea has been intensively surveyed for holothuroid species, and 37 are reported to 1180 m in the works of Gutt (1991, 33 species), Massin (1992, 3 new species) and Massin and Hétérier (2004, 1 new species). Since the work of Gutt (1991) there have been synonymies and reassignments to other genera (O'Loughlin et al., 2009). Some of the determinations by Gutt (1991) have been subjectively interpreted here by MO'L as follows.

The table ossicles in *Mesothuria bifurcata* and *Mesothuria lactea* (Théel, 1886) are similar, but the distal spires of the tables in *Mesothuria bifurcata* are frequently bifurcate. *Mesothuria lactea* is not known in the high Antarctic, and the species in question is judged to be *Mesothuria bifurcata*.

Molpadiodemas crinitus is similar in appearance to *Pseudostichopus villosus* Théel, 1886. The former is abundant at shelf and upper slope depths to ~1000 m in the high Antarctic, while the latter typically occurs deeper than 2000 m in other parts of the world ocean (see O'Loughlin and Ahearn, 2005). The high Antarctic species is judged to be *Molpadiodemas crinitus*.

Table 1
Holothuroid morpho-species recognized from all depths in the Antarctic

APODIDA
Chiridotidae Östergren
Kolostoneura species (S Orkney Is, 506 m; in preparation)
Paradota weddellensis Gutt, 1990
Scoliorhapis species (10 tentacles; S Shetland Is, 1544 m; in preparation)
Scoliorhapis species (12 tentacles; Shag Rocks, 206 m; in preparation)
Taeniogyrus antarcticus Heding, 1931
Taeniogyrus contortus (Ludwig, 1875)
Taeniogyrus magnibaculus Massin and Hétérier, 2004
Taeniogyrus species (10 tentacles; Prydz Bay, 109–830 m; in preparation)
Myriotrochidae Théel
Acanthotrochus antarcticus Belyaev and Mironov, 1981
Acanthotrochus species (S Orkney Is, 2914 m; Bohn in Gebruk et al., 2003)
Achiridota species (Prydz Bay, 788 m; in preparation)
Myriotrochus antarcticus Smirnov and Bardsley, 1997
Myriotrochus bipartitodentatus (Belyaev and Mironov, 1978)
Myriotrochus hesperides O'Loughlin and Manjón-Cabeza, 2009
Myriotrochus macquoriensis Belyaev and Mironov, 1981
Myriotrochus species (Ross Sea, 2283 m; in preparation)
Myriotrochus species (S Orkney Is, 2084–5190 m; Bohn in Gebruk et al., 2003)
Neolepidotrochus variodentatus (Belyaev and Mironov, 1978)
Prototrochus species (Shag Rocks, 206 m; in preparation)
Prototrochus species (S Shetland Is, 192–1544 m; in preparation)
Prototrochus species (S Orkney Is, 2375–5190 m; Bohn in Gebruk et al., 2003)
Synaptidae Burnmeister
Labidoplax species (S Orkney Is, 2893–3916 m; Bohn in Gebruk et al., 2003)

ASPIDOCHIROTIDA
Synallactidae Ludwig
Bathyplotes bongraini (Vaney, 1914)
Bathyplotes gourdoni (Vaney, 1914)
Bathyplotes moseleyi (Théel, 1886)
Bathyplotes cf *moseleyi* (Théel, 1886) (Ross Sea; this work)
Bathyplotes species 1 (Amundsen Sea; this work)
Bathyplotes species 2 (Bellingshausen Sea, Ross Sea; this work)
Bathyplotes species 3 (Scott Seamount; this work)
Mesothuria bifurcata Hérouard, 1901
Molpadiodemas crinitus O'Loughlin and Ahearn, 2005
Molpadiodemas involutus (Sluiter, 1901)
Molpadiodemas morbillus O'Loughlin and Ahearn, 2005
Molpadiodemas pediculus O'Loughlin and Ahearn, 2005
Molpadiodemas translucens O'Loughlin and Ahearn, 2005
Molpadiodemas villosus (Théel, 1886)
Molpadiodemas violaceus (Théel, 1886)
Paelopatides species (in Ekman 1927)
Pseudostichopus mollis Théel, 1886
Pseudostichopus peripatus (Sluiter, 1901)
Pseudostichopus spiculiferus (O'Loughlin, 2002)
Pseudostichopus species (Heard I.; this work)
Synallactes robertsoni Vaney, 1908
synallactid species (Heard I.; this work)

DACTYLOCHIROTIDA
Ypsilothuriidae Heding
Echinocucumis hispida (Barrett, 1857)
Echinocucumis kirrilyae O'Loughlin, 2009
Echinocucumis species (Heard I.; this work)
dactylochirotid species (Ross Sea; this work)

