THE SHARKCLUB OCTOPUS, *GALEOCTOPUS LATERALIS*, A NEW GENUS AND SPECIES OF DEEP-WATER OCTOPUS FROM THE WESTERN PACIFIC OCEAN (CEPHALOPODA: OCTOPODIDAE)

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ABSTRACT

French and Australian research expeditions over the past three decades, to the deeper waters of the tropical Pacific Ocean, have encountered a distinctive new octopus. *Galeoctopus lateralis* is described here from 200–400 m deep in the southern and western Pacific Ocean. This small octopus is recognized by a distinctive jaw-like ligula in mature males, superficially resembling the head and jaws of a shark (complete with teeth-like lugs). Other distinctive characters include a lateral mantle ridge, skin sculpture including stellate papillae, and swollen distal oviducts in females. This combination of characters warrants recognition as a distinct genus. Relationships with other octopodid genera are discussed. We propose that the unique form of the male reproductive organ has evolved as a mechanism for reduction of sperm competition. The mouth-like ligula pit may function to pierce, rupture, grip and/or remove the sperm bulbs of previous suitors from the distal oviducts of the female. This morphology is compared with parallel structures in other cephalopods.

INTRODUCTION

In the mid-1970s collaborations between the Muséum National d'Histoire Naturelle in Paris (MNHN) and the then Office de la Recherche Scientifique et Technique Outre-Mer (ORSTOM) instigated a series of deep-sea surveys throughout the tropical Pacific Ocean, which received the acronym MUSORSTOM. This extensive ongoing programme has undertaken major collecting surveys of the shallow and deep waters of the Philippines, New Caledonia, Vanuatu, Fiji, Wallis and Futuna Islands, Tonga and the Marquesas Islands, as well as deep-sea mountain ranges such as the Norfolk Ridge and Lord Howe Rise. Among the treasure trove of resulting material is a distinctive and unique deep-sea octopus which is described here.

This new deep-water octopus is one of the many undescribed taxa recognized in the Indo-Pacific region over the past two decades. More than 150 new species within the family Octopodidae await formal description (Norman & Hochberg, 2004).

Aside from descriptions of new species, the taxonomy of the family Octopodidae at a generic level is also in need of major revision. Over 90% of the more than 200 species included in this family to date have been placed in the catch-all genus *Octopus*, primarily on the basis of historical convention and the shared attributes of eight arms, an ink sac and two rows of suckers. A number of taxonomic studies based on morphology have recognized distinct species-complexes within the genus *Octopus* as it currently stands (e.g. Robson, 1929; Adam, 1954; Norman, 1992, 2000; Norman & Hochberg, 1994; Norman & Sweeney, 1997). Molecular studies of the phylogeny of octopuses of the family Octopodidae (Hudelot, 2000) have demonstrated that the genus *Octopus* is polyphyletic. Many of the groups proposed in the earlier morphological studies are supported by molecular sequence data. Historical generic names require reconsideration (and potential resurrection), and many new genera need to be introduced.

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Earlier work by the authors (Norman, Hochberg & Lu, 1997) on the octopuses in the Banda and Arafura Seas, Indonesia (also based on MUSORSTOM material) suggested that the octopod fauna of slope depths (200–1000 m) in tropical latitudes had no apparent phylogenetic links with the octopuses of adjacent shallow waters (<200 m). The new taxon described here follows this pattern and is sufficiently distinct to warrant status as a new genus.

MATERIAL AND METHODS

Specimens of this octopus were found amongst MUSORSTOM material from the Philippines, Indonesia, New Caledonia, Vanuatu, Fiji and Tonga during visits to the Paris Museum in 2001–2003. Four additional specimens were found in the collections of Museum of Victoria, Australia (MV), having been caught in Commonwealth Scientific and Industrial Research Organisation (CSIRO) surveys off the Great Barrier Reef in the mid-1980s. All specimens were captured by trawl, fixed in 10% formalin and stored in 70% ethanol.

Abbreviations: F, female; M, male; ML, mantle length.

The taxonomic methodology and diagnostic characters used in the description below follow Roper & Voss (1983) and Norman & Sweeney (1997).

SYSTEMATIC DESCRIPTIONS

Family Octopodidae d'Orbigny, 1840

Galeoctopus new genus

Diagnosis: Small moderately muscular octopus [mantle length (ML) to 37 mm, total length to 165 mm, wet weight to 18 g]; mantle muscular, spherical to roughly square; mantle aperture moderate, ~50% of neck circumference. Eyes of moderate size, head always narrower than mantle. Stylets long and chitinous

(not mineralized). Funnel organ very large, W-shaped with limbs of equal length. Arms of moderate length, thin and tapering to fine tips, 2.7–4.4 times ML, approximately equal in length, dorsal pair slightly shorter; arm autotomy absent. Suckers biserial and closely set; suckers normal, functional to tips of all arms other than hectocotylized arm of males; enlarged suckers absent; sucker counts on normal arms to 161; hectocotylized arm with 35–43 suckers. Webs deep (17–30% of longest arm) and approximately equal in length (dorsal web slightly shorter). Interbrachial aquiferous (water) pore system absent. Gills with 10–11 lamellae per demibranch plus terminal lamella. Third right arm hectocotylized, shorter than opposite arm (~40–60%); copulatory organ consists of large and unique barrel-shaped ligula (11–20% of arm length), with large calamus (>55% of ligula length); ligula groove enclosed deep within tip of ligula, opening reduced to transverse crescent-shaped mouth, floor of groove with paired raised papillae. Crop with large diverticulum; posterior salivary glands large, similar in length to buccal mass; intestine short and almost linear. Radula with all 7 series of teeth plus marginal plates. Rachidian tooth with long mesocone and asymmetrical arrangement of 1–2 lateral cusps each side, migrating from lateral to medial position over 7 rows. Terminal organ (penis) of moderate size with simple single diverticulum; spermatophores large (equal to or slightly larger than ML), unarmed. Females with swollen distal oviducts. Dorsal surfaces of body and arms mottled orange to red-brown in colour. Skin texture of numerous raised rounded papillae on dorsal surfaces, larger ones being stellate. Lateral ridge present.

Type species: *Galeoctopus lateralis* new species.

Etymology: From the Greek '*galeos*', shark, referring to the shark-like shape of the ligula.

