SYMPOSIUM

Unrecognized Antarctic Biodiversity: A Case Study of the Genus *Odontaster* (Odontasteridae; Asteroidea)

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Synopsis Antarctica has a complex and multifaceted geologic and oceanographic history that has influenced and shaped patterns of marine invertebrate diversity. This evolutionary history consists of major events on a wide range of time scales such as the formation of the Antarctic Polar Front (25–41 million years ago) to repeated glacial cycles during the past million years. These factors variably influenced genetic connectivity of fauna to produce a highly unique, but incredibly diverse marine community. Use of molecular phylogeographic methods is creating the need to revise our understanding of Antarctic patterns of biodiversity. In particular, almost every phylogeographic study carried out to date, suggests that the biodiversity of Antarctic marine shelf fauna is considerably underestimated. In discovering this diversity, some lineages (i.e., cryptic lineages) show no diagnostic morphological differences whereas others (i.e., unrecognized species) show differences that were unknown to science. The sea star genus *Odontaster* is among the best-studied of Antarctic invertebrate groups. Nonetheless, two unrecognized lineages were recently discovered along the Antarctic Peninsula, which is one of the best-studied regions in Antarctica. Herein, we elucidate the molecular and morphological uniqueness of these species and name them *O. roseus* and *O. pearsei*. The latter is in honor of John Pearse, an Antarctic biologist, as well as past President and long-time member of the Society of Integrative and Comparative Biology.

Introduction

Despite a cold and harsh environment, the Southern Ocean hosts amazing organismal diversity. In particular, levels of endemism and overall diversity observed in the marine fauna, are high south of the Antarctic Polar Front (APF) (Ekman 1953, Hempel 1985, Arntz et al. 1997). Understanding factors that promote, maintain, and influence the uniqueness and level of diversity is of great interest. Specifically, biologists, geologists and oceanographers are trying to better understand biotic and abiotic variables of the system. Although we currently have a relatively limited understanding, recent efforts have radically been reshaping our views of Antarctic marine invertebrate endemism and diversity. Genetic analyses of mitochondrial DNA, among others, have revealed a wealth of hitherto unknown organismal lineages found in, and around, Antarctic waters.

In this contribution, we compile literature demonstrating that Antarctic biodiversity is underestimated, outline some of the key elements that influence this diversity, and provide an example indicating that molecular tools are forcing us to critically re-examine morphological taxonomy. Moreover, we argue that there is a need for using more precise scientific language when discussing whether lineages of distinct species are difficult to detect (i.e., cryptic) or merely have not been noticed (i.e., unrecognized). For the purposes of this article, we will include species that are distributed south of the APF, including the sub-Antarctic islands, which mostly fall south of the APF boundary.

Geological setting

The APF is a steep temperature boundary in the Southern Ocean limiting north–south surface water exchange. Dramatic changes can be seen in surface

water temperatures and are often detectable to depths down to 1000 m. In addition, the Antarctic Circumpolar Current (ACC), known as the strongest current in the world, swirls around the continent and is driven by the world's mightiest westerly winds (Orsi et al. 1995). Both the APF and the ACC formed upon the opening of the Drake Passage, ~24–41 million years ago (MYA), after the South American and Antarctic continents separated. Earlier, on the opposite side of the Earth, Australia and Antarctica pulled apart creating the Tasmania Gateway (50–41 MYA), which also greatly contributed to the formation of the ACC (Wei 2004). These complex oceanographic features (separately or in combination) have been hypothesized to act as strong biogeographical barriers to most marine organisms, aside from migratory marine mammals and seabirds (Crame 1999; Pfuhl and McCave 2005; Scher and Martin 2006). Thus, fauna on either side of the APF are hypothesized to have a long (>24 MYA) evolutionary history of separation.

Whereas formation of the ACC and AFP are usually implicated in generating Antarctica endemic fauna, glaciations during the most recent glacial period, are credited with shaping much of the recent faunal distribution of Antarctic marine invertebrates (Thatje et al. 2005). Traditionally, authors (e.g., Brey et al. 1996) have argued that during glacial maxima, continental shelf fauna were largely expatriated and forced down on to the continental slope due to lack of habitat. However, in recent years, asynchronous glacial cycles and the presence of refugia on the continental shelf has been emerging as an explanation as to how Antarctic continental shelf fauna survived extensive glaciations (Thatje et al. 2005, 2008). Potential genetic outcomes of such refugia are two-fold. On one hand, reduced effective population size decreases genetic diversity "within" organismal lineages. In contrast, small population size in combination with multiple refugia can allow substantial genetic differences to quickly accumulate "between" lineages due to genetic drift. This latter scenario can result in genetically isolated lineages that are morphologically very similar as they recently diverged from a common ancestor.

