Polar Biol (2015) 38:1223–1237
DOI 10.1007/s00300-015-1689-9

ORIGINAL PAPER

The phylogenetic position and taxonomic status of *Sterechinus bernasconiae* Larrain, 1975 (Echinodermata, Echinoidea), an enigmatic Chilean sea urchin

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Received: 17 September 2014 / Revised: 28 March 2015 / Accepted: 31 March 2015 / Published online: 5 May 2015

Abstract *Sterechinus* is a very common echinoid genus in benthic communities of the Southern Ocean. It is widely distributed across the Antarctic and South Atlantic Oceans and has been the most frequently collected and intensively studied Antarctic echinoid. Despite the abundant literature devoted to *Sterechinus*, few studies have questioned the systematics of the genus. *Sterechinus bernasconiae* is the only species of *Sterechinus* reported from the Pacific Ocean and is only known from the few specimens of the original material. Based on new material collected during the oceanographic cruise INSPIRE on board the R/V *Melville*, the taxonomy and phylogenetic position of the species are revised. Molecular and morphological analyses show that *S. bernasconiae* is a subjective junior synonym of *Gracilechinus multidentatus* (Clark). Results also show the existence of two genetically distinct subclades within the so-called *Sterechinus* clade: a *Sterechinus neumayeri* subclade and a subclade composed of other *Sterechinus* species. The three nominal species *Sterechinus antarcticus, Sterechinus diadema*, and *Sterechinus agassizi* cluster together and cannot be distinguished. The species *Sterechinus dentifer* is weakly differentiated from these three nominal species. The elucidation of phylogenetic relationships between *G. multidentatus* and species of *Sterechinus* also allows for clarification of respective biogeographic distributions and emphasizes the putative role played by biotic exclusion in the spatial distribution of species.

Keywords *Sterechinus bernasconiae* · *Gracilechinus multidentatus* · Echinoidea · Antarctic · Phylogeny · Biogeography

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Introduction

For more than a century, species of the genus *Sterechinus* have been among the most frequently collected and commonly studied Antarctic echinoids (Agassiz 1869, 1881; Studer 1876, 1880; Meissner 1900, Koehler 1901, 1906, 1926; Döderlein 1906; Mortensen 1910). The genus includes six nominal species that were treated in many ecological and biogeographic studies devoted to Antarctic marine life (Brey and Gutt 1991; Arnaud et al. 1998; Barnes and Brockington 2003; Lee et al. 2004; David et al. 2005; Brandt et al. 2007; Linse et al. 2008; Díaz et al. 2011; González-Wevar et al. 2012a; Pierrat et al. 2012a, b). The genus *Sterechinus* is widely distributed across the Southern Ocean and extends northward along the coasts of Argentina until 35°S latitude (David et al. 2005; Pierrat et al. 2012b; Saucède et al. 2014). In the Antarctic, *Sterechinus neumayeri* (Meissner, 1900), *Sterechinus*

antarcticus (Koehler, 1901), and *Sterechinus dentifer* (Koehler, 1926) inhabit the inner (0–800 m depth), outer (200–1500 m depth), and deep shelf and slope (500–2400 m depth) of the Antarctic continent, respectively. *Sterechinus diadema* (Studer, 1876) is restricted to sub-Antarctic islands (Marion and Prince Edward Islands, Crozet and the Kerguelen Plateau), and the distribution range of *Sterechinus agassizi* (Mortensen, 1910) extends from sub-Antarctic islands (Falkland Islands, South Georgia, Shag Rocks, Bouvet Island, and Marion and Prince Edward Islands) to the coasts of Argentina as far northward as the mouth of Rio de la Plata at ca. 35°S latitude (David et al. 2005; Pierrat et al. 2012b). Finally, *Sterechinus bernasconiae* (Larrain, 1975) was only described from few localities off the coasts of southern Chile. It is the only species of *Sterechinus* recorded from the Pacific Ocean (Larrain 1975).

Despite the abundant literature devoted to *Sterechinus*, recent molecular and morphological results have shown that the three nominal species *S. diadema, S. agassizi*, and *S. antarcticus* cannot be distinguished (David et al. 2005; Díaz et al. 2011). In the past, the distinction between species often relied on the geographic origin of specimens as well as on subtle differences in morphology. However, most of the morphological characters show a wide range of within-species variation that tend to overlap among species and make the distinctions between them unclear (Mortensen 1943; David et al. 2005).

In this context, *S. bernasconiae* has attracted our attention as it is the only species of *Sterechinus* reported from the Pacific Ocean. It is recorded from a narrow area off the coast of southern Chile. In contrast, *S. agassizi* is much more widely distributed on the Atlantic side of southern South America; it extends from sub-Antarctic islands to the coasts and continental shelf of Argentina. Considering the few specimens of *S. bernasconiae* ever collected as compared with the numerous samples available for other *Sterechinus* species (Larrain 1975), the taxonomic status and distribution range of the species were not revised in studies devoted to the systematics and biogeography of Austral echinoids (David et al. 2005; Díaz et al. 2011; González-Wevar et al. 2012a; Pierrat et al. 2012b, 2013). In light of the taxonomic issues raised in a recent study (Díaz et al. 2011), the taxonomic status of *S. bernasconiae* and its phylogenetic relationships with *S. agassizi* and other species of *Sterechinus* had to be clarified.

The oceanographic cruise INSPIRE was led off the coasts of Chile (February–March 2010, R/V *Melville*) to explore chemosynthetic systems (i.e. hydrothermal vents and methane seeps) and study the associated marine life (Zapata-Hernández et al. 2014). The sampling effort was led between 400 and 3300 m depth and from ~ 33°S to ~ 46°S and allowed for obtaining specimens of rare species, among which specimens of *S. bernasconiae* were collected. Based on these newly collected specimens along with original samples including the type material (Larrain 1975), the present work aims to revise the systematics of *S. bernasconiae*, clarify phylogenetic relationships with other species of *Sterechinus*, and re-examine the biogeographic distribution of the genus *Sterechinus* in the Southern Ocean.

Materials and methods

Material studied

New specimens of *S. bernasconiae* were collected off the coasts of Chile during the oceanographic cruise INSPIRE aboard the R/V *Melville* along the Chilean continental margin (Fig. 1; Table 1). Eight specimens were caught by trawling at six stations, between about 600 and 1100 m depth (Tables 1, 2). They are housed at the Biological Collection of Universidad Católica del Norte (CBUCN, Coquimbo, Chile). The analysis of specimens was complemented by the examination of specimens of *S. bernasconiae* formerly collected in Patagonia during the Hero 72, 4b cruise (Larrain 1975). They are housed at the Museum of Zoology, Universidad de Concepción, Chile (Table 1). To perform the phylogenetic analysis, specimens of *S. bernasconiae* were sequenced along with specimens belonging to the five other nominal species of *Sterechinus* that were collected in six areas of the Southern Ocean (Adélie Land, South Shetland Islands, Antarctic Peninsula, Weddell/Bellingshausen seas, and around the Kerguelen Islands) and off the coasts of Argentina (Table 2). This material is housed at the Molecular Ecology Laboratory, Faculty of Ecology Sciences at Universidad de Chile, Santiago, Chile.