DENDROCHIROTIDA
Cucumariidae Blainville
Cladodactyla crocea (Lesson, 1830)
Cladodactyla crocea var *croceoides* (Vaney, 1908)
Clarkiella deichmannae O'Loughlin, 2009
Cucamba psolidiformis (Vaney, 1908)
Cucumaria dudexa O'Loughlin and Manjón-Cabeza, 2009
"*Cucumaria georgiana* (Lampert, 1886) group" (by Gutt, 1990) (? 6 species)
cucumariid species (Heard I.; this work)
cucumariid species 1 (Shag Rocks; this work)
cucumariid species 2 (Shag Rocks; this work)
Heterocucumis denticulata (Ekman, 1927)
Heterocucumis godeffroyi (Semper, 1867)
Heterocucumis steineni (Ludwig, 1898)
Heterocucumis species (Prydz Bay; this work)
Heterocucumis species (S Shetland Is; this work)
Microchoerus splendidus Gutt, 1990
Neopsolidium kerguelensis (Théel, 1886)
Parathyonidium incertum Heding, 1954

Table 1. (*continued*)

Parathyonidium species (Prydz Bay; this work)
Pseudocnus intermedia (Théel, 1886)
Pseudocnus laevigatus (Verrill, 1876)
Pseudocnus perrieri (Ekman, 1927)
Pseudocnus serrata (Théel, 1886)
Pseudocnus species (Ross Sea; this work)
Pseudopsolus ferrari Bell, 1908
Psolicrux coatsi (Vaney, 1908)
Psolicrux iuvenilesi O'Loughlin and Manjón-Cabeza, 2009
Psolidiella mollis (Ludwig and Heding, 1935)
Staurocucumis abyssorum (Théel, 1886)
Staurocucumis liouvillei (Vaney, 1914)
Staurocucumis turqueti (Vaney, 1906)
Staurocucumis species (Antarctic Peninsula; this work)
Trachythyone bouvetensis (Ludwig and Heding, 1935)
Trachythyone cynthiae O'Loughlin, 2009
Trachythyone lechleri (Lampert, 1885)
Trachythyone mackenzieae O'Loughlin, 2009
Trachythyone maxima Massin, 1992
Trachythyone muricata Studer, 1876
Trachythyone parva (Ludwig, 1875)
Trachythyone species 1 (S Shetland Is; this work)
Trachythyone species 2 (Amundsen Sea; this work)
Paracucumidae Pawson and Fell
Crucella hystrix Gutt, 1990
Crucella scotiae (Vaney, 1906)
Paracucumis turricata (Vaney, 1906)
Psolidae Forbes
Echinopsolus acanthocola Gutt, 1990
Echinopsolus parvipes Massin, 1992
Echinopsolus species (Scotia Sea; this work)
Ekkentropelma brychia Pawson, 1971
Psolidium emilyae O'Loughlin and Ahearn, 2008
Psolidium gaini Vaney, 1914
Psolidium incubans Ekman, 1925
Psolidium normani O'Loughlin and Ahearn, 2008
Psolidium pawsoni O'Loughlin and Ahearn, 2008
Psolidium poriferum (Studer, 1876)
Psolidium schnabelae O'Loughlin and Ahearn, 2008
Psolidium tenue Mortensen, 1925
Psolidium whittakeri O'Loughlin and Ahearn, 2008
Psolus antarcticus (Philippi, 1857)
Psolus arnaudi Cherbonnier, 1974
Psolus belgicae Hérouard, 1901
Psolus charcoti Vaney, 1906
Psolus cherbonnieri Carriol and Féral, 1985
Psolus dubiosus Ludwig and Heding, 1935
Psolus ephippifer Thomson, 1876
Psolus figulus Ekman, 1925
Psolus granulosus Vaney, 1906
Psolus koehleri Vaney, 1914
Psolus murrayi Théel, 1886
Psolus paradubiosus Carriol and Féral, 1985
Psolus parvulus Cherbonnier, 1974
Psolus patagonicus Ekman, 1925
Psolus punctatus Ekman, 1925
Psolus squamatus var *segregatus* Perrier, 1905
Psolus species (Marie Byrd Seamount; in preparation)
Psolus species (Shag Rocks; in preparation)
Psolus species (South Georgia; this work)
Psolus species (S Shetland Is; this work)
Psolus species (S Orkney Is; in preparation)
Psolus species (S Orkney Is; this work)

ELASIPODIDA
Deimatidae sensu Ekman
Oneirophanta mutabilis mutabilis Théel, 1879
Oneirophanta setigera (Ludwig, 1894)
Elpidiidae Théel
Amperima insignis (Théel, 1882)
Amperima naresi (Théel, 1882)
Amperima robusta (Théel, 1882)
Amperima velacula Agatep, 1967
Ellipinion facetum (Agatep, 1967)
Ellipinion papillosum (Théel, 1879)
Elpidia decapoda Belyaev, 1975
Elpidia glacialis sundensis Hansen, 1956
Elpidia cf *glacialis* Théel, 1876 (Amundsen Sea, 542–1518 m; this work)

Table 1. (*continued*)

