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www.publish.csiro.au/journals/mr *Molluscan Research*, 2004, **24**, 193–209

New Taxon

Microeledone mangoldi n. gen. and n. sp., a deep-water pygmy octopus from the Norfolk Ridge, New Caledonia (Cephalopoda : Octopodidae)

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Abstract

Microeledone mangoldi n. gen. and n. sp. is described from a male specimen collected from approximately one kilometre deep on the Norfolk Ridge south of New Caledonia in the south-west Pacific Ocean. This tiny octopus is characterised by a single row of suckers that are functional to the tips of the arms, the absence of an ink sac, the presence of a pair of chitinous stylets, a UU-shaped funnel organ, a copulatory organ with distinct ligula and calamus, and a distinctive radula. The radula has seven teeth per row. The unique central (rachidian) tooth has a long, sharp mesocone with a curved and grooved tip. The remaining rows of teeth are also unique, being flattened and plate-like. Marginal plates are absent. The body is smooth, without papillae, cartilaginous tubercles, or a lateral ridge. Functional chromatophores are absent. This octopus appears related to several other genera of deep-sea octopods with a single row of suckers, namely *Thaumeledone* Robson, 1930, *Bentheledone* Robson, 1932 and *Graneledone* Joubin, 1918, to which the new genus is compared. Definitions of the genus *Thaumeledone* are reviewed.

Additional keywords: deep-sea, Indo-Pacific, taxonomy.

Introduction

A distinctive new genus and species of octopus, *Microeledone mangoldi*, is reported from deep-water in the south-west Pacific Ocean. This new taxon is represented by a single submature male captured at a depth of ~1000 m in the Coral Sea, south of New Caledonia on the northern end of the Norfolk Ridge. This region of the Pacific Ocean is largely a bathyal plain dotted with submarine mountain ranges and isolated seamounts. Recent research into the deep-sea faunas of these poorly known habitats has uncovered highly diverse and largely unknown assemblages of organisms, many of which are endemic (Bouchet and Metivier 1982; Richer de Forges 1990; Richer de Forges *et al*. 2000; Valdéz 2001*a*, 2001*b*; Valdéz and Gosliner 2001).

The new taxon is described herein and compared with other octopods sharing similar morphological features. Geographic and phylogenetic aspects are discussed, particularly in relation to the Australian, New Zealand, and Antarctic deep-sea octopod fauna.

Material and methods

The single specimen described in this paper was collected in 1993 during a joint French cruise of ORSTOM and the Muséum National d'Histoire Naturelle (Paris) to New Caledonia and surrounding areas of the Coral Sea. It was captured with a beam trawl on the Bathus 3 Expedition at 980–1000 m depth on the northern end of the Norfolk Ridge. The preserved specimen is housed in the collections of the museum in Paris (MNHN). Additional species were examined from the collections of Museum Victoria, Melbourne, Australia (MV), The Natural History Museum, London, UK (BMNH), National Museum of Natural

 10.1071/MR04012 1323-5818/04/030193

History, Washington, DC, USA (USNM), Royal Museum of Natural History, Brussels, Belgium (MRHNB) and South African Museum, Cape Town, South Africa (SAM).

The taxonomic methodology and diagnostic characters used in the description below follow Norman and Sweeney (1997) and Norman *et al*. (1997).

Systematic descriptions

Family **OCTOPODIDAE** d'Orbigny, 1840

Microeledone n. gen.

Type species: *Microeledone mangoldi*, by monotypy.

Diagnosis

Small robust octopus; mantle muscular, roughly spherical; mantle aperture moderate (~40% of neck circumference); funnel organ large, UU-shaped, limbs of equal length with sharp tips; interbrachial aquiferous (water) pore system absent; stylets long, chitinous; eyes large; gills with 4–5 (typically five) lamellae per demibranch plus terminal lamella; arms robust, short, equal in length; arm autotomy absent; suckers uniserial, closely set; suckers normal, functional to tips of all arms, without modification except for hectocotylized arm of males; enlarged suckers absent; right arm III hectocotylized, shorter than opposite arm; copulatory organ with distinct ligula and large calamus; crop with distinct swelling but without anterior directed diverticulum; posterior salivary glands large, length similar to buccal mass; ink sac absent; intestine short, tapered, with single bend. Radula with serial rows of seven teeth; marginal plates absent. Rachidian teeth broad-based with elongate sickle-shaped mesocone with grooved anterior face. Other teeth flattened and blade-like, without obvious sharp cusps. Terminal organ (penis) short and straight with simple diverticulum. Skin smooth; papillae and lateral ridge absent; functional chromatophores absent, uniformly pink-grey in colour.

Remarks

Spermatophores of the species are unknown. Females unknown.

Erection of this new genus is based on the following unique suite of diagnostic characters: (*1*) small size at maturity; (*2*) suckers uniserial; (*3*) suckers at tips of arms in male are not modified; (*4*) radula with seven teeth per row, rachidian teeth with sickle-like elongate and grooved mesocone, other teeth flattened and blade-like, marginal plates absent; (*5*) copulatory organ with distinct ligula and calamus; (*6*) funnel organ large and UU-shaped; (*7*) webs are deep between all arms; (*8*) posterior salivary glands are very large; (*9*) crop swollen but without anterior diverticulum; (*10*) ink sac and anal flaps are absent; (*11*) skin smooth without texture or lateral ridge; and (*12*) functional chromatophores are absent and body appears relatively unpigmented.

Etymology

From the Greek *micros*, meaning 'small' in reference to the size of the animal.

Microeledone mangoldi n. sp.

(Figs 1–4; Table 1)

Material examined

Holotype. 18 mm ML male; south-west Pacific Ocean, Coral Sea, south of New Caledonia, northern end of Norfolk Ridge, 23°23′S, 167°52′E, 980–1000 m, 29 Nov. 1993, coll. P. Bouchet, B. Richer de Forges

and A. Warén, N/O *Alis*, cruise Bathus 3, station C-P823, beam trawl (MNHN 2105). Additional material examined are listed in Appendix 1.

Diagnosis (with characters of genus except as noted below)

Octopus small (mantle length 18 mm); arms short (1.3× mantle length). Webs deep and fleshy, extend almost half of arm length (deepest 45.8% of longest arm); dorsal and lateral webs equal in depth, ventral web shallowest. Sucker counts on normal arms 31–32; 22 suckers on hectocotylized arm of male. Male hectocotylized arm short (71% length of opposite arm); ligula small (*c.* 8% of hectocotylized arm length in submature male), copulatory groove wide and open; calamus large, wide (46% of ligula length); terminal organ short and straight with simple diverticulum. Skin colour uniform pink-grey with dark maroon pigment in oral webs for proximal third of arms.