Morphological study

New material was fixed in 96 % ethanol, the old specimens housed at the University of Concepción being preserved in formaldehyde. Morphological observations were performed with a binocular microscope, test measurements were taken with a digital caliper to the nearest 0.1 mm. Statistical tests were performed with PAST v. 1.93 (Hammer et al. 2001). Echinoid test plating was drawn using a binocular microscope equipped with a camera lucida. Secondary spines and pedicellariae were removed from tests of the newly collected specimens and placed into 96 % ethanol. They were bleached with a 10 % solution of sodium hypochlorite to remove soft tissue and to separate individual valves of pedicellariae. Then, they were washed in water, dried for 24 h, and mounted on SEM stubs. The

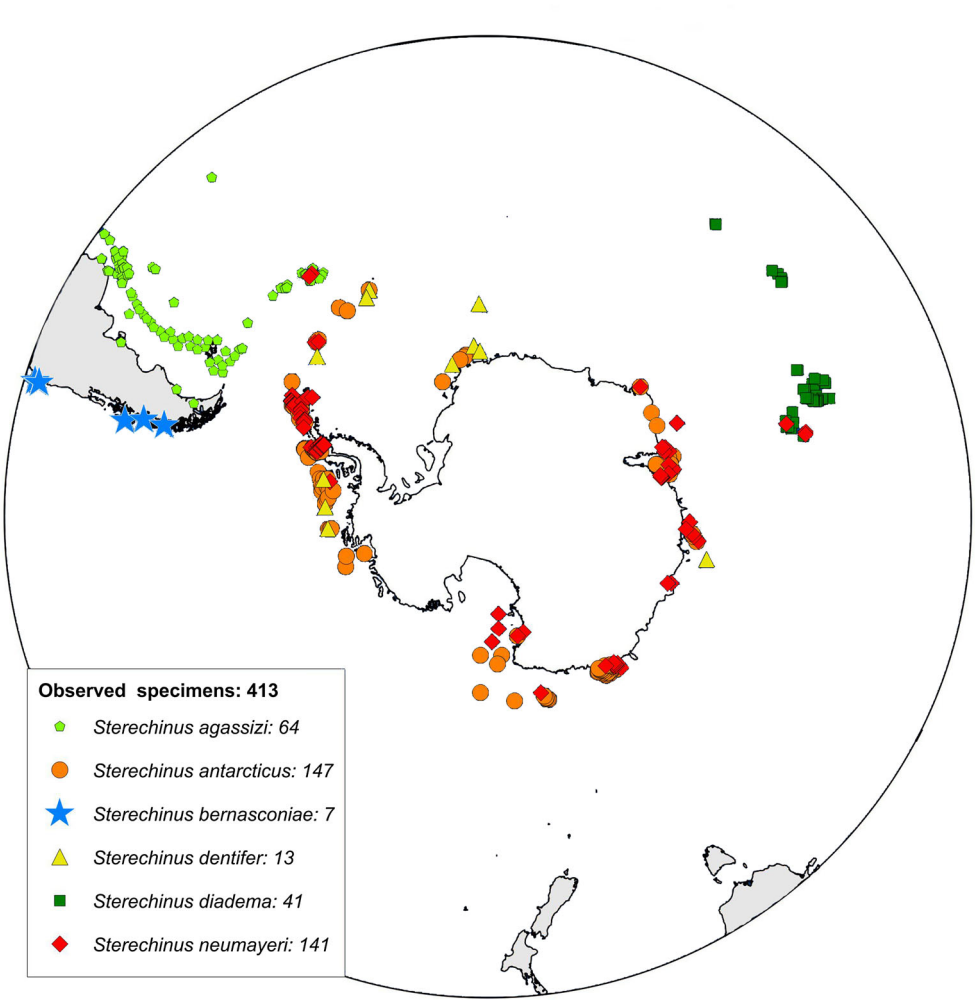

Fig. 1 Distribution map of the 413 specimens of *Sterechinus* spp. studied for this work. The number of studied specimens is given for each nominal species

Table 1 Origin of samples and number of specimens of *S. bernasconiae* studied for the morphological analysis

Location	Cruise	Station	Latitude	Longitude	Depth (m)	Specimen Number
Chilean margin	So-210	64	−35°58.56	−73°38.43	1034	1
Chilean margin	INSPIRE	AGT-1	−45°55.17	−75°35.12	628	2
Chilean margin	INSPIRE	AGT-2	−45°53.83	−75°35.97	579	1
Gulf of Penas[a]	Hero 72, 4b	–	−47°50	−74°40	300	8[b]
Topar Island	Hero 72, 4b	–	−50°08.5	−74°41	360	9

Newly collected specimens are from cruises So-210 and INSPIRE. Larrain's specimens are from cruise Hero 72, 4b

[a] *S. bernasconiae*'s type locality

[b] Including the holotype and the seven paratypes

entire process was performed under a binocular microscope. Details of pedicellariae and spines were examined with a tabletop scanning electron microscope, and digital images were recorded.

Extraction, amplification, and sequencing

Total DNA was extracted from gonadal tissue or spines of 30 specimens of *Sterechinus* including *S. bernasconiae*, i.e. 5 specimens per species, using the salt method (Aljanabi and Martínez 1997). PCR was used to amplify a fragment of the mitochondrial cytochrome oxidase I gene, using the primers described by Lee et al. (2004), LCOI1490 (5′-TCTA CAA ACC ACA ARG AYA TTG G-3′) and HCOIN (5′-CCC ATT GAA AGA ACG TAG TGA AAG TG-3′). For some samples that had degraded DNA, we used the intermediate primers designed by Díaz et al. (2011), ERZin-F (5′-GAC CGA CTG CCC TTA TTT-3′)

Table 2 Origin of specimens analysed for the molecular analysis (labelled as in the tree)

Species	Location	Programme	Station	Latitude	Longitude	Depth (m)	Specimens
S. neumayeri	Adélie Land	BENTHADEL	Emperor Bay	−66°40.19	140°00.61	26	1
	King George Is.	INACH 13-05	Ardley Pen. Bay	−62°07.79	−58°08.37	10	2
	King George Is.	ECOS C06B02	Ardley Pen. Bay	−62°07.79	−58°08.37	10	3
	Antarctic Pen.	INACH 02-02	O'Higgins	−63°19.23	−57°53.87	20	4
	Weddell Sea	INACH B01-07	Red Island	−63°44.22	−57°52.85	10	5
S. agassizi	Argentina	INIDEP 1608	Reclutas	−39°50.05	−56°12.24	100–200	1
	Argentina	INIDEP 1608	SAO	−40°45.22	−57°00.39	100–200	2
	Argentina	INIDEP 1608	Tango B	−43°38.12	−59°49.97	100–200	3
	Argentina	INIDEP 1608	Valdés	−43°21.55	−59°36.18	100–200	4
	Argentina	INIDEP 1608	SW SAO	−41°39.06	−58°05.40	100–200	5
S. diadema	Kerguelen Islands	BENTHOS-MAC	Portes Noires	−49°29.65	69°08.97	15	1
	Kerguelen Islands	BENTHOS-MAC	Ile Longue	−49°32.19	69°53.03	20	2
	Kerguelen Islands	BENTHOS-MAC	Ile Haute	−49°23.25	69°56.49	20	3
	Kerguelen Islands	BENTHOS-MAC	Port Couvreux	−49°17.38	69°42.67	20	4
	Kerguelen Islands	BENTHOS-MAC	Port Matha	−48°56.10	69°02.29	10	5
S. antarcticus	Weddell Sea	CHESSO	ISIS 152	−59°41.00	−28°21.00	1400	4
	Weddell Sea	BIOPEARL I	SG-EBS-35	−53°35.85	−37°54.13	502	5
	Adélie Land	CEAMARC	CEAMARC-08	−66°33.64	142°19.93	372	1
	Weddell Sea	ANT XXIII/8	PS69/603-5	−70°30.99	−08°48.08	285	2
	Weddell Sea	ANT XXIII/8	PS69/603-5	−70°30.99	−08°48.08	285	3
S. dentifer	Weddell Sea	CHESSO	ISIS 142	−60°02.00	−29°98.00	2400	4
	Weddell Sea	CHESSO	ISIS 152	−59°41.00	−28°21.00	1400	5
	Bellinghausen Sea	BENTART'06	MB 30	−69°58.00	−87°31.00	1814	1
	Bellinghausen Sea	BENTART'06	MB 30	−69°58.00	−87°31.00	1814	2
	Bellinghausen Sea	BENTART'06	MB 30	−69°58.00	−87°31.00	1814	3
S. bernasconiae	Chilean margin	So-210	69	−36°24.95	−73°42.15	680	1
	Chilean margin	INSPIRE	AGT-4	−36°23.59	−73°42.91	700	2
	Chilean margin	INSPIRE	AGT-3	−36°22.31	−73°43.00	854	3
	Chilean margin	So-210	64	−35°58.56	−73°38.43	1034	4
	Chilean margin	INSPIRE	AGT-1	−45°55.17	−75°35.12	628	5

and ERZin-R (5′-CTC GCT TTC CTG AGT AGT-3′). The amplified fragment has an extension of 774 bp, which corresponds to nucleotides 67 to 840 of the COI gene of *S. neumayeri* (GenBank accession AY275548, size 1077 pb). Polymerase chain reactions (PCR) were carried out in a Thermo PxE 0.5 thermocycler using Taq DNA polymerase (Invitrogen, Recombinant, 500 U) under standard amplification conditions with 25 µL of reaction volumes. Each reaction tube contained 1 µL (approx 10 ng) of genomic DNA extract, 2.5 µL 10XPCR buffer, 1.5 Mm MgCl2, 2.5 µL 10 mM each dNTP, 10 pmol of each primer, 0.2 U Taq polymerase. After 7 min of initial heating at 95 °C, amplification was performed in 35 repetitions of a three-step cycle (denaturation, 95 °C for 1 min; annealing, 58 °C for 1.5 min; extension, 72 °C for 1.5 min) and a final extension for 10 min. PCR products were purified with Qiagen QIAquick columns, and the sequencing was done by the Korean company Macrogen, in an ABI 3100 automatic sequencer (Applied Biosystems); the sequences obtained were aligned with the programs Proseq v. 3.0 (Filatov 2009) and ClustalX 1.8 (Thompson et al. 1997).

