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ORIGINAL ARTICLE

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Plectroninia celtica n. sp. (Calcarea, Minchinellidae), a new species of "pharetronid" sponge from bathyal depths in the northern Porcupine Seabight, NE Atlantic

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Abstract Recent pharetronid sponges were regarded as relict species in tropical and subtropical waters, inhabiting cryptic habitats on coral reefs and in caves. More recent findings of a new species of the genus *Plectroninia* off northern Norway, with an inner fused skeleton have changed that view. Recent investigations on the sponge fauna of the "Propeller Mound", northern Porcupine Seabight, focusing on sponges growing on the azooxanthellate cold-water coral *Lophelia pertusa* (Linné 1758) and *Madrepora oculata* Linné 1758, established the presence of a species of *Plectroninia* new to science. Its status as a common species within this deep-water coral habitat and the general status of the genus *Plectroninia* are discussed.

Keywords Porifera · Calcarea · Pharetronida · *Plectroninia* · *Lophelia* · Porcupine Seabight · Bathyal

Introduction

"Pharetronid" sponges, calcareous sponges retaining an archaic morphology with at least a partially fused skeleton and often possessing tuning-fork triactines, are familiar from the geological record (Vacelet 1991). They are known as important reef builders from the Mesozoic to the Cretaceous, with the few extant species being thought of as relicts, occupying cryptic habitats in the tropical Indo-Pacific and the Mediterranean where competition was low. Recent findings of a species of *Plectroninia* in a sponge-rich habitat off northern Norway (Könnecker 1989) and a number of findings of skeletal remains at bathyal depths in many parts of the world (Vacelet et al. 1989) have changed that view. It could therefore be expected that other species would be found, and this was confirmed when close examination of the sponge fauna, settled on the deep-water corals *Lophelia pertusa* and *Madrepora oculata*, revealed the presence of a hitherto undescribed species of *Plectroninia.*

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The new pharetronid sponge material was obtained during the RV *Poseidon* cruise 265 in September 2000. This cruise was a part of the EU-ACES Project (Atlantic Coral Ecosystem Study) which investigated environmental controls on deep-water coral frameworks along the northwestern European continental margin (Freiwald 2002). In the Porcupine Seabight and Rockall Trough area, these corals contribute substantially to the formation of so-called carbonate mounds (De Mol et al. 2002). One of these mounds is the "Propeller Mound", located in the northern Porcupine Seabight (Fig. 1a).

The Propeller Mound: structure and previous studies

The Propeller Mound forms a 140 m high structure consisting of three diverging spurs, which resemble the shape of a propeller. The summit area lies in the 'shaft zone' of the propeller at 52°09.80N and 12°46.40W at 653 m water depth (Fig. 1b). The Propeller Mound has become a prime target for interdisciplinary research. The modern sedimentary environment is characterised by sandy mud plains in the off-mound areas. An erosional moat with exhumed ice-rafted boulders and outcropping bathyal limestones is developed around the base of Propeller Mound. These hard substrates are colonised by psolid holothurians, brachiopods, stylasterids (*Pliobothrus symmetricus*), gorgonians and isolated scleractinian colonies (*Madrepora oculata, Lophelia pertusa*). The mid-slope environments of the mound show regular-furrowed sedimentary ridges and troughs with most intense coral framework—almost dead—on top of each ridge. The summit areas show large areas of coral rubble and fossil coral framework with dispersely distributed living *Lophelia* and *Madrepora* thickets