Remarks: The first step in reviewing the generic level taxonomy of the family Octopodidae is to delineate taxa clearly distinct from the genus *Octopus sensu stricto*, as represented by the type species of this genus, *Octopus vulgaris*, and its relatives (a group treated in the literature as the '*Octopus vulgaris* species-complex'; Norman & Sweeney, 1997). The new genus *Galeoctopus* described here is defined by the combination of the following characters (as compared with those features found in *Octopus s.s.*): distinctive barrel-shaped ligula with partially enclosed transverse ligula groove (*vs* simple and small ligula with open longitudinal groove); huge calamus, >55% of ligula length (*vs* small calamus <20%); short hectocotylized arm, 40–60% length of opposite arm (*vs* >80%); stellate larger papillae on dorsal surfaces (*vs* rounded or polygonal primary papillae); absence of enlarged suckers (*vs* enlarged suckers in mature males); lateral ridge (*vs* absent); linear and robust ejaculatory apparatus of the spermatophore with linear and narrow inner core (*vs* a narrow ejaculatory apparatus containing a coiled core). No other known octopus has a copulatory organ comparable to the distinctive form found in this new taxon (see Discussion for interpretation of the function of this highly modified structure).

Other octopuses, particularly many deeper water forms, also possess the lateral skin ridge found round the periphery of the mantle of *Galeoctopus lateralis* (Fig. 1B). This structure appears linked to a life in and/or on soft sediment substrates (see Life History below for discussion of its function). *Galeoctopus lateralis* can be clearly distinguished from these other octopuses. *Benthoctopus leioderma* (Berry, 1911) and members of the genus *Bathypolypus* Grimpe, 1921 possess a lateral ridge but are clearly distinguished from *Galeoctopus lateralis* as they all lack an ink sac. *Bathypolypus* is further distinguished by a V V-shaped funnel organ and the lack of a crop diverticulum. Members of the deep-water genus *Scaeurgus* Troschel, 1857 are similar in appearance to *Galeoctopus lateralis*, sharing a lateral ridge, large stylets and similar arm and web lengths. They are distinct from the new taxon through hectocotylization of the left third arm (instead of right), a peanut-shaped copulatory organ with open longitudinal groove and sharp calamus, a double-plaited sperm cord (*vs* single) and a colour pattern of four distinct large black spots on the dorsal mantle (*vs* none). Four Australian species currently placed in the genus *Octopus* also share some similarities with *Galeoctopus lateralis*. *Octopus australis* Hoyle, 1885, *O. berrima* Stranks and Norman, 1993, *O. bulbus* Norman, 2001 and *O. micros* Norman, 2001 all possess a lateral ridge. The morphologies of these taxa are compared against *Galeoctopus lateralis* in Table 1. None possess the distinctive ligula of our taxon and all possess fewer gill lamellae (<10 per demibranch *vs* 10–11), higher hectocotylized arm sucker counts (>60 *vs* 35–43) and a smaller calamus (<45% *vs* >55%). *Eledone palari* Lu & Stranks, 1992 (deep water Australia), *Tetracheledone spinicirrus* Voss, 1955 (deep water Cuba), the Antarctic octopus *Megaleledone senoi* Taki, 1961 and members of the genus *Pareledone* Robson, 1932 all possess a lateral ridge. They also possess a single row of suckers clearly delineating them from *Galeoctopus lateralis* (that possesses two rows of suckers).

Galeoctopus lateralis new species

Holotype: 1M: 24.6 mm ML, MNHN 3787, Tonga, North Kotu group, 19°52′S, 174°42′W, 417–424 m, N/O *Alis*, BORDAU 2, beam trawl, stn CP 1562, coll. Bouchet, Warén & Richer, 8 June 2000.

Paratypes: **New Caledonia**: 1M: 25.2 mm ML, MNHN 2115, Loyaute Ridge, off Lifou Island, 20°47′S, 167°05′E, 380 m, N/O

Table 1. Comparison of *Galeoctopus lateralis* with other Indo-West Pacific octopuses with a lateral ridge.

	G. lateralis	*Octopus australis*	*Octopus berrima*	*Octopus bulbus*	*Octopus micros*
Maximum size (mm ML)	37	72	105	50	25
Arm length (× ML)	2.7–4.4	3–4.3	2–4	4.9–5.6	2.3–2.7
Arm formula	4 = 3 = 2 > 1	3 > 2 > 4 > 1	2 = 3 > 4 > 1	1 > 2 > 3 > 4	4 = 3 = 2 > 1
Web depth (% arm)	17–30	15–32	20–25	10–12	22–27
Gill count	10–11	7–9	7–8	7–8	6
Sucker count max (normal arms)	M: 142, F: 161	124–217	138–218	190	150
Sucker size (% ML)	6–8	9–15	6–13	7–10	10–12
Hect. arm length (% opposite arm)	40–60	72–89	63–97	56	86
Hect. arm sucker count	35–43	62–77	66–78	91, 94	85–93
Ligula length (% arm)	11–20	11–16	11–16	8–9	6
Calamus length (% ligula)	>55	15–29	15–20	17–18	44

Table 2. *Galeoctopus lateralis* new species: male counts and measurements (mm).

