Graneledone gonzalezi sp. nov. (Mollusca: Cephalopoda): a new octopod from the Îles Kerguelen

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Abstract: A new octopod species, *Graneledone gonzalezi* sp. nov., is described from 19 specimens collected off the northern Îles Kerguelen. This is a bathyal octopus which is characterized by: the absence of supra-ocular papillae, short arms, a long ligula without copulatory ridges, a narrow head, six filaments per outer demibranch and radula exhibiting no archaic traits, medium size oocytes and a low number of very long spermatophores. *Graneledone gonzalezi* is compared with its other congeneric species and found most closely resemble *G. antarctica*. The geographic and bathymetric distribution of *G. gonzalezi* is also discussed.

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Introduction

The subfamily Graneledoninae was erected by Voss (1988a) and comprises the genera *Graneledone*, *Thaumeledone* and *Bentheledone*. Its diagnostic characters are summarized in Voss & Pearcy (1990).

Graneledone species live in lower bathyal and abyssal ecosystems of the northern Atlantic, northern and tropical eastern Pacific and Southern Ocean (Roper et al. 1985, Nesis 1987). Robson (1932) identified a number of diagnostic features of the genus which include a radula that exhibits archaic traits, the animal lacks an ink sac, the gills are very small, the hectocotylus is small but clearly differentiated into ligula and calamus and the terminal organ has a large and saccular diverticule. Two diagnostic characters for this genus were added by Palacio (1978): funnel VV and body covered by tubercules or papillae. A historical summary of the genus was given by Kubodera & Okutani (1994). Graneledone is composed of seven nominal species: G. verrucosa (Verrill, 1881) from the north-western Atlantic, G. challengeri (Berry, 1916) off Kermadec Islands, G. setebos Robson, 1932 from McMurdo Sound, G. antarctica Voss, 1976 from Ross Sea, G. macrotyla Voss, 1976 from Scotia Sea, G. boreopacifica Nesis, 1982 from Okhotsk Sea, and G. pacifica Voss & Pearcy, 1990 off Oregon. Furthermore, there are several unidentified species from the tropical eastern Pacific (Nesis 1987), the Gulf of Panama (sp. B, Voss 1988b), and the Southern Ocean (Kubodera & Okutani 1994).

Graneledone species show a somewhat bipolar distribution (Voss 1988b) which include species from the colder deep north Atlantic and north subarctic Pacific (G. verrucosa, G. boreopacifica and G. pacifica), and three others from deep waters of the Southern Ocean and south Pacific off New Zealand (G. antarctica, G. macrotyla and G. challengeri).

Recently, Voight (1998) studied 46 fresh specimens from the north-eastern Pacific Ocean at depths ranging from 1100 to 2450 m. This author indicated that the specimens from abyssal depths, referred to *G. pacifica*, can be distinguished from those at bathyal depths by subtle differences in the number of suckers on each arm, the number of gill lamellae and the number of papillae on the dorsal mantle. These differences may reflect ecophenotypic variation or, more probably, may signify the existence of a cryptic species isolated by depth. Isolation by depth and isolation by distance are considered as two important factors in taxonomic differentiation (Margalef 1974).

Bottom trawling around the Îles Kerguelen provided some interesting specimens of *Graneledone* that we studied in order to clarify their taxonomic status.

Material and methods

A total of 18 specimens of Graneledone was collected as by catch of the trawling fishery for Patagonian toothfish (Dissostichus eleginoides) off Îles Kerguelen aboard trawler Kerguelen de Tremarec. The specimens were taken from the upper continental slope (510-540 m) between 47°13'-47°18'S and 69°09'-69°16'E (Fig. 1) during February 1994. Samples were deep-frozen (-20°C) on board and were then fixed in 4% formalin for 24 hours and preserved in 70% alcohol. A further specimen was found in the stomach of a Dissostichus eleginoides collected from the same fishing ground. Data were collected on sex and maturity stage by reference to Guerra (1975). Definition of counts, measurements, and indices followed Roper & Voss (1983) except for beak measurements which followed Clarke (1986). Two new indices were defined and applied: (GiLI) Gill Length Index. length from the proximal filament to tip as a percentage of mantle length (ML) and Posterior Salivary Gland Index (PSGI), maximum length of the posterior right salivary gland as



Fig. 1. Location of trawl collection area, Kerguelen Plateau.

percentage of ML.

