

A REDESCRIPTION OF *GRANELEDONE VERRUCOSA* (VERRILL, 1881) (OCTOPODA: OCTOPODIDAE)

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(Received 17 January 2002; accepted 16 September 2002)

ABSTRACT

Graneledone verrucosa (Verrill 1881), the type species of the genus *Graneledone*, is redescribed based on historical material and previously unreported specimens that have resulted from an increase in deep-sea fishing in the North East Atlantic. *Graneledone verrucosa* var. *media* (Joubin 1918) was found to be invalid and is herein synonymized with *G. verrucosa*. *Graneledone verrucosa* is shown to inhabit deep water throughout the North Atlantic; its distribution extends from 20° to 65° N and from 9° to 75° W. A revised diagnosis is given for the genus *Graneledone* Joubin, 1918.

INTRODUCTION

Octopods dominate the benthic and demersal deep-sea cephalopod fauna, with incirrates on the upper slope, and cirrates on the lower slope and abyssal plains. Both commercial and research fishing in deep waters have expanded recently and, while these fishing activities have been primarily directed at fish, they have produced a by-catch of cephalopods, in particular octopods (Boyle, Collins & Williamson, 1998; Collins, Yau, Allcock & Thurston, 2001; Vecchione & Galbraith, 2001). This by-catch has provided new material for biological studies (Boyle & Daly, 2000; Daly, Boyle & Collins, 1998), but has also highlighted the paucity of knowledge of many cephalopod species. Some are new to science and others are poorly described, and these factors combine to hinder accurate identification of specimens.

The genus *Graneledone* appears to be widespread throughout the deeper waters of the North Atlantic (Voight, 2000). Collins *et al.* (2001) reported 12 specimens of *Graneledone verrucosa* (Verrill, 1881) from the Rockall Trough and Porcupine Seabight, to the west and southwest of the British Isles. This species has also been caught in the northwest Atlantic (Vecchione & Galbraith, 2001). Access to specimens of *G. verrucosa* on both sides of the Atlantic has enabled a review of the taxonomy of this species, which nominally comprises two subspecies *G. verrucosa verrucosa* and *G. verrucosa media* (Joubin, 1918). *Graneledone verrucosa*, the type species of the genus *Graneledone*, has been reported from the northwest, northeast and southeast Atlantic, yet remains poorly described. The widely dispersed material has never been critically examined. Until the 1970s the genus comprised three species: *G. verrucosa*, *G. challengerii* (Berry, 1916) and *G. setebos* Robson, 1932. The last of these has widely been regarded as *nomen dubium*, but is being reinstated in a different genus (Allcock, Hochberg & Stranks, in press). In 1976, Voss erected two new species, *G. antarctica* and *G. macrotyla*, from southern waters. Nesis (1982) described *G. boreopacifica* from Japanese waters. Voss & Percy (1990) described *G. pacifica* from the northeast Pacific, although this may be a junior synonym of *G. boreopacifica* (Hochberg, 1998). *Graneledone gonzalezii* has been described from the Kerguelen Islands (Guerra, Gonzalez & Chérel, 2000), *G. yamana* from the south west Atlantic (Kommritz, 2000) and *G. taniwha* from New Zealand (O'Shea, 1999). The generic diagnosis has been amended frequently during the rapid expansion of the genus.

Confusion concerning the genus has arisen as a result of the proliferation of recognized species and the present study examines specimens of the type species from across its wide distribution, including the syntypes of *G. verrucosa verrucosa* and the holotype of *G. verrucosa media*. A redescription based on historical and previously unreported specimens is given. *G. verrucosa media* is designated as a junior synonym of *G. verrucosa*. The diagnosis of the genus *Graneledone* is also corrected.

MATERIALS AND METHODS

Specimens of *Graneledone* were examined from the Discovery Collections, Southampton Oceanography Centre (DC-SOC), the US National Museum of Natural History, Smithsonian Institution (USNM), the National Museums of Scotland (NMSZ) and from recent captures by Aberdeen University research cruises in the Porcupine Seabight. Additional specimens attributed to *Graneledone* were examined from the University Museum, Bergen (UMB), the Zoologisk Museum, Copenhagen (ZMUC), the Muséum National d'Histoire Naturelle, Paris (MNHN), the Musée Océanographique, Monaco (MOM), the Natural History Museum, London (BMNH) and the Instituto de Ciencias del Mar, Barcelona (ICM).

All measurements, indices and abbreviations follow Roper & Voss (1983). Examples of counts and measurements taken from specimens are given in Table 1 although, because of the poor condition of some of the type material, much of this material was not suitable for extensive handling. Standard indices were calculated (Table 2) using as many specimens as possible. Because of specimen damage and sex and maturity constraints, the number of specimens used to calculate each index varies. All specimens included in the indices had a dorsal mantle length greater than 50 mm. Radular nomenclature follows Nixon (1995).

SYSTEMATIC DESCRIPTIONS

Graneledone Joubin, 1918

Type species: Graneledone verrucosa (Verrill, 1881).

Revised diagnosis: Sucker arrangement uniserial. Ink sac absent. Funnel organ VV-shaped. Hectocotylus is clearly differentiated into calamus and ligula; there are no transverse copulatory lamellae on the ligula. Gills small, with 6–9 lamellae per

Table 1. *Graledone verrucosa*: sample counts and measurements from type material and additional material in better condition.

