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Re-evaluation of *Graneledone setebos* (Cephalopoda: Octopodidae) and allocation to the genus *Megaleledone*

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The holotype of the Antarctic octopodid *Graneledone setebos* was re-examined and found to lack the epidermal warts characteristic of the genus *Graneledone*. It is similar in its large size to another Southern Ocean species, *Megaleledone senoi*. A comparative study of *G. setebos* and specimens attributed to *M. senoi* led us to conclude that *M. senoi* is a junior synonym of *G. setebos*. Although *M. senoi* is not valid, the genus *Megaleledone* can be separated from other genera by the structure of the radula (which lacks marginal plates) and we therefore consider the genus to be valid. We propose the new combination of *Megaleledone setebos* and have refigured the beaks and radula of the holotype herein and expanded the description. A search of museum specimens and the literature shows that *Megaleledone setebos* is more common in Antarctic waters than previously supposed.

INTRODUCTION

In the early part of the last century, the British Antarctic 'Terra Nova' Expedition established a base camp at Cape Evans on Ross Island. During 1911 and 1912, 'Miscellaneous collections' (Harmer & Lillie, 1914) were made from station 325, Cape Evans, and one of the specimens captured was an extremely large octopus collected from a tide pool. Massy (1916) discussed this specimen, which she described as being in 'deplorable condition,' under the name *Moschites* sp. Based on this specimen Robson (1932) described the species *setebos*, which he tentatively placed in the genus *Graneledone*. Robson's species was labelled *nomen dubium* by Voss (1976, 1988a) and has since rarely been given serious consideration in the literature. Lu & Stranks (1994) however, recognized the possibility that *G. setebos* might be synonymous with another very large octopus described from the Southern Ocean, namely *Megaleledone senoi* Taki, 1961. Taki had noted the similarities between *setebos* and *senoi* but was unable to examine personally the holotype of *G. setebos* and hence unable to draw firm conclusions.

Taki's (1961) original description of *Megaleledone senoi* was based on two females, one of which appeared to be mature. Nesis & Propp (1968) provided details of a mature female with spawned eggs captured by a SCUBA diver in 1966. Kubodera & Okutani (1986) figured the copulatory organs and briefly described the male reproductive systems of two immature males. Then, at the Southern Ocean Cephalopods Symposium held in Cambridge, England in July 1993 a number of presentations, including that of Lu & Stranks (1994), focused on *M. senoi* as an unusually large but rare Antarctic octopus species.

During a workshop session at the Cambridge meeting, the issue was raised, but not resolved, as to the taxonomic position of Robson's *Graneledone setebos*. As a result of this and previous discussions with several workers, we re-examined the holotype of *G. setebos* at the Natural History Museum, London (BMNH) together with many new specimens (Figure 1).

Measurements from four of the largest specimens reported by Lu & Stranks and held in the collections of the Museum Victoria, Melbourne (NMV) are included in this study and extensive new material has been collected by the National Museums of Scotland (NMSZ). Data are provided on additional specimens held by the Institute für Meereskunde, Kiel (IFM), the National Science Museum, Tokyo (NSMT), the Scripps Institute of Oceanography (SIO), the University of Miami Marine Laboratory [Rosenstiel School of Marine & Atmospheric Science], Miami, Florida (UMML), the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM) and the Zoological Museum, Academy of Sciences, St Petersburg (ZIN). Further comparative material was obtained from the Australian Museum, Sydney, NSW, Australia (AM), Muséum National d'Histoire Naturelle, Paris, France (MNHN) and the Musée Oceanographique de Monaco (MOM).

This paper aims to determine the appropriate specific name to use and to confirm the generic placement of the largest of the Antarctic octopuses. Abbreviations and indices are as defined in Roper & Voss (1983) except arm mantle index (AMI: arm length/mantle length×100), head width index (HWIw: head width/mantle width×100), egg thread length (EThL) and total fresh wet weight (TFW). The egg 'thread' (Figure 4C) attaches the egg within the

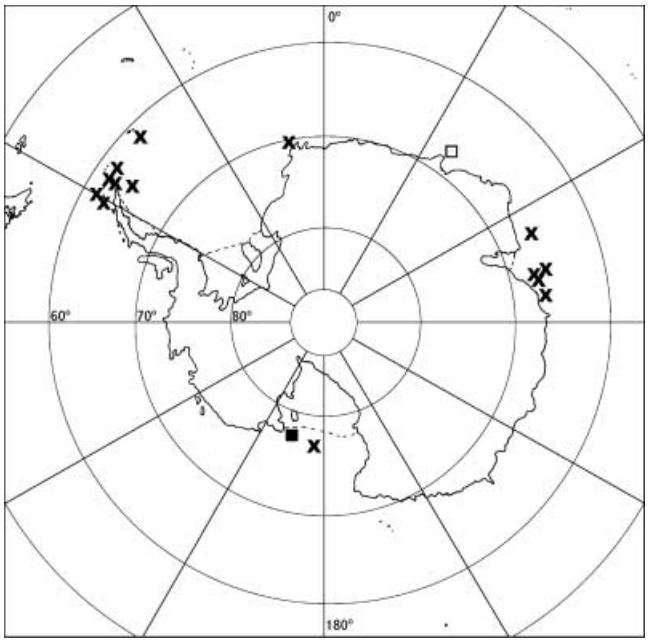

Figure 1. *Megaleledone*: distribution of specimens examined. ■, *Graneledone setebos*, holotype; □, *Megaleledone senoi*, holotype; **X**, specimens examined.

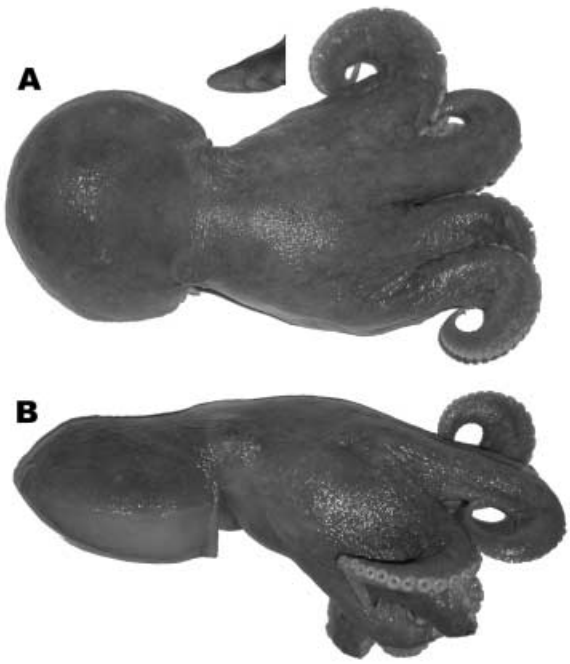

Figure 2. *Megaleledone setebos*: NMSZ 2002037.040, MLd 110 mm. (A) Dorsal view with enlarged view of hectocotylus (HcL 13 mm); (B) lateral view.

ovary and is so called to distinguish it from the 'stalk' used to attach deposited eggs of incirrate octopods.

