Proceedings of the 7th and 8th Symposia on Collection Building and Natural History Studies in Asia and the Pacific Rim, edited by Y. Tomida *et al*., National Science Museum Monographs, (34): 171–189, 2006.

Taxonomy and Biogeography of an Australian Subtropical Octopus with Japanese Affinities

Mark D. Norman[1] and Tsunemi Kubodera[2]

[1] Sciences, Museum of Victoria, Melbourne, VIC 3000, Australia
E-mail: mnorman@museum.vic.gov.au
[2] Department of Zoology, National Science Museum,
3–23–1 Hyakunin-cho, Shinjuku-ku, Tokyo 169–0073 Japan
E-mail: kubodera@kahaku.go.jp

Abstract A distinctive small octopus (*Amphioctopus* cf *kagoshimensis*) is here described from the subtropical waters of eastern Australia. Reports from northern New Zealand are also attributed to this taxon. This small crepuscular animal lives in shallow waters (typically <100 m) and feeds primarily on shellfish which it drills to poison and extract prey. The Australasian octopus reported here shows very strong morphological similarities with *Amphioctopus kagoshimensis* (Ortmann 1888), an octopus which occurs in comparable subtropical latitudes in the northern hemisphere (from southern Japan south to Taiwan). A number of marine species and genera have been reported in the past as having split distributions between subtropical latitudes in both hemispheres. This pattern has been termed "antitropical" or "bipolar", and three main theories have been coined to explain how such a disjunct distribution arose or is maintained. Prior reports of antitropical species are discussed and we suggest that few true bipolar species exist, these primarily being pelagic cool-water species capable of traversing large distances in their temperature-tolerant adult stages. Instead most records are likely to refer to either: 1) deep-water forms which are present in intervening latitudes but not detected due to low sampling effort, or 2) are closely-related forms (sibling taxa) such as the Australasian-Japanese octopus pair treated here. The "relict theory" coined to explain antitropical species may apply to species pairs or complexes marginalised to the boundaries of tropical waters.

Key words: *Octopus*, Cephalopoda, taxonomy, biogeography, bipolar, antitropical.

Introduction

Recent research into the octopuses of Australian and adjacent Indo-West Pacific waters has discovered a diverse, largely undescribed fauna (Stranks, 1988a-b, 1990; Norman, 1991, 1992, 1993a–d, 1998, 2001; Stranks & Norman, 1993; Norman & Hochberg, 1994, 2005a, 2005b; Norman & Sweeney, 1997; Norman *et al*., 1997; Nateewathana, 1997; Nateewathana & Norman, 1999; Norman & Lu, 2000; Norman & Finn, 2001; Norman, Boucher and Hochberg, 2004; Norman, Hochberg and Boucher, 2004, 2005). More than 150 new species have been recognised in the Australian and Indo-Pacific in the last decade alone (Norman & Hochberg, unpublished data). This rich fauna constitutes the greatest diversity of octopuses reported for any region of the world. Amongst recent finds is a small octopus species found in the subtropical waters of eastern Australia ("Eastern Transition Zone" *sensu* Wilson & Allen, 1987), from the southern Great Barrier Reef to southern New South Wales. The morphology, biology and distribution of this octopus are described here.

A recent review of the cephalopods of New Zealand (O'Shea, 1999) provided detailed morphological description of this same octopus from the northern tip of the North Island, treating it under the name *Octopus* cf *rugosus*.

This distinctive Australasian octopus shows strong parallels in morphology with a northern hemisphere species, *Amphioctopus kagoshimensis* (Ortmann, 1888), found at comparable latitudes in the subtropical waters off southern Japan. No other species of octopus found elsewhere in the world shares the distinctive morphology of these two taxa.

On the basis of a detailed earlier work on *kagoshimensis* by Sasaki (1929) and the limited museum material available, no morphological characters have yet been found to delineate the Japanese species from the Australasian taxon. In the absence of discriminating characters, we choose at this stage to treat the Australasian taxon under the name "*Amphioctopus* cf *kagoshimensis*".