Institution	USNM	USNM	MOM	ZMUC	ZMUC	ZMUC	MNHN	NMSZ	NMSZ	NMSZ	USNM	USNM
Catalogue no.	577583	729732	3437-1913	B5-78-10	B5-78-07	2013	1999158.096	2002159	815506	730993		
Identification	<i>E. verrucosa</i>	<i>E. verrucosa</i>	<i>M. verrucosa media</i>	<i>G. verrucosa</i>	<i>G. verrucosa</i>	<i>G. verrucosa</i>	<i>G. verrucosa</i>	<i>G. verrucosa</i>	<i>G. verrucosa</i>	<i>G. verrucosa</i>		
Authority	Verrill, 1881	Verrill, 1881	Joubin, 1918	(Verrill, 1881)	(Verrill, 1881)	(Verrill, 1881)	(Verrill, 1881)	(Verrill, 1881)	(Verrill, 1881)	(Verrill, 1881)		
Type status	Syntype	Syntype	Holotype	None	None	None	None	None	None	None		
Sex	Female	Male	Male	Male	Female	Female	Male	Female	Male	Female		
Total length	360	202	330	220	400	120	455	475	290	350		
Mantle length	100	58	77	65	110	33	88	105	90	85		
Mantle width	65	55	94	55	100	32	112	103	73	80		
Head width		49	80	56	75	26	90	92				
Pallial aperture				28	50	19						
Funnel length				26	37	15	42	49	35	30		
Free funnel length				14	18	4		31				
Funnel organ length				12	19	8						
Deepest web depth				44	70	30		68	65			
Arm lengths:												
L1	255	135	250	145	260	81	351	325	230	280		
L2	260	155	240	153	270	81	380	290	220	270		
L3	225	130	260	155	260	77	311	290	230	260		
Hectocotylized	-	103	215	125	-	-	296	-	210	230		
L4	210	145	215	144	240	78	339	285	200	230		
Arm width	18	12		11	21	7	20	-	5.8	5.5		
Sucker diameter	5	3	6	3	5	1	7	7.1				
Sucker count:												
L3				65	79	58		87	80	86		
Hectocotylized	-	45		44	-	-	42	-	45	-		
Gill lamellae count			7/7	7/7	7/7	7/7	7/8	7/7	6/7	7/7		
Ligula length	-		12		-	-	11	-	10	-		

All measurements in mm; -, indicates where character applies to males only.

REDESCRIPTION OF *GRANELEDONE VERRUCOSA*
Table 2. Average counts and indices that describe the morphology of *Graneledone verrucosa*.

Character	<i>n</i>	Mean	SE
Mantle width index	14	99.1	4.5
Head width index	25	86.8	2.9
Funnel length index	24	42.1	1.4
Arm length index	21	71.7	3.7
Arm mantle index, arm 1	26	296.7	10.0
Arm mantle index, arm 2	25	299.8	9.8
Arm mantle index, arm 3	21	288.2	10.3
Arm mantle index, hectocotylus	13	235.8	12.9
Arm mantle index, arm 4	25	269.4	11.0
Sucker diameter index	23	6.3	0.3
Sucker count, arm 1	22	81.6	1.8
Sucker count, arm 2	19	82.2	2.1
Sucker count, arm 3	10	81.8	5.0
Sucker count, hectocotylus	13	43.5	0.4
Sucker count, arm 4	19	79.8	2.0
Gill length index	11	23.5	1.4
Opposite arm index	9	83.1	2.2
Ligula length index	9	4.6	0.3
Calamus length index	5	49.3	3.8
Spermatophore length index	3	151.8	13.2

Abbreviations: *n*, number of specimens.

demibranch. Radula variable (homodont or heterodont). Posterior salivary glands small. Wart-like tubercles cover body surface variably and may extend over dorsal and ventral surfaces of mantle, head, arms and web.

***Graneledone verrucosa* (Verrill, 1881)**

(Figures 1–8)

Eledone verrucosa Verrill, 1881: 105, pls 5, 6. Verrill, 1882a: 380, pls 52, 53. Verrill, 1882b: 393, 435, pl. 44, figs 3, 3a. Verrill, 1884: 248.

Moschites verrucosa—Berry, 1917: 2, pl. 1, fig. 1. Joubin, 1918b: 340.

Graneledone verrucosa—Joubin, 1918b: 340. Joubin, 1924: 10, pl. 6, figs 15–17; pl. 9, figs. 1–3. Robson, 1932: 308. Boyle *et al.*, 1998: 1024. Collins *et al.*, 2001: 112. Vecchione & Galbraith, 2001: 387.

Moschites verrucosa var. *media* Joubin, 1918a: 1.

Moschites media—Joubin, 1918b: 340.

Graneledone media—Joubin, 1918b: 340. Joubin, 1924: 38.

Graneledone verrucosa var. *media*—Joubin, 1924: 13.

Graneledone verrucosa subsp. *media*—Robson, 1932: 309, fig. 70.

Material examined: **Syntype** *Eledone verrucosa* Verrill, 1881, off the coast of southern New England, 39° 50' N, 70° 11' W, 846 m, 1/7/1880, USNM 577583, ♀. **Syntype** *Eledone verrucosa* Verrill, 1881, 41° 33' N, 65° 21' W, 1470 m, 28/6/1880, USNM 729732, ♂.

Holotype *Moschites verrucosa* var. *media* Joubin, 1918, 42° 40' N, 62° 49' W, 1458 m, 26/8/1913, MOM 3437–1913, ♂. **Northwest Atlantic:** 39° 09' N, 72° 11' W, 1271 m, 6/3/1969, USNM 815506, 1♂. 39° 42' N, 71° 11' W, 1645–1737 m, 19/11/1973, USNM 730997, 1♂. 39° 45' N, 71° 07' W, 1645 m, 19/11/1973, USNM 730993, 1♀. 39° 12' N, 71° 51' W, 28/2/1973, USNM 730994, 1♂. 39° 44' N, 70° 29' W, 1830–1912 m, 8/7/1975, USNM 730996, 1♀. 37° 57' N, 72° 34' W, 2904 m, 21/7/1884, USNM 730989, 1♂. 39° 45' N, 70° 43' W, 1885–1967 m, 10/7/1975, USNM 730995, 1 indet. 34° 26' N, 75° 42' W, 363 m, 22/5/1967, USNM 576143, 1♀. 39° 56' N, 70° 48' W, 823–1061 m,