Measurements and indices are indicated in the text by mean and standard deviation or by the lowest or the highest values by sex. Maximum, mode and minimum number of suckers are given by sex.

The additional congeneric material was studied at the Natural History Museum (London) and the National Museum of Natural History (Washington, DC).

Taxonomic position

Family Octopodidae d'Orbigny, 1840 Subfamily Graneledoninae Voss, 1988 Genus *Graneledone* Joubin, 1918 Graneledone gonzalezi Guerra, González and Cherel, sp. nov.

Diagnosis: Medium size octopod (TL 335 mm, TW 344 g). Ink sac absent. Arm suckers in one row. Enlarged suckers absent. Dorsal surface of mantle, head, web and basal part of the arms beset by papillae. The papillae consist of a raised mound bearing from one to twelve cone shaped tubercules. Three or four papillae situated dorsally on each eye are greatly enlarged which do not constitute supra-ocular papillae. Head narrower than the mantle width (HWI = 60.4 ± 11.3). Arm Formula 2.1.4.3. Arms 1.6–2.7 times longer than the mantle length (ALI = 218 ± 47 in males and 211 ± 47 in females). Arm suckers counts on intact normal arms of immature and mature individuals ranged from 29 to 72 (mode = 35) in males and from 31 to 67 (mode = 40) in females. Third right arm hectocotylized (HcAI = 158-215). Number of suckers in hectocotylized arm ranged from 32 to 40. Ligula length represents 6% of the hectocotylized arm length. Calamus length $47.4 \pm 6\%$ of ligula length. Transverse copulatory lamellae on the ligula absent. Web formula variable, typically ACBDE or ACBED. Six filaments per outer demibranch. Radula with seven teeth and two marginal plates in each transverse row; first and second lateral teeth large and unicuspid with a narrow base. Medium size oocytes (EgLI = 12.5). Few number of very long spermatophores (SpLI = 119).

Etymology: Gonzalezi is the patronymic of González. The species is dedicated to the memory of the father of Angel F. González who died during this study.

Type species: Graneledone gonzalezi sp. nov. Guerra, González and Cherel, 2000

Type locality: off Îles Kerguelen, Southern Ocean, 47°15'S-69°14'E, 504 m.

Type specimens: Holotype: Male (mature), 84 mm ML, Museum National d'Histoire Naturelle, Paris, MNHN 3470, collected at 47°15'S–69°14'E, 504 m depth, bottom trawler Kerguelen de Tremarec, in February 1994, dissected specimen. Paratypes: Two mature females 77 and 80 mm ML, MNHN 3471 and 3472, collected at 47°13'S–69°15'E, from 504 m depth, bottom trawler Kerguelen de Tremarec, February 1994, fixed in formalin and preserved in 70% ethanol. Dissected specimens.

Additional material: Three immature females, 22, 40 and 48 mm ML, MNHN 3473, 3474 and 3475, collected at 47°13'S-69°15'E, from 504 m depth on 20 February 1994. Maturing male, 72 mm ML, MNHN 3476, collected at 47°14'S-69°18'E, from 540 m depth on 21 February 1994. Six immature females (24-54 mm ML) MNHN 3477-3482 and an immature male (25 mm ML), MNHN 3483, collected at 47°18'S-69°11'E, from 533 m depth on 23 February 1994. One immature female (28 mm ML), MNHN 3484, collected at 47°18'S-69°09'E, from 510 m depth on 23 February 1994. Two immature females, (23 and 29 mm ML), MNHN 3485-3486 and one immature male (24 mm ML), MNHN 3487, 47°13'S-69°16'E, from 511 m depth on 25 February 1994. Immature female (22 mm ML), MNHN 3488, collected at 47°18'S-69°10'E, from 525 m depth on 28 February 1994. These 16 specimens were collected by Yves Cherel aboard the bottom trawler Kerguelen de Tremarec.

Congeneric material examined: - Graneledone antarctica holotype (USNM 729679) and paratypes (USNM 729680, one male and three females; all paratypes with same data as holotype) from the National Museum of Natural History (NMNH), Washington DC, USA, which were preserved in 1968, and are still in good condition. The following counts which were not given by Voss (1976), were obtained from the holotype: ASCR1 = 62; ASCR2 = 61; ASCR3 = 40; ASCR4 = 49. The following measurements (in mm) and counts were undertaken from the male paratype: ASCR1 = 59; ASCR2 = 61; ASCR3 = 40; ASCR4 = 51. Maximum length of posterior salivary gland was 5.4 mm.