An accurate assessment of the timing of geological or oceanographic events is critical for understanding the cause and effect they have on organismal lineages. Unfortunately, accurately matching biological pattern to environmental underpinnings can be difficult (see Marko and Moran 2009, Marko et al. 2010). In the case of Antarctic fauna, factors that promoted isolation and endemism (e.g., APF), may be different from factors promoting diversity (recent glacial cycles) or genetic connectivity (e.g., life history, rafting). Recognition of differences in such events and timing can often be obscured. For example, establishment of the ACC has been hypothesized to be both a cause of isolation resulting in endemism (Arntz et al. 1997) and a factor promoting dispersal and establishment of circumpolar species (Fell 1961, Dell 1972, Fevolden and Schneppenheim 1989, Arntz et al. 1994, Thornhill et al. 2008, Waters 2008). Yet the timescales of ACC formation (25–41 MYA) and current connectivity among species (roughly the past million years) are vastly different. Thus, hypotheses seeking to explain Antarctic endemism and diversity need to carefully consider evolutionary timing within an appropriate geological or oceanographic construct.

Biogeography and genetics

Biogeographic understanding of Antarctic marine fauna, as in other regions, is based on observations of species collected in specific geographic regions. Because of this simple fact, our best understanding of species diversity is in regions with established research stations—e.g., along the Antarctic Peninsula and in the Ross Sea. When the "same" organism has been found in two disparate regions, most researchers have traditionally assumed them to be present between those sampling localities as well. Unfortunately, and in part due to logistical constraints such as ice cover and operating costs of ships, several regions of Antarctic waters are very poorly known and biologically explored (e.g., Amundsen Sea, much of the Eastern Antarctic, see Grant and Linse 2009), and taxonomists have often had a limited number of representatives with which to assess variation and delimit species. Likewise, we have very little information as to whether a given species occupies several disjunct locations, or has one large range that is occupied throughout. Many species, nonetheless, are currently regarded as having a circumpolar distribution (e.g., *Odontaster validus*, *Sterechinus antarctius*, *Parborlasia corrugatus*, *Lissarca notorcadensis*, Fisher 1940, Pawson 1969, Gibson 1983, Dell 1990; also see Brey et al. 1996, Arntz et al. 1997, Clarke and Johnston 2003, Thatje et al. 2005, Griffiths et al. 2009).

With the advent of molecular tools, taxonomic hypotheses can be tested with essentially independent data. Whereas some of the first phylogeographic studies on Antarctic species focused on cetaceans (Wada and Numachi 1991, Palsbøll et al. 1995, Hoelzel 1998, Pastene et al. 2005), pinnipeds (Gales et al. 1989, Slade et al. 1998, Wynen et al. 2000) and

penguins (Lambert et al. 2002, Ritchie et al. 2004), more complete aspects of Antarctic flora and fauna are now being tested using molecular approaches (see Rogers 2007). Fortunately, for the study of the marine continental shelf fauna, molecular phylogeographic techniques can be used to assess similarity and disparity between organismal populations, even with discontinuous sampling. These techniques have been producing interesting results, challenging some of our notions about Antarctic marine invertebrate biogeography and diversity.

Table 1 shows a compilation of Antarctic marine shelf fauna examined to date using molecular phylogeographic methods. The most striking feature of these studies is that previously unrecognized lineages were discovered in almost every case. Given that these studies are relatively restricted geographically (mainly Antarctic Peninsula and Weddell Sea), the data lend strong support to the notion that Antarctic marine biodiversity is underestimated (Clarke and Johnston 2003, Mahon et al. 2010). Having an accurate estimation of Antarctic biodiversity is critical for numerous reasons: for example, understanding organismal roles in ecosystem function; accurately monitoring effects of climatic change on fauna in the most rapidly warming region on Earth (Vaughan et al. 2003); inferring how geological and oceanographic processes have shaped organismal evolution in the region; assessing whether the same genetic lineage is repeatedly being used in biological experimentation; etc.

Cryptic versus unrecognized diversity

In documenting this unknown biodiversity, elucidating both the diversity of lineages and the disparity between lineages is important. The two concepts often become blurred in the phylogeographic literature. For example, the term "cryptic species" is often invoked to document additional genetic lineages that have been discovered. This situation is true in the Antarctic literature as well (e.g., Brierley et al. 1993, Held 2003, 2005; Raupach and Wagele 2006). However, the word "cryptic" implies that the diversity was hidden or hard to find. Such has been the case with the isopod *Ceratoserolis trilobitoides* (Held 2003) and with the brittle star *Astrotoma agassizii* (Hunter and Halanych 2008) which shows multiple genetic lineages but fail to display morphological characters that can be used to confidently assign them to distinct lineages.