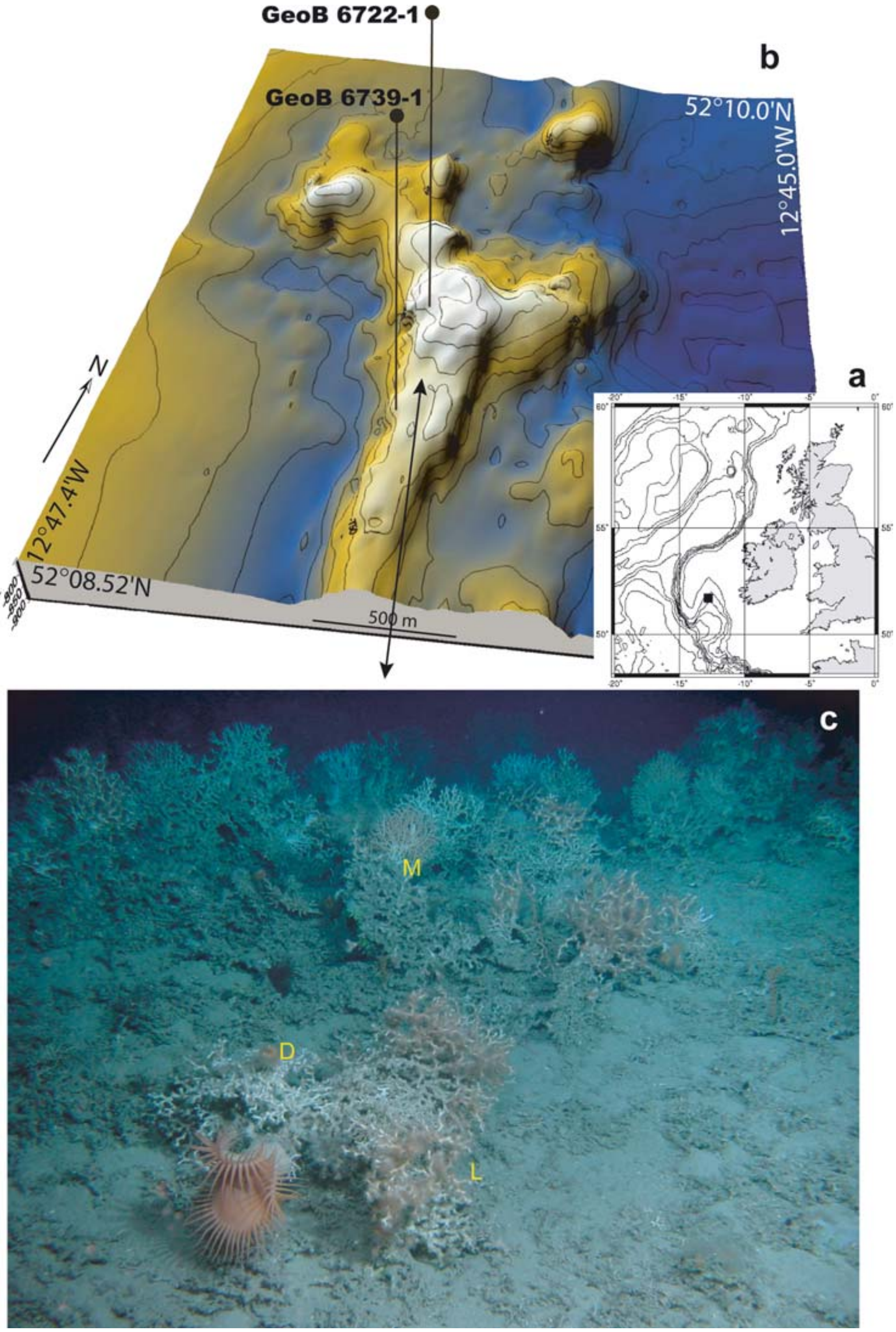

Fig. 1 **a** Geographic map showing the position of the Propeller Mound in the northern Porcupine Seabight (black box). **b** Oblique view on the Propeller Mound with coloured depth intervals (>800 m water depth in blue, 700–800 m water depth in brown and <700 m water depth in pale grey colour codes) with locations of the *Plectroninia celtica* n. sp. bearing stations GeoB 6722-1 (box corer) and GeoB 6739-1 (dredge haul; bathymetry data from RV *Poseidon* cruise 292). **c** Coral thickets (35–45 cm high) consisting of *Lophelia pertusa* (L), *Madrepora oculata* (M) and *Desmophyllum cristagalli* (D) from the summit area of Propeller Mound, which is the habitat of *Plectroninia celtica* n. sp. (735 m water depth; courtesy to IFREMER, CARACOLE cruise in 2001)

(Huvenne et al. 2005); see Fig. 1c. The taphonomy of the coral thickets is driven by bioerosion of a broad suite of heterotrophic organisms (Beuck and Freiwald 2005). The age of the fossil coral framework, obtained from U/Th-dating, ranges from Early Holocene to Mid-Pleistocene (Schröder-Ritzrau et al. 2003, 2005; Schröder-Ritzrau and Norbert Frank unpublished data). The stratigraphic framework and the sedimentary dynamic along with global climate change as documented from sediment cores collected from Propeller Mound were studied by Rüggeberg et al. (2005) and Dorschel et al. (2005).