- Graneledone macrotyla holotype at the NMNH (USNM

Table 1. Measurements, counts and indices (abbreviations according to Roper & Voss 1983, Clarke 1986 and present paper) of 19 specimens of Graneledone gonzalezi.

Specimen	3470	3471	3472	3473	3474	3475	3476*	3477	3478	3479	3480	3481	3482	3483	3484	3485	3486	3487	3488
ML (mm)	84	77	80	22	40	48	72	24	37	30	28	33	54	25	28	23	29	24	22
TW (g)	334	344	326	6.8	18.1	34.1	148.3	4.7	18.6	17.6	18.9	22.5	35.2	9.3	11.1	5.8	21.1	3.9	6.5
SEX	M	F	F	F	F	F	M	F	F	F	F	F	F	M	F	F	F	M	F
MS	IV-V	IV-V	III-IV	I-II	I-II	I-II	III-IV	I	I-II	I-II	I	I-II	II	I	I-II	I	I	I	I-II
TL	335	291	310	88	118.9	146.9	312	75	120	111	137	110.1	183	89.2	97	76	99.2	72	93.5
MWI	104	103.9	99.4	63.6	64.3	70.9	79.7	54.9	60	88.1	102.1	60.4	54.2	63.3	67.9	59.1	90.3	52.1	66.8
HWI	72.9	83.2	78.5	62.8	50	48.7	48	52.7	51.3	73.2	63.6	46.5	47	59.7	67.9	65.3	67.1	52.1	56.3
EDI	18.1	17.4	18	27.7	46.5	22	17.7	18.1	22.7	24.1	28.6	39.8	17.4	19.9	26.8	20.4	28.7	25.8	19.1
ALI:																			
Ll	240.5		210.3	231.8	162.7	192.1	256.9	192.0	178.4	237.3	325.0	211.8	188.9	179.2	235.7	183.5	221.4	175.0	222.7
L2	256.0		275.3		173.0	207.6	316.6		191.9	210.2				178.8	232.1		225.6	200.0	228.2
L3	209.5		244.1		151.2	191.5		192.0	167.6	254.2	343.9	203.6	187.0	176	253.6		193.7		203.2
L4	192.9	257.1	225.3		159.5	176.2	245.8		159.9	233.9	260.7	194.5	177.8	172.1	221.4		180.6	162.5	190.1
R1	276.2		241.6	218.2	150.5	193.2		211.0	178.3	257.6	357.1	187.6	205.6	182.4		182.6	202.7		215.5
R2	285.7	274.0	255.3		176.2		306.9		210.8	267.8			222.2	186.4	203.6		223.5	191.7	228.2
R3	181.0		215.3		147.0		215.2	170.9	151.3	213.6	350.0	202.7	161.1	162.1	210.7	178.6	214.5	175.0	188.6
R4	204.8	254.5	219.0		155.8	180.9	251.4	194.1	154.0	216.9	284.6	188.2	177.8	158.6	217.0		203.1	158.3	196.3
AF	2:1:3:4		2:1:3:4		2:4:1:3				2:1:4:3	2:1:4:3			2:1:4:3	2:1:3:4	3:1:2:4		2:3:4:1		2:1:4:3
ASC:																			
Ll	65		53	38	48	40		41	43	39			46	36	41		48		45
L2	62		66		51	44			47	38				38	38		51		46
L3	40		58		40	38			42	41			45	35	37		48		39
L4	52	58	60		41	37			44	39			41	35	35		40		42
R1	65		43	47	40	45		43	45	43			37	35			40		42
R2	67	67	56		43		72		48				47	36	34		42		45
R3	37		45		34		40	33	35	36		38	31	32	38		42		40
R4	42	63	49		38	39		39	40	39		43	40	29	39		37	31	41
SDI	6.6	6.7	4.5	7.3	4.8	4.7	6.9	5.1	4.0	7.1	8.2	6.9	4.3	4.8	7.1	4.8	6.2	5.4	6.8
LiLI	6.3						6.1												
CaLI	43.1						51.6												
WDI:																			
Α	54.2	54.9	55.1	64.5	35	44.1	43.3		41.0	38	68.9	38.6	32.8	64.1	35.7	72.0	45.3	22.9	50.9
В	68.3	73.1	66.3	50.9	31.8	47.2	39.9	44.3	35.6	56.3	64.3	39.9	26.9	58.9	48.2	12.5	45.6	33.3	35.0
C	64.6	62.7	67.6	31.8	43.3	45.1	39.2	42.2	34.3	58.6	87.5	41.7	38.9	48.6	48.2	53.8	43.2	25.0	30.0
D	92.8	56.5	60.1	43.6	55.7	40.6	35.7	32.9	39.2	50.8	73.6	38.9	43.1	43.4	25.0	40.0	48.1	19.6	27.3
E	80.5	52.2		54.5	51.3	39.2	42.2	29.5	30.8	69.5	78.6	47.4	30.6	36.6	32.1	39.5	29.7	25.0	44.1
PAI	52.3	57.7	53.3	35.0	43.0	43.2	45.3	44.3	48.6	74.6	64.3	33.5	40.7	48.2	23.2	38.6	42.2		36.8
GiLI	19.0	24.5		30.9		27.5	23.7		24.8				27.8			28.8		19.6	
FuLI	36.5	40.5	26.0	37.3	28.2	48.8	44.7	40.1	31.3	27.1	32.1	36.2	27.2	37	35.7	37.3	39.4		36.4
FFul	24.4	25.7	19.I	20.0	21.2	22.7	32.6	12.7	17.3	20.3	21.4	18.1	16.7	25.1	26.8	22.2	14.9		19.0
LHIL	6.5	6.5	5.9	1.9	2.3	3.1	5.6	1.6	2.4	2.6	2.3	2.9	3.1	1.9	1.9	1.8	2.6	2.0	1.7
LCL	14.0	14.4	14.0	4.0	5.1	6.5	10.3	3.5	5.8	5.8	5.8	6.7	6.9	4.1	4.9	4.0	6.6	4.1	3.9
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^{*} found in the stomach of Dissostichus eleginoides