In such cases, other features, such as diet or behavior may allow discrimination between lineages (de Aranzamendi et al. 2008). However, in the context of current Antarctic research, assigning taxa based on such features is not practical because we know so little about the biology of all but a few of invertebrate taxa, and we usually do not have the ability to observe them within their environment. Additionally, as mentioned above, we do not currently have a good understanding of the ranges of organisms due to very limited sampling; this limits our ability to assign names to taxa on geographic grounds. For all intents and purposes, species designations and taxonomic nomenclature is limited to our understanding of species boundaries based on morphological or molecular genetic tools.

In many cases, different genetic lineages may be associated with distinct morphology that was unrecognized. Cryptic or sibling species are defined when speciation occurs without detectable morphological change, yet the species are genetically distinct and often exhibit overlapping geographic ranges (Lomolino et al. 2006). In contrast to "cryptic" lineages, which display no obvious morphological differences, "unrecognized" species do have clear diagnostic morphology that has escaped detection. When novel genetic lineages are uncovered by use of molecular tools, verifying the similarity or disparity in morphology is informative and aids in improving the accuracy of taxonomic hypotheses. By extension, this improves accuracy and understanding of patterns of biodiversity.

Recognition of cryptic species complexes should be derived from a solid list of evidence, similar to that which Held (2003) and Held and Wagele (2005) described for serolid isopods. Specifically Held stated that there should be (1) bimodal distribution of pairwise distance measures with no intermediate values, (2) differentiation at a level known for this gene from other undisputed species pairs closely related to the studied species, and (3) persistence of high levels of genetic differentiation in sympatry. Combining haplotype networks and phylogenetic reconstruction with morphological characters, provides a sound foundation for testing species boundaries (Brandao 2010).

Case study: *Odontaster* species

The sea star genus *Odontaster* Verrill 1880, provides an interesting case study of unrecognized species diversity in Antarctic waters. This sea star, described in 1906 by Kohler, was hypothesized to have a circumpolar distribution (Fisher 1940) and is an important component of the Antarctic ecosystem. *Odontaster validus* spawns in the austral winter and boasts a planktotropic larva with high dispersal ability

Table 1. Phylogeographic studies on Antarctic fauna using molecular tools.

Clade	Species	Region	Previously unrecognized genetic lineages (number)	Marker (s)	References
Arthropoda					
Isopoda	Ceratoserolis trilobitoides	King George Island, Weddell Sea, Antarctic Peninsula	1	16S	Held 2003
	Glyptonotus antarcticus	Weddell Sea, Antarctic Peninsula, Ross Sea	3	16S	Held and Wagele 2005
	Acanthaspidia drygalskii	Weddell Sea	2	16S	Raupach and Wagele 2006
	Ceratoserolis trilobitoides	Weddell Sea, Antarctic Peninsula	1	Microsat.	Leese and Held 2008
	Macroscapha opaca	Sub-Antarctic	8	COI, ITS	Brandao et al. 2010
	Macroscapha tensa	Weddell Sea, Ross Sea			
Euphausiidae	Euphausia superba	Subantarctic, Antarctic Peninsula, Ross Sea	1	ND1	Zane et al. 1998
Pycnogonida	Colossendeis megalonyx	Subantarctic, Antarctic Peninsula	5	COI	Krabbe et al. 2010
	Nymphon australe	Antarctic Peninsula	2	COI, 16S	Mahon et al. 2008
Mollusca					
Bivalvia	Lissarca notocadensis	Subantarctic, Weddell Sea, Antarctic Peninsula, Ross Sea	1	COI	Linse et al. 2007
Cephalopoda	Pareledone turqueti	Subantarctic	1	Isozymes	Allcock et al. 1997
Cephalopoda	Martilia hyadesi	Antarctic Peninsula	1	Isozymes	Brierley et al. 1993
Gastropoda	Doris kerguelensis	Subantarctic, Weddell Sea, Antarctic Peninsula, Ross Sea	28	COI, ISSR-PCR	Wilson et al. 2009
	Nacella concinna	Antarctic Peninsula	1		de Aranzamendi et al. 2008
Nemertea					
	Parborlasia corrugatus	Subantarctic, Antarctic Peninsula, Ross Sea	1	COI,	Thornhill et al. 2008
	Multiple species	Antarctic Peninsula	19	16S	Mahon et al. 2010
Echinodermata					
Crinoidea	Promachocrinus kerguelensis	Subantarctic, Antarctic Peninsula	5	COI, CytB	Wilson et al. 2007
Ophiuroidea	Ophionotus victoriae	Subantarctic, Antarctic Peninsula	1	COI, 16S	Hunter and Halanych 2010
	Astrotoma agassizii	South America, Antarctic Peninsula	2	COII, 16S rRNA	Hunter and Halanych 2008
Asteroidea	Odontaster validus	Subantarctic, Antarctic Peninsula, Ross Sea	2	COI, 16S	A.M. Janosik et al. submitted for publication
Echiniodea	Sterechinus antarcticus/agassizi	South America, Subantarctic, Antarctic Peninsula	~1 (two species the same)	CO1, 16S	Cox et al. submitted for publication