SYSTEMATICS

Family OCTOPODIDAE Orbigny, 1840
Megaleledone Taki, 1961

Amended diagnosis

Mantle saccular. Stylets present. Arms with uniserial row of suckers. Right third arm of males hectocotylized; copulatory organ with clearly differentiated ligula and calamus; arm tips not otherwise modified. Suckers moderately large; distinct enlarged suckers absent. Web deep, well developed. Funnel organ VV-shaped. Ink sac present; anal flaps absent. Radula composed of seven teeth per transverse row; marginal plates absent. Rhachidian acuspid; lateral teeth unicuspid; marginal tooth unicuspid.

Type species

Megaleledone senoi Taki, 1961. By monotypy.

Included species

Graneledone setebos Robson, 1932.

Etymology

Genus name derived from the Greek *megale*, meaning 'large, great, big' in reference to the octopus' large size.

Remarks

Megaleledone can be differentiated from most other octopodid genera with uniserial suckers by the structure of the radula. *Eledone*, *Bentheledone* and *Tetracheledone* all have marginal plates (Palacio, 1978), as do *Pareledone* (A.L. Allcock, unpublished data), whilst *Thaumeledone* and *Vosseledone* lack marginal teeth (Palacio, 1978). *Megaleledone* is easily differentiated from *Graneledone* by the complex wart structure in the latter and from *Veledona* by the well developed web membranes in this species. Both morphological data (Voight, 1993, 1997) and molecular data (Carlini et al., 2001; Allcock & Piertney, 2002) suggest that the current concept of subfamilies (Sweeney & Roper, 1998) is flawed. An analysis of partial 16s rDNA sequence data showed that *Megaleledone* grouped within a clade containing *Graneledone* and *Pareledone* spp. (Allcock & Piertney, 2002) and we therefore believe that the subfamily Megaleledoninae, proposed by Taki, 1961, is not valid.

Megaleledone setebos (Robson, 1932) new combination
(Figures 2–4; Tables 1 & 2)

Graneledone setebos Robson, 1932: 313–314, text-figure 72, holotype, female, 170 mm ML, McMurdo Sound, off Cape Evans, in a rock pool, coll. British Antarctic Terra Nova Expedition, station 325, 1911–1912. Grimpe, 1933: 497. Castellanos & Menni, 1969: 78. Dell, 1972: 86. Voss, 1976: 457 [designation as *nomen dubium*].

Megaleledone senoi Taki, 1961: 297–304, text-figures 1–8, 16, plates 1–2, holotype [presumed not extant], female, submature, 135 mm ML, near Showa Base, 67°51.5′S 33°13.5′E, 630–680 m, coll. J. Senô, RV 'Umitaka-maru', 7 February 1957, beam trawl. Nesis & Propp, 1968: 66–68, text-figure 1. Dell, 1972: 86–87. Lipinski & Woyciechowski, 1981: 163–166, text-figure 1a,b. Kubodera & Okutani, 1986: 133–134, text-figure 2A–B, plate 2 (figures A–D); 1994: 210–212. Lu & Stranks, 1994: 233 text-figures 8, 9u–x. Piatkowski et al., 1998: 44. Ogden et al., 1998: 29–34.

Pareledone senoi Voss, 1988a: 302, text-figure 6 [map].

Moschites sp. Massy, 1916: 159–161, text-figure 33.

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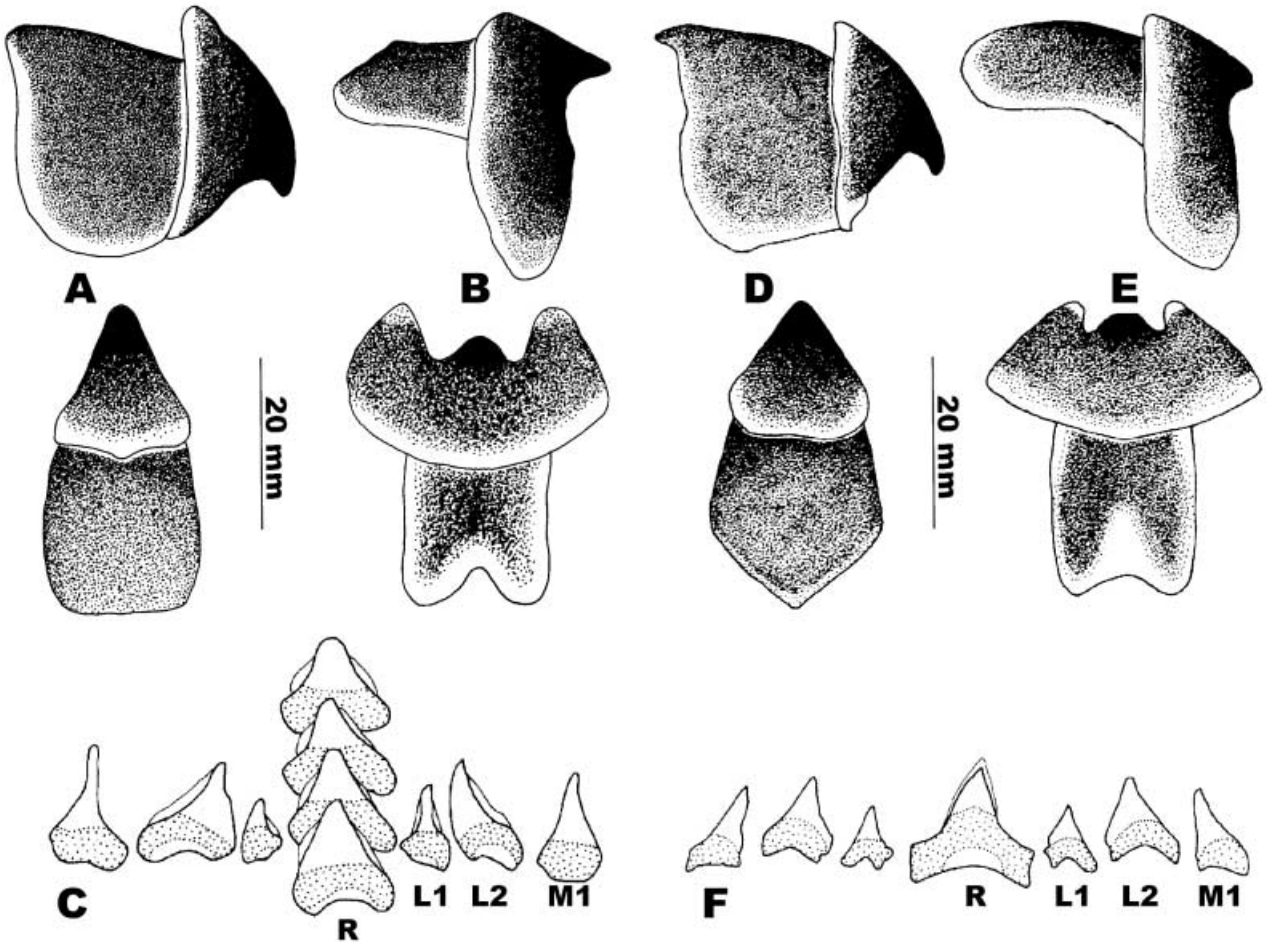