Elpidia gracilis Belyaev, 1975
Elpidia lata Belyaev, 1975
Elpidia ninae Belyaev, 1975
Elpidia theeli Hansen, 1956
Kolga cf *hyalina* Danielssen and Koren, 1879 (S Orkney Is, 1656 m; this work)
Peniagone affinis Théel, 1882
Peniagone diaphana (Théel, 1882)
Peniagone herouardi Gebruk, 1988
Peniagone incerta (Théel, 1882)
Peniagone mossmani Vaney, 1908
Peniagone papillata Hansen, 1975
Peniagone purpurea (Théel, 1882)
Peniagone vignoni Hérouard, 1901
Peniagone vitrea Théel, 1882
Peniagone willemoesi (Théel, 1882)
Peniagone cf *willemoesi* (Théel, 1882) (Ross Sea; this work)
Peniagone wiltoni Vaney, 1908
Protelpidia murrayi (Théel, 1879)
Rhipidothuria racovitzai Hérouard, 1901
Rhipidothuria verrucosa (Théel, 1879)
Scotoplanes globosa (Théel, 1879)
Laetmogonidae Ekman
Apodogaster alcocki Walsh, 1891
Laetmogone wyvillethomsoni Théel, 1879
Laetmogone species (Scotia Sea; in Gebruk, 1993)
Laetmogone species (Ross Sea; this work)
Laetmogone cf *scotoeides* (H. L. Clark, 1913) (Ross Sea; this work)
Pannychia species (Ross Sea; this work)
Psychropotidae Théel
Benthodytes sanguinolenta Théel, 1882
Benthodytes species (Scotia Sea; in Gebruk et al., 2003)
Psycheotrephes exigua Théel, 1882
Psycheotrephes recta (Vaney, 1908)
Psychropotes longicauda Théel, 1882
Psychropotes scotiae (Vaney, 1908)
Psychropotes species (Scotia Sea; in Gebruk, 1993)
swimming holothuroid species (? 2)

MOLPADIDA
Molpadiidae Théel
Molpadia abyssicola Pawson, 1977
Molpadia antarctica (Théel, 1886)
Molpadia discors Pawson, 1977
Molpadia liska Pawson, 1977
Molpadia musculus Risso, 1826
Molpadia species 1 (Ross Sea, Amundsen Sea; this work)
Molpadia species 2 (Admiralty Seamount; this work)
Trochostoma species (in Ekman, 1927)
Caudinidae Heding
Paracaudina species (Heard I.; this work)

Table 2
Documented species richness of Antarctic holothuroids.

Order	Described	Undescribed	Total
Apodida	10	12	22
Aspidochirotida	15	7	22
Dactylochirotida	2	2	4
Dendrochirotida	66	17	83
Elasipodida	38	9	47
Molpadida	5	4	9
TOTAL	136	51	187

Pseudostichopus spiculiferus is typically covered with a mat of sponge spicules, and is abundant in the high Antarctic. Gutt (1991) referred to sand grain cover of *Pseudostichopus mollis* Théel, 1886 specimens, and sponge spicule cover of *Pseudostichopus villosus* Théel, 1886 specimens in the Weddell Sea. *Pseudostichopus mollis* and *Pseudostichopus villosus* are typically not covered by sand grains or sponge spicules. The sponge spicule covered species is judged here to be *Pseudostichopus spiculiferus*.

The type locality for *Psolidium pawsoni* is the Weddell Sea. *Psolidium incertum* (Théel, 1886) was judged to be a junior synonym of *Psolidium poriferum* (Studer, 1876) by O'Loughlin and Ahearn (2008). It occurs typically on the Heard/Kerguelen plateau. The high Antarctic *Psolidium tenue* Mortensen, 1925 was raised out of synonymy by O'Loughlin and Ahearn (2008), and may occur in the Weddell Sea. The species in question is judged to be most probably *Psolidium pawsoni*.

A revision of the Gutt (1991) list, with the addition of the four subsequent new species, is given in Table 3.

Of the 37 holothuroid species reported for the Weddell Sea (Table 3), 32 have been found in Prydz Bay. The 5 species not found to date in Prydz Bay are: *Elpidia* cf. *glacialis*, *Psolidiella mollis*, *Psolus antarcticus*, *Trachythyone maxima*, *Trachythyone parva*. Nine additional species have been found in Prydz Bay, three described recently by O'Loughlin and Ahearn (2008), two by O'Loughlin (2009), and four remain undescribed.

In the Ross Sea, 31 of the 37 Weddell Sea holothuroid species have been found. The six species not found to date in the Ross Sea are: *Echinopsolus parvipes*, *Elpidia* cf. *glacialis* (found at 3386-3398 m), *Mesothuria bifurcata*, *Paradota weddellensis*, *Rhipidothuria racovitzai*, *Trachythyone parva*. Thirteen additional species have been found in the Ross Sea (to 1180 m), of which eight are undescribed.

Table 3
Holothuroid species reported from the Weddell Sea to 1180 m.