Description

The following description is based on the only known specimen, a submature male in good condition, fixed in formalin and preserved in 70% ethanol. Counts and measurements for this specimen are presented in Table 1. Relative indices are presented in the text.

Animal small, fleshy and robust (mantle length, 18 mm; total length, 46 mm; total body wet weight, 3.2 g). Mantle round (Fig. 1*a*); body wall relatively thick, muscular; skin thick, soft and semi-gelatinous. Mantle width almost equal to mantle length (index 92.8%). Head wide, slightly narrower than mantle width (index 82.9%). Eyes large. Stylets present (Fig. 1*b*), large (33.7% of mantle length), chitinous. Pallial aperture less than half mantle circumference (index *c.* 40%). Funnel short (35.4% of mantle length), wide; elongate lateral pouches present; free about one-third length of funnel (index 34.4%). Funnel organ (Fig. 1*c*) UU-shaped, located towards anterior end of dorsal funnel; anterior tips sharply pointed; organ large, occupies over half length of funnel (index 57.8%); lateral and medial limbs equal in length (index 97.3%).

Webs fleshy, deep (45.8% of longest arm); equal in depth except for ventral sector (formula A = B = C = D > E); web margins absent.

Arms short (longest 1.3× mantle length); robust (arm at widest point 16.0% of mantle length); roughly triangular in cross-section (with single sucker row as apex), taper evenly in width from arm base to distal tip. Arms equal in length. Arm autotomy absent. Suckers small (diameter of largest 5.0% of mantle length); tightly packed in single row (slightly bunched into zig-zag arrangement towards distal end of some arms); suckers slightly elevated, rim thickened, infundibulum narrow, acetabulum small. Suckers functional (but very small) to distal tips of normal arms. Enlarged suckers absent in single submature male specimen. Sucker counts on all normal arms 31–32; hectocotylized arm with 22 suckers.

Right arm III hectocotylized in males (70.8% of opposite arm length; 93.9% of mantle length). Copulatory organ (Fig. 1*d*) of moderate size relative to arm length (7.6% of hectocotylized arm length). Ligula wide with wide copulatory groove; calamus large, open (46% of ligula length). Spermatophore groove shallow, fleshy.

Gills with 4–5 lamellae per outer and inner demibranch; lamellae of inner demibranchs reduced in length, distinctly shorter than outer lamellae (index ~60%).

Digestive tract (Fig. 2*a*). Buccal mass large, about one-third length of mantle (index 33.7%); almost as large as digestive gland (index 80.3%). Anterior salivary glands relatively small, approximately one-quarter length of buccal mass (index 26.2%); posterior salivary glands very large, almost as long as buccal mass (index 88.5%) and three-quarters length of digestive gland (index 71.1%). Oesophagus short; crop distinctly swollen but

Table 1. ***Microeledone mangoldi*** **n. gen. & n. sp., counts and measurements (mm) of the holotype**

A–E, designation of web sectors from dorsal to ventral; 1–4 arm pairs numbered from dorsal to ventral

Sex	Male
Maturity	Submature
Total length	46
Total wet weight (g)	3.2
Dorsal mantle length	18
Ventral mantle length	16
Mantle width	17
Head width	15
Funnel length	6.4
Free funnel length	2.2
Funnel organ length	
Lateral limb	3.6
Medial limb	3.7
Web depth	11
A	11
B	Left = 11, right = 11
C	Left = 11, right = 10
D	Left = 11, right = 7[A]
E	7
Web depth formula	A = B = C = D > E
Arm lengths	
1	Left = 23, right = 23
2	Left = 24, right = 23
3/Hc	Left = 24, right = 17
4	Left = 22, right = 22
Arm length formula	Equal
Arm width	2.9
Sucker diameter	0.9
Sucker counts	
1	Left = 31, right = 31
2	Left = 31, right = 32
3/Hc	Left = 31, right = 22
4	Left = 31, right = 32
Gill count (outer/inner demibranch)	Left 5/5, 4/5
Stylet length	Left 6, right –
Ligula length	1.3
Calamus length	0.6
Terminal organ length	2.4
Diverticulum length	0.7

[A]Includes spermatophore guide.
Hc, hectocotylized right arm of male.

without diverticulum. Stomach bipartite; caecum with less than one whorl, ducts to digestive gland (pancreas) short and wide. Intestine short, broad, very wide at point of attachment to caecum, tapers to narrow, thin-walled rectum. Digestive gland ovoid with slightly elongate posterior lobes; pancreas present as small patch of light-coloured tissue at point of entry of ducts into digestive gland. Ink sac absent. Anal flaps absent.