9/7/1975, USNM 1009237, 1♀. 39° 24' N, 72° 06' W, 1170–1353 m, 17/11/1973, USNM 817333, 1♀. 39° 48' N, 71° 19' W, 913–940 m, 5/7/1994, USNM 1009236, 2♀. 39° 55' N, 67° 24' W, 1117–1200 m, 6/12/2000, USNM 1009133, 1♀. 39° 53' N, 70° 35' W, 588–832 m, 3/2/1999, USNM 1009235, 1 indet. **North Atlantic, Mid Atlantic Ridge:** 45° 27' N, 48° 18' W, 1100 m, 12/5/1973, USNM 815509, 1♂. **North Atlantic, Bassin du Cap Vert:** 20° 33' N, 18° 35' W, 2003 m, Stn CP04, 6/2/1991, MNHN 2013, 1♀. **North Atlantic, Porcupine Seabight:** 49° 27.3' N, 13° 21' W, 2045–2110 m, Stn 50518, 7/6/1979, DC-SOC, 2♀. 51° 07' N, 13° 17' W, 1930–1815 m, Stn 50602#3, 2/7/1979, DC-SOC, 2♂. 51° 20' N, 12° 57' W, 1635–1720 m, Stn 50715, 21/10/1979, DC-SOC, 1♂. 50° 57' N, 13° 12' W, 2095–2150 m, Stn 50822, 7/8/1980, DC-SOC, 3♀. 49° 30' N, 13° 19' W, 1794–1785 m, Stn 50517, 7/6/1979, DC-SOC, 1♂. 51° 05' N, 13° 04' W, 1925–1960 m, Stn 50510, 3/6/1979, DC-SOC, 1♂, 1♀. 51° 09' N, 12° 04' W, 1537–1545 m, 25/9/2000, Stn 13919#1a, NMSZ 2002159, 1♀. 49° 58' N, 12° 30' W, 2274–2300 m, 25/4/2001, Stn 13960, DC-SOC, 1♀. 48° 27' N, 10° 28' W, 1500 m, 12/9/1974, USNM 815507, 1♀. **North Atlantic, Rockall Trough:** 1500 m, 7/5/1995, NMSZ 1999158.034, 1♂. 1500 m, 7/5/1995, NMSZ 1999158.035, 1♀. 1500 m, 7/5/1995, NMSZ 1999158.036, 1♀. **North Atlantic, west of Hebrides:** 58° 42' N, 8° 55' W, 1500 m, 9/13/2000, NMSZ 1999158.096, 1♂. **North Atlantic, off Iceland:** 63° 48' N, 27° 00' W, 1110–1095 m, 10/3/1978, ZMUC B5-78-07, 1♀. 65° 22' N, 31° 37' W, 1060 m, 25/2/1981, ZMUC B3-81-6, 1♀. 63° 52' N, 27° 10' W, 1030–1050 m, 10/3/1978, ZMUC B5-78-10, 1♂. 63° 48' N, 27° 00' W, 1110–1095 m, 10/3/1978, ZMUC B5-78-07 1♀. 65° 22' N 32° 37' W. 1060 m, 25/2/1981, SMUC B3-81-6, 1♀. 63° 52' N, 27° 10' W, 1030–1050 m, 10/3/1978, ZMUC B5-78-10 1♂.

Congeneric material examined:

Moschites challengerii Berry, 1916, holotype, 29° 45' S, 178° 11' W, 630 fathoms, 14/7/1874, BMNH 1889.4.24.49, 1♂.

Graneledone antarctica Voss 1976, holotype, 75°06.5'S, 175°05'E, 2341 m, 8/2/1968, USNM (729679), 1♂.

Graneledone macrotyla Voss 1976, holotype, 54°43'S, 55°30'W, 1647–2044 m, 14/03/1966, USNM (729678), 1♀.

Graneledone sp. 23°05'S, 12°41'E, 1193 m, 9/8/1984, ICM-SA179, 1♀.

Diagnosis: Medium-sized octopodid (total length to 500 mm) with mantle broadly ovoid. Arms 2½–3 times as long as body. Uniserial suckers; no enlarged suckers. Ink sac absent. Funnel organ VV-shaped. Third right arm hectocotylized. Hectocotylus medium sized. Ligula small, simple without transverse ridges. Calamus of moderate length. Gills small with 6–8 lamellae on each demibranch. Radula with variable rachidian. Dorsal body surface covered in complex papillose warts. Warts consist of approximately 4–10 cone-shaped tubercles, 22–26 clusters across dorsal mantle, 12–16 clusters in transverse line between orbits. Multiple warts surround the eye, with 2–3 particularly large supra-ocular warts.

Description: Medium-sized octopodids with thick, firm broad mantle (Fig. 1A, B). Mantle width approximately equal to mantle length. Mantle of immature animals slightly longer than wide. Head wide, slightly narrower than mantle. Eyes medium to large and moderately prominent. Pallial aperture moderately narrow (occupying 30% of mantle circumference). Funnel moderately long and gently tapering with free portion approximately 50% funnel length. Funnel organ VV-shaped, but variable in shape (Fig. 2) with two common forms. Lateral and medial limbs of funnel organ symmetrical in both funnel organ forms. Web moderately deep, extending between ¼–½ of the length of the arms. Web bilaterally symmetrical with formula