Figure 3. *Megaleledone setebos*: beak and radula. (A–C) Holotype, BMNH 1919.12.30.27; (D–E) NMV F60488: originally identified as *senoi*; (F) NMV F65528: originally identified as *senoi*. L1, first lateral tooth; L2, second lateral tooth; M1, marginal tooth; R, rachidian tooth.

Eledoninae sp. B. Clarke & MacLeod, 1982a: 30; 1982b: 38, text figure 2.

Octopod unidentified Hoyle, 1907: 1.

Cephalopoda unidentified Hoyle, 1912: 274b.

'Octopus' Moss & deLeiris, 1988: 85, unnumbered text-figure.

Material examined

Holotype: female (according to Robson, 1932) 170 mm ML (according to Massy, 1916) [BMNH 1919.12.30.27]; McMurdo Sound, off Cape Evans (77°40′S 166°30′W), in a rock pool, coll. British Antarctic 'Terra Nova' Expedition, station 325, 1911–1912.

One male (ML and maturity unknown) [UMML 31.2597], arms only; Ross Sea, Balleny Islands, 2 miles [3 km] east of south end of Franklin Is, 76°02′S 168°21′E, 280 m, coll. R.B. Short & E.C. Powell, USS 'Glacier', station E172, 13 January 1965, 5ft Blake trawl. One male (submature), 160 mm ML [BMNH], Signy Island, coll. P.J. Tilbrook, near the shore, 15 March 1966. One male (mature), 200 mm ML [BMNH], 66°45′S 62°03′E, depth 219 m, coll. British Australian New Zealand Antarctic Research Expedition, station 107, 16 February 1931. One female (mature) 190 mm ML [USNM 884259], Weddell Sea, 74°36′S 29°36′W, depth 796–805 m, coll. RV 'Polarstern', EPOS III, station 250, 4 February 1989, bottom trawl. Two beak sets [SBMNH] from stomach contents of 6-y-old male southern elephant seal (*Mirounga leonina*), South Orkney Islands, Signy Island, Factory Cove, 60°43′S 45°38′W, coll. P.J. Tilbrook, Falkland Islands Dependencies Survey, 22 February 1963 (specimen no. 8, table I, Clarke & Macleod, 1982a). One female (submature) 234 mm ML [NMV F65528], Prydz Bay, 67°19′S 74°16′E, depth 464–465 m, coll. T.G. Cochran, Australian National Antarctic Research Expeditions (ANARE), MS 'Nella Dan', Station Prydz-87–47, 28 February 1987. One male (mature) 207 mm ML [NMV F60488], Prydz Bay, 67°00′S 74°23′E, depth 431–439 m, coll. C.C. Lu & T.N. Stranks, ANARE, RSV 'Aurora Australis', station AA91-87, 23 February 1991. One male (immature) 169 mm ML [NMV F60487], Prydz Bay, 67°00′S 75°01′E, depth 385–388 m, coll. C.C. Lu & T.N. Stranks, ANARE, RSV 'Aurora Australis, station AA91-86, 22 February 1991. One female (submature) 181 mm ML [NMV F65526], Prydz Bay, 67°54′S 76°37′E, depth 431 m, coll. T.G. Cochran, ANARE, MS 'Nella Dan', station Prydz-87-2, 16 February 1987. One female (mature) 230 mm ML [IFM], Antarctic Peninsula, 61°01′S 54°49′W, depth 441–512 m, coll. A.L. Allcock, S. Steimer, U. Piatkowski, M. Vecchione, ANT XIV/2, RV 'Polarstern',

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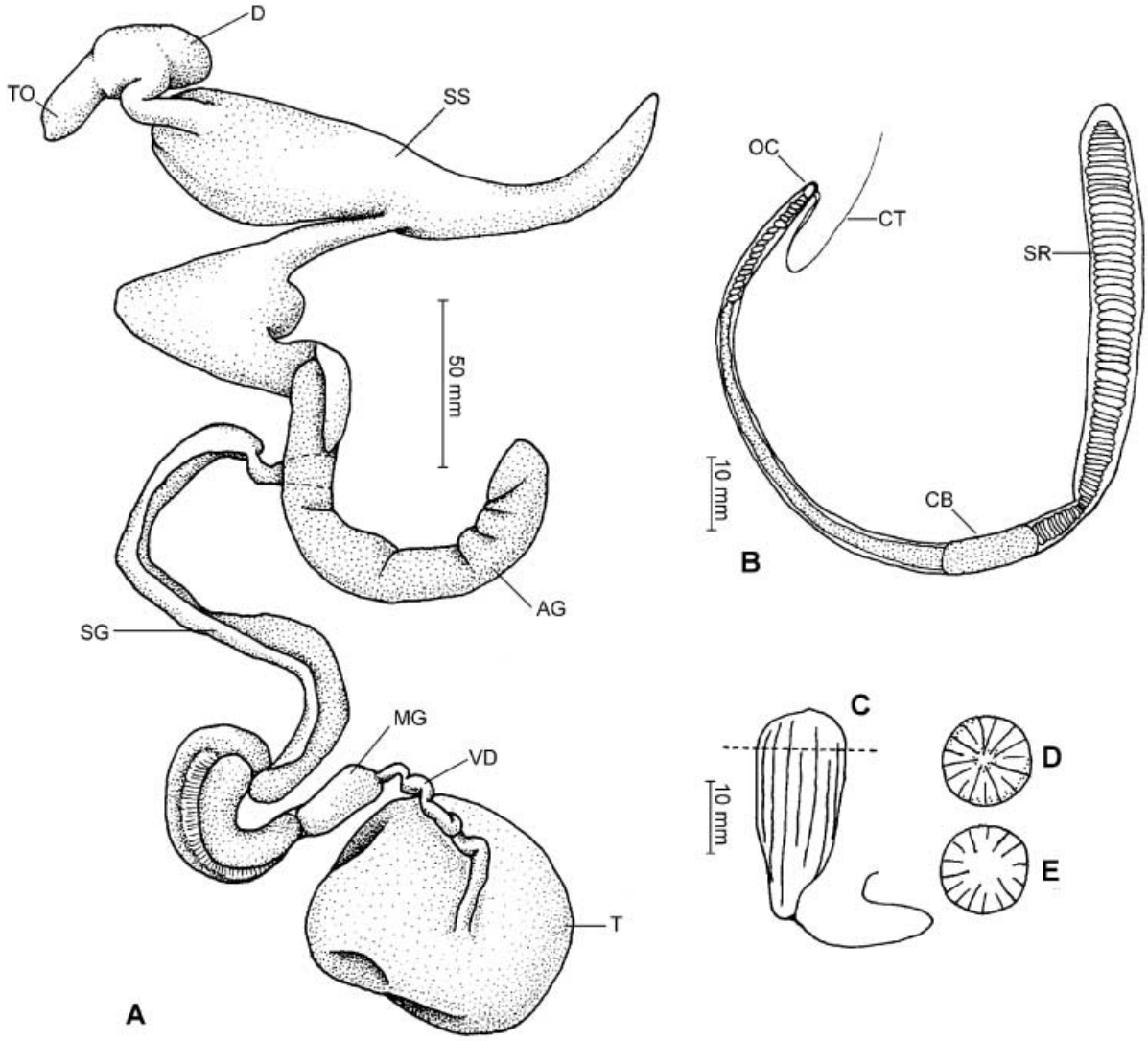