Material and methods

To obtain seabed samples from the various mound areas, a giant box corer was used yielding 0.5 m^2 undisturbed sediment surfaces. As the recovered coral material was intended primarily for geological research, it was completely air dried and stored in this condition. This treatment, however, still allowed analysis of the sponge fauna and other animals with a solid body or hard skeletal parts. The complete set of coral colonies of one box corer (station

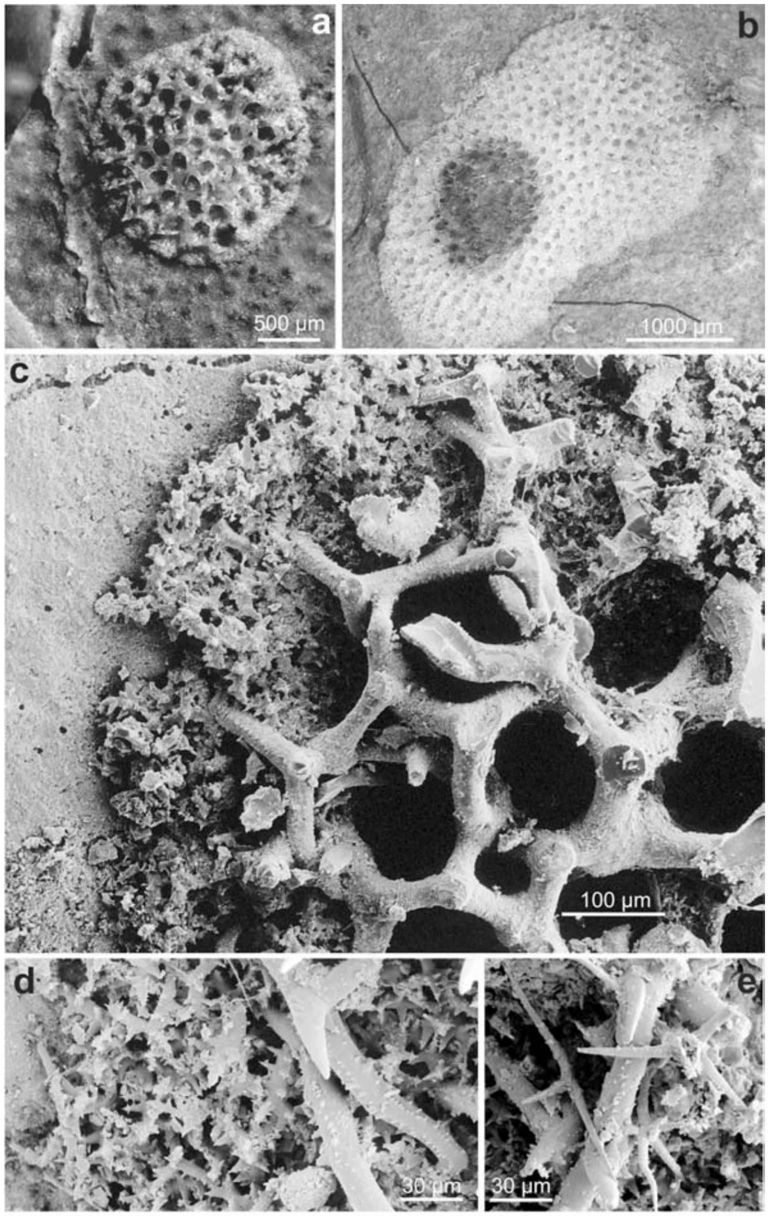

Fig. 2 *Plectroninia celtica* n. sp. **a** Overview of paratype specimen SMF 8013, station GeoB 6722-1. **b** Overview of holotype specimen SMF 8012, station GeoB 6722-1. **c** SEM image showing the large regular-fused tetractine meshwork (clearly visible as honeycomb pattern in (a) and (b) and the lamina layer around the perimeter of the sponge consisting of small, fused, irregular and spined tetractines. **d** SEM close up image showing parts of the large tectractines and how they are fused with the meshwork of the small irregular and spined tectractines (GeoB 6722-1). **e** SEM image of ectosomal triactines lying unconnected on the large tetractine meshwork (GeoB 6722-1)