(Pearse 1965, Pearse and Bosch 1986) and occurs over a wide range of depths and in a variety of habitats (Fisher 1940). Moreover, it is arguably one of the earliest known and best-studied marine invertebrate organisms in the Southern Ocean (see Pearse 1965, 1966, 1967, 1969, Belman and Giese 1974, Dayton et al. 1974, Pearse and Bosch 1986, 2002, Olson et al. 1987, McClintock et al. 1988, Bosch et al. 1990, Stanwell-Smith et al. 1998, Kidawa 2001, Peck and Prothero-Thomas 2002, Tyler et al. 2003, Janecki and Rakusa-Suszczewski 2004, Grange et al. 2007, McClintock et al. 2008, Peck et al. 2008).

While exploring phylogeographic structure of this species in the Western Antarctic, A.M. Janosik et al., (submitted for publication) discovered at least five deeply branched genetic lineages corresponding to individuals belonging to three recognized morphological species (*O. validus*, *O. penicillatus*, *O. meridionalis*). Using a combination of haplotype networks and phylogenetic reconstruction based on mitochondrial sequence data, Janosik et al. showed that all of the *Odontaster* lineages formed monophyletic clades and produced individual parsimony-based networks. As such, they warrant the status of full species because of their genetic uniqueness (CO1 divergence values from 3.5 to 10%) *sensu* Hart et al. (2006). Interestingly, both novel lineages occurred along the Antarctic Peninsula, a very well sampled area.

Moreover, further morphological investigation revealed that the species were not cryptic, but merely unrecognized. Diagnostic differences were found in the spines and plates of all taxa. Because diversity can remain unknown unless species are formally described (Oliver et al. 2009), the two previously unrecognized species of *Odontaster* from Antarctic waters (collected during two 5-week Antarctic research cruises aboard the *R/V Laurence M. Gould* in November/December of 2004 and May/June of 2006; using a Blake trawl, wire dredge, or epibenthic sled) are described below and compared with the other currently recognized species of *Odontaster* in Figs. 1, 2, and 3. In addition, a diagnostic key of the Southern Ocean of *Odontaster* species is presented. Terminology follows Lambert (2000) and Clark and Downey (1992).

Family ODONTASTERIDAE Verrill, 1899

Genus ODONTASTER Verrill, 1880

Odontaster roseus nov. sp. (Figs. 1d, 2d, and 3d):

Holotype: Antarctica, 63°24.961′S, 61°50.484′W, 132 m in depth, specimen wet (alcohol) $R = 1.3$ cm,

$r = 0.6$ cm (Fig. 1), USNM 1127023. Collected by K. M. Halanych and A. M. Janosik.

Paratypes: Two specimens were morphologically examined. Antarctica, 62°56.004′S, 61°28.751′W, $R = 2.5$ cm, $r = 0.9$ cm.

Etymology: The descriptor *roseus* describes the rosy to drab red and tan color of this species.

Diagnosis: A species with an almost pentagonal outline, rough spinelets on abactinal plates, four chevrons of plates on the actinal side, superomarginal and inferomarginal plates densely covered in slender, smooth spines with deep grooves between plates.

Description: Body relatively flattened with a stellate outline. Abactinal plates with distinct tabulum crowned with truncate paxillae, comprised of 10–12 spinelets per plate. Spinelets tapering and are of variable lengths, with small spines at end of spinelets (i.e., spinelets rough in appearance). Glassy granules absent on abactinal plates. Papulae on abactinal surface are restricted to the central disc and radial areas. Marginal plates form a distinct border with the abactinal and actinal plates, with deep grooves between plates. Specifically, superomarginal plates are paxillate, densely covered with ~18 spinelets per plate. Inferomarginal plates also paxillate, densely covered with 15–18 spinelets per plate. Spinelets on lateral side of inferomarginal plates are considerably longer than superomarginal spinelets and are rough in appearance. Oral surface possesses the characteristic *Odontaster* re-curved, glassy tipped spine on each mouth plate. Actinal plates with four complete chevrons, including 8–10 spinelets per plate, with one prominent longer spine. Spinelet circumference even from base to tip. Glassy granules also absent from actinal plates. Adambulacral plates with long armament. Spines tapering and rough in appearance. Approximately three to four furrow spines present along the ambulacral plates. Pedicellariae absent.