Phylogenetic analysis

The relatively best-fit DNA substitution model was selected by the Akaike Information Criterion deployed in jModelTest v. 0.1.1 (Posada 2008), and the model (GTR I + Γ) was used for subsequent Bayesian inference (BI) and maximum likelihood (ML) phylogeny inference. To root the phylogram, sequences of outgroups were chosen within the order Echinoidea following Lee et al. (2004). Three species were chosen within the family Echinidae: *Loxechinus albus* (GenBank access AY275550.1), *Paracentrotus lividus* (GenBank access NC_001572.1), and *Gracilechinus*

multidentatus (GenBank access EU8699-27.1, 28.1, 29.1 and 31.1), along with two species within the family Strongylocentrotidae: *Strongylocentrotus purpuratus* (GenBank access X12631.1) and *Hemicentrotus pulcherrimus* (GenBank access JQ742947.1). Finally, the species *Pseudechinus magellanicus* of the order Temnopleuroida (GenBank access AY275549.1) was selected as outgroup for the order Echinoidea. Maximum likelihood analysis was carried out using the software RAxML v7.03 (Stamatakis et al. 2008), and branch support values were estimated using 1000 bootstrap replicates (Felsenstein 1981). Bayesian phylogenetic analyses were performed using the program MrBayes v.3.1.2 (Huelsenbeck and Ronquist 2003). This method estimates the posterior probability that each recovered taxon forms a monophyletic unit. All Markov Chain Monte Carlo analyses were performed twice using independent runs of random trees for a total of 8×10^6 generations, and trees were sampled every 500 generations after discarding the first 25 % as a burn-in. Average standard deviation of split frequencies converged below 0.01. All remaining trees were used to construct a majority rule consensus phylogram.

To test for the reliability of the clades obtained in phylogenetic inferences we used the Automatic Barcode Gap Discovery (ABGD) species delineation tool (Puillandre et al. 2012a). Pairwise comparisons of COI sequences were performed within and among species, the shortest genetic distances being expected within species. Within the range of computed values, a barcode gap was expected between intra- and interspecific distance values. It provides a set of a priori threshold values for delineating genetically distinct species (Puillandre et al. 2012a, b). In addition to within and among species comparisons, genetic distances were calculated within and among clades and subclades. They were computed among the clades "GRA" (including sequences of *G. multidentatus* and *S. bernasconiae*), "LOX" (representing the sequence of *L. albus*), and "STER" (including sequences of the five remaining species of *Sterechinus*), within the clade "GRA" and "STER", and within the two subclades "NEU" (sequences of *S. neumayeri*) and "Stere" (including the four remaining species of *Sterechinus*). The software MEGA v6.06 (Tamura et al. 2013) with Kimura's two-parameter (K2P) model of base substitution (Kimura 1980) was used.

Results

Phylogenetic relationships

The length of the COI section obtained for the species of *Sterechinus* was 774 bp. Maximum likelihood analysis (ML) and the Bayesian inference (BI) resulted in a tree with similar topology in terms of branching and robustness of the nodes (Fig. 2). As expected, all the species of Echinidae included in the analysis form one single monophyletic group with respect to the representatives of the Strongylocentrotidae and Temnopleuroida. The Echinidae clade comprises the species *P. lividus* as sister group and two clades: a first one groups sequences of *G. multidentatus* and *S. bernasconiae* together (the "GRA" clade), and the second one is composed of the remaining *Sterechinus* sequences (the "STER" clade that includes *S. neumayeri*, *S. antarcticus*, *S. diadema, S. agassizi*, and *S. dentifer*). This second clade is composed of two well-differentiated and supported subclades. The first one includes all sequences of *S. neumayeri*, while the second one group together the sequences of other *Sterechinus* species. In the latter, sequences of *S. dentifer* form a supplementary grouping that it is not supported by posterior probability values (Fig. 2). *L. albus* forms a third group ("LOX"), but the clade is not well supported (Fig. 2).

Of the 12 species analysed, eight genetically distinct units (OTUs) were identified using the ABGD method. Threshold values for delineating the distinct species are comprised between 0.01 and 0.03 % (Kimura distance K80) (Table 3). The 8 OTUs comprise (1) *P. magellanicus*, (2) *H. pulcherrimus*, (3) *S. purpuratus*, (4) *P. lividus*, (5) *L. albus*, (6) the nominal species *G. multidentatus* and *S. bernasconiae*, (7) *S. neumayeri*, and (8) the cluster *S. agassizi*, *S. antarcticus*, *S. diadema*, and *S. dentifer*. These results are in line with the phylogenetic analyses (Fig. 2). The single OTU composed of the sequences of *G. multidentatus* and *S. bernasconiae* corresponds to the "GRA" clade identified in the phylogeny; OTUs 7 and 8 composed of other *Sterechinus* species correspond to the two subclades "NEU" and "Stere" of the "STER" clade (Fig. 2). Pairwise comparisons among the "GRA", "LOX" and "STER" clades show similar values for the distances "LOX"-"STER" and "GRA"-"STER" (0.2 %) and a lower value for the distance "LOX"-"GRA" (0.1 %). Within-clade comparisons give a genetic distance of 0.004 % (SE 0.001) for the "GRA" clade and 0.027 % (SE 0.004) for the "STER" clade. Genetic distances are 0.003 % (SE 0.001) within the "NEU" subclade and 0.004 % (SE 0.001) within the "Stere" subclade (Table 3).

Systematics

Measurement and examination of morphological characters of Larrain's original material (Universidad de Concepción) as well as of newly collected specimens of *S. bernasconiae* (Tables 1, 4) show that they all fall into the diagnosis of both *S. bernasconiae* Larrain, 1975 and *G. multidentatus* Clark, 1925. Hence, molecular and morphological results agree with each other and support the synonymy of the two species. The species is here assigned to the genus