APODIDA
Paradota weddellensis Gutt, 1990
Taeniogyrus contortus (Ludwig, 1875)
Taeniogyrus magnibaculus Massin and Hétérier, 2004

ASPIDOCHIROTIDA
Bathyplotes bongraini Vaney, 1914
Bathyplotes gourdoni (Vaney, 1914)
Mesothuria bifurcata Hérouard, 1901
Molpadiodemas crinitus O'Loughlin and Ahearn, 2005
Pseudostichopus spiculiferus (O'Loughlin, 2005)

DENDROCHIROTIDA
Cucamba psolidiformis (Vaney, 1908)
Crucella hystrix Gutt, 1990
Crucella scotiae (Vaney, 1906)
Cucumaria acuta Massin, 1992
"*Cucumaria georgiana* (Lampert, 1886) group" (by Gutt, 1990)
Echinopsolus acanthocola Gutt, 1990
Echinopsolus parvipes Massin, 1992
Heterocucumis denticulata (Ekman, 1927)
Heterocucumis steineni (Ludwig, 1898)
Microchoerus splendidus Gutt, 1990
Paracucumis turricata (Vaney, 1906)
Psolicrux coatsi (Vaney, 1908)
Psolidiella mollis (Ludwig & Heding, 1935)
Psolidium gaini Vaney, 1914
Psolidium pawsoni O'Loughlin and Ahearn, 2008
Psolus antarcticus (Philippi, 1857)
Psolus charcoti Vaney, 1906
Psolus dubiosus Ludwig & Heding, 1935
Staurocucumis liouvillei (Vaney, 1914)
Staurocucumis turqueti (Vaney, 1906)
Trachythyone bouvetensis (Ludwig & Heding, 1935)
Trachythyone maxima Massin, 1992
Trachythyone parva (Ludwig, 1875)

ELASIPODIDA
Elpidia cf *glacialis* Théel, 1876
Laetmogone wyvillethomsoni Théel, 1879
Peniagone vignoni Hérouard, 1901
Protelpidia murrayi (Théel, 1879)
Rhipidothuria racowitzai Hérouard, 1901

MOLPADIDA
Molpadia musculus Risso, 1826

Of the 21 holothuroid species listed for the Heard/Kerguelen Islands, only 6 occur on the Antarctic continental coast; only one at Bouvet Island; but four in the Magellanic region of South America. The species common to the Magellanic Region (north of the Antarctic Convergence) and the Heard/Kerguelen Islands (at the Convergence) are: *Heterocucumis godeffroyi*; *Psolus paradubiosus*; *Taeniogyrus contortus*; *Trachythyone lechleri*. Of these only *Taeniogyrus contortus* has been found on the Antarctic continental coast.

3.2. Genetic results

Twenty-nine species complexes, represented by 375 specimens, included samples from multiple localities at least 1000 km apart (Table 4, Fig. 2). We define species complexes for this study as clades whose members share the same morpho-specific identification, or that have different identifications but are within 5% K2P pair-wise distance in COI. Twenty-eight of these are represented by multiple samples within the Antarctic Region, while seven include samples from within the region as well as north of the Antarctic Convergence.

Seventeen of 28 species complexes sampled from around Antarctica show reciprocally monophyletic differentiation among localities and thus are comprised of multiple ESUs, while 11 do not. In several of these 17 all major localities sampled host reciprocally monophyletic populations, although sample sizes are often small (Table 4, Fig. 2). Level of inter-ESU genetic differentiation is typically substantially greater than intra-ESU variation, further demonstrating that these populations have been on independent evolutionary trajectories. One additional species, *Laetmogone wyvillethomsoni* shows two genetic clusters that appear to stratify by depth (from 1620-1990 m vs. 2281-3485 m).

Five of seven taxa sampled across the Antarctic Convergence show differentiation. The five that are differentiated include eight ESUs north of the Convergence. The *Psolus antarcticus* complex shows remarkably little differentiation among populations from the Ross Sea, the Chatham Rise and Tristan da Cunha, while two specimens sampled of an unidentified *Paracaudina* species are only 1.4% divergent (K2P pairwise) between Heard Island and SE Australia.

The 29 species complexes studied are comprised of 39 nominal species (see below), representing 71 genetic ESUs. Most of the ESUs are allopatric to each other and thus their species-status is currently subjective. However 12 are sympatric with other ESUs within larger species complexes (Table 4), and thus likely represent full biological species.

3.3. Morphological and genetic species delineations

Although there was good correspondence between morphological and genetic species delineations, ESUs defined on mtDNA sequences did not always correspond with morphologically identified species.

First, several morphospecies were complexes of multiple, geographically differentiated ESUs: *Peniagone incerta, Benthodytes sanguinolenta, Laetmogone wyvillethomsoni, Staurocucumis liouvillei, Pannychia moseleyi, Psolicrux coatsi, Mesothuria bifurcata, Molpadia musculus, Cucumba psolidiformis, Trachythyone bouvetensis, Psolus charcoti, Crucella hystrix, Crucella scotiae, and Psolidium gaini.* While some of these complexes show relatively shallow genetic differentiation among populations, others are comprised of deeply differentiated lineages, sometimes including sympatric clades. For example the 16 specimens sequenced of the supposedly cosmopolitan (described from the Mediterranean) *Molpadia musculus*, included two Antarctic and three Australian ESUs up to 23% (pairwise K2P) divergent. *Molpadia* species are notorious for their difficult taxonomy, a result of simple morphology (no tube feet, smooth body wall, simple tentacles) and ossicles that change and deteriorate with age (Pawson, 1977). Thus it is not surprising that traditional taxonomic characters would fail in species delineations.

Table 4
Antarctic species sequenced from more than one locality.