DNA: Two adults and two larvae were molecularly characterized. Unique diagnostic sequences from the mitochondrial COI and 16S rDNA genes are deposited to GenBank under the following accession numbers: COI—GQ29359 Holotype; GQ29489, GQ29490 Paratypes; 16S—GQ294413 Holotype; GQ294414, GQ29447 Paratypes.

Color note: Live color rosy to drab red and tan compared to the typical bright red of *Odontaster validus*, but still brighter red than *O. pearsei* nov. sp.

Distribution: Northern Antarctic Peninsular, South Shetland Islands, collected at 132–188 m.

Odontaster pearsei nov. sp. (Figs. 1e, 2e, and 3e):

*Holotype:* Antarctic Peninsula 54°29.071′S, 62°12.857′W 132 m in depth, specimen wet (alcohol)
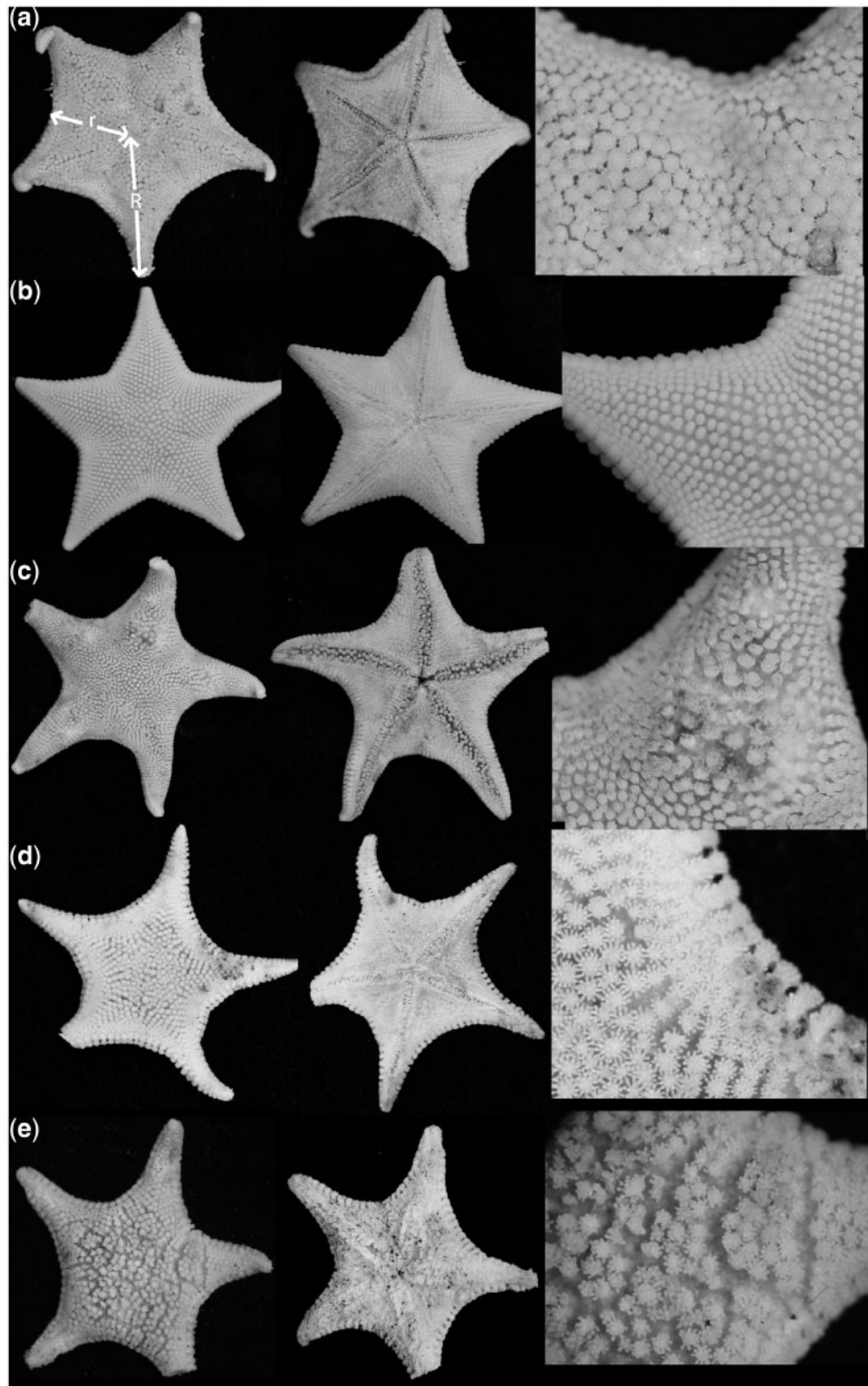
Fig. 1 *Odontaster* morphology. Aboral, oral, and close-up of aboral side are pictured, respectively for: (a) *Odontaster meridionalis*, (b) *Odontaster penicillatus*, (c) *Odontaster validus*, (d) *Odontaster roseus* nov. sp., and (e) *Odontaster pearsei* nov. sp.