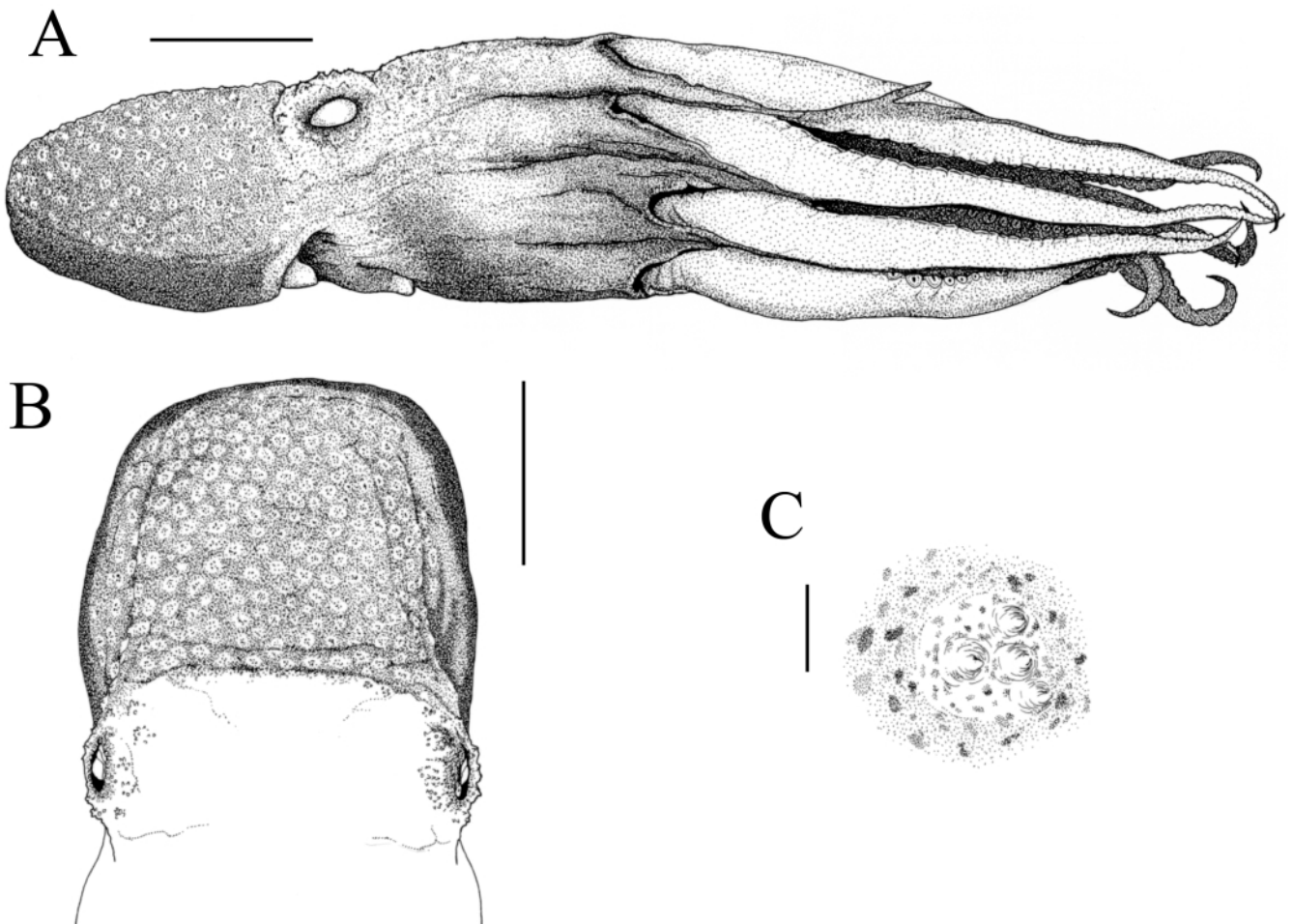


Figure 1. *Graneledone verrucosa*. **A.** Lateral view of female (NMSZ 2002159). **B.** Detail of the dorsal view of the head. **C.** Detail of one of the warts. Scale bars: **A, B** = 50 mm; **C** = 5 mm.

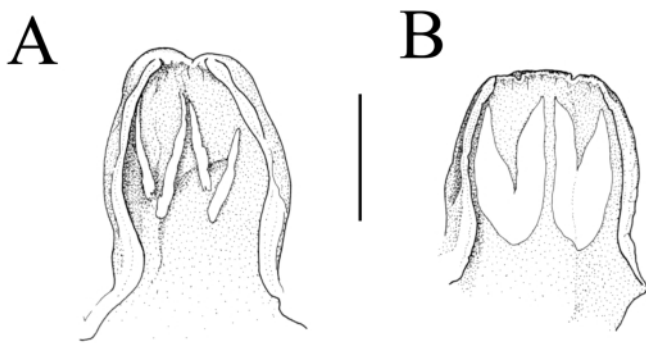


Figure 2. *Graneledone verrucosa*. Variation in funnel organ after fixation; **A.** USNM 1009237. **B.** USNM 815506. Scale bar = 15 mm.

highly variable. Arms medium length, stout and muscular, gently tapering (Fig. 3A). Dorsal arms typically slightly longer than ventral arms ($1 = 2 > 3 > 4$), although showing some variation. Suckers uniserial and small; no enlarged suckers. Arm sucker counts increase linearly with mantle length (Fig. 4). Right third arm hectocotylized and shorter than opposite arm, showing little variability. Hectocotylized arm sucker count ranging from 40 to 46, with some apparent regional variation (see Fig. 5). Ligula small, simple, without transverse ridges. Calamus moderately

large (Fig. 3B). Gills medium length with 6–8 lamellae per demi-branch (typical configuration of 7/7). Ink sac absent.

Digestive tract (Fig. 6): buccal mass large, anterior salivary glands small. Posterior salivary glands small. Crop without diverticulum. Anal flaps absent. Beaks of normal octopodid form. Radula with rachidian, two laterals, one marginal tooth and one marginal plate. Rachidian variable from classic octopod unicuspid form (Fig. 7B) to unicuspid ‘wishbone’ form (Fig. 7C). Small lateral cusps may be present if the rachidian is classically shaped, but the presence of these may vary along length of radula. Extremes of form have not been seen on the same radula. First lateral tooth small, second lateral tooth larger, curving medially, marginal tooth similar in size to second lateral but with a tendency to be worn.