729678). In good condition.

- Graneledone pacifica holotype at the NMNH (USNM 730716). In good condition.
- Graneledone setebos holotype at the British Museum of Natural History, London (NHM 1919.12.30.27). In bad condition.
- Graneledone challengeri holotype at the British Museum of Natural History, London (NHM 1889.4.2449). In bad condition.

Description

Based on one mature and three immature males, and two mature and thirteen immature females. Measurements, counts and indices are given in Table I.

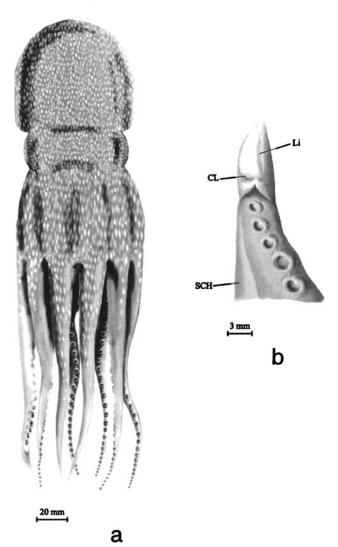


Fig. 2. Graneledone gonzalezi Guerra, González and Cherel sp. nov. a. Dorsal view of the holotype, MNHN 3470; mature male, 84 mm ML, b. Copulatory organ of the same specimen. Abbreviations: CL = calamus; Li = ligula, SCH = spermatophoric channel.

Animals medium size (TL to 335 mm; TW to 344 g); mantle short (22-84 mm ML), thick, firm and muscular and broadly ovoid (Figs 2a & 3a). Mantle of immature animals longer than wide (MWI 52-90) whereas in mature animals the mantle is as long as it is wide (MWI 99-104). Head narrower than mantle (HWI 60.4±11.3). Neck distinct and slightly narrower than head. Eyes medium to large (EDI 24.1 ± 7.9) and moderately prominent. Pallial aperture (Fig. 3b) wide (PAI 45.8 ± 11.9). Funnel stout and muscular, moderately long (FuLI 35.7 \pm 6.2) with free portion approximately 59% funnel length (FFuLI 21.1 \pm 4.7). Funnel organ not visible. Web deep (WDI 45-48) symmetric and sector of each side unequal; sector A always deeper, sector E or D always shallower and formula typically A C B D E or A C B E D. Arms short (ALI 200-225), stout and muscular tapering to finely attenuated tip and formula typically 2.1.4.3. Suckers uniserial and small (SDI 5.9 ± 1.3). Enlarged suckers absent. Arm suckers counts on intact normal arms of immature and mature individuals