Repository	MNHN	MNHN	MNHN	MNHN	MNHN	MNHN	MV	MV	MNHN
Catalogue no.	3787	3771	2115	2114	3786	2118	F97379	F97380	???
Locality	Tonga	Fiji	New Caledonia	Vanuatu	Tonga	New Caledonia	Australia	Australia	Indonesia
Status	Holotype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype	Paratype
Maturity	Mature	Mature	Mature	Mature	Mature	Mature	Mature	Mature	Mature
Total length	103	144	106	121	131	112	165	154	130
Total wet weight (g)	9.7	17.8	9.2	16.5	14.2	11.3	15.1	15.4	12.0
Dorsal mantle length	24.6	32.3	25.2	31.0	29.8	25.8	36.7	36.7	28.0
Ventral mantle length	18.4	23.2	17.7	25.5	27.1	18.6	31.2	30.8	21.2
Mantle width	21.5	25.7	21.7	25.9	23.5	21.9	23.3	25.0	23.4
Head width	17.6	20.2	16.7	22.4	19.7	16.9	18.0	19.2	18.0
Funnel length	11.2	13.4	10.4	14.1	12.7	11.7	d	13.4	10.9
Free funnel length	3.5	2.8	4.2	5.7	5.0	4.2	d	2.7	4.5
Funnel organ length: lateral limb	6.1	7.9	7.0	8.0	8.5	7.1	d	InD	InD
Funnel organ length: medial limb	6.8	8.7	8.0	8.5	9.4	7.8	d	InD	InD
Web depths (L, R)									
A	13	18	d	18	17	18	d	16	16
B	15 14	21 19	15 d	21 d	17 20	19 19	d d	22 22	15 18
C	19 16	23 18	14 17	23 d	20 23	19 20	d d	22 21	18 19
D	20 17SpG	19 22SpG	17 18SpG	25 20SpG	20 20SpG	20 19SpG	d d	21 17SpG	19 20SpG
E	d	19	15	21	18	19	d	17	15
Web depth formula	C = D > B > A	~ =	~ =	B = C = D = E > A	~ =	~ =	d	B=C=D>A=E	B = C = D > A = E
Arm lengths (L, R)									
1	59 d	d d	d d	68 d	d d	63 65	d 99	d 90	65 67
2	68 72	d 93	66 76	d d	d 73	82 79	d 120	111 103	D 69
3	73	105	76	d	95	75	d	d	97
Hc	41	54	43	58	47	46	50	45	39
4	65 d	d d	73 d	d 84	d 81	76 77	97 d	d d	D 88
Arm length formula	~Equal	n/a	Equal	4 > 3 = 1	3 > 4 > 2	4 = 3 = 2 > 1	2 > 1 = 4	n/a	2 > 4 > 1
Arm width	3.5	4.6	4.2	5.3	4.3	4.0	5.0	4.6	3.7
Sucker diameter	1.9	2.3	2.0	2.2	1.9	1.7	2.2	2.3	2.0
Sucker counts (L, R)									
1	98 d	d d	d d	104 d	d d	96 98	–	–	–
2	116 122	d 122	116 119	d d	d 108	116 d	– 116	– 126	–
3	127	130	131	d	119	108	–	–	142
Hc	37	40	39	41	38	43	43	37	35
4	119 d	d d	115 d	100 98+	d 115	106 105	–	–	–
Gill count: outer/inner demibranch (L, R)	10/11 10/10	10/10 10/10	10/10 10/10	10/11 10/11	10/11 11/11	10/10 10/11	10/10 10/10	10/10 10/11	10/10 10/10
Ligula length	6.7	7.6	5.8	6.7	6.6	5.1	6.6	7.8	7.8
Calamus length	4.5	5.1	4.4	3.8	4.0	3.4	5.0	5.2	4.8
Terminal organ length	6.6	9.0	8.5	8.4	9.3	7.1	11.0	9.2	5.9
Diverticulum length	2.8	3.8	3.7	3.1	4.5	3.4	4.5	3.9	3.3
Spermatophore count	3	3	3	8	5	3	2	3	4
Spermatophore length	26	33	25	28	30	31	28	27	27
Spermatophore width	0.8	1.0	0.7	0.8	0.9	0.8	0.7	0.8	0.8
Sperm reservoir length	8	13.5	8	10	11	10	12	11	10
Spermatophore cord whorls	~70	>50	~60	~60	InD	71–88	~70	InD	d

A–E, Web sectors starting from dorsal sector; d, damaged; InD, indistinct; Hc, hectocotylized arm of male; n/a, not applicable.

Table 3. *Galeoctopus lateralis* new species: female counts and measurements (mm).

Repository	MV	MV	MNHN
Catalogue no.	F76981	F97989	???
Locality	Australia	Australia	Indonesia
Status	Paratype	–	–
Maturity	Submature	Submature	Submature
Total length	135	143	152
Total wet weight (g)	15.5	8.5	11.2
Dorsal mantle length	31.5	28.9	27.0
Ventral mantle length	24.2	23.4	19.8
Mantle width	24.7	21.0	21.3
Head width	18.9	d	17.5
Funnel length	12.2	10.7	9.9
Free funnel length	3.3	d	3.0
Funnel organ length – lateral limb	6.3	d	5.5
Funnel organ length – medial limb	7.4	d	6.1
Web depths (L, R)			
A	19	20	16
B	21 19	19 20	18 19
C	22 21	d d	19 17
D	22 21	d d	20 d
E	20	17	18
Web depth formula	~ =	A = B > E	B = C = D = E > A
Arm lengths (L, R)			
1	73 74	77 83	70 82
2	d 96	97 106	105 118
3	110 97	95 101	115 d
4	91 d	87 89	99 d
Arm length formula	4 = 3 = 2 > 1	2 = 3 > 4 > 1	2 = 3 > 4 > 1
Arm width	5.5	3.4	4.1
Sucker diameter	2.3	2.1	2.1
Sucker counts (L, R)			
1	–	–	–
2	–	–	–
3	161 159	155 160	151 d
4	–	–	–
Gill count: outer/inner demibranch (L, R)	10/10 10/10	10/InD 10/InD	d/d 10/10

A–E, Web sectors starting from dorsal sector; d, damaged; InD, indistinct.

Alis, MUSORSTOM 6, Waren dredge, stn DW397, 13 February 1989; 1M: 25.8 mm ML, MNHN 2118, east coast, 20°35′S, 164°58′E, 410–430 m, N/O *Alis*, BATHUS 1, beam trawl, stn CP695, 17 March 1994. **Tonga**: 1M: 29.8 mm ML, MNHN 3786, North Ha'apai group, 19°42′S, 174°31′W, 391–402 m, N/O *Alis*, BORDAU 2, beam trawl, stn CP 1572 coll. Bouchet, Warén & Richer, 11 June 2000. **Vanuatu**: 1M: 31.0 mm ML, MNHN 2114, south of Espiritu Santo Island, 15°41′S, 167°02′E, 398–400 m, N/O *Alis*, MUSORSTOM 8, beam trawl, stn CP1136, 11 October 1994. **Fiji**: 1M: 32.3 mm ML, MNHN 3771, south-east Vanua Levu, 16°39′S, 179°37′E, 360–380 m, N/O *Alis*, BORDAU 1, beam trawl, stn CP 1406, coll. Bouchet, Warén & Richer, 25 February 1999. **Australia**: Queensland, off Great Barrier Reef, east of Tully: 1F: 31.5 mm ML, MV F76981, 18°00′S, 147°01′E, 220 m, station SO1/86/20, *Soela*, 12 January 1986, 0155 h; 1M: 36.7 mm ML, MV F97380, 17°59′S, 147°05′E-17°59′S, 146°06′E, 302–300 m, 0500 h, station SO1/86/15, *Soela*, 11 January 1986; 1M: 36.7 mm ML, MV F97379, 17°59′S, 147°01′E–17°57′S, 146°58′E, 220 m, 0925 h, station SO1/86/40, *Soela*, 15 January 1986. **Indonesia**: Makassar Strait: 1M: 28.0 mm ML, MNHN unreg, 1°57′S, 119°15′E, 252–215 m, CORINDON 2, stn CH271, 7 November 1980; 1F: 27.0 mm ML, MNHN unreg, 1°57′S, 119°15′E, 220–180 m, CORINDON 2, stn CP273, 7 November 1980.