Male reproductive tract with no special features (Fig. 8A). Spermatophores long, slender, few in number (approximately five). Female reproductive tract with no special features (Fig. 8B). Mature ovary packed with up to 80 oocytes (maximum length 17 mm).

Dorsal surface of mantle, head, web and basal part of arms covered by complex papillose warts, consisting of a raised mound bearing approximately 4–10 papillae. Animal has a purple hue, which is deeper on ventral surface, paler on head and oral surface. Deep purple rims occur around the eyes and suckers (Fig. 1).

Distribution: In deep water throughout the North Atlantic. The species extends across the North Atlantic from 9° to 75° W

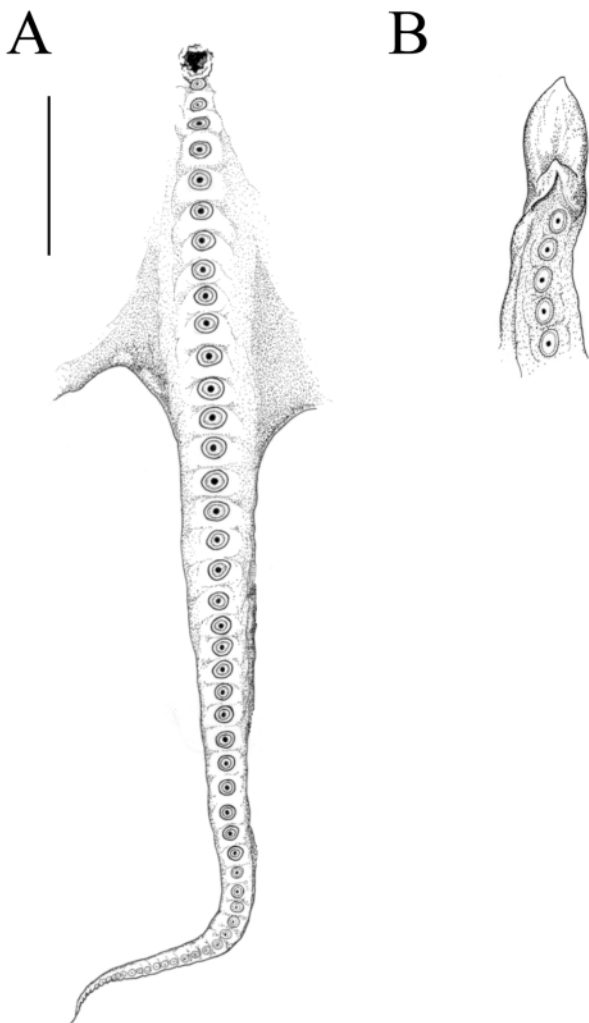


Figure 3. *Graneledone verrucosa*. **A.** Dorsal arm of female (NMSZ 2002159). **B.** Hectocotylus of male (NMSZ 1999158.096). Scale bars **A** = 10 mm; **B** = 10 mm.

occurring most commonly in water depths between 1000 and 2000 m, including on the Mid-Atlantic Ridge. The latitudinal range of *G. verrucosa* appears to be greatest in the eastern Atlantic where it extends from 20° to 65° N.

DISCUSSION

Verrill (1881) described *Eledone verrucosa* from two specimens captured off the eastern coast of the United States during a cruise of the *RV Blake* led by Alexander Agassiz in 1880. The specimens comprised a female taken in 466 fathoms (846 m) and a male taken in 810 fathoms (1470 m), both of which were designated syntypes. An additional male was captured by the *Fish Hawk* in 1882 off Nantucket in 787 fathoms (1429 m) and four further specimens (one male, three females) were taken in 1050–1255 fathoms (1906–2278 m) in the NW Atlantic (30–42° N, 69–72° W) by the *Albatross* in 1883 (Verrill, 1884).

A similar-looking specimen was brought up by *Challenger* near the Kermadec Islands (29° 45'S, 178° 11'W) in the Pacific Ocean. Hoyle (1886) identified this specimen as *Moschites* [a name rejected by the ICZN (1954) *verrucosa*, but Berry (1916) subsequently erected a new species, *Moschites challengerii* to accommodate this specimen.

In 1913 the *Prince de Monaco*, while trawling off the east coast of the United States, captured another specimen from near to the type locality of *E. verrucosa*. Joubin (1918a) felt that the papillae of this specimen resembled those of the syntypes of *Eledone verrucosa* Verrill, but that the hectocotylus resembled instead that of the holotype of *Moschites challengerii* Berry, although he did not personally examine Verrill's holotype, but relied on a photograph provided by S. Berry. Joubin (1918a) admitted that 'et d'autre part il est possible que l'étude de l'hectocotyle de *M. verrucosa* dont M. Berry a donné le photographie soit insuffisant' [on the other hand, it is possible that the hectocotylus study of *M. verrucosa*, for which Mr Berry produced the photography, is inadequate]. He added that the hectocotylus of Verrill's holotype was contracted and may have been modified by its long period in alcohol. Nonetheless, he erected a new subspecies *Moschites verrucosa* var. *media* to accommodate his specimen. Robson (1932) commented on Joubin's (1918b)