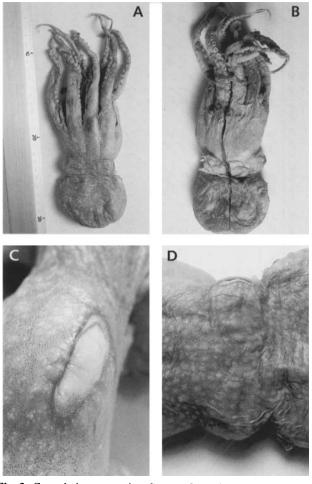


Fig. 3. Graneledone gonzalezi Guerra, González and Cherel sp. nov. a. Dorsal view of the paratype, MNHN 3471 (scale in cm), mature female, 77 mm ML, b. ventral view of the same specimen, c. Detail of the left eye, d. Detail of the papillae between the eyes.

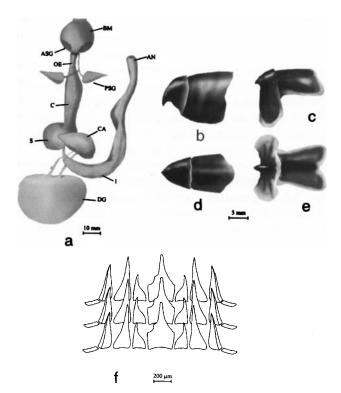


Fig 4. a. Digestive tract of the holotype, b. & d. Upper beak, c. & e. Lower beak, f. Radula. Terminology: AN = anus, ASG = anterior salivary gland, BM = buccal mass, C = crop, CA = caecum, DG = digestive gland, I = intestine, OE = oesophagous, PSG = posterior salivary gland, S = stomach.

a

ranged from 29 to 72 (mode = 35) in males and from 67 to 31 (mode = 40) in females. Right arm 3 hectocotylized (HcAI 158–215) shorter than opposite (OAI 87–90). Number of suckers in hectocotylized arm ranged from 32 and 40. Conspicuous spermatophore groove, narrow and without transverse ridges. Copulatory organ (Fig. 2b) long (LiLI 6.2 \pm 0.1), ligula conical without transverse laminae. Calamus large (CaLI 47.4 \pm 6). Gills large (GiLI 25.2 \pm 4), leaflets thick and fleshy with six lamellae per outer demibranch.

Digestive tract illustrated in Fig. 4a. Bucal mass voluminous. Anterior salivary glands large. Beaks and radula illustrated in Figs. 3b-f. Radula with seven teeth and two marginal plates in each transverse row. Rachidian tooth with one lateral cusp in one side of a long medial cone. There is no seriation in the lateral cusp. First lateral tooth small and sharp. Second lateral tooth sharp, taller than the first one and slightly curved at its base. Third lateral one tall and sharp. Marginal plates exist on each side of each transverse row. Posterior salivary glands relatively well developed and its maximum length varied from 2.5 and 10.7 mm (PSGI = 10.5 ± 1.6). Crop wide and long without diverticulum. Stomach bipartite, one part thickwalled and muscular, the other one thin-walled. Caecum striate coiled in single whorl. Digestive gland round-shaped. Intestine stout lacking of anal flaps. Ink sac absent. Stomach contents composed of remains of tissue, bristles and mandibles of polychaeta and some other hard structures of small crustaceans.

Male reproductive tract shown in Fig 5a. Vas deferens short and ampulla absent. Spermatophoric gland long and convolute.

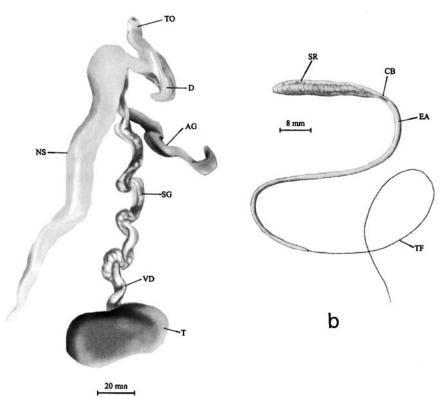


Fig. 5. a. Male reproductive system of the holotype, b. Spermatophore.

Terminology: AG = accessory gland,
CB = cimentary body, D = diverticullum,
EA = ejaculatory apparatus,
NS = Needham sac, SG = spermatophoric gland, SR = sperm reservoir, T = testis,
TF = terminal filament, TO = terminal organ, VD = vas deferens.