Genus	species	Ross Sea	Amundsen Sea-Marie-Byrd	Bellingshausen Sea	S Shetland-Antarctic Peninsula	Powell Basin-Orkneys	S Georgia	S Sandwich	Bouvet	Heard	Falkland	SE Aus	NZ	NW Aus	W Aus	Tristan	Chatham
Bathyplotes	bongraini	6	1		2				2								
Bathyplotes	moseleyi cpx	12	2		1				2		1						
Benthodytes	sanguinolenta	1												3			
Crucella	hystrix	3	1														
Crucella	scotiae	4			1												
Cucamba	psolidiformis	3			2			1	3								
Cucumaria	georgiana cpx	4			1			1									
Cucumaria	georgiana cpx	1			1												
Cucumaria	georgiana cpx	6															
Elpidia	glacialis		16		2												
Heterocucumis	steineni	6	3					6									
Laetmogone	wyvillethomsoni	5	1														
Laetmogone	wyvillethomsoni	7															
Mesothuria	bifurcata	1	8														
Molpadia	musculus	6			5					1				2	1		
Molpadia	musculus														1		
Molpadia	sp (musculus)	2	1														
Molpadiodemas	cpx	4	1					4				1	1				
Pannychia	moseleyi 1	8										5					
Pannychia	moseleyi 2											1					2
Paracaudina										1		1					
Paracucumis	turricata	3	2														
Peniagone	incerta	2				2	1										
Peniagone	vignoni	7	4	6													
Protelpidia	murrayi	4			1	3		1									
Psolicrux	coatsi	5			1		1		3								
Psolidiella	mollis	8			4		1	2	3								
Psolidium	gaini	4			1												
Psolidium	tenue cpx 1	3	4		1												
Psolidium	tenue cpx 2	14	2		3				2	3							
Psolus	antarticus cpx	7								1						2	1
Psolus	charcoti					1		1	5								
Psolus	charcoti	4			7			1									
Psolus	dubiosus cpx	16			4		1		3								
Psolus	dubiosus cpx				6												
Psolus	koehleri				6		2										
Staurocucumis	liouvillei 1	3	4		1		1		2	1							
Staurocucumis	liouvillei 2	1			3						1						
Trachythyone	bouvetensis	5	2		2		4	1	3								
Trachythyone	bouvetensis				4												

Locations arranged W to E in light blue from S, in pale yellow from N, of Antarctic Convergence. Number of specimens sampled given; each ESU in a species complex is colored differently. cpx = complex, denoting multiple identified morphospecies in group (see text). Complexes with sympatric ESUs are listed on multiple lines to separate these ESUs.