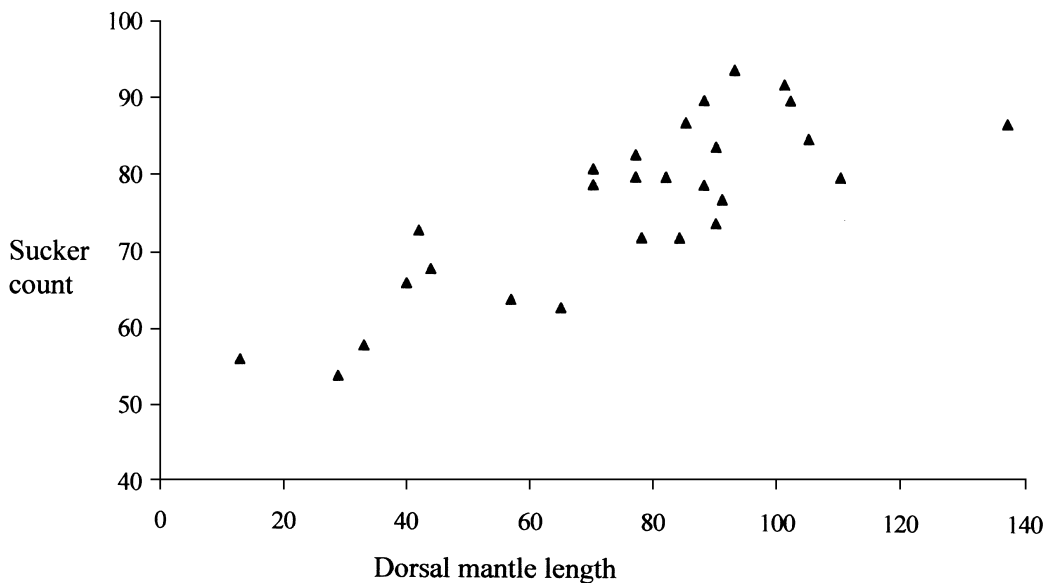


Figure 4. Relationship between sucker count (arm 1) and mantle length in *Graneledone verrucosa*.

treatment of *media* as a distinct species, but added little to the argument as, like Joubin, he did not personally examine the holotype of *Eledone verrucosa* Verrill. Re-examination of both specimens during the present study show both hectocotyli to be very similar (although in poor condition because of their long period of preservation) and the basis for dividing *Graneledone verrucosa* into two subspecies is therefore invalid.

Although most of the early conjecture surrounded specimens from the western Atlantic, the first specimen of *G. verrucosa* recorded from the eastern Atlantic was captured off the Faroe Islands in 1892. It was deposited in the Zoological Museum of Copenhagen and found in the collections by Nielsen (1930), however, it does not appear still to be extant. Grieg (1933), reporting on the catch of the Danish research vessel *Thor*, recorded a female *Graneledone verrucosa* taken off Iceland, originally reported in 2150 m [Thomsen (1931) *vide* Bruun (1945)]

but, again, this specimen (ZMUC 20-11-1903) appears to be lost. Grieg also cited several specimens taken in shallow water (20–200 m) off Bergen, Norway, but subsequent re-examination of these specimens (held by the UMB) as part of this study revealed these to be *Eledone cirrhosa*. Indeed, Kjennerud (1962) suggests that *G. verrucosa* should be excluded from the Norwegian fauna. A search of the collections held by ZMUC, however, revealed that *Graneledone verrucosa* is, in fact, common in latitudes up to 65° N, although few of these records have been previously published. Additional material provided from fishing expeditions off the Porcupine Seabight shows that this species is relatively common in the eastern Atlantic at latitudes just south of 50° N. Only one record could be found further south, although this was from 20° N, suggesting that the species extends some distance; lack of fishing activity in certain areas may account for its absence from the records.

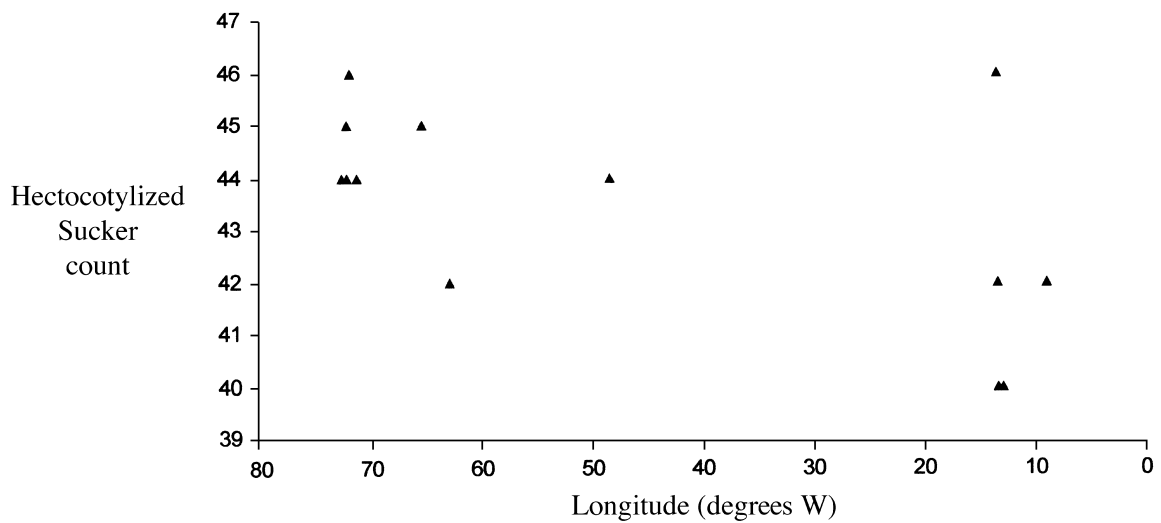


Figure 5. Regional variation of hectocotylized arm sucker count.