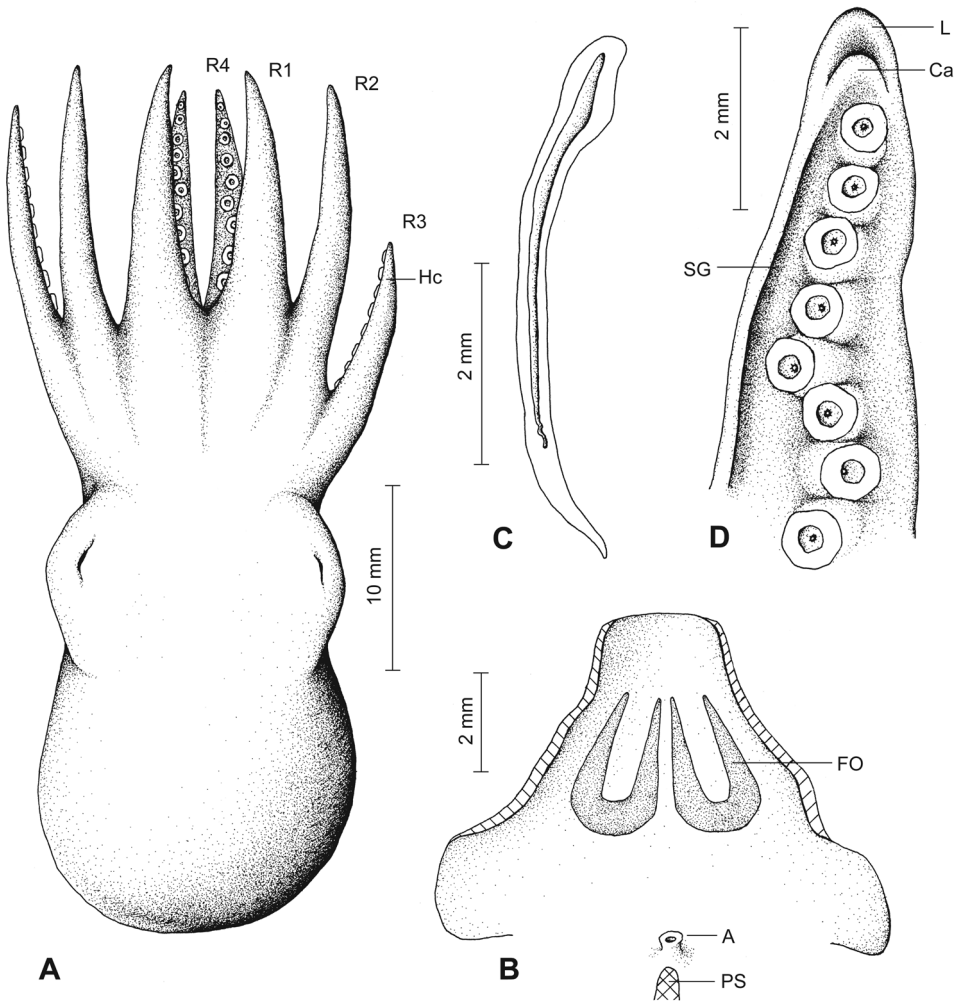

Fig. 1. *Microeledone mangoldi* n. gen. and n. sp. *a–d*, male holotype (18 mm ML, MNHN 2105). *a*, dorsal view of whole animal; *b*, stylet (right side) within shell sac; *c*, funnel cut open to display funnel organ *in situ*; *d*, distal end of male hectocotylized arm with copulatory organ, oral view. A, anus; Ca, calamus; FO, funnel organ; Hc, hectocotylized arm; L, ligula; PS, pallial septum (cut); R1–4, right arms 1 to 4; SG, spermatophore groove. Scale bars: *a*, 10 mm; *b–d*, 2 mm.

Upper beak (Fig. 2*b*) hood of moderate size, almost half of beak length (index 46.0%); rostrum bluntly hooked, cutting edge rounded; crest slightly rounded. Lower beak (Fig. 2*c*, *d*), hood and crest slightly rounded; rostrum pointed, cutting edge sharp; lateral walls parallel with slightly concave posterior margin. Radula (Fig. 3) with seven teeth per transverse row; marginal plates absent. Rachidian tooth acuspid, with broad base; mesocone sickle-shaped and blade-like (elongate, curved and flattened), oriented perpendicular to main axis of radular ribbon. Other teeth flattened, plate-like (Fig. 3*e*). First lateral teeth small, elongate, rectangular to square in shape; acuspid. Second lateral teeth triangular, rounded, swollen at medial end; acuspid. First marginal teeth slightly curved to triangular with blunt medial tip; acuspid.

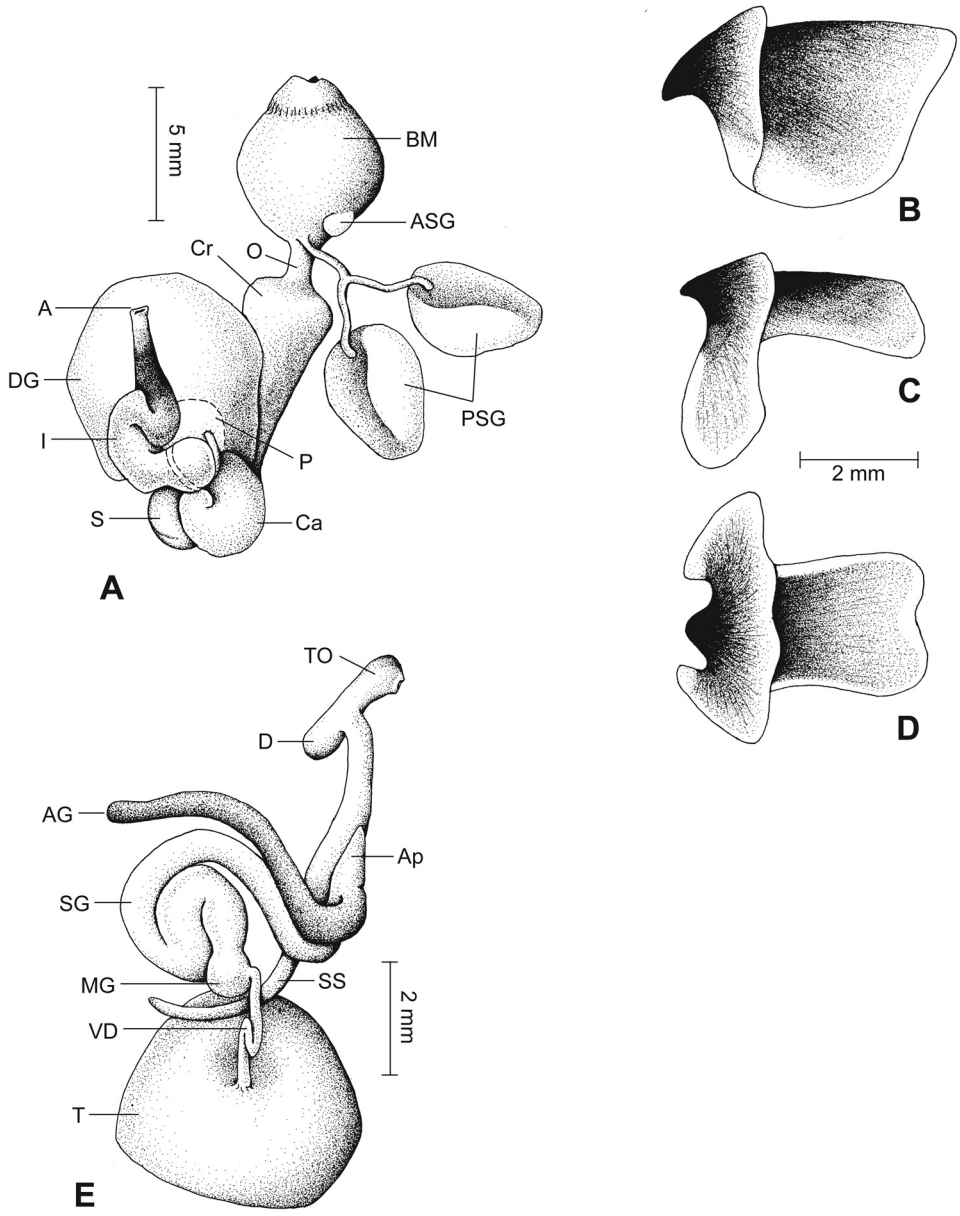

Fig. 2. *Microeledone mangoldi* n. gen. and n. sp. *a–e*, digestive and reproductive systems (male holotype, 18 mm ML, MNHN 2105). *a*, digestive tract; *b*, upper beak, lateral view; *c*, lower beak, lateral view; *d*, lower beak, ventral view; *e*, reproductive tract, ventral view. A, anus; Ap, appendix; AG, accessory gland; ASG, anterior salivary gland; BM, buccal mass; Ca, caecum; Cr, crop; D, diverticulum; DG, digestive gland; I, intestine; MG, mucilaginous gland; O, oesophagus; P, pancreas; PSG, posterior salivary gland; S, stomach; SG, spermatophoric gland; SS, spermatophore storage sac; T, testis; TO, terminal organ; VD, vas deferens. Scale bars: *a*, 5 mm; *b–e*, 2 mm.