Accessory gland large and spermatophore storage sac (Needham's sac) very long. Spermatophores (Fig. 5b) long (SpLI = 119), produced in low numbers (5 in Needham's sac ofholotype), the terminal filament representing the 65% of the spermatophore length. Terminal organ long with large diverticulum.

Reproductive tract of mature female illustrated in Fig. 6a. Mature ovary large round packed with 70–80 striated oocytes (maximum size = 10 x 3.5 mm; EgLI = 12.5). Widest part of the oocyte at the posterior end (Fig. 6b). Proximal oviducts considerably shorter and narrower than distal oviducts which are large, swollen, lacking eggs and terminate in small pores nearly at the level of anus. Oviducal glands oval-shaped and grey.

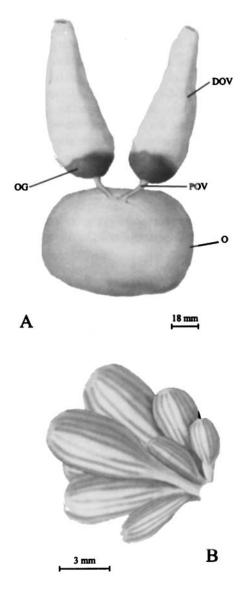


Fig. 6. a. Female reproductive tract of the paratype, female, 80 mm ML, b. Oocytes of the same specimen.

Terminology: DOV = dorsal oviduct, O = ovary, OG = oviducal gland, POV = proximal oviduct.

The surface of the animal is covered by a very tough, thin skin which is covered dorsally on the mantle head, web and basal part of the arms by numerous evenly spaced close set papillae (Figs 2a & 3a). There are twelve papillae of 3.3 mm on horizontal line between the eyes (Fig. 3d). The papillae consist of a raised mound bearing from one to a dozen cone shaped tubercules yellowish in colour. The papillae are regularly distributed and they are especially dense in the dorsal surface of the mantle, head, web and basal parts of the arms. Three or four papillae situated dorsally on each eye are greatly enlarged but do not constitute supra-ocular papillae (Fig. 3c). The papillae decrease in number towards the arm tips and the ventral surface of the mantle. The ventral surface of the mantle, head, web and arms is smooth (Fig. 3b).

Ground colour of preserved specimens pale brown dorsally, suffused with purplish hues at the base of the brachial crown and between the arm bases. On this ground colour, mantle, head, funnel and arms have small purple chromatophores uniformly distributed. Spermatophore groove yellowish.

Discussion

Graneledone verrucosa is a well described species and it has been reported widely throughout the Northwest Atlantic from south of Iceland to Cape Hatteras at depths ranging from 850 to 2300 m. Joubin (1918) described the sub-species media from a single specimen collected south-west of Halifax and deposited in the Oceanographic Museum of Monaco. The validity of this taxon has been questioned and requires further studies to be published to validate the sub-species (Robson 1932, Sweeney & Roper 1998). According to the descriptions of Verrill (1881) and Robson (1932), the differences between G. verrucosa and G. gonzalezi can be summarized as follows:

- a) G. verrucosa has longer arms (72-85% of the ML) than G. gonzalezi (50-70%),
- b) the number of gill lamellae in *G. verrucosa* varies from 7 to 8 whilst in *G. gonzalezi* there are 6,
- c) web formula in *G. verrucosa* is C>D>B>A>E whilst *G. gonzalezi* it is A>C>B>D>E,
- d) G. gonzalezi lacks supra-ocular papillae which are present in G. verrucosa (3-5) and
- e) the sculpture of the skin in *G. verrucosa* consists of stellate papillae scattered over the dorsal side of the mantle and head reaching almost the dorsal side of the web and arms. In contrast, the mantle, web and the base of the arms of *G. gonzalezi* are covered dorsally by numerous space close set papillae.

Graneledone challengeri has only been characterized from five specimens from the type locality (off Kermadec Islands). The holotype (NHM 1889.4.2449) was examined in April 1998. It was in bad condition. From the original (Berry 1916)

and Robson (1932) descriptions, the main differences between this species and G. gonzalezi are:

- a) the size of the ligula (3.3% vs 6.2%),
- b) the copulatory ridges are marked in *G. challengeri* whilst the ligula of *G. gonzalezi* lacks copulatory ridges,
- c) the size of the calamus (55% of ligula length vs 47%), and
- d) the sculpture of the skin of *G. challengeri* is formed by papillae on dorsal side of mantle, head and web which are closely set and almost connect each papillae with small white tubercules. The papillae of *G. gonzalezi* are evenly spaced with small yellowish tubercules.