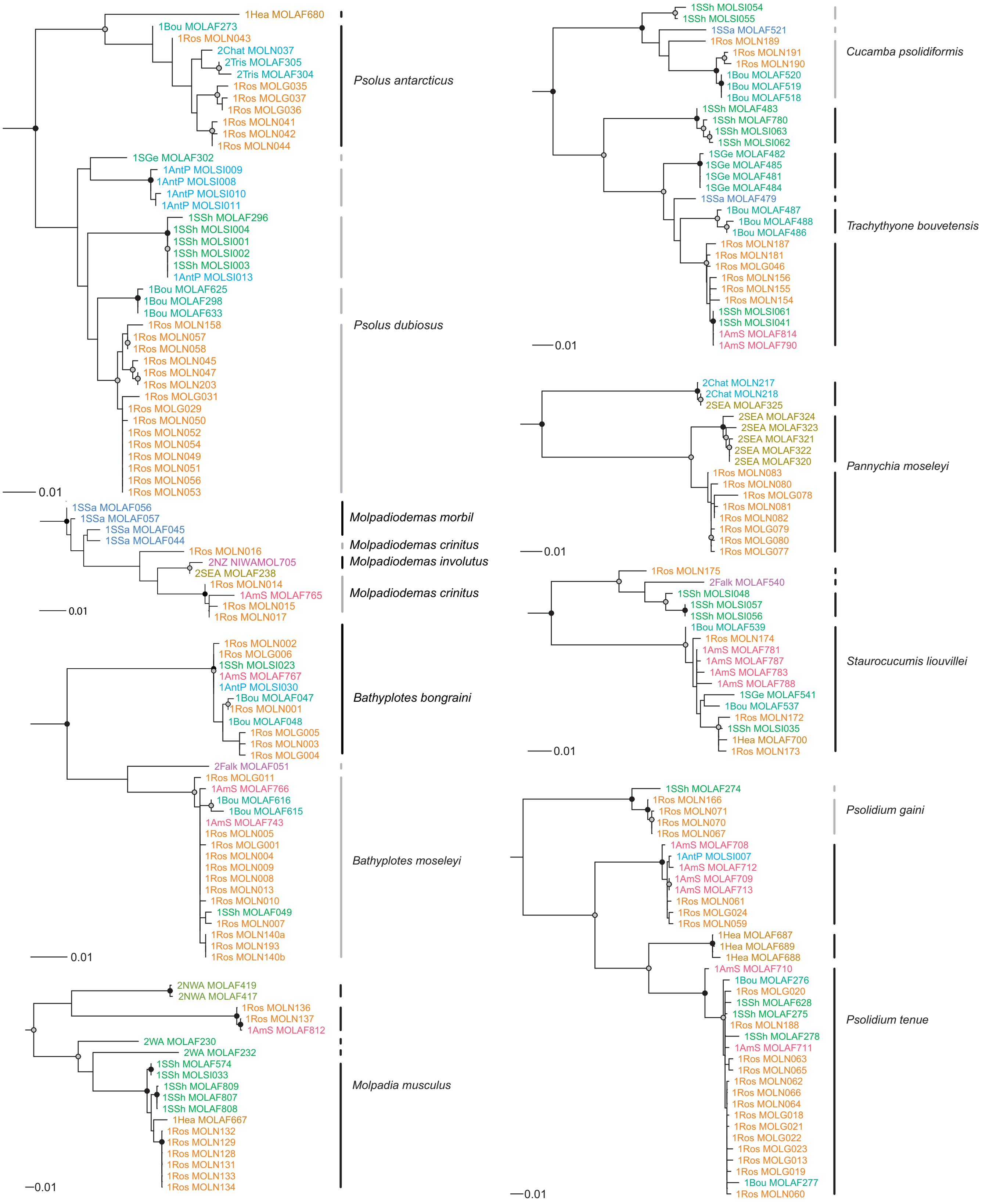

Fig. 2. Phylogenetic relationships of species complexes studied based on Maximum Likelihood estimation of COI sequence data (see Methods for details). Scale: distance based on expected number of substitutions per site under the GTR+GAMMA model. Bootstrap confidence indicated by black spot on node: >95%, grey spot on node: >75%. Locations color marked, OTUs marked with region-location-sample as follows: 1: Antarctic, 2: Subantarctic/cold temperate. AmS: Amundsen Sea, AntP: Antarctic Peninsula, Bell: Bellingshausen Sea, Bou: Bouvet Island, Hea: Heard Island, MByrd: Mairie Byrd Seamounts, Pow: Powell Basin, Ros: Ross Sea, SGe: South Georgia, SOrk: South Orkney Islands, SSa: South Sandwich Islands, SSh: South Shetland Islands, Chat: Chatman Islands, Falk: Falkland Islands, NWA: Northwest Australia, NZ: New Zealand, SEA: Southeast Australia, Tris: Tristan da Cunha Island, WA: Western Australia. ESUs indicated by vertical lines beside species complex (Table 4) designations.