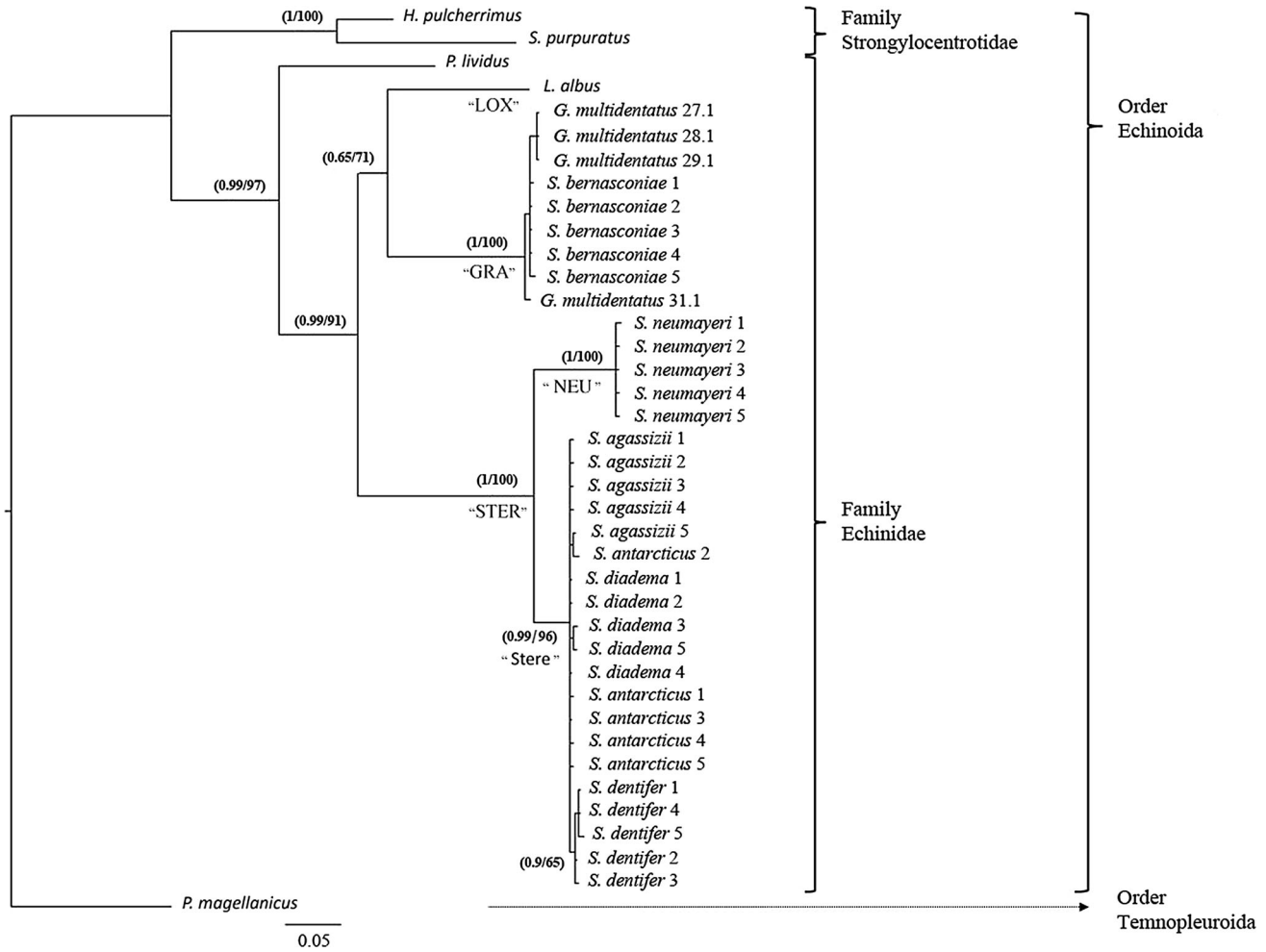

Fig. 2 Bayesian inference (BI) tree based on COI sequences. Branch support values are given for main nodes, Bayesian posterior probabilities preceding bootstrap values (analysis with 1000 replicates)

Gracilechinus Fell and Pawson 1966, not *Sterechinus* Koehler 1901.

Gracilechinus multidentatus (Clark, 1925)

Echinus acutus Agassiz, 1881; p. 114 (pro parte, St. 170, non *Echinus acutus* Lamarck, 1816).
Echinus multidentatus Clark 1925; p. 115–116, Pl. VI. 1–2.
Gracilechinus multidentatus McKnight 1968: 94–99; Figs. 4–6.
Sterechinus bernasconiae Larrain 1975: 94–105; Figs. 109–129; Tabs. 9–11, maps 9, 11, and 15.

Holotype Specimen housed at the Natural History Museum, collected during the cruise of the H.M.S. Challenger near the Kermadec Islands (northeast of New Zealand), station 170, 1135 m depth, on a rocky bottom.

Material See Tables 1, 2 for examined material.

Diagnosis One primary tubercle on each ambulacral plate, primary tubercles forming two distinct vertical rows in each ambulacrum. Primary tubercles irregular in size and arrangement; they can be replaced by secondary tubercles adorally and adapically on every alternate or third plate. Valves of globiferous pedicellariae with two to five lateral teeth near the tip. Large tridentate pedicellariae with long (up to 2.5 mm), narrow, and slightly curved valves, blade edges finely serrate at the tip. Shaft of secondary spines smooth. Buccal plates without spines.

Description Test measurements are shown in Table 4. Test circular at the ambitus. In lateral view, test hemispherical in shape, flattened orally (Fig. 3). Mean test height 57 % the diameter of the test but relative test height highly variable, test profile varying from high subconical to flattened aborally. There is an allometric relationship

Table 3 Pairwise genetic distances within and between OTUs based on the Automatic Barcode Gap Discovery (ABGD)

OTUs	Species	Number of sequences	% K2P sequence divergence							
			Within OTU	Between OTUs						
				1	2	3	4	5	6	7
1	*P. magellanicus*	1	n/a							
2	*H. pulcherrimus*	1	n/a	0.2 ± 0.02						
3	*S. purpuratus*	1	n/a	0.2 ± 0.02	0.1 ± 0.01					
4	*P. lividus*	1	n/a	0.2 ± 0.02	0.2 ± 0.02	0.3 ± 0.02				
5	*L. albus*	1	n/a	0.2 ± 0.02	0.2 ± 0.02	0.2 ± 0.02	0.2 ± 0.02			
6	*G. multidentatus*	4	0.004 ± 0.001	0.2 ± 0.02	0.2 ± 0.02	0.2 ± 0.02	0.2 ± 0.02	0.1 ± 0.01		
	S. bernasconiae	5								
7	*S. neumayeri*	5	0.003 ± 0.001	0.2 ± 0.02	0.2 ± 0.02	0.2 ± 0.02	0.2 ± 0.02	0.2 ± 0.02	0.2 ± 0.01	
8	*S. agassizii*	5	0.004 ± 0.001	0.2 ± 0.02	0.2 ± 0.02	0.3 ± 0.02	0.2 ± 0.02	0.2 ± 0.02	0.2 ± 0.02	0.1 ± 0.01
	S. antarcticus	5								
	S. diadema	5								
	S. dentifer	5								

between test diameter and relative test height (H/D), relative test height increasing with size, as shown in Fig. 6 where a natural logarithm regression model is fit to morphological data. The regression model was tested significant (10,000 replicate permutation test; $p < 0.005$), but the value of the coefficient of determination is low ($R^2 = 0.26$) due to strong among-individual variability. This is in agreement with very first studies (Clark 1925). Mean peristome diameter 32 % the diameter of the test, relative peristome size (P/D) decreasing with size (Fig. 6). The allometric relationship between relative peristome size and test diameter can be described by a natural logarithm regression model ($R^2 = 0.83$, $p < 0.005$, 10,000 replicate permutation test). Mean apical disc diameter 0.28 % the diameter of the test, relative apical size (A/D) decreasing with size (Fig. 6) following an allometric relationship ($R^2 = 0.7$, $p < 0.005$, 10,000 replicate permutation test). The peristome diameter significantly exceeds the size of the apical disc (paired t test, $p < 0.01$). Peristome with five separated pairs of buccal plates carrying no spines, but with ophicephalous and some tridentate pedicellariae. Beside the buccal plates, pedicellariae also scattered on plates of the peristomial membrane. There is no significant difference in test measurements between the specimens originally attributed to *S. bernasconiae* by Larrain and the other specimens of *G. multidentatus* (NPMANOVA not significant, $p > 0.1$), both those recently collected off the coasts of Chile and those described in the literature (McKnight 1968).

All studied specimens along with specimens described in the literature (Clark 1925; McKnight 1968) have dicyclic apical systems, that is, the five ocular plates are exsert (out of the genital plate ring) and do not contact the periproct (Fig. 4a; Table 1). Some ocular plates covered with one small tubercle, genital plates covered with one to five small tubercles. Surface of genital plate 2 almost entirely covered with hydropores. Periproctal membrane without spines, anus excentric towards genital plate 5, and surrounded by small periproctal plates.