Other material: **New Caledonia**: 1M: 18.1 mm ML, MNHN, 19°01'S, 163°16'E, 275–330 m, N/O *Vaubin*, MUSORSTOM 4, beam trawl, stn CP172, 17 September 1985. **Vanuatu**: 1M: 20.1 mm ML, MNHN 2117, south of Espiritu Santo Island, 15°42′S, 167°03′E, 360–371 m, N/O *Alis*, MUSORSTOM 8, beam trawl, stn CP1137, 11 October 1994. **Philippines**: Off Lubang Island: 1M: 18.9 mm ML, MNHN, 14°01′N, 120°20′E, 192–209 m, MUSORSTOM 2, beam trawl, stn CP66, 29 November 1980; 1M: 37.0 mm ML, MNHN, 14°00′N, 120°18′E, 188–195 m, MUSORSTOM 2, beam trawl, stn CP18, 22 November 1980. **Australia**: 1F: 28.9 mm ML, MV F97989, Queensland, 70 km east of Dunk Island, 18°00.7′S, 147°01.4′E–17°57.4′S, 146°58.3′E, 202–212 m, station SO6/85/43, *Soela*, 29 November 1985. **Indonesia**: Makassar Strait: 1M: 21.0 mm ML, MNHN, 1°57′S, 119°15′E, 220–180 m, CORINDON 2, stn CP273, 7 November 1980, coll. ORSTOM/IRD; 2M: 25.0, 26.8, 1F: 19.2 mm ML, MNHN, 1°57′S, 119°15′E, 252–215 m, CORINDON 2, stn CH271, 7 November 1980, coll. ORSTOM/IRD.

Etymology: Specific name from the Greek *lateralis*, referring to the skin ridge or keel around the lateral mantle.

Diagnosis: As this new genus is currently monotypic, the above diagnosis for the genus applies at both the generic and specific levels.

Description: The following description is based on nine mature males and three submature females. Counts and measurements for this material are presented in Tables 2 and 3. Indices are provided in the text as means followed by ranges in parenthesis.

Small moderately robust species (Fig. 1A), mantle length (ML) to at least 37 mm in males, 32 mm in females; total length to 165 mm; weight (wet) to 18 g. Mantle round to squat-ovoid (Fig. 1A, B) with muscular walls; mantle width approximately equal to ML [M, 79.5 (63.5–87.4)%; F, 76.7 (72.7–78.9)%]. Head of moderate width, approximately two-thirds of ML [M, 63.3 (49.0–72.3)%; F, 60.0, 64.8%]. Head narrower than mantle [M, 79.6 7 (6.9–86.5)%; F, 76.5, 82.2% of mantle width]. Eyes of moderate size and slightly pronounced. Stylets present, long, almost half ML (13.7 mm long in MNHN 3786, 46.0% ML) and non-mineralized (Fig. 1F). Pallial aperture of moderate width, approximately half mantle circumference. Funnel large and wide [M, 42.1 (36.5–45.5)%; F, 37.5 (36.7–38.7)% ML); free portion short, less than half funnel length [M, 33.7 (20.1–41.3)%; F, 27.0, 30.3%]. Funnel organ W-shaped (Fig. 1C), located towards anterior end of dorsal funnel; very large, medial limbs about two-thirds length of funnel [M: 67.3 (60.3–76.9)%; F, 60.7, 61.5%]; lateral limbs almost as long as medial limbs [M, 90.6 (87.5–94.1)%; F, 85.1, 90.2%].

Arms of moderate length, longest approximately three to four times ML [M, 3.1 (2.7–3.5); F, 3.9 (3.5–4.4)]; width moderate [M, 14.6 (12.5–17.1)%; F, 14.8 (11.8–17.5)% ML]; arms roughly square in cross-section, evenly tapering in width from base to long thin distal tip. Arms approximately equal in length, dorsal pair often slightly shorter. Arm autotomy absent. Suckers biserial, small and closely spaced; infundibulum fleshy with fine radial cushions; rim finely scalloped; diameter of suckers small [M, 6.9 (6.0–7.9)%; F, 7.5 (7.3–7.8)% ML]. No enlarged suckers in either sex. Sucker counts around 130–150 on normal arms (116–142 in males; 151–161 in females). Hectocotylized arm of males with 35–43 suckers.

Webs thick, deep relative to arm length [deepest M, 24.0 (19.8–29.8); F, 18.6 (16.9–20.0)% of longest arm length]; webs approximately equal in length, dorsal sector slightly shorter. Web margins poorly developed. Interbrachial aquiferous (water) pore system absent.

Third right arm hectocotylized in males; short [1.6 (1.2–1.9) times ML], approximately half of length of opposite arm [52.5 (40.2–61.3)% of opposite arm]. Copulatory organ (Fig. 1D, E) large and fleshy [14.6 (11.1–20.0)% of hectocotylized arm length]. Ligula barrel-shaped with groove represented as unique deep pit opening to exterior through transverse crescent-shaped slit. Floor (proximal face) of opening lined with small paired papillae. Calamus very large, over half ligula length [66.5 (56.7–75.9)%]. Spermatophore groove and associated web wide and robust, restricting straightening of hectocotylized arm in preserved material.

Gills with 10–11 lamellae per demibranch (typically 10) plus terminal lamella.

Digestive tract (Fig. 2A). Buccal mass of moderate size, around two-thirds length of digestive gland. Anterior salivary glands of moderate size, approximately one-third length of buccal mass; posterior salivary glands well developed, slightly larger than buccal mass. Crop with distinct diverticulum. Stomach bipartite; caecum with approximately one whorl, ducts to digestive gland short and wide. Intestine short and wide, almost linear, without distinct U-shaped loop. Digestive gland square to ovoid in shape, completely enclosed in an iridescent silver membrane. Pancreatic tissue not evident through iridescent membrane. Ink sac large and embedded in mid-ventral surface of digestive gland. Anal flaps present, elongate with distinct paddles.