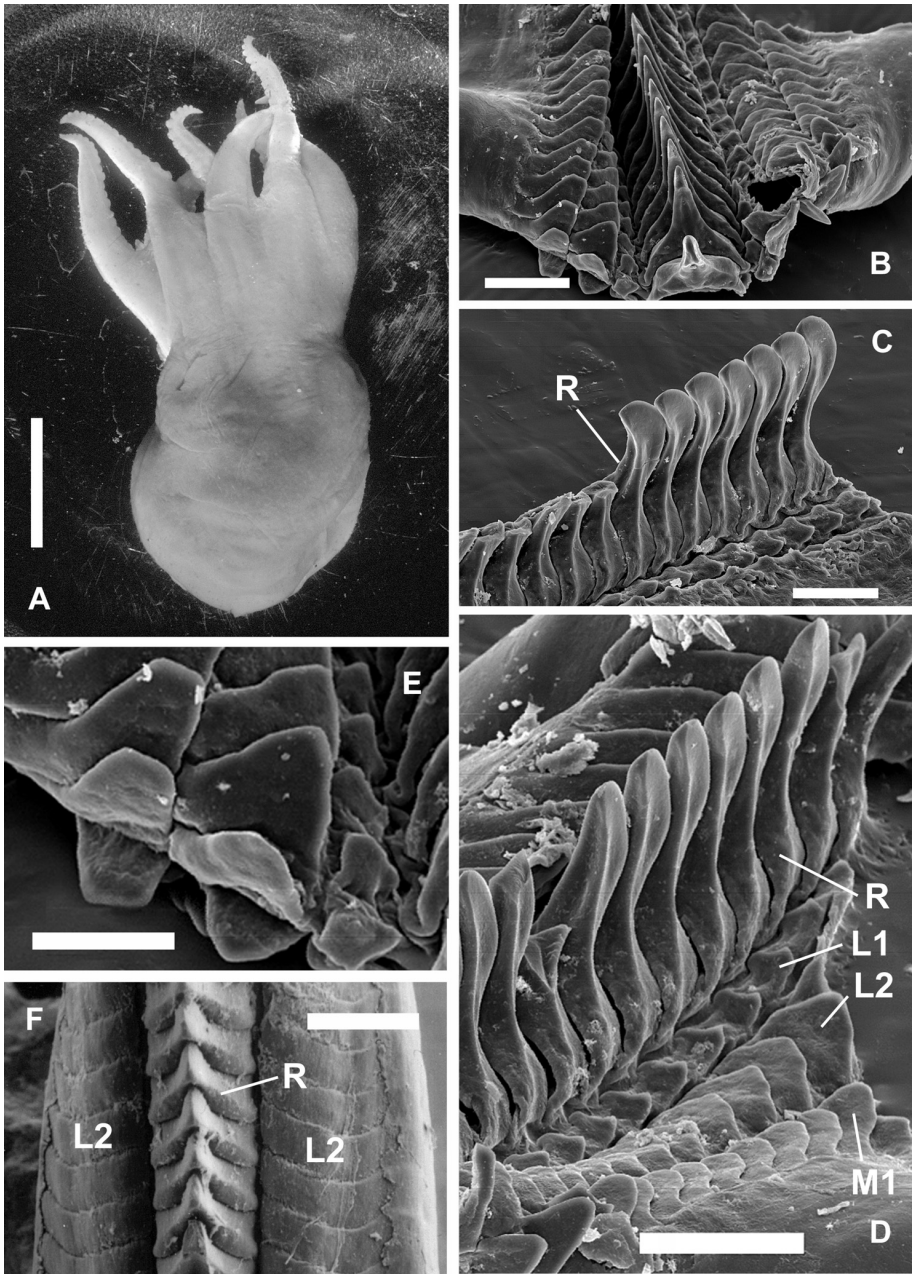

Fig. 3. *Microeledone mangoldi* n. gen. and n. sp. *a–f*, photographs of holotype and radula (18 mm ML male, MNHN 2105). *a*, dorsal view of whole animal; *b–e*, scanning electron micrographs of radula; *b*, anterior view of radula; *c*, anterior lateral view of broken and intact rachidian tooth row showing curved and grooved tips; *d*, anterior lateral view of radula showing tooth nomenclature; *e*, close up of first marginal tooth (left), second lateral tooth (centre) and first lateral tooth (right); *f*, radula of *Thaumeledone gunteri* (MV F65706). L1, first lateral tooth; L2, second lateral tooth; M1, first marginal tooth; R, rachidian tooth. Scale bars: *a*, 10 mm; *b–d*, 0.1 mm; *e* = 50 μm; *f* = 0.2 mm.

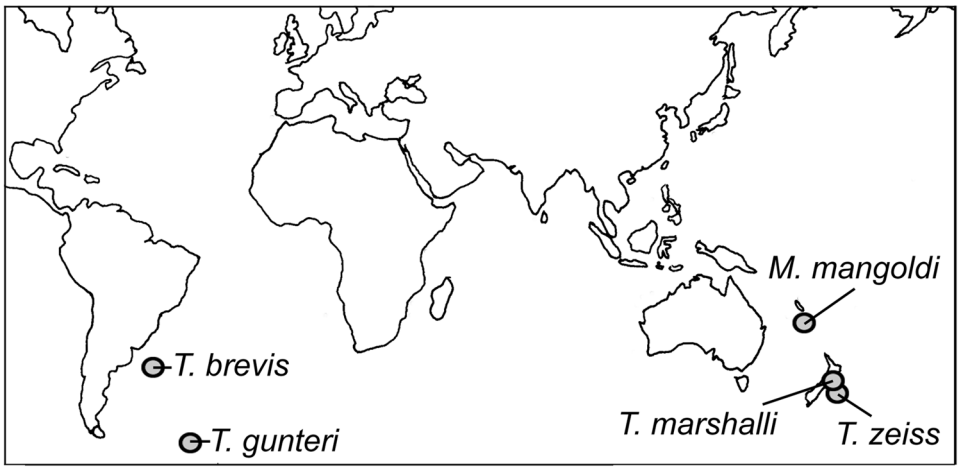

Fig. 4. *Microeledone mangoldi* n. gen. and n. sp. Collection locality of only known specimen, and type localities of other species assigned to the genus *Thaumeledone*.