$R = 2.4$ cm, $r = 1.3$ cm. USNM 1127022. Collected by K. M. Halanych and A. M. Janosik.

Paratypes: Eight individuals were morphologically examined. Antarctic Peninsula 64°24.62′S, 64°30.13′W, $R = 1.7$ cm, $r = 1.0$ cm, Antarctic Peninsula 67°43.607′S, 69°18.103′W, $R = 0.9$ cm, $r = 0.5$ cm, Antarctic Peninsula 63°24.961′S, 61°50.484′W, $R = 1.8$ cm, $r = 0.9$ cm, Antarctic
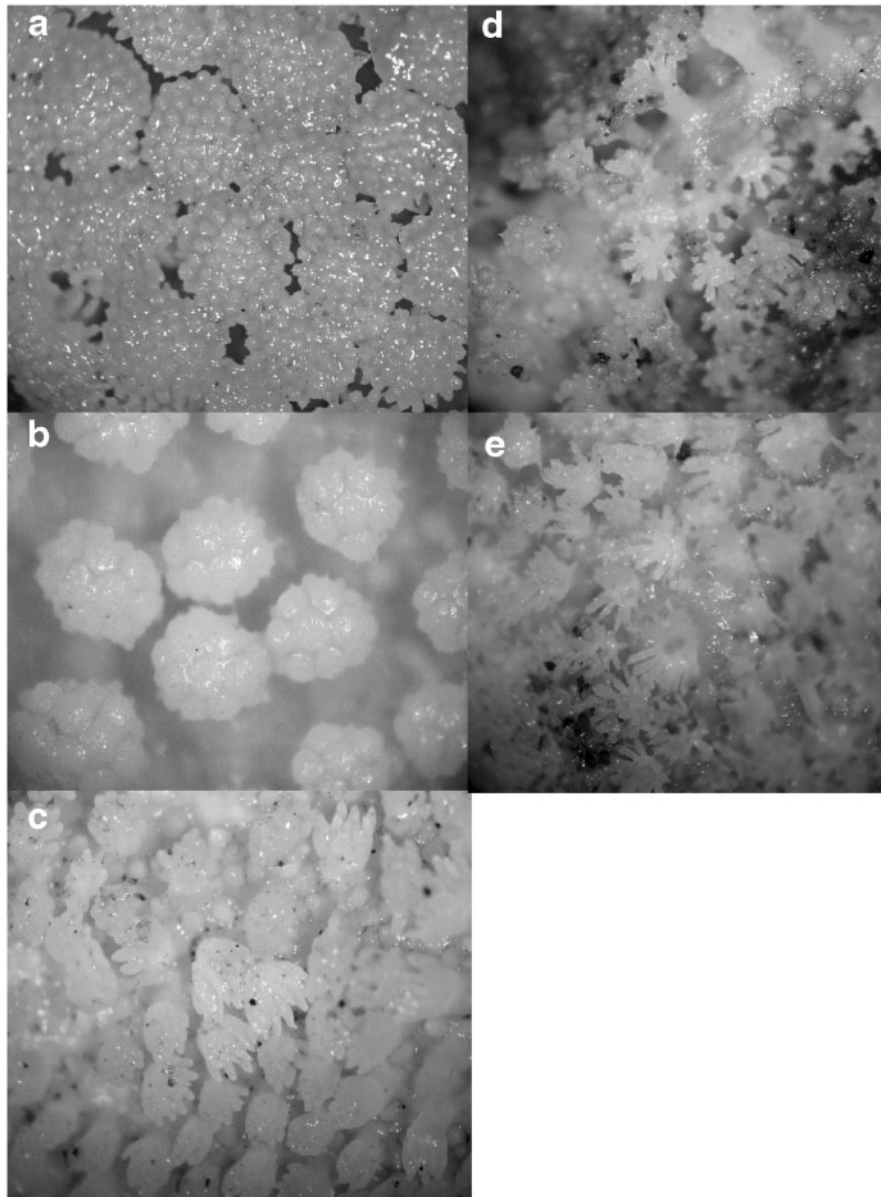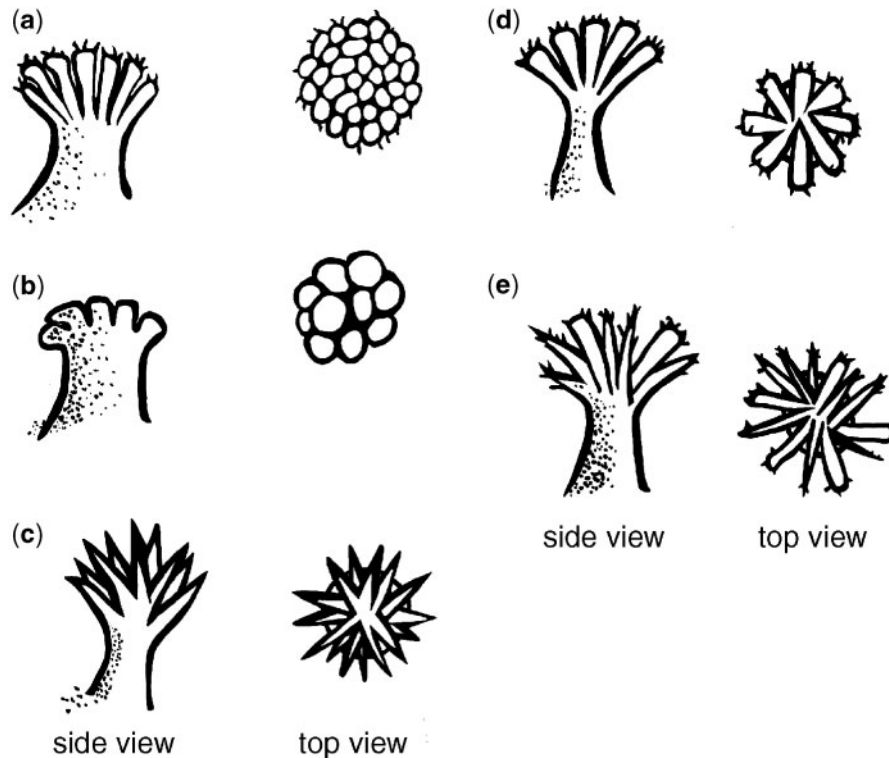
Fig. 2 Photograph of the spine morphology of *Odontaster*. Spine on paxillae are pictured for: (a) *Odontaster meridionalis*, (b) *Odontaster penicillatus*, (c) *Odontaster validus*, (d) *Odontaster roseus* nov. sp., and (e) *Odontaster pearsei* nov. sp.