The holotype of *Graneledone setebos* (NHM 1919.12.30.27) was examined in April 1998. It is in very bad condition and did not allow any comparison with our material. However, according to Voss (1976) and Voss & Pearcy (1990) we consider *G. setebos* as a *species dubia*.

Graneledone macrotyla was described from one female caught near the Falkland Islands (USNM 729678) at 1647–2044 m depth, which was examined in September 1998 and preserved in good condition. Among other characters, G. macrotyla is clearly different from our specimens since it has few and very large tuberculations on the dorsal side of the mantle and head.

There is some controversy regarding the taxonomic status of *Graneledone boreopacifica* and *G. pacifica*. It is uncertain whether or not *G. pacifica* is synonymous with *G. boreopacifica* and until a detailed description of *G. boreopacifica* is published (Voss & Pearcy 1990) this comparison cannot be undertaken.

Graneledone pacifica was characterized from 14 males and 14 females collected off Oregon (Voss & Pearcy 1990). The holotype (USNM 730716) is in good condition and it was examined in September 1998. The main characters that differentiate our specimens from *G. pacifica* are:

- a) the radula of *G. pacifica* is degenerated and often with various teeth missing;
- b) the head of G. pacifica is narrower than the mantle;
- c) the ligula has low transverse ridges;
- d) the calamus is larger than in G. gonzalezi (CaLI = 58.6– 66.7 vs 47.4 ± 6); and
- e) the gills have 7–8 lamellae per outer demibranch.

Comparing the original description (Voss 1976) of Graneledone antarctica and the measurements and counts obtained by us on the type material with the specimens collected from Kerguelen waters it is concluded that Graneledone gonzalezi resembles G. antarctica. However, several differences were found:

a) the head in G. gonzalezi is narrower (HWI = 60.4 ± 11.3) than in G. antarctica (HWI = 87.2-100);

- b) the arms of G. antarctica are considerably longer than in G. gonzalezi (ALI = 354–400 in males and 248–297 in females G. antarctica vs ALI = 218 \pm 47 in males and 211 \pm 47 in females in G. gonzalezi);
- c) the hectocotylized arm of G. antarctica (HcAI = 289–353) is longer than in G. gonzalezi (HcAI = 158–215);
- d) the ligula of G. antarctica is considerably shorter (LiLI = 2.9) than in G. gonzalezi (LiLI = 6.2 ± 0.1);
- e) G. antarctica has 9–10 transverse copulatory ridges on the ligula whilst these are not present in G. gonzalezi;
- f) the teeth of the radula in G. antarctica are different to those in G. gonzalezi. Furthermore, Voss (1976) indicated that marginal plates are absent in G. antarctica whereas they are present G. gonzalezi;
- g) a clear difference between our specimens and those described by Voss (1976) is that the papillae on the mantle, head, web and arms in the *G. gonzalezi* are less pronounced than in *G. antarctica*.

However, when Voight (personal communication 1999) compared the holotype of *G. pacifica* preserved from July 1969 and fresh animals of this species, she observed that the papillae were considerably less pronounced in the fresh animals than in the preserved ones. Furthermore, Voight found than the preserved animals had lost tissular fluid which could be the reason for the different appearance of the skin sculpture. This could also explain why the papillae in of *G. gonzalezi* are embedded in the skin instead of being similar to the type material of *G. antarctica*.

The specimens of Graneledone gonzalezi were captured north off Îles Kerguelen, on the continental slope at the Kerguelen Plateau. Therefore, it appears to be a bathyal species living near or on the upper slope of the Kerguelen-Heard Plateau (Lu & Mangold 1978, Nesis 1987). Concerning the bathymetric distribution, Graneledone antarctica is an abyssal species inhabiting deeper waters (2341 m) in the Ross Sea (Voss 1976). The localities of the present material and of G. antarctica were collected from distinct regions (present material 47°13'S-47°18'S and 69°01'E-69°18'E; G. antarctica 74°05.6'S-175°05.2'W). We therefore conclude, from morphological, bathymetrical and geographical differences, that G. gonzalezi is a new species. This could be confirmed by further molecular genetic studies. Nesis (1987) suggested the existence of a similar form of G. antarctica living near Kerguelen and Heard Islands in the upper-bathyal. Furthermore, Kubodera & Okutani (1994) indicated that the specimen from 45°44'S-59°46'E, caught at 848 m depth off Îles Crozet resembles G. antarctica except for slight differences in papillae distribution on the arms and the structure of the radula teeth. This animal was identified as Graneledone sp. A (National Science Museum of Tokyo, NSMT Mo 67837). Due to the considerable distance between Îles Crozet and the Ross Sea, Kubodera & Okutani (1994) hesitated to consider the materials conspecific.