Reproductive tract of submature male (Fig. 2*g*). Terminal organ linear, short (13.2% of mantle length); diverticulum small (29.2% of organ length); genital aperture subterminal. Appendix present at junction of accessory gland, spermatophoric duct and spermatophore storage sac. Spermatophores unknown.

Females unknown.

Colour of live animal unknown. Preserved specimen uniform light pink-grey in colour on both dorsal and ventral surfaces. Oral web dark maroon in colour for proximal third of arms. Functional chromatophores not evident. Crop, posterior salivary glands, stomach, and distal two-thirds of intestine enclosed within darkly-pigmented (maroon) membrane. Skin smooth without apparent tuberculate, granular, or papillate texture; patch and groove system absent.

Distribution

Known only from the type locality (Fig. 4).

Life history

Nothing is known about the life history or behaviour of this rare species. Numerous prey remains were found in the stomach. Contents included setae and at least seven jaw fragments from polychaetes, and the radula of an unidentified gastropod mollusc. Foraminiferans (whole and broken) and sand grains were present, most likely ingested incidentally along with other prey.

Externally, the proximal oral surfaces of the webs between the arms are darkly pigmented. In addition, sheaths of dark maroon pigmented tissue envelop the salivary glands, crop, stomach, and part of the intestine. This suggests the animal's ability to mask out light produced during the capture and ingestion of luminescent prey. Other deep sea octopods are similarly pigmented both externally and internally (e.g. *Benthoctopus karubar*, see Norman *et al*. 1997).

Oocysts of the apicomplexan parasite *Aggregata* were present in large numbers throughout the digestive tract, especially caecum and proximal intestine. This indicates that

the animal had presumably fed extensively on crustaceans, known to be the intermediate hosts for this protozoan parasite (see Hochberg 1990).

Etymology

Named in honour of our late colleague and friend the eminent cephalopod researcher Dr Katharina M. Mangold (1922–2003). For many years she was Directeur de Recherche at the Laboratoire Arago, Banyuls-sur-Mer, France.

Common name

Sickletooth pygmy eledone.

Discussion

Taxonomy

Four morphological features characterise this interesting octopus and distinguish it from other known octopuses of both shallow and deep waters: (*1*) a single row of suckers; (*2*) loss of ink sac; (*3*) distinctive and unique radula; and (*4*) small size.

Sucker rows

The majority of benthic octopus species (>90% of nominal species) possess two rows of suckers. The following genera possess a single row of suckers: *Adelieledone* Allcock *et al*., (2003); *Bentheledone* Robson, 1932; *Eledone* Leach, 1817; *Graneledone* Joubin, 1918; *Megaleledone* Taki, 1961; *Pareledone* Robson, 1932; *Tetracheledone* Voss, 1955; *Thaumeledone* Robson, 1930; *Velodona* Chun, 1915 and *Vosseledone* Palacio, 1978.

Loss of ink sac

Many deep-sea octopuses lack a functional ink sac, ink having less value in lightless depths (Voss 1988*a*). Of the taxa that possess a single row of suckers, only three genera lack an ink sac: namely *Graneledone*, *Bentheledone* and *Thaumeledone*.

Radula

The most distinctive feature of the new octopus described herein is the radula. It consists of seven teeth per row but lacks marginal plates. The mesocone of the rachidian tooth is modified into a vertically-oriented sickle-shaped structure with a grooved anterior surface (Fig. 3*c*). All other teeth are flattened and blade-like. The only other octopus with a radula that contains blade-like structures is *Vosseledone charrua* Palacio, 1978. In *Vosseledone* the rachidian tooth is modified into a trident of wide transverse blades, more suited to scraping.

Size

Microeledone mangoldi is the smallest octopus species described to date with a uniserial arrangement of suckers. The male specimen is close to mature at a mantle length of 18 mm and total body wet weight of 3.2 g. Although the testes were well developed, spermatophores were not present. The modified tip of the third right arm of this animal is well developed with a distinct ligula and calamus.

Primary differences between *Microeledone* and other octopodids with a single row of suckers are summarised in Table 2. The genera that appear to be most closely related in form to *Microeledone* are *Graneledone, Bentheledone* and *Thaumeledone*. All are easily distinguished from the new genus.

Table 2. ***Microeledone mangoldi*** **n. gen. & n. sp., comparison with other octopus genera that possess a single row of suckers on the arms**
Terminology for vertical distribution and associated depth ranges: abysso, abyssobenthic (> 2500 m); bathy, bathybenthic (1000–2500 m); epi, epibenthic (0–200 m); meso, mesobenthic (200–1000 m)

Character	*Microeledone*	*Thaumeledone**	*Bentheledone*	*Graneledone*	*Megaleledone*	*Pareledone*	*Adelieledone*	*Tetracheledone*	*Velodona*	*Vosseledone*	*Eledone*	*'Eledone'*
Source material	See 'Material examined'	See 'Material examined'	See 'Material examined'	Joubin 1918; Robson 1932; Voss and Pearcey 1990	Taki 1961; Lu and Stranks 1994	Lu and Stranks 1994; Allcock *et al.* 2003	Allcock *et al.* 2003	See 'Material examined'	See 'Material examined'	Palacio 1978	See 'Material examined'	Norman *et al.* 1997
No. species	1	2+	2+	8+	1	7+	3	1	1	1	4	1
Genotype	*M. mangoldi*	*T. brevis*	*B. rotunda*	*G. verrucosa*	*M. setebos*	*P. charcoti*	*A. adelieana*	*T. spinicirrus*	*V. tongata*	*V. charrua*	*E. cirrhosa*	*E. palari*
Depth range	Meso	Meso-abysso	Abysso	Meso-abysso	Epi-meso	Epi-meso	Epi	Meso	Meso	Epi	Epi-meso	Epi-meso
Ink sac	Absent	Absent	Absent	Absent	Reduced	Present	Present	Present	Present	Present	Present	Present
Gill count	4–5	4–5	4–5	6–9	10–11	6–11	7–8	6–9	8	6–7	8–13	5
Arm length	1.3	1.3–1.5	2–3	2.1–4.2	2.0–2.6	1.5–3.6	1.5–2.7	1.5–2.4	3–4.5	1.9–2.5	1.8–4.5	1.5–2
Web	46	41–50	29–43	17–37	40–45	20–50	25–37	43–45	18–26	34	20–37	38–67
Stylets	Present	Present	NI	Absent	Absent	Present	Absent	Present	Present	Unknown	Present	Present
Radula teeth per row	7	3–5	7	7	7	7	7	7	7	3	7	7
Rachidian modifications	Elongate homodont, concave tip	Homodont	Homodont	Homodont	Homodont	Normal	Normal	Normal	Normal	Trident blades	Normal	Normal
Crop diverticulum	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Present	Present	Present
Posterior salivary glands	Large	Moderate	NI	Small to tiny	Moderate	Moderate	Very large	Moderate	Moderate	Moderate	Large	Large
Funnel organ	UU	VV, IIII	Wide V in *B. albida*	VV	UU	UU	W	IIII	VV	VV	UU/W	UU
Ligula	Normal with calamus	Normal with calamus	Normal with calamus	Normal with calamus	Normal with calamus	Normal with calamus	Normal with calamus	Normal with calamus	Normal with calamus	Normal with calamus	Spongy or no calamus	Normal with calamus
Male arm tip modifications	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Ridges or fingers	Spongy tissue
Lateral ridges on mantle	Absent	Absent	Absent	Absent	Present	Present or absent	Absent	Present	Absent	Absent	Present or absent	Present
Skin texture	Smooth	Low papillae	Smooth	Cartilaginous warts	Low papillae	Papillae	Scattered papillae	Spiked papillae	Regular papillae	Low papillae	Patch and groove	Low papillae