We feel that four factors justify production of this paper:

1. The Australasian taxon is a poorly-known octopus which is harvested as bycatch in commercial fisheries in New South Wales. Production of a detailed morphological description and summary of life history traits enables identification of this animal and may provide useful information for biological and fisheries research.
2. As mentioned above, the closest living relative to this taxon is *Amphioctopus kagoshimensis*. This Japanese species is poorly diagnosed and limited well-preserved material exists. Detailed description of the Australasian taxon may aid future comparisons and delineation should additional northern hemisphere material emerge.
3. Both the Australasian and Japanese taxa belong in the genus *Amphioctopus*, a group around which there has been considerable taxonomic confusion (see Norman & Hochberg, 2005a; Huffard & Hochberg, 2005). This publication provides an opportunity to describe in detail a member species.
4. *Amphioctopus kagoshimensis* occurs in comparable subtropical latitudes in the northern hemisphere, separated from the Australasian taxon by extensive intervening tropical waters. Such a distributional pattern has been termed "bipolar", "amphitropical" or "antitropical" (Ekman, 1953). This pattern has been reported in the past for both single species and related species in other taxonomic groups of Indo-West Pacific marine organisms, particularly fishes (Randall, 1981). Such reports are discussed and interpreted in the light of more recent studies, along with potential mechanisms by which these biogeographic patterns may have arisen.

Species Account

Family Octopodidae

Amphioctopus* cf *kagoshimensis

Figures 1–4

Octopus sp. 3: Norman, 1993c: 120–128, figs 4.7.22–26, plate 7
Octopus sp.: Davie, 1998: 192, textfig
Octopus cf *rugosus* (Bosc, 1792): O'Shea, 1999: 127–129, figs 79–81
Octopus sp.: Norman & Reid, 2000: 75, textfigs
Octopus cf *kagoshimensis*: Norman, 2000: 229, textfigs.
Amphioctopus cf kagoshimensis: Norman & Hochberg, 2005a; Huffard and Hochberg, 2005: 115, 124.

Material Examined

Abbreviations: M=male, F=female. Institutions: AMS: Australian Museum; MV=Museum Victoria.

QUEENSLAND: Capricorn Bunker Group, One Tree Island, 23°30′S, 152°05′E: 1M: 10.6 mm ML, MV F60119, 24.3 m; 1M: 20.1 mm ML, MV F60118, 2 m; 1F: 30.6 mm ML, AMS C159278, near shore; 2F: 31.2, 32.3 mm ML, AMS C159277, tide pool; 1F, 1M: 35.0, 43.5 mm ML, AMS C159279, in lagoon; 1M: 38.1 mm ML, AMS C159277, tide pool; 1M, 1F: 39.1, 40.9 mm ML, AMS C159276, on reef; 1M: 42.9 mm ML, MV F60114, 1 m; 1F: 43.1 mm ML, MV F60120, 1–3 m; 1M: 43.4 mm ML, MV F60113, 1m,; 1F: 44.5 mm ML, MV F60117, 1 m; 1F: 55.7 mm ML, MV F60116, 1 m; 1F: 67.3 mm ML, MV F60115, 1 m; 1F: 31.8 mm ML, MV F82871, 3–4 m; 1M: 39.7 mm ML, MV F82875, 3–4 m; 1F: 46.3 mm ML, MV F82873, 3–4 m; 1F: 35.4 mm ML, MV F82876, 2 m; 1F: 49.3 mm ML, MV F82874, 2 m; 1M: 45.7 mm ML, MV 82877, 1.5 m; 1F: 42.0 mm ML, MV F82870, 1.5 m; 1M: 32.6 mm ML, MV F82872, 3 m; 1M: 74.6 mm ML, MV F60122, 1 m; 1M, 1F: 50.5, 61.5 mm ML, MV F60121, 1 m; 1F: 72.1 mm ML, MV F82878, 1 m. Other Queensland: 1M: 20.3 mm ML, MV F82881, Moreton Bay, 27°4.82′S, 153°21.90′E, 10–6 metres; 1?: 6.34 mm ML, MV F82882, Moreton Bay, 27°5.2′S, 153°21.9′E, 9 m; 1M, 2F: 60.0 mm ML, 55.7 mm ML, 62.3 mm ML, MV F82879, 20 km east of South Stradbroke Island, Queensland, “shot 1”, 27°45′S, 153°40′E, 83 m, 6 Nov 1981, 0715–0830 hrs, otter trawl, 3 net rig, coll. C. C. Lu, “Iron Summer” Acc. No. 81–26; 2F: 61.5 mm ML, 64.8 mm ML, MV F82880, east of Noosa, Queensland, “Mooloolaba Cruise”, shot 6, 63 fms, 12 Dec 1980, coll. M. Potter, Qld. Fish. “Rhonda Lane” Acc. No. 81–9. NEW SOUTH WALES: 1M: 57.6 mm ML, AMS C304880 (part), off Tathra, 36°36′S, 150°01′E – 36°44′S, 150°05′E, 37–59 m, 7 Mar 1994, FRV “Kapala”, cruise no. K94-03-10/13; 1M: 64.8 mm ML, MV F82679, off Wreck Bay, 35°12′S, 150°43′E, 43–61 m, 23 Feb 1993, FRV “Kapala”, cruise no. K93-03-01; 1M: 67.6 mm ML, MV F78284, off Newcastle, 32°53′S, 152°00′E, 64–66 m, 20 Apr 1995, FRV “Kapala”, cruise no. K95-03-13; 2M: 70.6 mm ML, 87.0 mm ML, MV F78366, off Wreck Bay, 35°13′S, 150°43′E, 35–62 m, 15 Feb 1994, FRV “Kapala”, cruise no. K94-01-03; 1M: 26.6 mm ML, AMS C164182, off Balmoral, New South Wales, 8 fms, 21 Aug 1966, dredge, coll. Pres. Mal. Society of Australia.