Upper beak (Fig. 2B) hood of moderate size, under 40% of beak length (37.1% in male paratype, MNHN 2115); rostrum bluntly hooked, cutting edge rounded; crest slightly rounded. Lower beak (Fig. 2C, D) hood and crest slightly rounded; rostrum worn in specimen examined (Fig. 2D); lateral walls

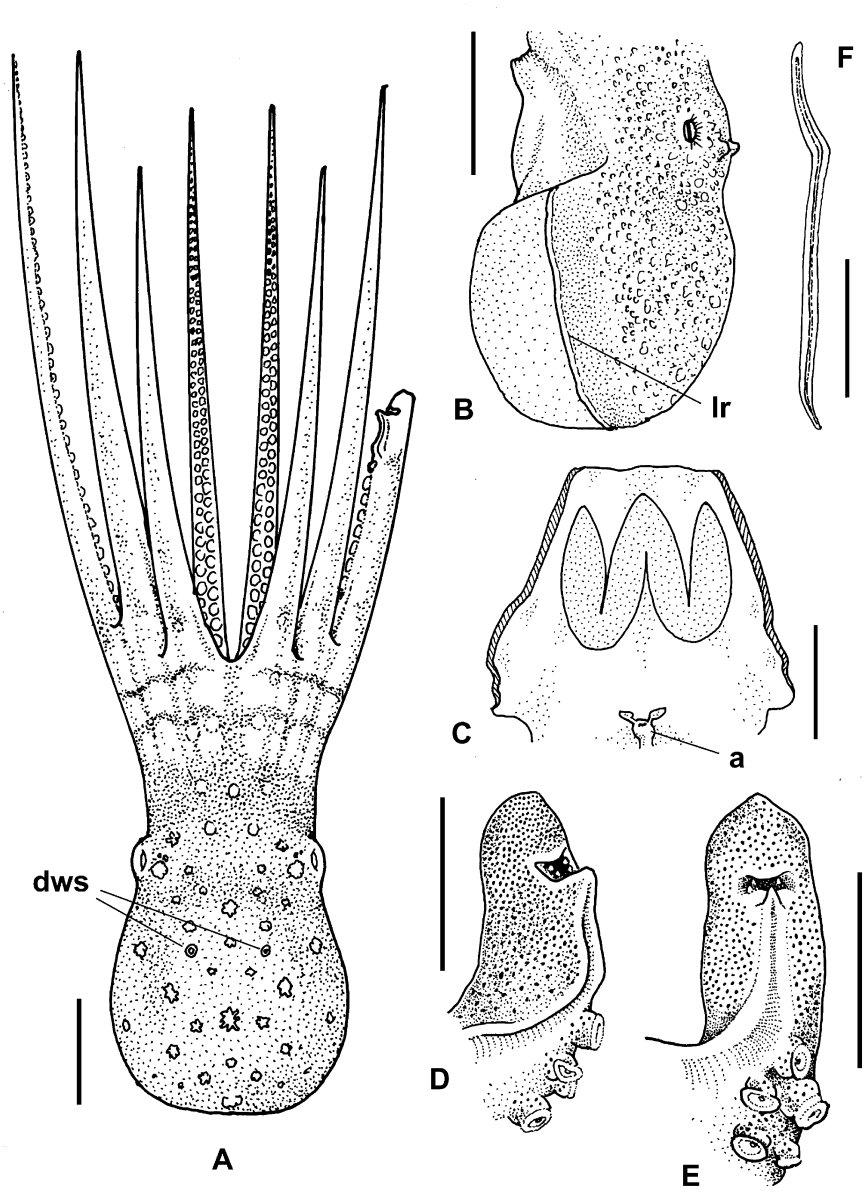

Figure 1. *Galeoctopus lateralis* new species. Holotype (24.6 mm ML male, MNHN 3787). **A.** Dorsal view of whole animal. **B.** Lateral view of mantle. **C.** Funnel organ showing position in funnel. **D.** Copulatory organ, left lateral view. **E.** Copulatory organ, oral view. **F.** Stylet from 29.8 mm ML male paratype (MNHN 2114). Abbreviations: a, anus; dws, dorsal white spots *sensu* Packard & Sanders (1971); lr, lateral ridge. Scale bars: **A**, **B** = 10 mm; **C–F** = 5 mm.

slightly flared with moderately incised posterior margin. Radula (Fig. 4D, E) with 7 teeth plus 2 marginal plates per transverse row. Rachidian tooth has long mesocone with 1 (rarely 2) cusp on each side in an asymmetrical arrangement. Lateral cusps migrate from medial to lateral position over approximately seven rows. First lateral teeth almost square with single medial cusp. Second lateral teeth with single large cusp at medial end. First marginal teeth tusk-shaped. Marginal plates square.

Male reproductive tract (Fig. 3A). Terminal organ linear and of moderate size [27.8 (21.1–33.7)% ML]; diverticulum simple and of moderate size [44.5 (36.9–55.9)% of organ length]; genital aperture subterminal. Vas deferens duct relatively short and robust. Spermatophoric gland long and thin with loose recurved coil. Accessory gland long and thin, distal end reflexed. Appendix large, extending to anterior tip of spermatophore sac. Spermatophore storage sac long and thin; spermatophores present in low numbers (2–8 in storage sacs of examined males).

Spermatophores (Fig. 3B, D) long (25–33 mm), equal to or longer than ML [1.0–(0.7–1.2) times ML]; narrow [width 2.9 (2.5–3.1)% of spermatophore length]; spermatophores unarmed. Ejaculatory apparatus with numerous fine coils (Fig. 3C), which may form external ridges on everted spermatophore. Sperm reservoir <50% spermatophore length [36.6 (30.8–42.9)%]; sperm cord coiled in approximately 50–90 regular coils.

No mature females reported. Reproductive tract of submature females (Fig. 3E) with distinct swollen distal oviducts. Muscular flange of unknown function at distal tip of oviducts. Eggs distinct in submature ovary but mature egg size unknown.

Colour of live animals unknown. Dorsal body and arms of well-preserved specimens mottled orange brown in colour. Papillae orange cream in colour. Three slightly darker transverse bands present across dorsal arm crown (Fig. 1A). Lateral mantle with band of dense small chromatophores between lateral ridge and ventral limit of papillae. Ventral surfaces of mantle below the lateral skin ridge are white with numerous, slightly larger, evenly scattered chromatophores (Fig. 1C). Faint 'dorsal white spots' (*sensu* Packard & Sanders, 1971) present on dorsal mantle (Fig. 1A). Visceral mass encased in membrane containing numerous large chromatophores.