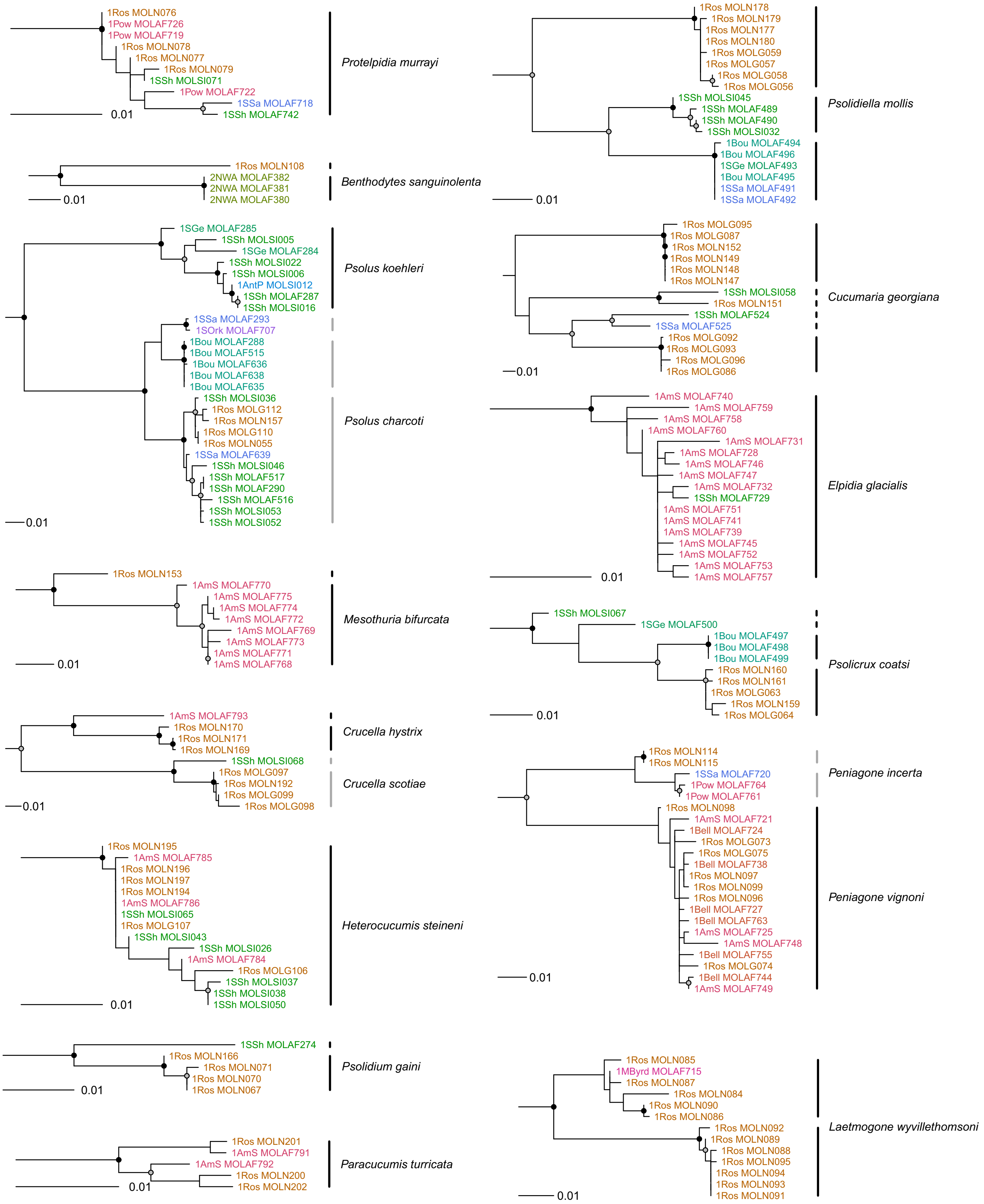

Fig. 2. (*Continued*)

Second, in four complexes genetic and morphological identifications were inconsistent. In these, multiple species were initially identified, but species boundaries did not correspond well with mtDNA delineated ESUs. These are the *Bathyplotes moseleyi* complex (including specimens initially identified as *B. bongraini* and *B. gourdoni*), the *Psolidium tenue* complex (including some *P. pawsoni* and *P. whittakeri*, as well as *P. poriferum* reliably identified from Heard Island that falls as an ESU among these taxa), the *Psolus antarcticus* and *dubiosus* complexes (also including some *P. cherbonnieri* and *P. arnaudi*), and the "*Cucumaria georgiana*" complex (including some *C. attenuata* and *C. acuta*). All four of these complexes are taxonomically challenging groups, that appear to have differentiated fairly recently, and require additional study.

4. Discussion

Holothuroids are remarkably diverse in the Antarctic region: the 187 morpho-species recorded (Table 1) represent ~10% of the known global fauna of ~1700 sea cucumbers (Paulay et al., unpublished data). Genetic results show a substantial additional diversity of cryptic species; with 74 ESUs evident among the limited samples examined of 39 named species. Integrative taxonomic approaches, utilizing traditional morphological characters, field appearance and biology, and DNA sequence data, are demonstrating that cryptic species are quite pervasive and diverse among sea cucumbers (e.g. Uthicke et al., 2004; Michonneau et al., 2008). In numerous species groups ossicles are not sufficiently variable to distinguish species defined on the basis of field and genetic characteristics. External morphological characteristics can get badly damaged by sampling gear, especially in taxa with soft, even gelatinous body walls, further constraining possibilities for morphological identification. With specimens resulting mostly from rough, ship-based sampling methods, limited availability of live/fresh material for specialists, and no previous genetic studies, it is not surprising that Antarctic holothuroid taxonomy and diversity is in need of reevaluation. High diversity is also reflected in the importance of sea cucumbers in the biota: almost 4% of known Antarctic benthic species are sea cucumbers (Clarke and Johnston, 2003).

Local holothuroid diversity is also high, with 37 species documented in the Weddell Sea, 41 species in Prydz Bay, and 43 in the Ross Sea, from shallow to moderately deep waters (to 1180 m to facilitate comparisons). Such high local diversity compares with that of coral reefs, although Antarctic compilations are across a broader depth range than available at, or compiled for, tropical locations. For example the well studied holothuroid fauna of the Mariana Islands, not far from the global marine diversity center, has 47 species (Paulay, 2003); while 114 species are recorded from shallow waters of the entire tropical insular Pacific (Pawson, 1995).

What is the source of this diversity? Conditions in the Antarctic are clearly favorable for holothuroids, and for echinoderms in general. That these animals handle the physical conditions of the region well is evidenced by the taxonomic breadth of the fauna, as well as the abundance, even local dominance of many species. All six orders of holothuroids are represented in the Antarctic, 13 of the 25 currently recognized families, and a broad range of genera and species. Thus conditions in the Antarctic do not seem to exclude many major groups of holothuroids. Abundant planktonic productivity provides ample food resources for deposit and suspension feeders at least seasonally, and some high latitude holothuroids have the ability "shut down" during unfavorable winter conditions, even undergoing visceral atrophy (Fankboner and Cameron, 1985). Echinoderms are not alone in their success in the Antarctic; other taxa that are unusually diverse include pycnogonids, amphipods, and polychaetes (Child, 1995; Clarke and Johnston, 2003).

Suitable ecological conditions do not in themselves lead to diversity. To build diversity, species have to enter the biota through dispersal or to diversify *in situ*. Both are important for holothuroids. The Antarctic Convergence poses a filter barrier to marine life, but is expressed most strongly as a surface feature, so is less effective in deep than shallow water (Brandt et al., 2007b). While the shallow faunas south and north of the Convergence are largely distinct, the Convergence is not a formidable barrier to taxa that do well in polar seas (Clarke et al., 2005). Islands near the boundary of the Convergence, such as the Heard-Kerguelen group, have intermediate faunas as demonstrated above, mixing high Antarctic and cold temperate elements in roughly equal proportions. The broad representation of families and orders in the Antarctic fauna shows this connection at deeper phylogenetic levels. There are relatively few genera restricted to the Antarctic: 45 of the 55 genera present are also recorded north of the Convergence. Not surprisingly 9 of the 10 endemic genera are dendrochirotids, a generally shallow water group, indicating that the barrier is stronger in neritic waters.