Figure 4. *Megaleledone setebos*: reproductive tract. (A) Male tract, mature male NMV F60488; (B) spermatophore, mature male NMV F60488; (C–E) eggs, mature female, NMSZ 2002037; (C) lateral view; (D) view from top; (E) transverse section. AG, accessory gland; CB, cement body; CT, cap thread; D, diverticulum; MG, mucilaginous gland; OC, oral cap; SG, spermatophoric gland; SR, sperm reservoir; SS, spermatophoric sac; T, testes; TO, terminal organ; VD, vas deferens.

station 42/040, 26 November 1996. One female (immature) 105 mm ML [SIO M8733], Antarctic Peninsula, Anvers Island, Wylie Bay, depth 100 fathoms, coll. SIO, January 1969. One juvenile 28 mm ML [NMSZ 2000081.014], Weddell Sea, 70°50′S 10°35′W, depth 237–266 m, coll. A.L. Allcock, EASIZ III, RV 'Polarstern', station 119-1, 07 April 2000. One juvenile 16 mm ML [NMSZ 2000081.024], Antarctic Peninsula, 63°05′S 59°33′W, depth 858–859 m, coll. A.L. Allcock, EASIZ III, RV 'Polarstern', station 164-1, 28 April 2000. One male (immature) 85 mm ML [NMSZ 2000081.038], Antarctic Peninsula, 63°01′S 61°09′W, depth 352–279 m, coll. A.L. Allcock, EASIZ III, RV 'Polarstern', station 173-1, 30 April 2000. One male (mature) 280 mm ML [NMSZ 2000081.047], Antarctic Peninsula, 61°58′S 60°18′W, depth 804–930 m, coll. A.L. Allcock, EASIZ III, RV 'Polarstern', station 178-2, 02 May 2000. One female (immature) 105 mm ML [NMSZ 2000081.054], Antarctic Peninsula, 62°07′S 60°22′W, depth 200–204 m, coll. A.L. Allcock, EASIZ III, RV 'Polarstern', station 183-1, 03 May 2000. Six males (immature) 28, 32, 33, 35, 41, 42 mm ML, 3 females (immature) 32, 35, 61 mm ML [NMSZ 2000081.061], Antarctic Peninsula, 62°01′S 60°21′W, depth 338–374 m, coll. A.L. Allcock, EASIZ III, RV 'Polarstern', station 184-1, 03 May 2000. Two females (immature) 65, 73 mm ML [NMSZ 2002037.036], Antarctic Peninsula, 60°58.2′S 55°06.6′W, depth 308–399 m, coll. A.L. Allcock, ANT XIX/3, RV 'Polarstern', station 61/044-1, 29 January 2002. One female (immature) 75 mm ML [NMSZ 2002037.037], Antarctic Peninsula, 60°59.4′S 55°11.4′W, depth 196–269 m, coll. A.L. Allcock, ANT XIX/3, RV 'Polarstern', station 61/045-1, 29 January 2002. One male (immature) 160 mm ML [NMSZ 2002037.038], Antarctic Peninsula, 61°04.2′S 54°36.6′W, depth 190 m, coll. A.L. Allcock, ANT XIX/3, RV 'Polarstern', station 61/047-1, 30 January 2002. One male (immature) 140 mm ML [NMSZ 2002037.039], Antarctic Peninsula, 61°09.6′S 54°33.6′W, depth 343–278 m, coll. A.L. Allcock, ANT XIX/3, RV 'Polarstern', station 61/048-1, 30 January 2002. Two males (immature) 105, 155 mm ML [NMSZ 2002037.040], Antarctic Peninsula, 61°16.8′S 55°42.6′W, depth 136–172 m,

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Table 1. Megaleledone setebos*: measurements and indices for selected female specimens. Data on holotype of* M. senoi *Taki, 1961 are taken from the literature, as are data on ZIN 1 (Nesis & Propp, 1968).*