Dorsal surfaces of skin covered in numerous small and rounded papillae, larger ones roughly stellate in shape (Fig. 4A). Patch and groove system absent. Arrangement of larger papillae symmetrical as shown in Figure 1A. Larger papillae extend to lateral mantle, ceasing dorsal to the lateral ridge (Fig. 1B). Small rounded papillae visible on ventral mantle in several

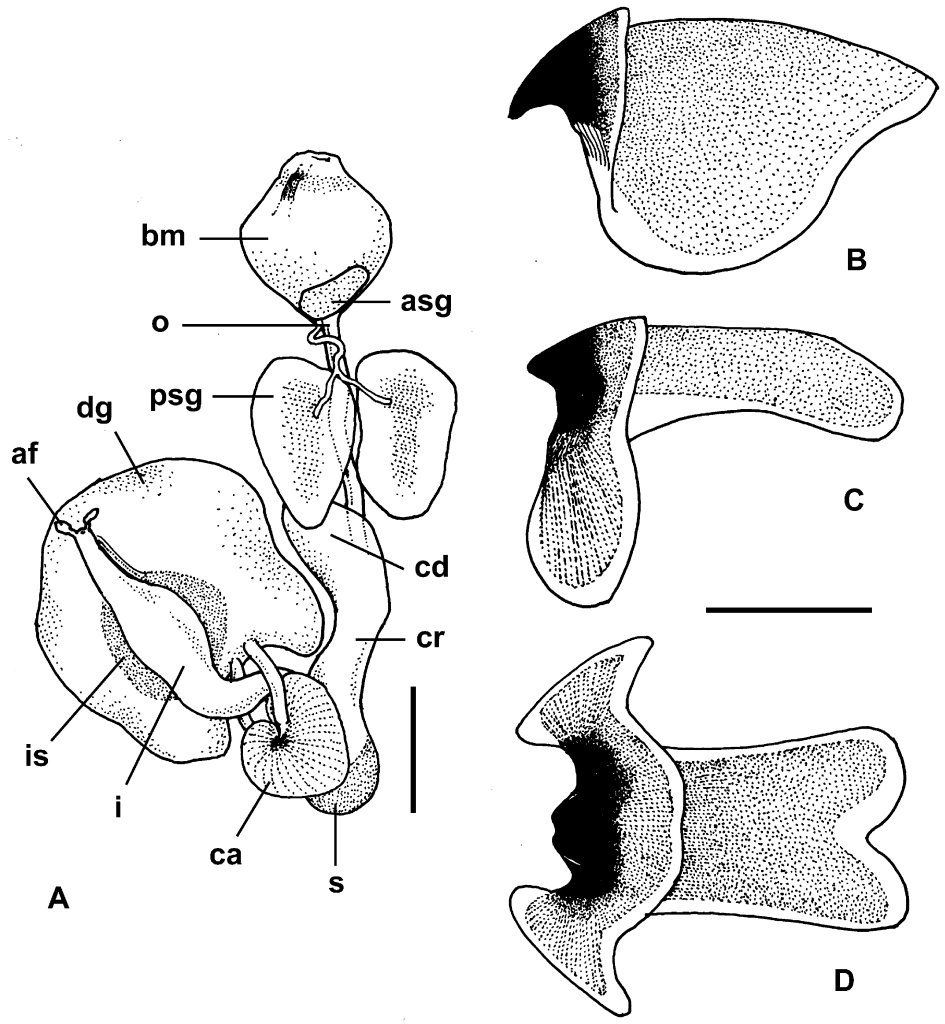

Figure 2. *Galeoctopus lateralis* new species. Digestive system of 25.2 mm ML male paratype (MNHN 2115). **A.** Digestive tract. **B.** Upper beak, left lateral view. **C.** Lower beak, left lateral view. **D.** Lower beak, ventral view with worn tip of rostrum. Abbreviations: af, anal flaps; asg, anterior salivary gland; bm, buccal mass; ca, caecum; cr, crop; cd, crop diverticulum; dg, digestive gland; i, intestine; is, ink sac; o, oesophagus; psg, posterior salivary gland; s, stomach. Scale bars: **A** = 5 mm; **B–D** = 2 mm.

specimens. Single large and several smaller papillae over each eye (Fig. 1B). Lateral mantle ridge present (Figs 1B, 4B).

Distribution: This species occurs at slope depths off the continental shelf of Australia and oceanic islands in the tropical central and western Pacific Ocean. It is reported here from Tonga, Fiji, Vanuatu, New Caledonia, Coral Sea (Australia), Makassar Strait (Indonesia) and the Philippines (Fig. 5). The shallowest depth record is a trawl at 188–192 m, the deepest a trawl from 410–430 m.

Life history: Nothing is known of the behaviour of this small octopus. The presence of a lateral ridge is typically found in octopuses that inhabit mud or sand habitats (Norman, 2001). The well-developed lateral ridge in *Galeoctopus lateralis* suggests that it may also be a soft-sediment species.

The diet of *Galeoctopus lateralis* consists of at least fish and crustaceans. The contents of the digestive system were examined in one animal (MNHN 2115). The crop and stomach were empty but the intestine contained unidentified fish scales and small broken pieces of crustacean exoskeleton.

This octopus occurs at slope depths (~200–400 m deep) on isolated island systems (Fig. 5) that rise out of much deeper waters (>1000 m). Its presence from the Philippines to Tonga suggests that its young are capable of planktonic dispersal. In the absence of mature females, egg size and hatchling behaviour remain unknown.

Common name: 'Sharkclub octopus', referring to the distinctive ligula of this species.

DISCUSSION

The distinctive form of the male reproductive organ in this octopus has no parallels amongst other octopod species. Most benthic octopuses (family Octopodidae) possess a ligular groove on the copulatory organ. In these animals this open or closed channel is parallel with the arm axis. In *Galeoctopus lateralis*, the ligula opening is uniquely transverse and mouth-like, complete with teeth-like lugs (Fig. 1D, E). We propose that this highly modified structure is likely to play a sperm-removing role, an adaptation for reducing sperm competition from previous suitors. We propose that the similarity to a toothed mouth corresponds to a mouth- or jaw-like function by this reproductive organ.