About two ambulacral plates to each interambulacral plate ambitally, ambulacra one-third the width of interambulacra. Ambulacral plates trigeminate, pore pairs arranged in arcs of three, with one tubercle on each compound plate (Fig. 4b), primary tubercles forming two distinct vertical rows in each ambulacrum. Size of primary tubercles decreases from the ambitus to the peristome adorally, and to the apex adapically. However, primary tubercles are irregular in size and arrangement, and can be replaced by secondary tubercles adorally and adapically on every alternate or third plate. Secondary tubercles and granules scattered over the plates above the ambitus, except in the bare perradial area, which is slightly sunken. Secondary tubercles numerous adorally where they

Table 4 Morphological measurements of the studied specimens of *S. bernasconiae*

Specimens	D (mm)	H (mm)	A (mm)	P (mm)	H/D	A/D	P/D
INSPIRE AGT-1 426	48	24.7	12.3	–	0.51	0.26	–
INSPIRE AGT-2 536	46.7	25.1	12.8	–	0.54	0.27	–
INSPIRE AGT-1 423	49.6	29.3	12.8	15	0.59	0.26	0.30
So-210 64	18.4	8.5	6.6	7.6	0.46	0.36	0.41
Hero 72.4b GP 7969	47.4	27.8	13	15.2	0.59	0.27	0.32
Hero 72.4b GP 7970	49	31	14	17	0.63	0.29	0.35
Hero 72.4b GP 7971	45	25	13	15	0.55	0.29	0.33
Hero 72.4b GP 7972	46	27	12	15	0.59	0.26	0.33
Hero 72.4b GP 7973	48	27	15	15	0.56	0.31	0.31
Hero 72.4b GP 7974	43	24	12	14	0.56	0.28	0.33
Hero 72.4b GP 7975	40	27	12	13	0.67	0.3	0.32
Hero 72.4b GP 7976	42.7	26.8	11.9	13	0.63	0.28	0.30
Hero 72.4b TI 1	50.8	31.9	12.6	14.2	0.63	0.25	0.28
Hero 72.4b TI 2	53.4	31.3	16.2	17	0.59	0.30	0.32
Hero 72.4b TI 3	49	27.2	12.7	14.7	0.55	0.25	0.30
Hero 72.4b TI 4	48.8	27.3	14.7	15	0.56	0.30	0.31
Hero 72.4b TI 5	47.1	28.9	13.2	14.1	0.61	0.28	0.30
Hero 72.4b TI 6	53.3	28.2	14.6	13.9	0.53	0.28	0.26
Hero 72.4b TI 7	52.1	28.8	13.2	15	0.55	0.26	0.29
Hero 72.4b TI 8	47.1	29.2	14.2	14.3	0.62	0.31	0.30
Hero 72.4b TI 9	37.2	19.3	10.7	12.1	0.52	0.29	0.32
Clark S 170[a]	78	52	19	22	0.67	0.25	0.28
Studer	10	5	4	5	0.5	0.4	0.5
McKnight E148	32	15	8.5	10	0.47	0.27	0.31
McKnight D138	63	33	14	18	0.52	0.22	0.28
McKnight E76	97	58	24	26	0.60	0.25	0.27

Values of test diameter (D), test height (H), size of apical disc (A), and size of peristome (P) are given in mm. Relative test height (H/D), apical size (A/D), and peristome size (P/D) were computed over test diameter (D). Newly collected specimens are from cruises So-210 and INSPIRE. Larrain's specimens are from cruise Hero 72, 4b. They were measured. Other values were taken from Clark (1925), Studer (1880), and McKnight (1968)

[a] Holotype of *G. multidentatus*

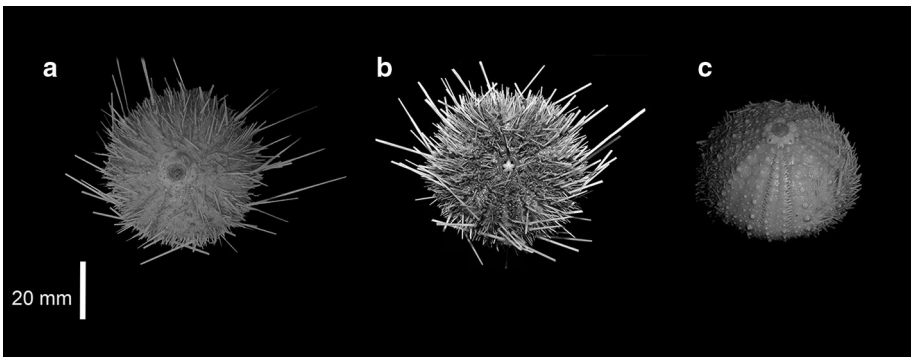

Fig. 3 *Gracilechinus multidentatus*. **a** Apical and, **b** oral views of specimen Hero 72.4b GP 7969. **c** View of the denuded ambulacrum I of specimen Hero 72.4b GP 7973

partially encircle primary tubercles. Aborally, one primary tubercle on each interambulacral plate, located near the adoral and adradial plate sutures (Fig. 4c). Primary tubercles form two distinct vertical rows in each interambulacrum. Secondary tubercles and granules scattered over the plates above the ambitus, except in the bare interradial area. Adorally and ambitally, several series of primary tubercles form up to three distinct vertical rows in

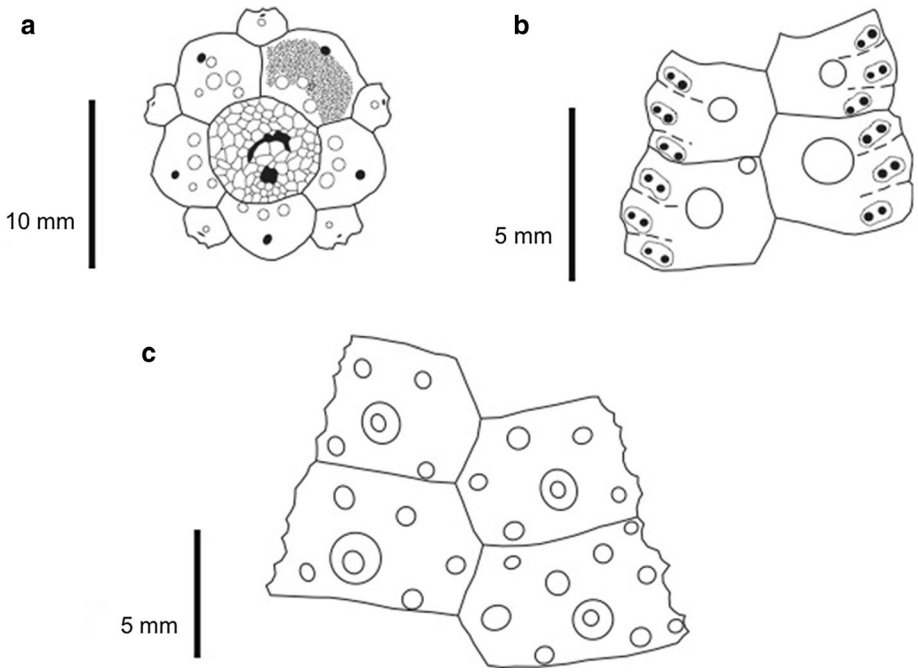

Fig. 4 *Gracilechinus multidentatus*, details of test plating. **a** Apical disc of specimen Hero 72.4b GP 7969. **b** Aboral plates of ambulacrum I, specimen Hero 72.4b GP 7971. **c** Aboral plates of interambulacrum 5, specimen Hero 72.4b GP 7971

each interambulacrum. The adradial series continuous from the ambitus to the peristome, the interradial series continuous only in large specimens. Secondary tubercles and granules numerous adorally with no distinctive organization. Interradial area slightly sunken aborally, flush with test ambitally and orally.

Ophicephalous and globiferous pedicellariae abundant over the test. Valves of ophicephalous pedicellariae low, wide, scarcely constricted in the middle, blade edges indented and finely serrate (Fig. 5a–b). Valves of globiferous pedicellariae with blade sharply differentiated from base, forming a more or less tubular rostrum (Fig. 5e–f). Crossbeams linking the sides of the rostrum. Tip of the blade forming a robust hook, presence of two to five lateral teeth on each side of the rostrum near the tip. Basal part with an irregular, thorny apophysis, and rounded outer corners. Two forms of tridentate pedicellariae (Fig. 5c–d). Small rostrate-like form with slender, curved valves (Fig. 5c). Large forms with long (up to 2.5 mm—Clark 1925), narrow valves, slightly curved, and finely serrate at the tip (Fig. 5d). Edges of the blade thick in the lower part, with small teeth arranged in transverse series. Triphyllous pedicellariae present, of the classical type of the family. Primary spines straight, ovoid to flatten distally, length of primary spines up to 60 % (3/5) the test diameter, the longest ones near the ambitus in interambulacra. Secondary spines few, short, with smooth shaft (Fig. 5g–h), although small forms may have a finely serrate shaft and tip (Fig. 5i). Below the ambitus, primary and secondary spines may have flattened and slightly expanded distal parts (Fig. 5g–h), while others have pointed tips (Fig. 5i).