[A]Excludes O'Shea 1999 species: *T. marshalli* and *T. zeiss* (see 'Discussion' and Table 3).
NI, not indicated.

Table 3. *Microeledone mangoldi* n. gen. & n. sp, comparison with three other species currently referred to the genus *Thaumeledone*

Characters	*M. mangoldi*	*T. brevis*	*T. gunteri*	*'T'. zeiss*	*'T'. marshalli*
Ink sac	Absent	Absent	Absent	Absent	Absent
Crop: anterior diverticulum	Absent	Absent	Absent	Absent	Absent
Radula					
Teeth per transverse row	7	3	5	7	5
Marginal plate	Absent	Absent	Absent	Present	Absent
Rachidian mesocone	Blade-like	Absent	Triangular	Triangular	Triangular
Gill lamellae counts	4–5	4–5	4–5	4–5	5
Eye size	Large	Large	Large	Large	Large
Stylets	Present	NI	Present	NI	NI
Funnel organ shape	UU	IIII	VV	VV	VV
Posterior salivary glands (% buccal mass)	Very large (89)	Large	Large	Large (72)	Large (72)
Arm lengths (x ML)	1.3	~1.7	1.4–1.5	1.0–1.4	1.2–1.3
Web depths (% longest arm)	46	68	41–51	38–53	50–65
Web margins	Absent	NI	3/4 length	Absent	Absent
Sucker diameter (% ML)	5	5	7–8	4–5	4–7
Enlarged suckers: males	Absent	NA (female only)	Absent	Absent	Absent
Sucker counts					
Normal arms	31–32	25–29	35–36	29–33	28–31
Hectocotylized	22	NA (female only)	22	19	17–20
Modified arm tips: males	Absent	NA (female only)	Absent	Absent	Absent
Ligula: shape	Normal ligula and calamus	Female only	Normal	Normal	Normal
Skin sculpture	Smooth	Papillose	Papillose	Papillose	Smooth/faint
Lateral ridge	Absent	Absent	Absent	Absent	Absent
Papillae: supra-ocular	Absent	Present	Absent	Present (2)	Absent
Reverse counter-shading	Absent	NI	Present	Present	Present
Dark oral web	Proximal 1/3	Present	All	All	All
Type locality	Norfolk Ridge, New Caledonia	S. Atlantic, SE of Uruguay	Antarctica, S. Georgia I.	Chatham Rise, New Zealand	Chatham Rise, New Zealand
Latitude	23°S	37°S	53°S	44–45°S	37–42°S
Longitude	168°E	~54°W	35°W	173–178°E	176–177°E
Depth (m)	980–1000	1096	400	1050–1400	2000–2500

NA, not applicable; NI, not indicated

Microeledone resembles *Graneledone* in that they both lack an ink sac and an anterior directed crop diverticulum. *Graneledone* is clearly distinguished by the presence of numerous raised cartilaginous tubercles on the body and arms, and longer arms (2–5× the mantle length *v.* 1.3).

Microeledone is similar to *Bentheledone* in the absences of body texture, ink sac and anterior-directed crop diverticulum. *Bentheledone*, however, differs in having a single broad V-shaped funnel organ (*v.* UU), small eyes (*v.* large), very small posterior salivary glands (*v.* large), and longer arms (2–3× the mantle length *v.* 1.3). The genus *Bentheledone* is in critical need of detailed study.

The taxa most similar to *Microeledone mangoldi* have been placed in the genus *Thaumeledone* (Table 3). This genus was originally erected by Robson (1930) on the basis of a degenerate radula with only a single tooth per transverse row, gill counts of 5–6 lamellae, and short subequal arms with very deep webs. Robson included two species in this genus, *T. brevis* (Hoyle, 1885) and *T. gunteri* Robson, 1930. Both species had characters that challenged Robson's own generic diagnosis, i.e. *T. brevis* had 4–5 gill lamellae and *T. gunteri* had a radula with 'faint traces of admedians and of an oblong second lateral with a low cusp' (Robson 1932: 317). Voss (1988*a*) amended Robson's generic diagnosis reporting the presence of marginal plates on the radula and adding three new characters: a tall and narrow VV funnel organ (despite IIII reported for *T. brevis*), vestigial posterior salivary glands, and a papillose dorsum.

The typical radula for most members of the family Octopodidae consists of seven teeth per transverse row plus adjoining marginal plates. Terminology for these teeth are as follows: *rachidian* (R): this single central tooth typically has a tall medial mesocone that may lack cusps ('acuspid'), bear a single cusp ('unicuspid') or multiple cusps ('multicuspid'); *first laterals* (L1): typically a small low tooth with a single cusp; *second laterals* (L2): typically a larger curved tooth with a single cusp towards the medial end of the tooth; *first marginals* (M1): an elongate and curved tooth; and *marginal plates* (MP): square to oblong plates lacking cusps and anchored within the radula tissue.

In *Thaumeledone brevis* and *T. gunteri* the radula is considered degenerate: only 3–5 teeth are present in a transverse row. Figure 3*f* shows the radula of *Thaumeledone gunteri* with three visible teeth per row: the central unicuspidate rachidian row, and two rows of large and flattened lateral teeth. Robson (1932: 317) reported that *T. gunteri* showed 'faint traces of *admedians* (= first lateral teeth) and of an oblong second lateral with a low cusp'. We concur with Robson in considering the large flattened tooth to be a highly modified second lateral tooth. There has been some confusion in the literature in the interpretation of this flattened wide tooth. We believe Voss (1988*a*) incorrectly defined this tooth as a marginal plate, hence adding this character to the generic diagnosis.