	Holotype of *G. setebos*	Holotype of *M. senoi*									
Repository	BMNH	unknown	ZIN	NMV	NMV	USNM	IFM‡	NMSZ	NMSZ	NMSZ	SIO
Catalogue No.	1919.12.30.27		1	F65528	F65526	884259		2000081.054	2000037.041	2002037.043	M8733
Sex		(sub)	(mat)	(sub)	(sub)	(mat)	(mat)	(imm)	(sub)	(mat)	(imm)
Depth (m)	tide pool	630–680	32–35	464–465	431	800	441–512	204–200	298–326	327–317	~200
TL (mm)		460	715	696	601	527	750	335‡ 330	620	650	
ML (mm)	170	135	195	234	181	190	230	105‡ 90	150	200	104.7
TFW (g)		2860	[6200]	[6530]	[2950]				7000	9140	[1430]
MWI	120.6	105.9	92.3	83.8	76	94.2	113	120.0	126.7	110.0	115.4
HWIw		62.2	65	59.7	71.1	62.6		63.0	63.2	59.1	60.1
HWI		65.9	60	50	54	58.9	56.5	75.6	80.0	65.0	69.3
FLI	29.4	18.5		33.8	36.5	34.7	30.4	36.7	48.0	34.0	39.5
AL 1	402	281	370	445	389	332	530	230	490	410	202
2	407	292	405	485	386	353	510	240	460	500	225
3	425	285	395	507	398	355	500	230	460	420	240
4	412	295	370	512	446	360	510	230	480	430	260
AMI longest	250	218.5	207.7	218.8	246.4	189.5	230.4	288.9	326.7	255.0	248.3
AMI shortest	236.5	205.9	189.7	188.9	195	171	217.4	244.4	286.7	205.0	192.9
AWI	6.6			17.1	14.6	9.4	21.7	27.8	32.0	22.5	19.1
SD (mm)	17	15	21	17.2	14.9	20.2	21	11	20	16	14
SDI	10	11.1	10.7	7.4	8.2	10.6	9.1	12.2	13.3	8.0	13.4
S Count 1		62	61	67	64	53		55	59	66	62
2		63	63	68	67	55		58	58	66	61
3		62	63	69	65	54	51	56	59	65	62
4		63	64	59+	67	53		59	59	65	64
Egg Count		ca. 50	88			78				130	
EL (mm)		17*	34**	18–19*		41.5**	29**			34**	
ELI		13*	14.5**	8.1*		21.8**	12.6**			17**	
EThL (mm)		14*	25**	12–18*						44**	

[ ], preserved wet weight; *, immature ovarian egg (largest); **, mature ovarian egg; ‡, measurements on fresh tissue. imm, immature; sub, submature; mat, mature; *G. setebos*, *Graneledone setebos*.

Table 2. Megaleledone setebos*: measurements and indices for selected male specimens. Data on NSMT specimens are taken from the literature (Kuboderal & Okutani, 1986).*

Repository	NMV	NMV	ZIN	UMML	NSMT	NSMT	NMSZ	NMSZ	NMSZ	BMNH	BMNH
Catalogue No.	F60488	F60487	2	31.2597	Mo-63960	Mo-63961	2002037.038	2002037.040	2000081.047	unregistered	unregistered
Sex	(mat)	(imm)	(mat)		(imm)	(imm)	(imm)	(imm)	(mat)	(mat)	(sub)
Depth (m)	431–439	385–388	670–830	280	120	120	190	136–172	804–930	219	near shore
TL (mm)	748	542	590		470	350	420	410	900‡ 840	830	600
ML (mm)	207	169		170	145	110	115	110	280‡ 250	200	160
TFW (g)	14000	4730	[4850]						14500		
MWI	105.3	96.4	97.1		96.6	90.9	108.7	131.8	92.0	115.0	103.1
HWIw	63.3	54.8	61.2		67.8	60	66.4	62.1	60.9	56.5	66.7
HWI	66.7	52.8	59.4		65.5	54.6	72.2	81.8	56.0	65.0	68.8
FLI	42	42			37.9	34.6	44.3	47.3	32.0	45.0	51.9
AL 1	482	388	345		305	225	290	260	530	580	385
2	540	402	405		330	240	320	330	510	580	435
3	497+	365	376		310	235	340	340	620	510	435
Hc	537	343	312	450+	285	205	220	330	580	520	375
4	586	403	406	590+	310	240	290	310	670	470	435
AMI longest	283.1	238.5	238.2		227.6	218.2	295.7	318.2	268.0	290.0	271.9
AMI shortest	229	216	202.9		210.3	200	191.3	236.4	204.0	235.0	234.4
AWI	23.9	16.6					22.6	29.1	20.0	25.0	23.1
SD (mm)	38.6	18.3	22	26	17	11.4	16	16	35	27	25
SDI	18.7	10.8	12.9		11.7	10.4	13.9	14.5	14.0	13.5	15.6
S Count 1	63	63	54		54	53	60	59	62	58	65
2	66	63	55		55	58	60	59	63	59	68
3	66	58	47		55	58	59	58	62	57	
Hc	38	38	36	33+	38	39	35	38	37	39	40
4	66	64	51	43+	58	58	59	58	64	56	70
HAMI	259.4	203	183.5		196.6	184.6	191.3	300.0	232.0	260.0	234.4
OAI		94	83		91.9	87.2	64.7	97.1	93.5	102.0	86.2
LLI	3.6	3.9	5.4	5.1	3.4	3.9	5.0	3.9	4.0	3.8	4.5
CLI	42.7	45.2	29.4	56.5	39.6	55	45.4	46.2	39.1	25.0	41.2
SpLI			50						48.0		

[ ], preserved wet weight; ‡, measurements on fresh tissue. imm, immature; sub, submature; mat, mature.

coll. A.L. Allcock, ANT XIX/3, RV 'Polarstern', station 61/055-1, 01 February 2002. One female (submature) 200 mm ML [NMSZ 2002037.041], Antarctic Peninsula, 61°25.2′S 56°09.0′W, depth 298–326 m, coll. A.L. Allcock, ANT XIX/3, RV 'Polarstern', station 61/059-1, 02 February 2002. One male (immature) 175 mm ML [NMSZ 2002037.042], Antarctic Peninsula, 61°21.6′S 56°02.4′W, depth 355–353 m, coll. A.L. Allcock, ANT XIX/3, RV 'Polarstern', station 61/060-1, 02 February 2002. Three males (immature) 35, 50, 74 mm ML, 1 female (immature) 53 mm ML, 1 female (mature) 240 mm ML [NMSZ 2002037.043], Antarctic Peninsula, 61°17.4′S 56°13.2′W, depth 327–317 m, coll. A.L. Allcock, ANT XIX/3, RV 'Polarstern', station 61/061-1, 02 February 2002.

Comparative material examined

Pareledone adelieana (Berry 1917). Holotype [AM C40889]. Adelieland, off Mertz Glacier, 66°55′S 145°21′E, depth 450–549 m, coll. Mawson Antarctic Expedition, station 2, 28 December 1913.

Pareledone aurorae (Berry 1917). Holotype [AM C40891]. Off Queen Mary Land, 66°08′S 94°17′E, depth 219 m, coll. Mawson Antarctic Expedition, station 8, 27 January 1914.

Pareledone turqueti (Joubin 1905). Holotype [MNHN 5.7.1089]. Baie Carthage, Ile Wandel, 65°05′S, depth 25 m, coll. 'Charcot' Antarctic Expedition, 15 March 1904.