Living specimens pale cream. Specimens preserved in ethanol whitish, pale pink or light brown. Dried specimens straw-coloured to light brown, denuded test and spines white.

Distribution *G. multidentatus* is known between 35.05°S and 50.94°S latitude, between 73.38°W and 117.21°E longitude, and between 300 and 1800 m depth (see Fig. 7 and Pierrat et al. 2012b for occurrence records).

Remarks The species now included in the genus *Gracilechinus* were formerly assigned to the genus *Echinus* Linnaeus, 1758. The genus *Gracilechinus* was erected by Fell and Pawson (1966) (in Fell and Pawson 1966, p. 431, Fig. 322-1) based on the type species *Echinus gracilis* A. Agassiz, 1869. Diagnosis is as follows: (1) presence of primary tubercles on each ambulacral plate, (2) a peristome larger than the apical disc, (3) secondary spines with smooth shafts, and (4) valves of globiferous pedicellariae with blade sharply differentiated from base, forming a tubular rostrum. McKnight (1968) noticed that the original description of the holotype of *G. multidentatus* (Clark, 1925) is not in line with the diagnosis of the genus *Gracilechinus*. Clark (1925) states that primary tubercles are present on every second or third ambulacral plate, which partly corresponds to the amended diagnosis of the genus *Echinus* (Fell and Pawson 1966, p. 431, Fig. 322-2). However, in his re-examination and re-description of *G. multidentatus*, McKnight (1968) indicates that primary tubercles are irregular in size and arrangement aborally, but are present on every ambulacral plate, a situation typical of the genus *Gracilechinus*.

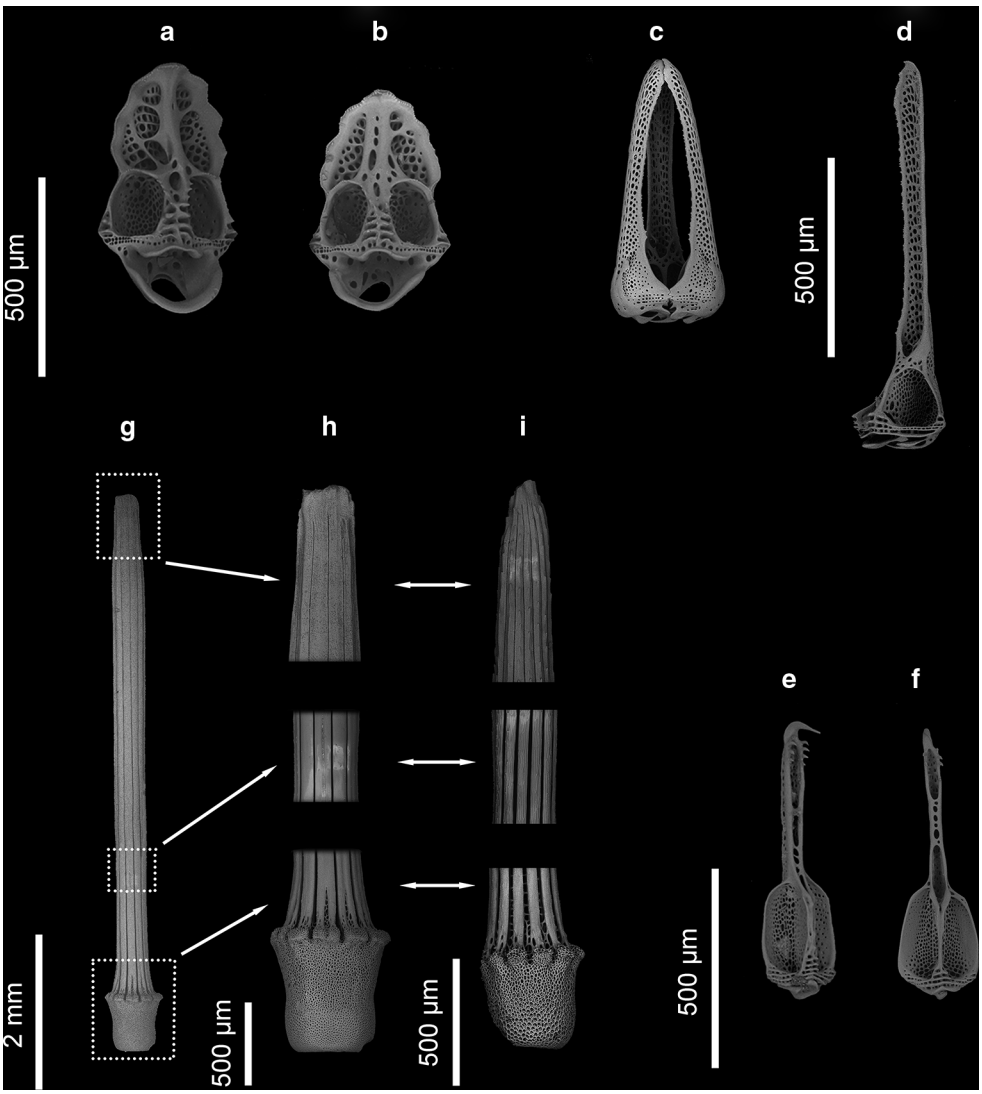

Fig. 5 *Gracilechinus multidentatus*. **a**, **b** Isolated valves of ophicephalous pedicellariae, **a** specimen AGT-1 426 and **b** AGT-1 423. **c**, **d** Valves of tridentate pedicellariae, specimen SO-210 64, **c** three valves of the small form in connection, **d** isolated valve of the large form. **e**, **f** Isolated valves of globiferous pedicellariae, **e** specimen Hero 72.4b TI 9, **f** specimen SO-210 64. **g**, **i** Secondary spines of specimen AGT-1 426, **g** form with smooth shaft and flattened tip, **h** details of the basal, mid, and upper parts of **g**, **i** small form with finely serrate shaft and pointed tip

Species of the genus *Gracilechinus* are characterized by the presence of primary tubercles on every ambulacral plate, whereas primary tubercles are on every alternate, or every third ambulacral plate in the genus *Echinus* Linnaeus, 1758. *Gracilechinus* also differs from *Sterechinus* Koehler, 1901, in which primary and secondary spines are well-differentiated, secondary spines are thorny, numerous, and densely packed. Moreover, in *Sterechinus* the apical system is monocyclic to hemicyclic, with oculars I and V insert, and test and spines are bright red in life. Species of *Dermechinus* Mortensen, 1942 have primary tubercles on every ambulacral plate as in *Gracilechinus*, but the test is extremely high in the former, equalling or exceeding the diameter of the test. Moreover, secondary spines are thorny, numerous, densely distributed (such as *Sterechinus*), and the peristome is smaller than the apical disc. *Gracilechinus* is different from *Parechinus* Mortensen, 1903 only in the shape of globiferous pedicellariae, which have triangular valves, with blade not sharply differentiated from base in *Parechinus*. Specimens of both genera that lack pedicellariae (e.g. denuded tests and fossil material) cannot be distinguished from each other (Fell and Pawson 1966).