In order to incorporate two new taxa from New Zealand waters (*T. marshalli* and *T. zeiss*) O'Shea (1999: 246) further amended the diagnosis for *Thaumeledone* as reproduced here:

> 'Small-bodied muscular benthic octopodids characterised by papillose dorsal and ventral surfaces of mantle, head, arms and web; arms short; non-hectocotylised (*sic*) arm sucker counts very low (less than 20); non-hectocotylised arm sucker counts very low, less than 40 at maturity; penis diverticulum hammer-shaped, with or without pronounced spiral; distal oviducts expanded, length less than or equal to that of proximal oviducts. Posterior salivary glands large to small; radula dentition simple, rachidian without lateral cusps, marginal plates present; lateral teeth vestigial to absent; funnel organ VV; outer gill lamellae few, 4 or 5, inner demibranch little reduced (amended from Voss, 1988)'.

Many of the characters within O'Shea's (1999) generic diagnosis for *Thaumeledone* are problematic. Several character states contradict descriptions and illustrations that O'Shea provides, both for existing members of this genus and his new included species, for example: (*1*) *'papillose dorsal and ventral surfaces of mantle, head, arms and web*' (yet *T. marshalli* is reported as 'entire animal smooth or with extremely faint traces of papillation' (p. 252)); (*2*) '*distal oviducts …. length less than or equal to that of proximal oviducts*' (yet distal oviducts are longer than the proximal oviducts in O'Shea's fig. 153*E* of

the holotype of *T. gunteri*); (*3*) *'marginal plates present'* (O'Shea's illustration of the radula of *T. marshalli* appears analogous to that of *T. gunteri* with reduced first lateral tooth and a broad and flattened second lateral tooth. As such we would interpret this radula as lacking marginal plates. In describing the lateral teeth of *T. marshalli*, O'Shea does not distinguish between the marginal plate or first marginal tooth, simply referring to it as: 'single block-like marginal.'); (*4*) *'lateral teeth vestigial to absent'* (*T. zeiss* possesses the full compliment of seven teeth per row, none of which appear reduced in size. The second lateral teeth in *T. marshalli* appear very well developed, as stated above).

Certain characters within O'Shea's diagnosis offer little diagnostic value, namely: (*1*) penis diverticulum hammer-shaped, with or without pronounced spiral; and (*2*) posterior salivary glands large to small.

As illustrated by O'Shea (1999: 261), the character of vestigial posterior salivary glands does not hold true for either the syntype of *T. brevis* or the holotype of *T. gunteri*. The glands of both are smaller than that of *Microeledone* but hardly constitute vestigial organs (such organs being reported for other, non-type material attributed by Voss to *Thaumeledone*, see O'Shea). As a consequence it is appropriate that this character should be removed from the diagnosis.

It appears that O'Shea found it difficult to place his two new taxa in existing genera. As a consequence he emended and broadened the diagnosis of *Thaumeledone* to include these New Zealand species. His concluding remarks make this apparent: 'As *T. zeiss* and *T. marshalli* are not particularly alike, and because equally dissimilar species are found in southern oceans, it is possible that two genera exist amongst this complex of small-bodied, short-armed species (with low total arm-sucker counts)…' (1999: 255).

We do not agree that the definition of *Thaumeledone* should be modified to accommodate O'Shea's new taxa. If O'Shea's diagnosis truly encompassed his two species as well as *T. brevis* and *T. gunteri*, the diagnosis would be left with no diagnostic characters other than short arms, low sucker counts and a VV funnel organ (that does not encompass the IIII funnel organ reported for *T. brevis*). Similarities suggest that there may be phylogenetic affinities amongst the suite of small southern hemisphere species that possess a single row of suckers (including our new taxon); however, excessive modifications to the diagnosis of *Thaumeledone* have resulted in one that lacks any real distinguishing diagnostic characters.

In light of these partial (and questionable) revisions to the genus, it is clear that there are few remaining characters that diagnose *Thaumeledone*. As a consequence we choose to restrict the diagnosis of *Thaumeledone* to include both taxa originally placed within this genus (*T. brevis* and *T. gunteri*) based on the following core characters: (*A*) degenerate radula, reduced number of teeth (3–5) per transverse row; (*B*) papillose skin; (*C*) tall and narrow VV funnel organ or four separate linear components (IIII): (*D*) low gill counts (4–6 per demibranch); (*E*) short arms (1–1.7× ML); and (*F*) deep webs (~30–60% longest arm).

If we restrict our consideration to these characters, *Microeledone* is similar to *Thaumeledone* in having short subequal arms, deep webs and low gill counts (4–5 *v.* 4–6). However it is clearly delineated by the nature of the radula (complete and highly modified *v.* the degenerate form of *Thaumeledone*). *Microeledone* also differs in funnel organ (a distinct deep UU *v.* the narrow and shallow VV or IIII of the two *Thaumeledone* species) and smooth skin (*v.* papillose).

The generic placement of O'Shea's species *T. marshalli* and *T. zeiss* require further consideration and await a more thorough description of the core characters of radula structure and attributes of the digestive systems for these two species. Full descriptions of

the mature reproductive systems of all taxa are also required. It is clear that the genus *Thaumeledone* requires a thorough revision.

Biogeography

Geographic and vertical distributional patterns may provide clues into the phylogenetic affinities of the new genus. Amongst the octopodid genera that possess a single row of suckers, the majority of genera and species occur in two regions:

(*1*) Temperate and tropical latitudes of the Atlantic Ocean: all *Eledone* species (except '*Eledone*' *palari* Lu and Stranks, 1992, see comments below); *Tetracheledone* and *Vosseledone*.
(2) Antarctic and subantarctic waters: *Pareledone*, *Megaleledone, Adelieledone*, *Bentheledone* and *Thaumeledone*.

The genus *Graneledone* is scattered throughout the world's oceans: primarily in the northern Pacific Ocean, north-west Atlantic Ocean, southern Pacific and Indian Oceans, and Antarctica (Voight 2000). The species that have been placed in *Graneledone* need to be critically re-evaluated to determine if more than one genus is represented. The two remaining uniserial genera have more restricted distributions. *Velodona togata* Chun, 1915 occurs at tropical latitudes in the western Indian Ocean. '*Eledone*' *palari* occurs on the continental slopes around Australia and in southern Indonesia. It's placement within the genus *Eledone* has been questioned (Norman *et al*. 1997) and is the topic of current research (Hudelot, Boucher-Rodoni and Hochberg unpublished data).