Pareledone charcoti (Joubin 1905). Holotype [MNHN 5.7.1095]. Ile Wandel, 65°05′S, on the shore, coll. 'Charcot' Antarctic Expedition, 3 September 1904.

Pareledone framensis Lu & Stranks 1994. Paratype [NMV F65667]. Prydz Bay, 67°27.35′S 68°50.34′E, depth 145–150 m, coll. RV 'Aurora Australis', station AA91-100, 28 February 1991.

Pareledone prydzensis Lu & Stranks 1994. Paratype [NMV F65625]. Prydz Bay, 66°47′S 72°36′W, depth 526–532 m, coll. RV 'Aurora Australis', station AA91-89 (2), 24 February 1991.

Pareledone harrissoni (Berry 1917). Holotype [AM C40892]. Queen Mary Land, off Shackleton Glacier, 65°06′S 96°13′E, depth 494–595 m, coll. Mawson Antarctic Expedition, station 10, 29 January 1914.

Pareledone polymorpha (Robson 1930). Holotype [BMNH 1951.4.26.26]. East Cumberland Bay, South Georgia, depth 120–204 m, coll. Discovery Expedition, 1 April 1926.

Graneledone verrucosa (Verrill, 1881). Syntype [USNM 729732]. Eastern coast of the United States, 41°33′N 65°21′W, depth 810 fathoms (1470 m), coll. RV 'Blake', 28 June 1880.

Graneledone verrucosa var *media* (Joubin, 1918). Holotype [MOM 3437-1913]. Eastern coast of the United States, 42°40′N 62°49′W, 1458 m, coll. RV 'Prince de Monaco', 26 August 1913.

Graneledone challengeri (Berry, 1916). Holotype [BMNH 1889.4.24.49]. Kermadec Islands, 29°45′S 178°11′W, depth 630 fathoms (1152 m), coll. RV 'Challenger', 14 July 1874.

Graneledone antarctica Voss, 1976. Female [USNM 100829]. Antarctic Peninsula, 61°18.6′S 57°01.8′W, depth 1440–1512 m, coll. RV 'Polarstern', station 42/077, 8 December 1996.

Diagnosis

Large benthic octopus, maturing at over 200 mm ML. Total length to 900 mm. Mantle saccular and broad. Stylets present. Arms with uniserial row of suckers. Arms 2–3 times length of body. Right third arm of males hectocotylized; copulatory organ with clearly differentiated ligula and calamus. Ligula simple, without transverse ridges, calamus of moderate length. Arm tips not otherwise modified. Suckers moderately large; distinct enlarged suckers absent. Web deep, well developed. Funnel organ VV-shaped. Gills with 10–13 lamellae per outer demibranch. Ink sac present; anal flaps absent. Radula composed of seven teeth per transverse row; marginal plates absent. Capsule length of spawned eggs over 40 mm.

Description

Animals large sized (ML to 280 mm, TL to 900 mm). Mantle spherical, maybe slightly broader than long or slightly longer than broad. Eyes medium sized (mean EDI 20.4). Funnel large (mean FuLI 34.3), tapered; funnel organ VV shaped, lateral limbs similar in length to median limbs. Arms long, 2–3 times mantle length. Arm lengths approximately equal. Suckers uniserial, moderately large (mean ASI 8.5) reaching >50 mm on large animals but without obvious sucker enlargement in sexually mature animals. Third right arm of males hectocotylized, slightly shorter than opposite number (OAI 93.2). Ligula small (mean LLI 4.2), ligula groove long, well marked and shallow. Calamus distinct and long (mean CLI 42.3). Hectocotylized arm with 35–40 suckers, opposite arm with up to 69 suckers. Web deep, extending to nearly half way down the arms (mean WDI 45.0), web formula usually C=D.B.A=E. Ink sac present. Gills with 10–13 lamellae per outer demibranch with some regional variation (mode Weddell Sea 11, Antarctic Peninsula 12, eastern Antarctica 11). Gills often heavily parasitized in large mature animals. Beak large but takes usual octopodid form. Radula with acuspid rachidian, unicuspid lateral teeth and unicuspid marginal teeth (Figure 3). Reproductive tract takes normal octopodid form. Mature ovarian eggs large, up to 41.5 mm attached within the ovary by a long thread which may be longer than the eggs (Figure 4). Spermatophores long, up to 235 mm (maximum SpLi 87.0) and slender (Figure 4). Males and females mature at approximately 200 mm ML.

The integument is thick and loose and in life the animal is mottled in hues of brown and red. The integumental sculpture consists of fine, widely scattered papillae on the dorsal surface. There are no enlarged papillae in the supraocular region. A ventrolateral integumentary line is well defined (Figure 2B). The ventral and oral surfaces are smooth and slightly paler in coloration than the dorsal surface.

Distribution

Circum-Antarctic but not extending to sub-Antarctic islands such as South Georgia (Figure 1). Depth ranges from 32 m (Nesis & Propp, 1968) to 850 m.

Etymology

Although not specified by Robson, the trivial epithet most likely refers to *Setebos*, a deity worshiped by the Patagonians. The cult was first known in Europe through reports of Magellan's Voyage. *Setebos* was later introduced by Shakespeare into his *Tempest* as the god of Sycorax, Caliban's mother. It is possible that Robson was alluding to lines from Robert Browning's poem, *Caliban on Setebos*; or *Natural Theology in the Island*:

> 'Careth but for Setebos
> The many-handed as a cuttle-fish'

Remarks

The holotype is represented by the remains of a large, robust specimen contained in a tall, glass cylinder. The specimen is macerated and unfortunately in very poor condition. The muscular cores of all eight arms are present although the skin and suckers are sloughed off. Several large pieces of mantle musculature are present but neither the head nor the internal organs could be identified. It is immediately apparent that the specimen is lacking the warts that are characteristic of the genus *Graneledone* (Allcock et al., in press). The suckers were found in a slurry of skin, macerated muscle and body organs in the bottom of the container. The arms of the holotype are detached from the body. Two additional small jars identified under the name assigned by Massy, namely *Moschites* sp., were located in the general collection. These contained the radula (BMNH 1919.12.30.56) and the beaks, anterior and posterior salivary glands and funnel (BMNH 1919.12.30.57). All parts of the holotype have been recombined under the earliest catalogue number (BMNH 1919.12.30.27; F. Naggs, personal communication). The funnel is in poor condition and the funnel organ is not visible. The beaks and radula are in good condition and are refigured here (Figure 3).