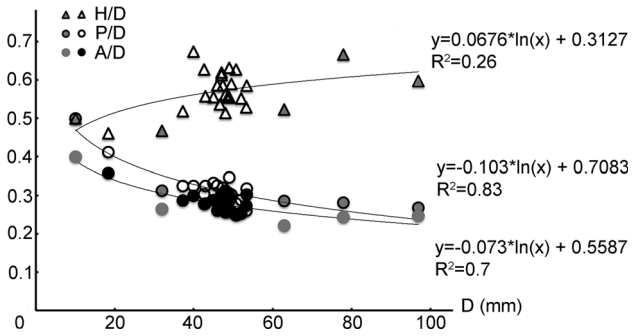

Fig. 6 Regression plot of test relative height (H/D), relative peristome size (P/D), and relative apical size (A/D) against test diameter (D). See Table 4 for values and sample details. Data taken from the literature about *Gracilechinus multidentatus* are shown as *grey shaded triangles* and *circles*. Natural logarithm models best fit the regressions

Discussion

Molecular phylogeny and morphological features

In this work, morphological and molecular analyses are congruent and provide evidence for synonymizing *S. bernasconiae* and *G. multidentatus*. Molecular results show an inconsistency within *Sterechinus*, sequences of *S. bernasconiae* and *G. multidentatus* clustering together (only 0.004 % of intraspecific genetic distance), while other *Sterechinus* species do form a distinct, robust clade (0.2 % of genetic distance to *G. multidentatus*) composed of two subclades. The first one corresponds exclusively to the Antarctic species *S. neumayeri*, which is separated from other species of *Sterechinus* (0.1 % of genetic distance), both Antarctic and sub-Antarctic. The second one groups together *S. agassizi* from the continental shelf of Argentina, *S. diadema* from the Kerguelen Plateau, *S. antarcticus* from the deep Antarctic shelf, and the Antarctic deep-sea *S. dentifer* (only 0.004 % of genetic distance within the subclade). This challenges their different taxonomic status as the four nominal species could be considered a single group or subclade (i.e. *S. diadema*). Within this subclade, all sequences of *S. dentifer* cluster together. Interestingly, Díaz et al. (2011) showed that specimens of *S. dentifer* could be distinguished from other *Sterechinus* based on the morphology of globiferous pedicellariae. However, the cluster is not well-supported and the short genetic distances within the *S. diadema* subclade suggest that *S. dentifer* is not much differentiated and does not form a distinct species.

The present molecular phylogeny totally agrees with results of Díaz et al. (2011) who showed that distinct *Sterechinus* subclades could be distinguished also using morphological criteria, and more precisely using the morphology of globiferous pedicellariae. In contrast, the three nominal species *S. antarcticus, S. diadema*, and *S. agassizi* cannot be distinguished from each other based on either genetics or morphology. David et al. (2005) had already noticed that morphological differences between *Sterechinus* species were unclear and that patterns of geographic distribution provide us with more significant features to distinguish between certain species (e.g. between *S. diadema* and *S. antarcticus*). They suggested that only details of the morphology of globiferous pedicellariae could be used to distinguish among the three species *S. neumayeri*, *S. dentifer,* and *S. antarcticus*, while *S. antarcticus, S. diadema*, and *S. agassizi* only differ in their respective geographic distributions.

Within the genus *Sterechinus*, the taxonomy established by previous authors (Koehler 1906, 1926; Döderlein 1906; Mortensen 1943) relied on the examination of a small number of specimens (David et al. 2005). Subsequently, the morphological characters they regarded as diagnostic (mostly the structure of the apical system) proved to be highly variable, with wide and overlapping ranges of variation (David et al. 2005). Hence, there is no real discrepancy between molecular data and morphology in *Sterechinus*; the inconsistency between the current taxonomic status of species and recent molecular results (Díaz et al. 2011, this work) is due to an insufficient appraisal of morphological variations.

Comparative biogeography of *G. multidentatus* and *Sterechinus*

Previously, *G. multidentatus* was known exclusively in deep-sea areas off the coasts of New Zealand, south of Australia, and Tasmania (McKnight 1968; Pierrat et al. 2012b—Fig. 7). In light of the present taxonomic revision, it turns out that the distribution area of *G. multidentatus* is much broader than previously thought. It extends across the South Pacific Ocean from the southwest of Australia to the coasts of Chile (Fig. 7). Interestingly, Chilean specimens from Patagonia were collected in relatively shallow waters considering the average depth (ca. 900 m) and range (300–1800 m) of the species. Larrain's specimens were collected in Patagonia at 300 m and recent specimens from Patagonia (INSPIRE AGT-1 and AGT-2) were collected at 628 and 579 m depth, respectively (Table 1). The huge expanse of water that separates the continental shelves of New Zealand and Chile suggests that *G. multidentatus* can disperse with currents or across the ocean floor. Considering its known bathymetric range, the species can be expected on seamounts of the South Pacific Ocean as well. New occurrence data are needed to address this topic and better characterize the apparent, fragmented pattern of species distribution. Future oceanographic programmes in this part of the Ocean are expected to provide such data. They also could

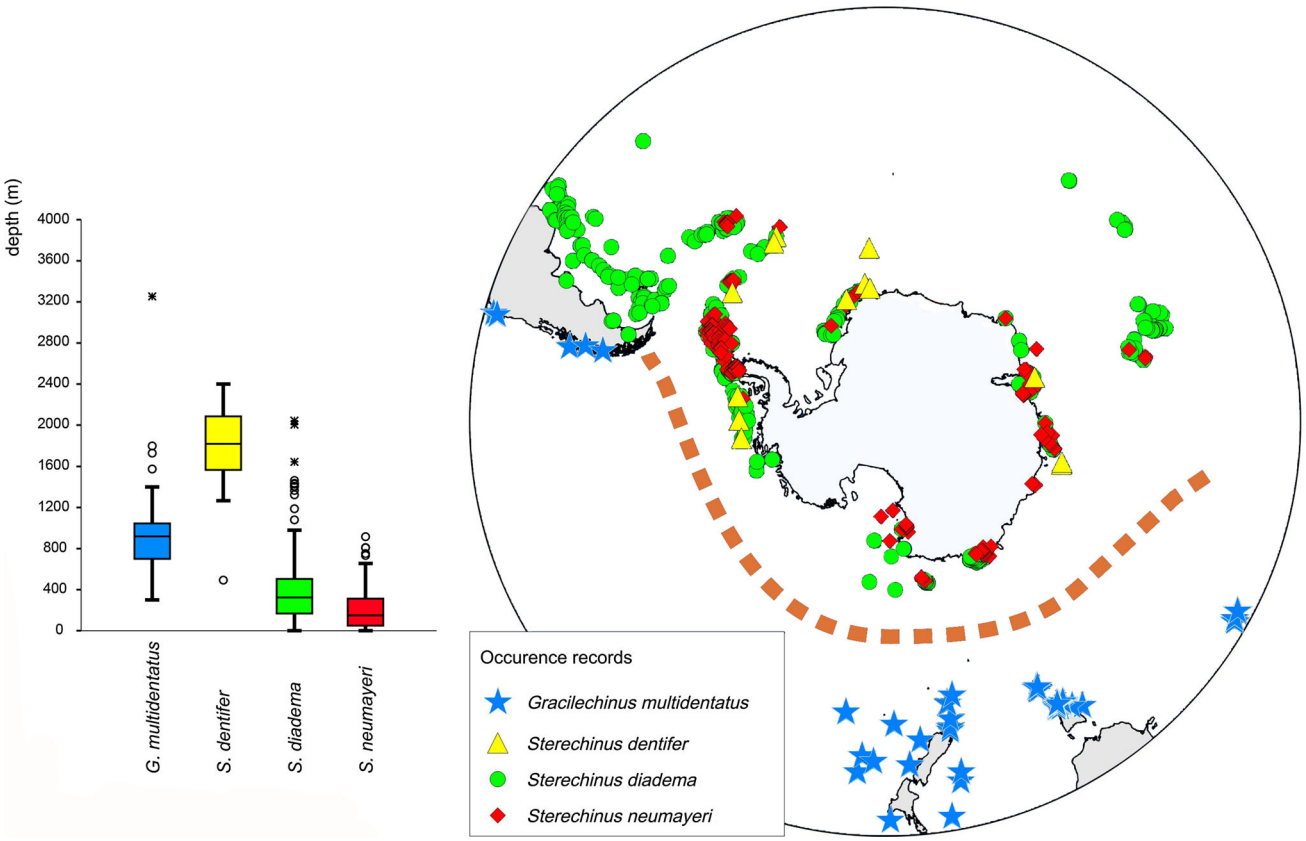

Fig. 7 Distribution map and depth range of *Gracilechinus multidentatus* along with *Sterechinus* subclades. The *orange dotted line* symbolizes the biogeographic boundary between the two adjacent, but not overlapping distribution areas of *G. multidentatus* and of *Sterechinus* subclades. Depth range shown as a *box plot*. *Each box* shows the 25–75 % quartiles with the median value (*horizontal line inside the box*). Whiskers are drawn from the *top of the box* up to the highest value less than 1.5 times the 25–75 % quartiles, and similarly *below the box*. *Circles* show values outside the whiskers, *stars* corresponding to outliers more than 3 times the *box height*. Additional data taken from Pierrat et al. (2012a, b). (Color figure online)

help refine the southern boundary of the species distribution and determine whether it crosses the Antarctic Polar Front.