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References

- Berry, S.S. 1916. Cephalopoda of the Kermadec Islands. *Proceedings of the Academy of Natural Sciences of Philadelphia* 68, 45-66.
- CLARKE, M.R. 1986. A handbook for identification of cephalopod beaks. Oxford: Clarendon Press, 273 pp.
- Guerra, A. 1975. Determinación de las diferentes fases del desarrollo sexual de *Octopus vulgaris* mediante un índice de madurez. *Investigación Pesquera*, **39**, 397–416.
- JOUBIN, L. 1918. Études préliminaires sur les céphalopodes recueillis aucours des croisières de S.A.S. le Prince de Monaco, 5° note: Moschites verrucosa (Verrill, 1918). Bulletin de l'Institut Océanographique, Monaco, 339, 9 pp.
- KUBODERA, T. & OKUTANI, T. 1994. Eledonine octopods from the Southern Ocean: systematics and distributions. *Antarctic Science*, 6, 205-214.
- Lu, C.C. & Mangold, K. 1978. Cephalopods of the Kerguelenian Province of the Indian Ocean. Proceedings of the International Symposium on Marine Biogeography and Evolution, Southern Hemisphere, Auckland, 567-574.
- MARGALEF, R. 1974. Ecología. Barcelona: Editorial Omega, 951 pp. NESIS, K.N. 1987. Cephalopods of the world Neptune City: TFH Publications, 351 pp. [English version of the Russian published in 1982].

- PALACIO, F.J. 1978. Vosseledone charrua: a new Patagonian cephalopod (Octopodidae) with notes on related genera Bulletin of Marine Science, 28, 282-296.
- ROBSON, G.C. 1932. A monograph of recent Cephalopoda Vol 2, Part 2. The Octopoda (excluding the Octopodinae). British Museum (Natural History), London, 359 pp.
- ROPER, C.F.E. & Voss, G.L. 1983. Guidelines for taxonomic descriptions of cephalopod species. *Memoirs of the National Museum of Victoria*, 44, 49-63.
- ROPER, C.F.E., SWEENEY, M.J. & CLARKE, M.R. 1985. Cephalopods. In FISCHER, W. & HUREAU, J.C., eds. FAO species identification sheets for fishery purposes: Southern Ocean (Fishing Areas 48, 58 and 88) (CCAMLR Convention Area) vol. 1. Rome: Food and Agriculture Organisation, 1, 117-205.
- Sweeney, M.J. & Roper, C.F.E. 1998. Classification, type localities, and type repositories of recent Cephalopoda. *In* Voss, N.A., VEECHIONE, M., TOLL, R.O. & Sweeney, M.J., *eds.* Systematics and biogeography of cephalopods. *Smithsonian Contribution to Zoology* No. 586, Vol. 2, 561-595.
- VERRILL, A.E. 1881. Report on the cephalopods and on some additional species dredged by the US Fish Commission Steamer Fish-hawk, during the season of 1880. Bulletin of the Museum of Comparative Zoology, Harvard, 8(6), 99–116.
- Voight, J.R. 1998. Biological investigations of the genus Graneledone from abyssal and bathyal depths of the North Pacific Ocean. In Bieler, R. & Mikkelsen, P.M., eds. Abstracts, World Congress of Malacology. Washington, DC: Unitas Malacologica, 344.
- Voss, G.L. 1 976. 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. Evolution and phylogenetic relationships of deepsea octopods (Cirrata and Incirrata). In Clarke, M.R. & Trueman, E.R., eds. The Mollusca: Paleontology and neontology of cephalopods. London: Academic Press, 253-276.
- Voss, G.L. 1988b. The biogeography of deep-sea octopoda. Malacologia, 29, 295-307.
- Voss, G.L. & PEARCY, W.G. 1990. Deep-water octopods (Mollusca: Cephalopoda) of the northeastern Pacific. Proceedings of the California Academy of Sciences, 47(3), 47.