GeoB 6722-1) and those from a short dredge haul (station GeoB 6739-1) from the summit area and upper flank of Propeller Mound were analysed semi-quantitatively. Particular attention was given to small encrusting poriferans. Altogether 500 sponge specimens were found representing 97 species of Porifera (see Appendix). The samples yielded 17 specimens of *Plectroninia* from the box corer station where it represented the most common species of Porifera and five from the dredge. The specimens were photographed under a high-power stereo-microscope (OLYMPUS SX-12). This was equipped with a high-resolution 3-chip-colour-CCD video camera linked to a computer running an Enhanced Focussing Imaging (EFI) programme based upon the ANALYSIS software package. This system was able to build up a composite 3D-image stacked up from several pictures taken at successive focussing stops; it also allowed point-to-point measurements of spicules or spicule rays. In addition, a CamScan scanning electron microscope was used for photographic documentation. Two specimens, one with a section of fairly intact ectosome, were selected as holotype and paratype and have been stored at the Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany, inventory numbers SMF 8012 and SMF 8013. The reminders are held in the collection at the Institute of Paleontology, Erlangen University, Germany. The systematic classification follows Borojevic et al. (2000).

Systematic description

Class: Calcarea Bowerbank, 1964
Subclass: Calcaronea Bidder, 1898
Order: Lithonida Vacelet, 1981

Table 1 Comparative spicule data (lengths of rays) for all extant species of *Plectroninia* (given in μm)

Species	Basal fused tetractines	Large fused tetractines, free ray	Diactines	Endosomal tetractines	Endosomal triactines	Tuning-fork spicules	Ectosomal tetractines	Ectosomal triactines	Habitus
P. celtica n. sp.	40–60	140–170				45–49		140–250	Encrusting
P. deansi		150	120			12–150			Encrusting
P. hindei	18–35	250–300	200–500			300–400 and 5–90		60–100 and 60–170	Encrusting
P. lepidophora	17–30	150–200	60–70 and 60–165					50–100	Encrusting
P. microstyla	indet	indet	35–110			10–12	15–20		Encrusting
P. minima	70–110	80–100	70–120			15–60	40–55	90–100	Encrusting
P. neocaledoniense	40–70	110–170			70–100	50–55		40–60	Encrusting
P. norvegica	50–80	500	500–700	50–130	90–150	40–70	50–130	90–150	Upright, unattached?
P. pulchella	70–110	80–100	90–330			25–45	30–130	40–60 and 45–130	Encrusting
P. radiata	70–110	80–100	100–120 and 60–140			40–50	60–95	50–110	Encrusting
P. sp.	30–40	80–100							Encrusting
P. tecta	70–110	80–100	150–300 and 50–90		30–36	28–30	50–80	60–80	Encrusting
P. tetractinosa	40–70	150	50–100			40–90	15–220		Encrusting
P. vasseuri		150					100–120	110–130	Encrusting

Family: Minchinellidae Dendy and Row, 1913
Genus: *Plectroninia* Hinde, 1900
Type species: *Plectroninia halli* Hinde, 1900

Holotype: Stored at Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany, inventory number SMF 8012; Propeller Mound, station GeoB 6722-1, 52°08.88N, 12°46.30W, 735 m water depth, substrate *Lophelia pertusa*, measurements 5×3 mm, collected 18th August 2000; see Fig. 2b.

Paratype: Inventory number SMF 8013; Propeller Mound, same station, substrate dead skeletal portions of the scleractinian *Lophelia pertusa*, measurements 4×2.5 mm; see Fig. 2a. Other 15 specimens same location, identical data, and 5 specimens from station GeoB 6739-1, 52°08.71N, 12°46.33W, 780–735 m water depth, general substrate and data as above.

Shape, size and consistency: Sponge encrusting, initially circular (Fig. 2a), with increased growth achieving a slightly irregular outline. Maximum size observed 5 mm×3 mm (Fig. 2b). Height generally not more than top of large fused tetractines; these may form a second layer above first leading to slightly dome-shaped appearance. Surface where observed smooth due to tangential arrangement of ectosomal spicules. Oscula not observed.

Colour: Colour in living specimens not observed, in the dried state dark purple.

Ectosome: Thin smooth layer with scattered nearly equal-rayed triactines which are lying separate and parallel to the surface without touching (Fig. 2e). Tuning-fork spicules observed near the edge of specimen.