The occurrence of *G. multidentatus* off the coasts of both Australia and New Zealand is a common biogeographic pattern in echinoids. The similarity of echinoid faunas between Australia and New Zealand has been explained by the existence of recurring trans-Tasman faunal exchanges between southeastern Australia and New Zealand throughout the Cenozoic (Foster and Philip 1978; Saucède et al. 2013). The existence of a faunal connectivity between New Zealand and southern South America is more atypical, though it was demonstrated by previous authors (Beu et al. 1997; Del Rio 2002; Saucède et al. 2013) to have occurred in some benthic invertebrates since the Oligocene owing to dispersal through the Antarctic circumpolar current at its early stages of development (Lawver and Gahagan 2003). In echinoids, the two genera *Pseudechinus* and *Austrocidaris* are present off the coasts of New Zealand and southern Chile, but they both diversified into distinct species on each side of the South Pacific Ocean (Pierrat et al. 2012b). It is postulated that the two genera originated in Australasia then dispersed to the west after the Early Miocene (Saucède et al. 2013). *Dermechinus horridus* is the only echinoid species to have a circum-polar, sub-Antarctic distribution. It is known from off southern Chile, off southern Africa, on the Kerguelen Plateau, and between Tasmania and Victoria (David et al. 2005; Pierrat et al. 2012b). Hence, like *G. multidentatus*, it occurs on both the eastern and western sides of the South Pacific Ocean, and interestingly, both species have similar depth ranges (between 150 and 1800 m depth and mean depth of ca. 800 m for *D. horridus*). Most deep-sea species of pourtalesiid and plexechinid echinoids are known to occur below 2500 m all around Antarctica. Therefore, some of them could also extend across the South Pacific Ocean, but occurrence records are too sparse to provide a clear representation of distribution patterns (David et al. 2005).

To date, no species of *Sterechinus* has ever been recorded along the coast of southern Chile, the specimens previously described as *S. bernasconiae* being reassigned to *G. multidentatus* here (Fig. 7). The absence of

Sterechinus in Pacific Patagonia contrasts with the extended distribution of the genus along the southwestern Atlantic coast. On the Atlantic side, the genus is represented by *S. agassizi* (*S. diadema* subclade) that is known from off Atlantic Patagonia and over the Argentinian continental shelf as far northward as 35°S latitude (Pierrat et al. 2012b). Based on presence data and on a set of 10 oceanographic variables, Pierrat et al. (2012a) modelled the distribution of two *Sterechinus* species, *S. antarcticus* and *S. neumayeri*, using the "maximum entropy" modelling procedure (Phillips et al. 2006), which is a correlative approach for assessing species distribution probabilities (Gutt et al. 2012). The distribution of *S. antarcticus* was modelled all around Antarctica, on the Campbell Plateau (South New Zealand), and on both the Pacific and Atlantic sides of southern South America (Pierrat et al. 2012a). According to the model, areas suitable to *Sterechinus* occur on both the Atlantic and Pacific sides of southern South America. The discrepancy observed between the modelled distribution and true absence data can be explained alternatively by the accuracy of the model, by the impact of biogeographic processes and/or by the results of biotic interactions.

Along the shorelines of Patagonia, interactions among winds, tides, freshwater discharges, local geomorphology, and oceanographic currents determine coastal marine fronts that have a key role in local ecology (e.g. areas of large primary production, retention areas for larvae of benthic species) and structure the spatial distribution of marine species (Acha et al. 2004; Miloslavich et al. 2011; González-Wevar et al. 2012b). In the biogeographic Magellanic Province, interactions between the Cape Horn Current and the Patagonian cold estuarine front can promote dispersal of organisms from the Pacific to the Atlantic Ocean (Acha et al. 2004; González-Wevar et al. 2012b), while the Atlantic Patagonian cold estuarine front constitutes an oceanographic barrier to dispersal between Pacific and Atlantic Patagonia (Miloslavich et al. 2011; González-Wevar et al. 2012b). In contrast to *Sterechinus*, many invertebrates are known to occur along both Pacific and Atlantic Patagonia among which the echinoids *Arbacia dufresni* and *P. magellanicus*, the gastropod *Nacella magellanica*, the octopus *Enteroctopus megalocyathus*, and the bivalve *Aequipecten tehuelchus* (Real et al. 2004; González-Wevar et al. 2012b; Pierrat et al. 2012b). Therefore, the role played by oceanographic currents cannot be considered as decisive in explaining the absence of *Sterechinus* along the Chilean coast.

Pierrat et al. (2012a) proposed a putative exclusion pattern between *G. multidentatus* and *S. antarcticus* to explain the absence of *S. antarcticus* on the Campbell Plateau (Figs. 1, 7) although it is a suitable area according to models. Such an exclusion pattern between *G. multidentatus* and *S. agassizi* (*S. diadema* subclade) can be also invoked to explain the absence of *Sterechinus* in Pacific Patagonia. The clear-cut distinct distribution areas of *G. multidentatus* and *Sterechinus* subclades also suggest the existence of an exclusion pattern between the two clades at ocean scale (Fig. 7). *Sterechinus* subclades occur in the Southern Ocean and in sub-Antarctic areas of the Atlantic and Indian Oceans, while *G. multidentatus* is present exclusively in the South Pacific Ocean. The two distinct distribution areas are adjacent, especially in the Magellanic region, and do not seem to overlap.

Conclusion

The molecular phylogeny performed in this work resulted in synonymizing the two species *S. bernasconiae* and *G. multidentatus*. Molecular results are congruent with morphological data and imply that the species name *S. bernasconiae* should not be used anymore and that echinoids formerly identified as *S. bernasconiae* belong to the species *G. multidentatus*.

Molecular results also show the existence of two genetically distinct subclades within the *Sterechinus* clade: the *S. neumayeri* and *S. diadema* subclades. This totally agrees with previous results of Díaz et al. (2011) who showed that the two subclades could be distinguished also upon morphological criteria, and more precisely upon the morphology of globiferous pedicellariae. In contrast, the three nominal species *S. antarcticus, S. diadema*, and *S. agassizi* belong to the same subclade; they cannot be genetically or morphologically distinguished from each other (Díaz et al. 2011). The genus *Sterechinus* requires more comprehensive taxonomic revision.

The elucidation of phylogenetic relationships between *Gracilechinus* and *Sterechinus* also allowed for clarification of their respective biogeographic distributions and emphasized the putative role played by biotic exclusion in the spatial structuring of marine biodiversity. The family Echinidae is represented by two more genera in the Antarctic and sub-Antarctic regions: *Loxechinus* and *Dermechinus*. If phylogenetic relationships among *Sterechinus*, *Gracilechinus*, and *Loxechinus* seem clear (Lee et al. 2004; this study), the position of *Dermechinus* is still uncertain. Forthcoming studies should identify phylogenetic relationships among all representatives of Antarctic and sub-Antarctic Echinidae, thereby clarifying biogeographic patterns in the family.

Acknowledgments Samples were collected during oceanographic campaigns through IPEV (formerly IFRTP) programmes No. 195 BENTHOS-MAC, No. 345 BENTHADEL, and No. 1044 PROTEKER; Chilean programmes INACH 13-05, INACH 02-02, INACH B01-07, ECOS C06B02, and INIDEP 1608; and oceanographic cruises INSPIRE, Antarktis XXIII/8, CEAMARC, CHESSO, BIOPEARL I, and Bentart'06. The authors are indebted to the staff of the

Marine Research Station of Las Cruces (Chile), CBUCN (Biological Collection of Universidad Católica del Norte, Coquimbo, Chile), ZMUC (Concepción, Chile), NIWA (Wellington, New Zealand), BAS (Cambridge, UK), and AWI (Bremerhaven, Germany). This study was supported by the European Community through an ASSEMBLE Grant (Grant No. 22779). This is Contribution No. 4 to the vERSO project (www.versoproject.be), funded by the Belgian Science Policy Office (BELSPO, Contract No. BR/132/A1/vERSO). This is a contribution to team BioME of the CNRS laboratory Biogéosciences (UMR 6282).

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