As Taki (1961) noted, 'the radular characters of this species [*Megaleledone senoi*] somewhat resemble those of *Graneledone setebos*.' Comparison of the beaks and radula of *Graneledone setebos* with Taki's drawings show close agreement, and it is the radula characters which validate placement of *G. setebos* in *Megaleledone*. It is the morphology of the hard structures, together with the large size of these animals (unique in the Southern Ocean) and their similarity in 'the broadness of mantle' (Taki, 1961) and general body proportions (Tables 1 & 2), the sucker size and the configuration of the ligula that convince us that *M. setebos* and *M. senoi* are synonymous. The one difference is in the form of the funnel organ which we believe may have been described inaccurately by Taki. Unfortunately he never published catalogue numbers for his type material, it has not been located and we are therefore unable to verify this. Several authors have commented on the 'ribs' of the ligula groove but these are not to be confused with the deep ridges found, for example, on the ligula of *Pareledone polymorpha* (Robson, 1930). The general looseness of the integument of *M. setebos* leads to a creasing or folding of skin on the ligula of the live animal which, when fixed, can appear as shallow grooves.

DISCUSSION

There is a notable lack of reference not only to *Graneledone setebos* Robson, 1932 but to *Megaleledone senoi* Taki, 1961, the other very large octopus described from the Southern Ocean, in papers referring to the octopods or cephalopod fauna of Antarctic waters (see Roper, 1981; Roper et al., 1985; Voss, 1967, 1988b). Some authors (e.g. Kühl, 1988; Voß, 1988) have probably mistakenly identified giant octopus specimens and recorded specimens of *Megaleledone* in their reports as more moderately sized species such as *Pareledone turqueti* (Joubin, 1905). Others have been unable to resolve identities beyond subfamilial level.

Hoyle (1907) was the first to document the presence of a pair of mandibles 'belonging to an octopod a couple of feet in total length' in the stomach contents of an unidentified male seal collected 10 November 1902 at Hut Point, Ross Island, the winter quarters of the British National Antarctic Expedition (Hoyle specimen 1346). As originally published, the position 54°01¼′S 170°49′E is incorrect; maps produced during the expedition show Hut Point at 77°50′50″S 166°44′45″E. Hoyle's report most likely refers to *Megaleledone* based on size. The beaks have not been located. Hoyle (1912) documents the mandibles from the stomach of a Weddell seal taken at station 325, South Orkneys, 21 September 1903 during the Scottish National Antarctic Expedition. These mandibles have been located at the National Museums and Galleries of Wales (NMWZ 78.014.333; Hoyle specimen 939) and identified as *Megaleledone*.

A number of authors have reported on the importance of cephalopods in the diet of seals in the Antarctic (e.g. Rodhouse et al., 1992; Daneri et al., 1999). Dearborn (1965) was the first to specifically identify eledonine octopods in stomach contents of Weddell seals (*Leptonychotes weddelli* Lesson, 1826). Lipinski & Woyciechowski (1981) published a detailed report on the octopods in the diet of Weddell seals captured in Admiralty Bay, King George Island, South Shetland Islands during the Third Polish Antarctic Expedition in 1978–1979. Beaks of *Megaleledone* were encountered in the stomach contents of six of the 17 seals examined. A set of beaks is figured in their paper. In order to confirm identifications, comparative octopus material was collected by otter trawl at depths of 470–550 m from the same locality. Of 31 specimens collected, two were identified as *M. senoi* based on size (male, ML 210 mm, TL, 840 mm; female, ML 78 mm, TL 330 mm). The male was, until recently, the largest known specimen of the genus ever collected. The specimens were originally housed in the collections of the Sea Fisheries Institute (MIR) but were moved in 1988 and currently are presumed to be stored in the Marine Museum and Aquarium, Al. Zjednoczenia, Poland (M.R. Lipinski, personal communication).

A large species of eledonine octopod was reported in the diet of southern elephant seals (*Mirounga leonina* Linnaeus, 1758) from Signy Island, South Georgia Islands (Clarke & MacLeod, 1982a) and in the stomach contents of Weddell seals from Deception Island, South Shetland Islands (Clarke & MacLeod, 1982b). In the first instance specimens of 'Eledoninae sp. B' were estimated to have an average weight of 5259 g while in the second case the octopods had an average weight of 1390 g.

These weights are well within the range of *Megaleledone* and much higher than weights recorded for any species of the endemic Antarctic genus *Pareledone*. Two sets of beaks from a 6-y-old male (specimen no. 8, table I, Clarke & MacLeod 1982a) were re-examined and identified as *Megaleledone*.

A subsequent study on the cephalopod prey of southern elephant seals from Husvik, South Georgia Islands encountered only *Pareledone* beaks. This is consistent with extensive fishing around South Georgia that has failed to yield *Megaleledone* specimens (Yau et al., in press).

It is clear that *M. setebos* is more common in the high Antarctic than the literature suggests. It has been found in great abundance particularly on the Antarctic Peninsula (Piatkowski et al., 1998, in press) and it is hoped that this redescription will facilitate further studies on a species that contributes greatly to the benthic cephalopod biomass of the Antarctic.

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REFERENCES

Allcock, A.L., Collins, M.A. & Vecchione, M., in press. A redescription of *Graneledone verrucosa* (Verrill, 1881) (Octopoda: Octopodidae). *Journal of Molluscan Studies*.

Allcock, A.L. & Piertney, S.B., 2002. Evolutionary relationships of Southern Ocean Octopodidae (Cephalopoda: Octopoda) and a new diagnosis of *Pareledone*. *Marine Biology*, **140**, 129–135.

Carlini, D.B., Young, R.E. & Vecchione, M., 2001. A molecular phylogeny of the Octopoda (Mollusca: Cephalopoda) evaluated in the light of morphological evidence. *Molecular Phylogenetics and Evolution*, **21**, 388–397.

Castellanos, Z.J.A. & Menni, R.C., 1969. Nota preliminar sobre la distribución de los cefalopodos del Atlantico Sudoccidental. Lista de especies incluyendo las las del sector Antartico. *Anales de la Sociedad Cientifica Argentina*, **188**, 205–221.

Clarke, M.R. & MacLeod, N., 1982a. Cephalopods in the diet of elephant seals at Signy Island, South Orkney Islands. *British Antarctic Survey Bulletin*, **57**, 27–31.

Clarke, M.R. & MacLeod, N., 1982b. Cephalopod remains in the stomach of eight Weddell seals. *British Antarctic Survey Bulletin*, **57**, 33–40.

Daneri, G.A., Piatkowski, U., Coria, N.R. & Carlini, R., 1999. Predation on cephalopods by Antarctic fur seals, *Arctocephalus gazella*, at two locations of the Scotia Arc, Antarctica. *Polar Biology*, **21**, 59–63.