Choanosome: Basal layer formed of small fused tetractines, irregular and spined, with straight rays and forming a lamina around the perimeter of young specimens (Fig. 2c, d). Main skeleton formed of large regular fused tetractines (Fig. 2a–c), with the smaller rays angled halfway and fusing with neighbouring rays and the basal layer, building a honeycomb pattern; large apical rays pointing upwards and supporting ectosome. Smaller tetractines along the growing edge.

Spicules: Endosomal basal small fused tetractines, with large and nearly regularly arranged conical spines, with the base and height nearly equal to the diameter of the rays; with straight rays of 40–60 μm (Fig. 2c, d); endosomal large regular fused tetractines, apical rays 140–170 μm, angled section 50–60 μm (Fig. 2a–c). The SEM photos show them to be partially and minutely hispid. Tuning-fork spicules, paired rays 45–49 μm long. Regular ectosomal triactines, with straight rays 140–250 μm long (Fig. 2e). No other spicules observed; for the small tetractines of the growing edge see Discussion.

Ecology: All specimens were found growing on the dead skeletal portions of *Lophelia pertusa* and *Madrepora oculata* from the upper summit area of the Propeller Mound between 780 and 735 m water depth. The ambient seawater temperature and salinity CTD-data were 9.4°C and 35.49‰respectively.

Discussion

The species differs from *Plectroninia norvegica* Könnecker, 1989, the nearest species geographically, in its wide attachment base and different ectosomal spicules as well as the lack of ectosomal tetractines, as well as in spicule dimensions. From *Plectroninia hindei* Kirckpatrick, 1900, it differs in ectosomal spicules and the lack of diactinal spicules. The same contingent of spicules is only shared by *Plectroninia neocaledoniense* Vacelet, 1981 (see Vacelet 1981); it differs from this species in its spicules being smooth, a much less dense and not overlapping ectosomal spiculation and in spicule dimensions. A recent finding of an hitherto undescribed species of *Plectroninia* from the eastern Mediterranean (Ilan et al. 2003) shows some similarity in the fused skeleton; it differs, however, in the dimensions of the free apical rays and lacks the heavy conical spines of the basal fused tetractines; the spines being smaller at the base, slimmer and not straight conical. No information on the ectosomal skeleton is available due to their degraded condition. For comparison, spicule types and dimensions of all species of *Plectroninia* are given in Table 1.

The smaller tetractines along the growing edge present somewhat of an enigma. They are confined to that location and were not observed anywhere else in the ectosomal layer. The authors suggest that they are development forms of the large fused tetractines for the following reasons:

1. They are only found along the growing edge.
2. They are similarly arranged to the large fused tetractines, resting on the sagittal ray and two of the apical rays.
3. Continuing growth of the large fused tetractines is evidenced in Fig. 2 and would in any case be a requisite for a secondarily fused skeleton.

Nothing is reported in the literature on growth and development or the formation of the fused internal skeleton of this genus, and this question will require detailed analysis of better-preserved or live material to reach a definite conclusion on the status of these small tetractines.

The genus *Plectroninia* was established by Hinde (1900) for *Plectroninia halli*, a fossil species from Eocene strata in Australia. However, these sponge-bearing deposits were revised by Pickett (1983) and represent an Early and Middle Miocene age (see Vacelet et al. 2002). Kirckpatrick (1900, 1911) described two recent species from the Indian and Pacific Oceans. Further species were described by Vacelet (1967a, b, 1977, 1981), again from the Indian and Pacific Oceans, and he recorded one species, *Plectroninia hindei*, from the Mediterranean (Pouliquen and Vacelet 1970). Könnecker (1989) recorded the first fully described species from the Atlantic Ocean off northern Norway, far out of the geographical range recorded until then. The collection of recent *Plectroninia* remains at bathyal depths down to 1600 m (however confined to the fused skeleton and therefore not allowing distinction of species) and the current find extends the known distribution of this genus geographically as follows: Northeast Atlantic from northern Norway, Mediterranean, Azores, Brazil, South Africa, southern and tropical Indian Ocean and western Pacific, with the majority of species recorded from the western Pacific. The depth range at present reaches from shallow water to about 1600 m, and the temperature regime from cold to tropical. It is highly likely that the geographical range and number of species will be extended once proper attention is given to the small encrusting forms of Porifera. Their small size virtually precludes detection with the naked eye. Notable is the fact that in both areas—northern Norway and Porcupine Seabight—*Plectroninia* represents the most numerous calcareous sponge. This indicates flourishing populations of what was once thought of as rare relict forms, and that they can thrive under intense competition.