Peninsula (two individuals) 65°39.843′S, 68°02.224′W, $R = 1.6$ cm, $r = 0.8$ cm, $R = 1.6$ cm, $r = 0.8$ cm, Antarctic Peninsula 67°44.420′S, 69°17.379′W, $R = 1.5$ cm, $r = 0.7$ cm, sub-Antarctic 54°38′S, 3°50′W, $R = 1.2$ cm, $r = 0.6$ cm.

Etymology: This species is named for Dr John S. Pearse in honor of his numerous contributions to Antarctic marine invertebrate ecology and asteroid biology.

Diagnosis: A species with a stellate outline, rough spinelets on abactinal plates, three chevrons of plates on the actinal side, superomarginal and inferomarginal plates densely covered in rough spines with deep grooves between plates.

Description: Body relatively flattened, with a stellate to sub-pentagonal outline. Abactinal plates with distinct tabulum crowned with truncate paxillae, comprised of 16–20 spinelets per plate. Spinelets taper towards base, with small spines at end of each spine (i.e., rough in appearance). Glassy granules absent on abactinal plates. Papulae on abactinal surface also restricted to the central disc and radial areas. Marginal plates form a distinct border with the abactinal and actinal plates, with deep grooves between plates. Specifically, superomarginal plates are paxillate, densely covered with ~15 spinelets per plate and are rough in appearance. Inferomarginal plates also paxillate, densely covered with 10–12

Fig. 3 Drawing of the spine morphology of *Odontaster*. Spine on paxillae are pictured for: (a) *Odontaster meridionalis*, (b) *Odontaster penicillatus*, (c) *Odontaster validus*, (d) *Odontaster roseus* nov. sp., and (e) *Odontaster pearsei* nov. sp.

spinelets per plate. Spinelets on lateral side of infero-marginal plates considerably longer than supero-marginal spinelets and rough in appearance with small spines at end of spinelet. Oral surface possesses the characteristic *Odontaster* re-curved, glassy tipped spine on each mouth-plate. Actinal plates with three complete chevrons, including five to eight spinelets per plate. Spinelets taper from tip to base, being more slender at the base. Glassy granules also absent from actinal plates. Adambulacral plates with long armament, with spines tapering and rough in appearance. Three furrow spines present along the ambulacral plates. Pedicellariae absent.