Dearborn, J.H., 1965. Food of Weddell seals at McMurdo Sound, Antarctica. *Journal of Mammology*, **46**, 37–43.

Dell, R.K., 1972. Antarctic benthos. In *Advances in marine biology*, vol. 10 (ed. F.S. Russell and C.M. Yonge), pp. 1–216. New York: Academic Press.

Grimpe, G., 1933. Die Cephalopoden des arktischen Gebietes. *Fauna Artica*, **6**, 489–514.

Harmer, S.F. & Lillie, D.G., 1914. List of collecting stations. *British Antarctic 'Terra Nova' Expedition, 1910, Natural History Reports, Zoology*, **2**, 1–12, pl. 1–4.

Hoyle, W.E., 1907. Mollusca. I. Cephalopoda. *British National Antarctic Expedition, 1901–1904. Natural History Reports*, **2**, Zoology, 1–2.

Hoyle, W.E., 1912. The Cephalopoda of the Scottish National Antarctic Expedition. *Transactions of the Royal Society of Edinburgh*, **48**, 273–283.

Kubodera, T. & Okutani, T., 1986. New and rare cephalopods from the Antarctic waters. *Memoirs of the National Institute of Polar Research*, **44**, 129–143. [Special Issue.]

Kubodera, T. & Okutani, T., 1994. Eledonine octopods from the Southern Ocean: systematics and distribution. *Antarctic Science*, **6**, 205–214.

Kühl, S., 1988. A contribution to the reproductive biology and geographical distribution of Antarctic Octopodidae (Cephalopoda). *Malacologia*, **29**, 89–100.

Lipinski, M. & Woyciechowski, M., 1981. Cephalopods in the food of Weddell seals from the Admiralty Bay (King George Island, South Shetland Islands). *Polish Polar Research*, **2**, 163–167.

Lu, C.C. & Stranks, T.N., 1994. Synopsis of *Pareledone* and *Megaleledone* species, with description of two new species from East Antarctica (Cephalopoda: Octopodidae). *Memoirs of the Museum of Victoria*, **54**, 221–242.

Massy, A.L., 1916. Mollusca. Part. II. Cephalopoda. *British Antarctic 'Terra Nova' Expedition, 1910, Natural History Reports, Zoology*, **2**, 141–176.

Moss, S. & deLeiris, L., 1988. *Natural history of the Antarctic Peninsula*. New York: Columbia University Press.

Nesis, K.N. & Propp, M.V., 1968. Samyi bodshoi osminog Antarktiki [The biggest octopus of the Antarctic]. *Priroda*, **12**, 66–68. [English translation available from senior author.]

Ogden, R.S., Allcock, A.L., Watts, P.C. & Thorpe, J.P., 1998. The role of beak shape in octopodid taxonomy. *South African Journal of Marine Science*, **20**, 29–36.

Palacio, F.J., 1978. *Vosseledone charrua*: a new Patagonian cephalopod (Octopodidae) with notes on related genera. *Bulletin of Marine Science*, **28**, 282–296.

Piatkowski, L., Allcock, L., Hevia, M., Steimer, S. & Vecchione, M., 1998. Cephalopod ecology. In *The expedition ANTARKTIS XIV/2 of RV Polarstern in 1996/1997* (ed. G. Kattner). *Berichte zur Polarforschung*, **274**, 41–47.

Piatkowski, U., Allcock, L. & Vecchione, M., in press. Cephalopod diversity and ecology. *Berichte zur Polarforschung*.

Robson, G.C., 1932. *Monograph of the Recent Cephalopoda*. Part II. *Octopoda (excluding Octopodinae)*. London: British Museum (Natural History).

Rodhouse, P.G., Arnbom, T.R., Fedak, M.A., Yeatman, J. & Murray, A.W.A., 1992. Cephalopod prey of the southern elephant seal, *Mirounga leonina* L. *Canadian Journal of Zoology*, **70**, 1007–1015.

Roper, C.F.E., 1981. Cephalopods of the Southern Ocean region: potential resources and bibliography. *Biological Investigations of Marine Antarctic Systems and Stocks (BIOMASS)*, **2**, 99–105.

Roper, C.F.E. & Voss, G.L., 1983. Guidelines for taxonomic descriptions of cephalopod species. *Memoirs of the National Museum of Victoria*, **44**, 13–27.

Roper, C.F.E., Sweeney, M.J. & Clarke, M.R., 1985. Cephalopoda. In *Species identification sheets for fishery purposes. Southern Ocean (Fishing areas 48, 58 and 88) (CCAMLR Convention Area)*. Vol. I (ed. W. Fischer and J.C. Hureau), pp. 117–205. Rome: FAO.

Sweeney, M.J. & Roper, C.F.E., 1998. Classification, type localities, and type repositories of recent Cephalopoda. In *Systematics and biogeography of cephalopods*, vol. II (ed. N.A. Voss et al.). *Smithsonian Contributions to Zoology*, **586**, 561–599.

Taki, I., 1961. On two new eledonid octopods from the Antarctic Sea. *Journal of the Faculty of Fisheries and Animal Husbandry, Hiroshima University*, **3**, 297–316.

Voight, J., 1993. A cladistic reassessment of octopodid classification. *Malacologia*, **35**, 343–349.

Voight, J., 1997. Cladistic analysis of octopods based on anatomical characters. *Journal of Molluscan Studies*, **63**, 311–325.

Voss, G.L., 1967. Systematics and distribution of Antarctic cephalopods. *Antarctic Journal of the United States*, **2**, 202–203.

Voss, G.L., 1976. Two new species of octopods of the genus *Graneledone* (Mollusca: Cephalopoda) from the Southern Ocean. *Proceedings of the Biological Society of Washington*, **88**, 447–458.

Voss, G.L., 1988a. The biogeography of the deep-sea Octopoda. *Malacologia*, **29**, 295–307.

Voss, G.L., 1988b. Evolution and phylogenetic relationships of deep-sea octopods (Cirrata and Incirrata). In *The Mollusca*. Vol. 12. *Palaeontology and neontology of cephalopods* (ed. M.R. Clarke and E.R. Trueman), pp. 253–276. San Diego: Academic Press.

Voß, J., 1988. Zoogeographie und Gemeinschaftsanalyse des Makrozoobenthos der Weddellmeeres (Antarktis). *Berichte zur Polarforschung*, **45**, 1–145.

Yau, C., Allcock, L., Daly, H.I. & Collins, M.A., in press. Distribution of *Pareledone* spp. (Octopodidae: Eledoninae) around South Georgia. *Bulletin of Marine Science*.

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