Plectroninia celtica n. sp. is the most abundant sponge belonging to the Calcarea on the Propeller Mound. The other Calcarea recorded are *Clathrina coriacea* (Montagu, 1818) and *Ute gladiata* Borojevic, 1967. The sponge assemblage that colonises the dead azooxanthellate coral framework on Propeller Mound is dominated by Demospongiae with 92 species identified (see Appendix). Hexactinellidae are represented by two species, *Aphrocallistes bocagei* Schulze, 1886 and *Rossella nodastrella* Topsent, 1915.

Taba

	Overview of Porifera from Propeller Mound	Box corer	Dredge
		GeoB 6722-1	**GeoB** 6739-1
	Class: Demospongiae		
	Subclass: Tetractinomorpha		
	Order: Astrophoridae		
	Family Geodidae		
1	*Geodia barretti* (Bowerbank, 1858)	1	1
2	*Geodia atlantica* (Stephens, 1915)	4	17
	Order: HADROMERIDA		
	Family: Clionidae		
3	*Cliona vermifera* Hancock, 1867		1
4	*Alectona millari* Carter, 1879		1
	Family: Hemiasterellidae		
5	*Paratimea constellata* (Topsent, 1893)		6
6	*Paratimea loennbergi* (Alander, 1942)	1	1
	Family: Polymastiidae		
7	*Polymastia radiosa* Bowerbank, 1866	1	
8	*Radiella sol* Schmidt, 1870	1	8
9	*Spinularia spinularia* (Bowerbank, 1866)		1
	Family: Stylocordyliidae		
10	*Stylocordyla borealis* (Loven, 1868)	1	
	Subclass Ceractinomorpha		
	Order: Poecilosclerida		
	Family: Microcionidae		
11	*Clathria anchorata* (Carter, 1874)	2	21
12	*Clathria acanthotoxa* (Stephens, 1916)	1	7
13	*Clathria tenuissima* (Stephens, 1916)	2	
14	*Clathria microchela* (Stephens, 1916)	4	8
15	*Clathria ditoxa* (Stephens, 1916)		2
16	*Clathria armata* (Bowerbank, 1866)		4
17	*Clathria laevis* (Bowerbank, 1866)		1
18	*Clathria dianae* (Schmidt, 1875)		1
19	*Clathria bitoxa* (Burton, 1930)		2
20	*Clathria laciniosa* (Bowerbank, 1874)		3
21	*Antho beanii* (Bowerbank, 1866)	1	1
	Family: Raspailidae		