Microeledone is closest in form to species placed in the genera *Thaumeledone*, *Bentheledone* and *Graneledone*. These genera, the closest geographically to *Microeledone*, also occur at the greatest depths amongst those octopuses with a single row of suckers. Depth information provided below comes from Voss (1988*a*, 1988*b*), Voss and Pearcy (1990), Lu and Stranks (1992, 1994), O'Shea (1999) and Norman and Hochberg (unpublished data).

Microeledone was trawled from 980–1000 m deep. *Thaumeledone brevis* has been recorded between 800 and 3931 m, while *T. gunteri* is known only from the female holotype collected from 410 m. O'Shea's new species were captured from depths over 1000 m: *T. marshalli* 1999–2542 m; *T. zeiss* 1052–1386 m. *Bentheledone rotunda* (Hoyle, 1885) was collected from 3596 m and *B. albida* (Berry, 1917) from 3111 m. A specimen of an undescribed species of *Bentheledone* also has been collected at a depth of 3475 m off Peru (Cardosa and Hochberg unpublished data). Except for *Graneledone gonzalezi* Guerra, González and Cherel, 2000 found at depths of 200–950 m in the subantarctic Indian Ocean (Heard Island), all records of the seven or more species of *Graneledone* are from 477–2756 m deep.

The Antarctic genera with a single row of suckers show wider depth ranges, extending from shallow depths into deeper waters (e.g. *Pareledone* 15–1116 m; *Megaleledone* 120–761 m). This may reflect the absence of temperature thermoclines in polar latitudes. The remaining genera with a single row of arm suckers are from shallower waters: *Eledone moschata* (Lamarck, 1798) (< 300 m), *E. cirrhosa* (Lamarck, 1798) (10–800 m), *E. caparti* Adam, 1951 (60–170 m), *E. massyae* Voss, 1964 (73 m), '*Eledone*' *palari* Lu & Stranks, 1992 (110–620 m), *Vosseledone charrua* (10–200 m), *Tetracheledone spinicirrus* Voss, 1955 (183–544 m) and *Velodona togata* Chun, 1915 (290–749 m).

It is unknown whether the morphological similarities between *Microeledone* and the other three deeper genera (*Graneledone, Thaumeledone* and *Bentheledone*) constitute

evidence of shared evolutionary history or are instead habitat-related convergences in form. Voss (1988*a*) suggested many characters of deep-water octopuses related to their environment. The following of Voss' characters are found in this suite of deep-water taxa with a single row of suckers: loss of ink sac, loss or reduction of crop diverticulum, reduction in number of gill lamellae and marked extension of the web. Insights into the influence of phylogeny *v.* convergence (due to habitat) will not be possible until better reference material is obtained, more detailed morphological descriptions are produced for all groups, and several phylogenetic studies based on molecular characters that are currently in progress are completed.

The single specimen of *Microeledone mangoldi* was collected through the MUSORSTOM surveys of seamounts and deep habitats in tropical latitudes of the Pacific Ocean. These surveys encountered many rare and unusual forms including numerous taxa previously thought extinct (see Richer de Forges 1990). At this stage there are limited insights offered by a single specimen of this new taxon; however, the distinctive radula of this octopus is unlike any previously reported. Four other new genera are currently being described from deep waters in this south-west corner of the Pacific Ocean (works in progress). With so many weird and wonderful animals coming to light, it is an exciting time for octopus systematics.

Acknowledgments

This study was funded by Visiting Curator grants to the senior authors (MDN and FGH) between 2001 and 2003. These authors would like to thank the third author, Renata Boucher-Rodoni and her husband Guy for their kind hospitality during our stays in Paris. Phillipe Bouchet collected and preserved the specimen upon which this description is based. This research was supported through funding to the senior authors by the Australian Biological Resources Study. Line illustrations were prepared by Peter Gaede.

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Appendix 1. Additional material examined

Bentheledone rotunda (Hoyle, 1885)

Holotype. 1F (immature and poor condition): total length ~150 mm, Southern Ocean, 53°55′S, 108°35′E, 1950 fms, 3 Mar. 1874, coll. Challenger Expedition (BMNH 1890.1.24.6).

Eledone cirrhosa (Lamarck, 1798)

1M (mature): 74.4 mm ML, Delante de Barcelona, Spain, 41°23′N, 2°11′E, 180 m, 12 Nov. 1978, coll. E. Morales (USNM 730592).

Eledone moschata (Lamarck, 1798)

1M (mature): 77.1 mm ML, Gulf of Tunisia, 36°57′N, 10°28′E, 64–75m, 30 Mar. 1967 (USNM 577099).

Tetracheledone spinicirrus Voss, 1955

1M (mature): 71.9 mm ML, Off Oregon, Stn 1547, 24°28′N, 83°30′W, 210 fms, 17.VI.1956 (MRHNB IG 22810).

Thaumeledone brevis (Hoyle, 1885)

Syntypes. 3F (immature), largest 20 mm ML, south Atlantic Ocean, off Monte Video (off mouth of Rio de la Plata), 37°17′S, 53°52′W, 600 fm (1097 m), 14 Feb. 1876, coll. H.M.S. Challenger, station 320, trawl, green sand (BMNH 89.4.24.50–1).

Thaumeledone gunteri Robson, 1930

Holotype. **Antarctica:** 1F (mature), 34 mm ML, (Scotia Sea, NE of South Georgia Island), 53°48.5′S, 35°57.1′W, 401–411m (219–224 fm), 21 Jan. 1927, coll. R/V Discovery, station 158, large dredge (net DLH), rock bottom (BMNH 1951.4.26.50); 1F (mature), 39 mm ML, off Enderby Land, 66°03.0′S, 49°50.0′E; 690–911 m; 29 Nov. 1985, coll. M. D. Norman, ANARE, M/S Nella Dan, station HRD-013, epibenthic sled, through sea-ice (MV F65706); 1F (mature), 50.5 mm ML, 1M (immature), 38.5 mm ML, 62°11.3′S, 42°43.3′W, 1228–1400 m; 20 Feb. 1976, coll. USARP/SOSC, R/V Islas Orcada, cruise 876, station 117, 10 ft Blake trawl (USNM 817378). South Shetland Islands: 1M (mature), 37mm ML, 1M (immature), 23.7 mm ML, 1F (submature), 23.8 mm ML, 62°00′S, 61°09′W, 0–1437 m; 8 Aug. 1962, coll. Johnson, Matsudo, J. Mohr & J. Paxton, R/V Eltanin, station USC-138, 10 ft Blake trawl (USNM 817371).

Velodona togata Chun, 1915

1M (mature), 94.0 mm ML, off Mozambique, 16°20.0′S, 40°8.0′E, 500 m, 16 Jun. 1994 (SAM S3061).