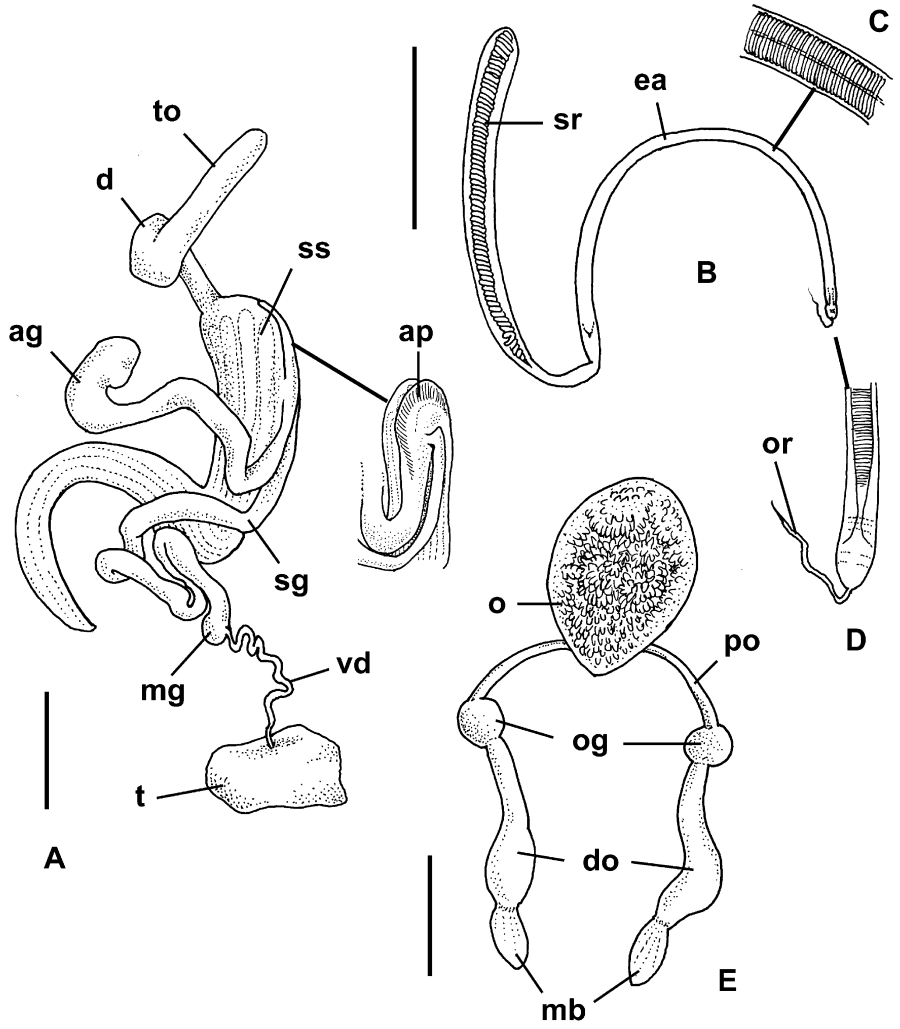

Figure 3. *Galeoctopus lateralis* new species. **A–D.** Male reproductive system (31.0 mm ML paratype, MNHN 2114). **A.** Reproductive tract, ventral view. **B.** Spermatophore. **C.** Close-up of rings of fine ridges within ejaculatory apparatus. **D.** Close-up of oral cap. **E.** Reproductive tract of submature female (31.5 mm ML paratype, MV F76981). Abbreviations: ag, accessory gland; ap, appendix; d, diverticulum; do, distal oviduct; ea, ejaculatory apparatus; mb, muscular base, mg, mucilagenous gland; or, oral cap thread; o, ovary, og, oviducal gland; po, proximal oviduct; sg, spermatophoric gland; sr, sperm reservoir; ss, spermatophore storage sac; t, testis; to, terminal organ; vd, vas deferens. Scale bars: **A**, **B, E** = 5 mm.

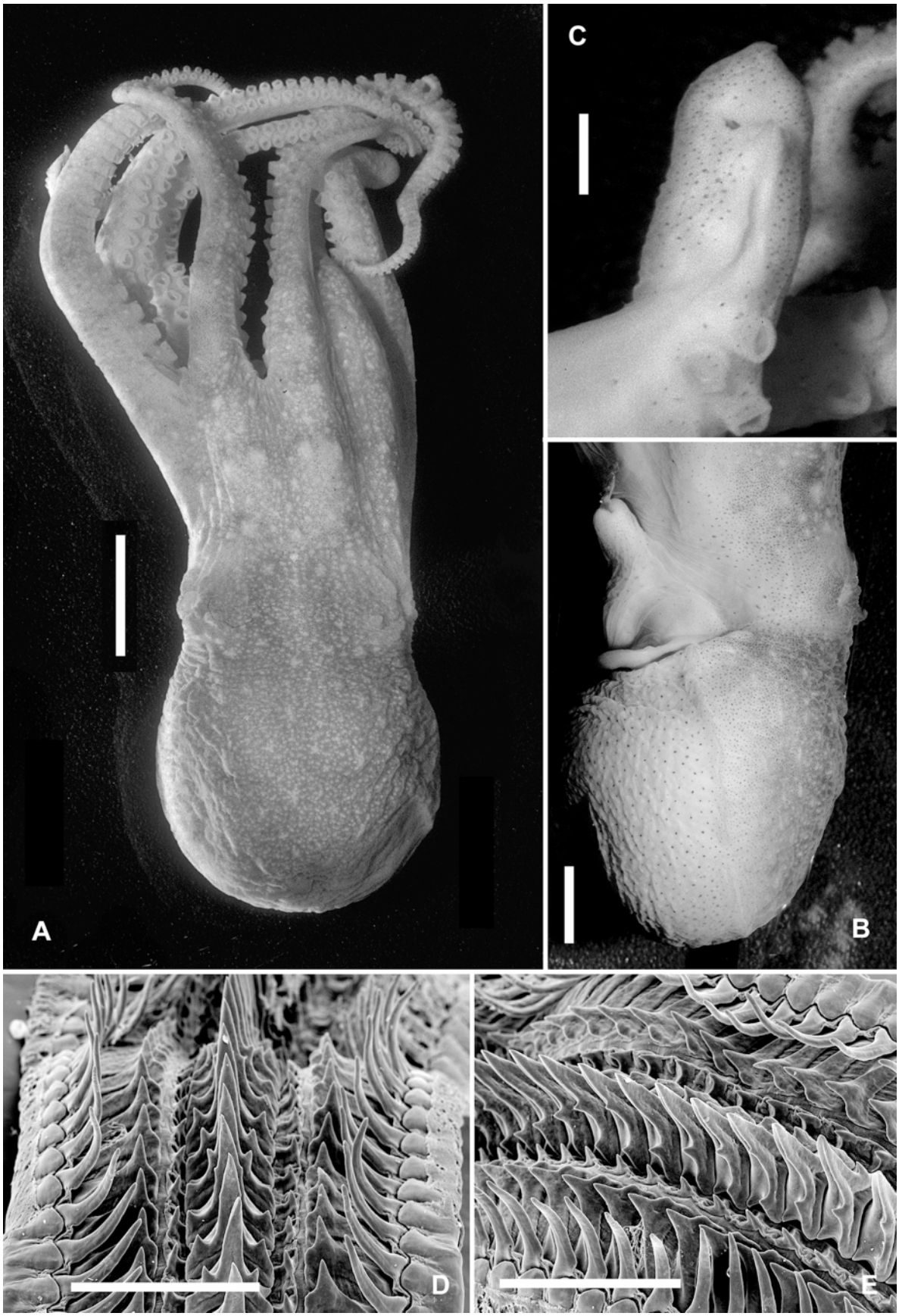

Figure 4. *Galeoctopus lateralis* new species. **A–C.** Photographs of holotype (24.6 mm ML male, MNHN 3787). **A.** Dorsal view of whole animal. **B.** Lateral mantle view showing lateral ridge. **C.** Ligula. **D, E.** Radula of 28.9 mm ML female (MV F97989). Scale bars: **A** = 10 mm; **B** = 5 mm; **C** = 3 mm; **D, E** = 0.5 mm.