Taba

	Overview of Porifera from Propeller Mound	Box corer	Dredge
22	*Cyamon spinispinosum* Topsent, 1904		11
23	*Eurypon clavatum* (Bowerbank, 1866)		5
24	*Eurypon viride* (Topsent, 1889)	3	3
	Family: Anchinoidae		
25	*Phorbas perarmatus* (Bowerbank, 1866)		1
26	*Phorbas* sp.		1
27	*Phorbas* cf. *salebrosus* Koltun, 1958		1
28	*Plocamionida ambigua* (Bowerbank, 1866)	2	
29	*Plocamionida microcionides* (Carter, 1876)		3
30	*Plocamionida tornotata* Brondsted, 1932		5
	Family: Coelosphaeridae		
31	*Histodermella ingolfi* Lundbeck, 1910		3
32	*Histodermella* sp.		2
33	*Lissodendoryx diversichela* Lundbeck, 1905	1	3
34	*Lissodendoryx indistincta* (Fristedt, 1887)	1	
35	*Lissodendoryx* sp.		3
36	*Ectyodoryx atlanticus* Stephens, 1916		1
	Family: Crellidae		
37	*Crella* sp.		1
38	*Crellomima imparidens* Rezvoj, 1925	2	
	Family: Hymedesmiidae		
39	*Hymedesmia baculifera* (Topsent, 1901)		7
40	*Hymedesmia koehleri* (Topsent, 1896)	2	8
41	*Hymedesmia mucronata* (Topsent, 1904)	1	5
42	*Hymedesmia occulta* Bowerbank, 1869	10	5
43	*Hymedesmia poicilacantha* Alander, 1942	1	3
44	*Hymedesmia digitata* Lundbeck, 1910		2
45	*Hymedesmia donsi* Alander, 1937		1
46	*Hymedesmia irregularis* Lundbeck, 1910		1
47	*Hymedesmia consanguinea* Lundbeck, 1910	1	
48	*Hymedesmia perforata* Lundbeck, 1910		2
49	*Hymedesmia rugosa* Lundbeck, 1910		2
50	*Hymedesmia storea* Lundbeck, 1910		1
51	*Hymedesmia* sp. I	2	7
52	*Hymedesmia* sp. II		6
53	*Stylopus stylifera* Alander, 1942	1	1
54	*Stylopus aceratus* (Topsent, 1904)		1
55	*Styloporus aequatus* (Lundbeck, 1910)		1
56	*Spirorhabdia vidua* (Schmidt, 1875)		1
	Family: Myxillidae		
57	*Iotroata acanthostylifera* (Stephens, 1916)		1
58	*Melonancora emphysema* (Schmidt, 1875)		2
59	*Melonancora elliptica* Carter, 1874		1
60	*Myxilla* (*Pseudomyxilla*) sp.	1	
	Family: Tedaniidae		
61	*Tedania suctoria* (Schmidt, 1870)		2
62	*Tedania* sp.		1
	Family: Desmacellidae		
63	*Desmacella inornata* (Bowerbank, 1866)	1	2
64	*Desmacella* sp.		3
	Family: Hamacanthidae		
65	*Hamacantha falcula* (Bowerbank, 1874)	2	2
66	*Hamacantha johnsoni* (Bowerbank, 1864)	5	2
	Family: Mycalidae		
67	*Mycale lingua* (Bowerbank, 1866)		1
68	*Mycale placoides* (Carter, 1876)		2
69	*Mycale ovulum* (Schmidt, 1870)		1
70	*Rhaphidotheca rhopalophora* (Schmidt, 1875)		1
	Order: Halichondrida		
	Family: Axinellidae		
71	*Axinella pyramidata* Stephens, 1916	2	1
72	*Bubaris vermiculata* (Bowerbank, 1862)		1
73	*Stylotella inornata* (Bowerbank, 1874)		1
	Family: Desmoxyidae		

Taba

	Overview of Porifera from Propeller Mound	Box corer	Dredge
74	*Halicnemia verticillata* (Bowerbank, 1866)	3	2
	Family: Halichondridae		
75	*Halichondria sitiens* (Schmidt, 1870)	1	3
76	*Halichondria oblonga* (Hansen, 1885)	2	13
77	*Topsentia fibrosa* (Fristedt, 1887)	1	17
78	*Topsentia genitrix* (Schmidt, 1870)		1
	Order: Haplosclerida		
	Family: Chalinidae		
79	*Haliclona voeringii* (Lundbeck, 1902)	2	4
80	*Gellius jugosus* (Bowerbank, 1866)	6	2
81	*Gellius couchi* (Bowerbank, 1874)	1	
82	*Gellius pumiceus* (Fristedt, 1885)	1	
83	*Gellius flagellifer* Lundbeck, 1902	1	11
84	*Gellius* sp.		3
85	*Metschnikowia spinispiculum* (Carter, 1876)	1	3
	Family: Niphatidae		
86	*Aka coralliophaga* (Stephens, 1915)		9
87	*Aka labyrinthica* (Hancock, 1849)		2
	Family: Petrosiidae		
88	*Petrosia crassa* Carter, 1876		1
89	*Phlaeodictyon elongatum* (Topsent, 1892)		1
	Order: Dendroceratida		
	Fam. Dysidiidae		
90	*Dysidea fragilis* (Montagu, 1818)		5
91	*Spongionella pulchella* (Sowerby, 1806)	1	
	Family: Darwinellidae		
92	*Aplysilla rosea* (Barrois, 1878)		1
	Class: Calcarea		
	Subclass: Calcinea		
	Fam. Clathriidae		
93	*Clathrina coriacea* (Montagu, 1818)	5	
	Family: Grantiidae		
94	*Ute gladiata* Borojevic, 1967	1	1
	Order: Lithonida		
	Family: Minchinellidae		
95	*Plectroninia celtica* n. sp. (this study)	17	5
	Class: Hexactinellida		
	Subclass: Hexasterophora		
	Order: Hexactinosida		
	Family: Aphrocallistidae		
96	*Aphrocallistes bocagei* Schulze, 1886	5	5
	Family: Rosselidae		
97	*Rossella nodastrella* Topsent, 1915		1

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