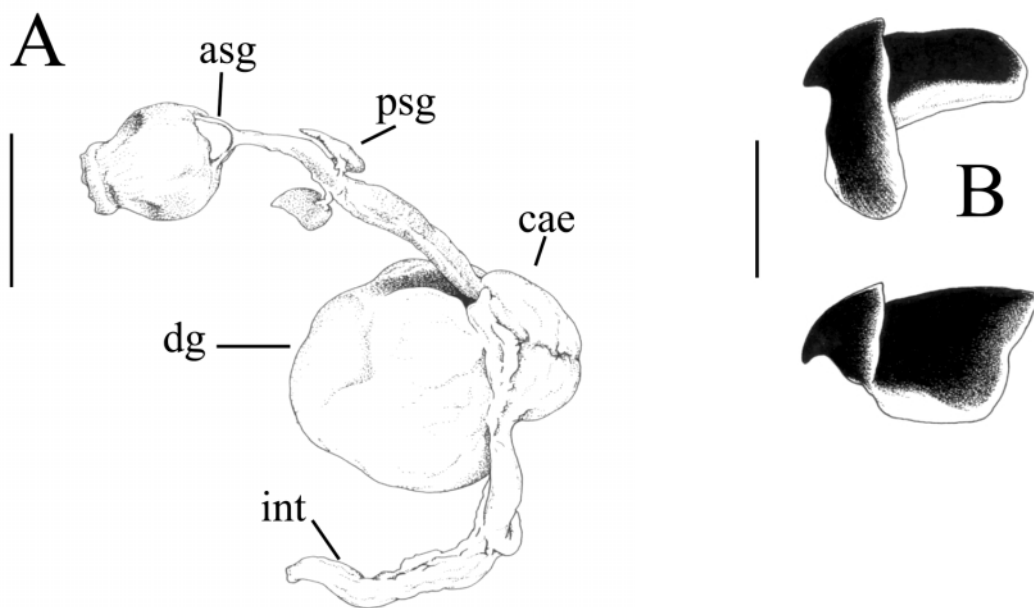


Figure 6. *Graneledone verrucosa*. Digestive tract (NMSZ 1999158.286). **A.** Digestive system. **B.** Lower and upper beaks. Abbreviations: asg, anterior salivary gland; cae, caecum; dg, digestive gland; int, intestine; psg, posterior salivary gland. Scale bars **A** = 30 mm; **B** = 20 mm.

REDESCRIPTION OF *GRANELEDONE VERRUCOSA*

Specimens attributed to *Graneledone verrucosa* from the South Atlantic held by the South Africa Museum, Cape Town (SAM 2734, SAM 2735, SAM S807 and SAM S3569) were determined not to be this species during a taxonomic workshop in 1997, on the basis of wart configuration (S. O’Shea, personal communication). A specimen (ICM SA179) attributed to *Graneledone* sp. by Villanueva & Sanchez (1993) from 23° 05’ S, 12° 41’ E and examined during this study is also not attributable to *G. verrucosa*. It therefore appears that the distribution of *G. verrucosa* is restricted to the North Atlantic.

Graneledone verrucosa does show some variation over this wide distribution as illustrated by the variation in hectocotylized arm sucker count (Fig. 5). Additional variation was seen in the morphology of the funnel organ (which may be due to preservation artefacts; Fig. 2), in the number of gill lamellae and in the distribution of papillae. However, there was neither pattern to this variation nor any apparent linkage between the characters. We believe that only a single species of *Graneledone* occurs in the North Atlantic.

The genus *Graneledone* was proposed by Joubin (1918b) to accommodate the deep-water species *Moschites verrucosa*, *M. media* (raised without comment to specific status) and *M. challengeri*, together with the Antarctic species *M. charcoti* (Joubin, 1905) and *M. turqueti* (Joubin, 1905) (now *Pareledone*). Joubin’s diagnosis of the new genus was limited to ‘les espèces benthiques et polaires à peau grenue et à gros hectocotyle d’*Octopus*’ [benthic and polar species with granular skin and large hectocotylus like that of *Octopus*] adding that ‘nous ne connaissons pas l’anatomie’ [we do not know the anatomy]. This diagnosis was slightly expanded by Robson (1932) who removed *Pareledone charcoti* and *P. turqueti* from the genus *Graneledone*. The diagnosis has been amended many times and that given here is unlikely to be contentious, save for the statement that the radula may be homodont or heterodont. Several authors have stated the generic diagnosis of the radula to be homodont (e.g. O’Shea, 1999; Kommritz, 2000), yet many species have a tricuspid rachidian (e.g. *G. taniwha*, *G. yamana*, *G. macrotyla*), although *G. antarctica*