Filter barriers like the Antarctic Convergence can facilitate diversification by inter-regional speciation. Dispersal and divergence across the barrier can build diversity in both Antarctic and cold temperate waters. The great diversity and radiation of southern temperate holothuroids, especially in the Australian region (O'Loughlin and O'Hara, 1992; Rowe and Gates, 1995), provides a rich fauna for biotic interchange to draw on. At least seven holothuroid morphospecies traverse the Convergence among the 39 sampled. Five of these have divergent (and sometimes multiple, divergent) ESUs across this boundary indicating past dispersal followed by differentiation, while two (*Psolus antarcticus* complex, *Paracaudina* sp.) show little genetic differentiation indicating recent or ongoing gene flow (Fig. 2). Genetic connections with differentiation are also evident in other species studied across the Convergence (e.g., Hunter and Halanych, 2008; Wilson et al., 2009).

In situ diversification has also been substantial. Powerful circum-Antarctic currents have facilitated the dispersal of marine life and together with the prevalence of circum-Antarctic morphospecies, would suggest that allopatric differentiation has been limited (Briggs, 1974; Pawson, 1994). As the reviewed faunistic comparisons demonstrate, there is substantial homogeneity around Antarctica: many holothuroid morpho-species have circum-polar distributions. However, genetic scrutiny demonstrates that circum-Antarctic differentiation is pervasive among these circumpolar holothuroids, with 17 of 28 species complexes sampled showing differentiation around Antarctica. Even with the limited geographic sampling on hand, these 17 complexes encompass 51 ESUs within the Antarctic region, or on average 3 ESUs per morpho-species (Table 4). Additional sampling will no doubt challenge the validity of some ESUs, while uncovering others. Overall however the story is clear: the Antarctic holothuroid fauna is substantially more diverse and geographically differentiated than previously documented. The numerous islands, seas, and other isolated habitats create ample opportunities for speciation, facilitated by the transport potential of powerful currents. Allopatric differentiation around the polar region may have been facilitated by contraction of populations to select refugia during the even more extreme environments prevalent during glacial times, and have substantially contributed to the radiation of marine life in the region (Clarke and Crame, 1992; Briggs, 2003; Brandt et al., 2007b). Thus conditions for speciation are ideal: sufficient dispersal to spread populations, yet not enough to prevent their differentiation (cf. Paulay and Meyer, 2002). The large number of relatively isolated habitats allows relatively contemporaneous differentiation of multiple populations, thus getting around even potential thermodynamic rate limitations for evolutionary diversification at these cold latitudes.

Evidence for circum-Antarctic differentiation and diversification is also emerging from other genetic studies. While little differentiation has been found in pelagic taxa (Zane et al., 1998;

Jarman et al., 2002), brooding species that lack pelagic stages, including philobryid bivalves (Linse et al., 2007) and isopods (Held and Wägele, 2005; Raupach and Wägele, 2006), show substantial allopatric genetic structuring. Genetic differentiation around the continent has also been demonstrated in a benthic octopod with presumed benthic paralarvae (Allcock et al., 1997), and southern bull kelp (Fraser et al., 2009). Studies on echinoderms are available to date only from smaller spatial scales in the region, and show limited genetic differentiation (Hunter and Halanych, 2008; Wilson et al., 2007). Studies are as yet too few to test for the importance and generality of faunal breaks established from classical biogeographic studies: between east and west Antarctica, and between these and South Georgia (Hedgpeth, 1970; Clarke and Johnston, 2003).

The diversity and abundance of sea cucumbers (and echinoderms in general) in the Antarctic is comparable to that in the deep sea (Gage and Tyler, 1991). The close biotic affinity between these realms is well known, a result in part of deep shelves, weak stratification, substantial mixing, consequent expanded depth ranges of many species, and more facile biotic exchange across depth (Lipps and Hickman, 1982; Brandt et al., 2007a; Rogers, 2007). Nevertheless, differences between shallow and deep faunas remain. Thus dendrochirotids dominate Antarctica shelf habitats, accounting for about half the sea cucumber species, but are largely absent from the deep sea, reflective of their suspension feeding mode of life.

In conclusion, we suggest the following scenario for the anomalously great, high latitudinal diversity of Antarctic holothuroids (and likely other echinoderms). Favorable biological and physical conditions allow for the invasion/exchange and ecological success of many lineages that inhabit the remarkably diverse neighboring regions. Connections between the deep sea and the Antarctic are well documented, but shallow water taxa also show substantial (if more limited) links across the Convergence (Clarke et al., 2005). Thus dispersal into and out of the Antarctic has been high; allowing inter-regional speciation to lay down a diverse foundational diversity. Colonizing species can undergo intra-regional diversification, facilitated by limited dispersal by circum-Antarctic currents, changes in connectedness of populations as a result of glacial cycles, and resulting relatively contemporaneous differentiation of numerous species from successful founders.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dsr2.2010.10.011.

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