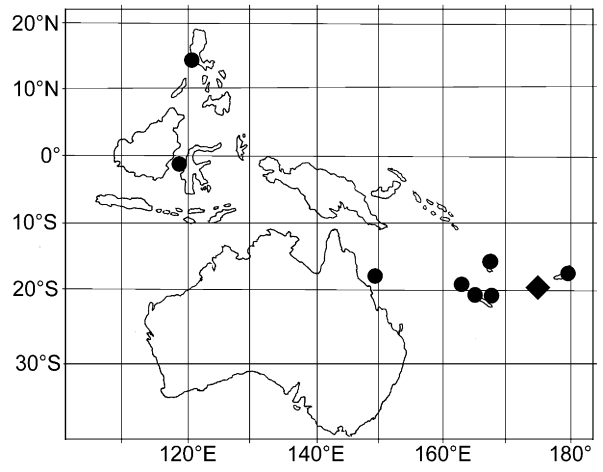

Figure 5. Distribution of *Galeoctopus lateralis* new species. Diamond indicates type locality.

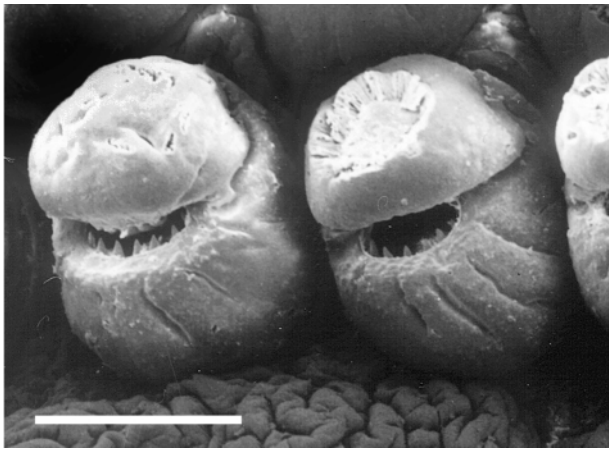

Figure 6. Modified suckers on the hectocotylized arm of the sepiolid squid, *Euprymna tasmanica*, showing the jaw-like modifications (from Norman & Lu, 1997). Scale bar = 0.5 mm.

The shape of the ligula of *G. lateralis* is reminiscent of the shape of highly modified suckers on the hectocotylized arm of the sepiolid squid, *Euprymna tasmanica*. Norman and Lu (1997) illustrated that a row of fleshy suckers on the tip of the hectocotylized arm in male *Euprymna* have mouth-like openings, armed with sharp teeth on a chitinous ring (Fig. 6). In females of these sepiolid squids, the spermatophores are embedded in a fleshy pouch adjacent to the opening of the single oviduct. The hectocotylized arm of *Euprymna* is placed within this pouch during copulation.

We propose that the distinctive ligula of *G. lateralis* and the 'biting suckers' of *Euprymna* are likely to be used to rupture the outer casings of the sperm bulbs of previous suitors. Once the bulbs have been ruptured, the male would be able to dislodge and/or flush out the free sperm present before depositing his own spermatophores.

No mature females of *Galeoctopus lateralis* are known. The distal oviducts of the submature females are swollen with an unusual, fanned, muscular base embedded in the body wall adjacent to the medial septum (Fig. 3E). The latter structure has not previously been reported. Swollen distal oviducts have previously been reported in other deep-sea octopuses, namely *Graneledone, Thaumeledone* and *Bentheledone* (Voss, 1988). Voss suggested that this enlargement did not correlate with egg size and its function was unclear. We propose that this swelling indicates that the distal oviducts of such species are the site of sperm storage (acting as spermathecae). This differs from other octopuses (that have narrow oviducts), where the sperm is stored within chambers of the oviducal gland or penetrates into the ovary (Mangold, 1989). In describing *Graneledone pacifica*, Voss & Pearcy (1990) described swollen distal oviducts in their single mature female. One of these oviducts contained a mass of whitish material that they proposed was sperm.

We speculate that the swollen distal oviducts evident in our submature females of *G. lateralis* play the same sperm-storing role. Everting spermatophores are likely to form rounded sperm bulbs in these sections of the oviducts. Male *Galeoctopus* may use the mouth-like transverse groove of the muscular ligula to grip and rupture the sperm bulbs of previous suitors. The position of this groove, close to the distal tip, and the tooth-like lugs within the ligula pit both support this hypothesis. The muscular flange on the distal oviducts of the female may be related to a vigorous mating process, these muscles potentially anchoring the oviducts during copulation to prevent them tearing free from the visceral wall.

The depth records for *G. lateralis* cleanly fit the vertical stratification previously reported for benthic octopuses from tropical latitudes. Norman *et al.* (1997) reported a shift in species composition around 200 m deep for the benthic octopuses of northern Australia and Indonesia. This depth corresponds with the limits of the continental shelf and a marked drop in seawater temperature. The authors also proposed that there was no clear phylogenetic affinity between the faunas of the tropical shallows and those deeper than 200 m at the same latitudes.

The new octopus described here shows little affinity with other octopods. There are several morphological similarities with the mid-depth genus *Scaeurgus*, namely presence of a lateral ridge, large stylets, similar arm lengths and web depths, and a similar rachidian tooth in the radula (asymmetrical, 1–2 cusps per side). They differ, however, in many aspects of their reproductive systems: *Scaeurgus* has left-handed hectocotylization, a different copulatory organ, spermatophores with a double-strand sperm cord and four large dorsal mantle black spots.

Superficial similarities between *Galeoctopus* and *Scaeurgus* may represent shared ancestry or be due to convergence in form as both genera share similar depth ranges and habitats. Further resolution of the origins and affinities of this new taxon await the results of current molecular phylogenetic studies.

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