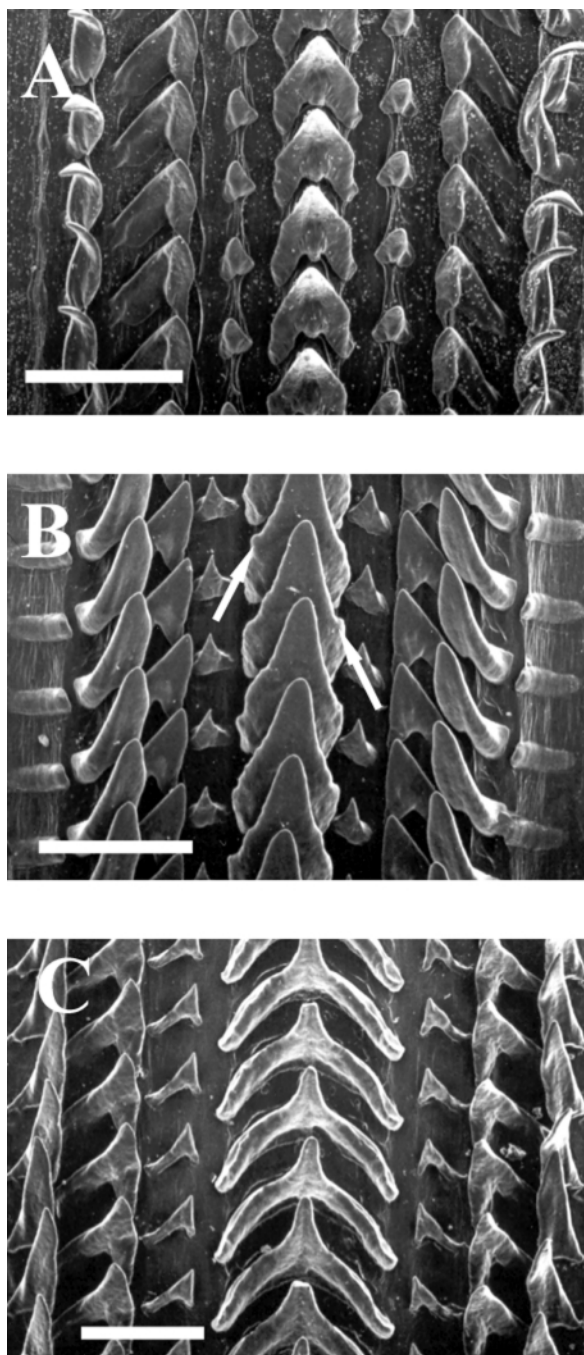


Figure 7. *Graneledone verrucosa*. Variation in radula. All photos from unworn section of radula. **A.** DC-SOC, Stn 50510, 51° 05’ N, 13° 04’ W, 1925–1960 m, 3/6/1975. **B.** DC-SO C, Stn 50602, 51° 07’ N, 13° 17’ W, 1930–1815 m, 2/7/1979. **C.** Commercial catch from West of Lewis (Hebrides), 1996. Rachidian cusps indicated by arrows. Scale bars = 0.5 mm.

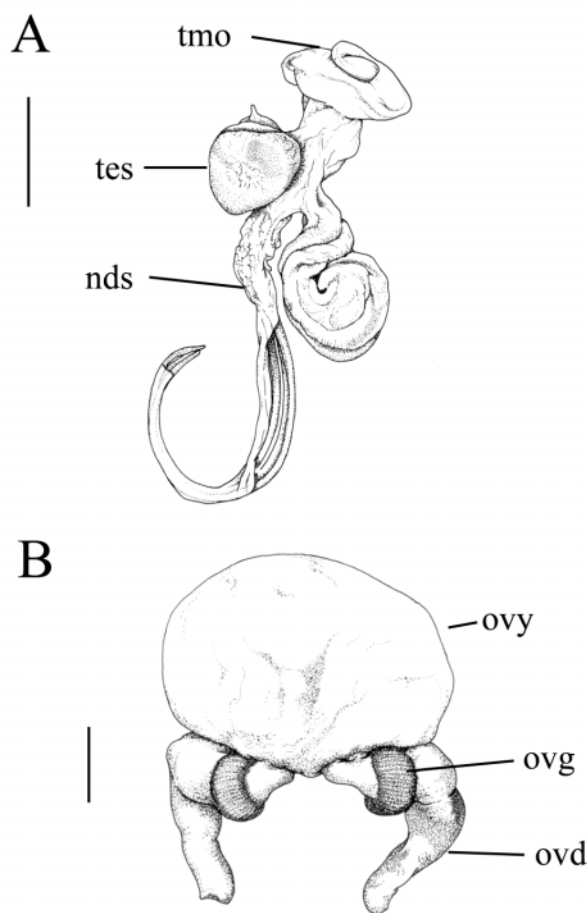


Figure 8. *Graneledone verrucosa*. Reproductive systems. **A.** Male (NMSZ 1999158.096). **B.** Female (NMSZ 2002159). Abbreviations: nds, Needhams sac; ovd, oviduct; ovg, oviducal gland; ovy, ovary; tes, testes; tmo, terminal organ. Scale bars = 15 mm.

has an apparently homodont radula (Voss, 1976). In *G. pacifica* the rachidian may range from multicuspid (with up to eight cusps) to simple (Voss & Percy, 1990). The comment by Robson (1932) 'I think it is actually unicuspid' (which refers to the rachidian of the radula of *G. challengerii*) illustrates the problems associated with examining radulae with the light microscope. In *G. verrucosa* the radula is highly variable and may be homodont or heterodont (Fig. 8), with variation on different portions of the same radula. The cusps (when present) may not be well marked, which illustrates the importance of using electron microscopy to examine this character.

Graneledone verrucosa can be distinguished from many other *Graneledone* species by the wart configuration. O'Shea (1999) lists figures for the number of wart clusters across the dorsal mantle in *G. antarctica* (34–36) and *G. challengerii* (34–39). The figure for *G. verrucosa* is only 22–26. The wart configuration of *G. boreopacifica* and *G. verrucosa* is similar, but these species can, nevertheless, be separated on the basis of hectocotylized sucker count (36–38 in the former and 40–46 in the latter). *G. verrucosa* can be distinguished from *G. yamana* by the presence of two large supraocular cirri in this species (Kommritz, 2000) and from *G. macrotyla* because of the unusual structure of the warts in the latter species (Voss, 1976). Differences in wart structure on the dorsal mantle, web and arms in *G. gonzalezi* and *G. verrucosa* can similarly be used to distinguish between these two species (Guerra *et al.*, 2000).

ACKNOWLEDGEMENTS

Mike Sweeney provided the information on the ICZN ruling on *Moschites* and assisted with access to specimens. Fred Naggs, Ole Tendal, Philippe Bouchet, Sankurie Pye, Conchita Allue, Roger Villanueva and Andre Willasen facilitated specimen loans. Steve O'Shea provided the information on the specimens held by the South African Museum. Ian Rendall drew the figures under a Linnean Society (NERC Fund for Taxonomic Illustration) grant to MAC. Lyndsay Brown assisted with specimen measurement. Alex Ball provided access to SEM facilities at the BMNH under a Sharing Museum Skills Millennium Award to ALA. ALA completed much of this work while employed by the National Museums of Scotland.

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REDESCRIPTION OF *GRANELEDONE VERRUCOSA*

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