DNA: Eight adults were characterized molecularly. Unique diagnostic sequences from the mitochondrial COI and 16S rDNA genes are deposited to GenBank under the following accession numbers: COI—GQ294358 Holotype; GQ294357, GQ294358, GQ294372, GQ294383, Paratypes; 16S—GQ294412; Holotype, GQ294411, GQ294412, GQ294415, GQ294423, GQ294426, GQ294439 Paratypes.

Color note: Color of live specimen orange to tan, more drab than *O. roseus* or the typical bright red of *Odontaster validus*.

Distribution: Northern Antarctic Peninsula, South Shetland Islands, Anvers Island, Beer Island, and Marguerite Bay, collected at 132–282 m.

Key to the *Odontaster* species of the Southern Ocean

The genus *Odontaster* is characterized by a recurved, glassy-tipped spine on each mouth-plate, two side-by-side, at each mouth angle. In addition, *Odontaster* spp. have abactinal plates with a distinct tabulum crowned with short to rather long spinelets; marginal plates small, to well-developed, more or less tabulate, spinulose; actinal area densely spinulose.

(1) Radial paxillae with 20–30 spinelets, the middle ones markedly clavate (Figs. 2a and 3a); actinal plates also with numerous radiating spines, up to ~15, central ones more clavate than the peripheral (Antarctic, circumpolar, including South Georgia, Marion Island, and Kerguelen):............*Odontaster meridionalis*

Radial paxillae with fewer than 20 spinelets:...2

(2) Outline more pentagonal than stellate, marginal plates obvious with short, usually granuliform spinelets, barely longer than wide; abactinal spinelets as in Figs. 2b and 3b; dorsal side flat or slightly convex (Patagonia, Falkland Plateau):...*Odontaster penicillatus*

Outline more stellate; spinelets of marginal plates otherwise:.......................................3

(3) Radial paxillae with about a dozen spinelets that are smooth, slender and tapering (Figs. 2c and 3c); five actinal plate chevrons, actinal plates with up to seven similar, slender spinelets that are even from base to tip, two to three furrow spines (Antarctic, circumpolar, including South Georgia and Bouvet Island): ....*Odontaster validus*

Radial paxillae with rough, tapering spinelets with little spines at the tips; two to four (commonly three) furrow spines: 4

(4) Radial paxillae with 10–12 spinelets (Figs. 2d and 3d); four complete actinal plate chevrons, actinal plates with spines of different lengths (8–10), specifically with one prominent spine in the middle, (Antarctic Peninsula):..*Odontaster roseus*

Radial paxillae with 16–20 spinelets (Figs. 2e and 3e); three complete actinal plate chevrons, actinal plate with slender tapering (from tip to base) spines of equal length (five to eight) (Antarctic Peninsula):..*Odontaster pearsei*

Current and future directions

Although many studies attempt to estimate biodiversity in the Antarctic, assessing how many species are present is not simple. Specifically, Arntz et al. (1997) estimated 5,200 species and Clarke and Johnston (2003) estimate 4100 species, while Gutt et al. (2004) estimated anywhere from 11,000 to 17,000 macrozoobenthic species using statistical methods. Based on the phyogeographic studies listed in Table 1, considerable diversity in the Antarctic remains to be discovered and distinguished as either cryptic or unrecognized. Using the publications in Table 1 as a guide, we can approximate how much additional marine benthic diversity has yet to be discovered in the Antarctic. For example, there are currently ~400 species of echinoderms recognized in the Antarctic (Arntz et al. 1997). Specifically, four nominal echinoderm species from the Antarctic have been examined by phylogeographic studies and at least ten unrecognized lineages were discovered. Thus, there are 3.5 times as many echinoderms species than expected, leading to an estimate of a total of 1400 echinoderm species in the Antarctic. Of note, these studies were also conducted in the well-examined areas. By the same logic, there are currently 900 species of crustaceans recognized and but preliminary genetic evidence suggests that this group may be underestimated by three-fold. Similarly, although 500 species of pycnogonids are known, estimates based on under-representation observed in phylogeographic analyses suggest as many as 2250 spp. in the Antarctic. These numbers are at best very rough estimates, and as more data are gathered probably will be refined. Clearly, we have much more to discover in the waters around Antarctica.

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