Amphioctopus kagoshimensis (Ortmann, 1888): 2M: 72.9, 76.3 mm ML, 1F: 59.7 mm ML, The Natural History Museum, London (BM) unreg., Awa, Okinawa, Japan, 26°36′N, 127°56′E, 26 Feb 1891.

Diagnosis: *Small to moderate-sized species (mantle length to around 90 mm) with skin sculptured in distinct regular patch and groove system, patches typically pentagonal or hexagonal, largest on ventral arm crown. Grooves darkened to form net-mesh pattern on arm crown, dorsal faces of arms and oral surface of dorsal web. Dark longitudinal eye bar bordered by narrow white lines, visible in fresh dead and preserved specimens as four short white lines radiating from eye. 8–9 gill lamellae per demibranch. Approximately 150–210 suckers on intact arms of mature animals. 73–87 suckers on hectocotylised arm of males. Moderate size copulatory organ (4–7% of arm length) with wide ligular groove. Terminal organ (“penis”) greatly elongated and recurved. Diverticulum bilobed and robust. Spermatophores very long, up to twice mantle length. Small to moderate eggs (to 4 mm).*

Description: Counts and measurements are presented in Tables 1–2. Terminology follows Roper and Voss (1983) except for suckers counts, which are total counts per arm. Arms are num-

Table 1. Counts and measurements (mm) for 14 males of *Amphioctopus* cf *kagoshimensis*. (d=damaged, H=hectocotylised arm, InD=indistinct, A–E=web sectors from dorsal sector)

Museum Reg. No.		MV F60119	MV F60118	AMS C159277	AMS C159276	MV F60114	MV F60113	AMS C159279	MV F60121	AM C304880	MV F82679	MV F78284	MV F78366(b)	MV F60122	AMS F78366(a)
Maturity		Immature	Submature	Mature	Mature	Mature	Mature	Mature	Mature	Mature	Mature	Mature	Mature	Mature	Mature
Mantle length		10.6	20.1	38.1	39.1	42.9	43.4	43.5	50.5	57.6	64.8	67.6	70.6	74.6	87.0
Total length		30.5	66.0	135.0	119.0	147.0	163.0	160.0	185.0	225.5	203.5	251.5	259.5	271.0	334.5
Weight (g)		0.6	2.9	—	—	23.2	23.5	—	39.4	92.2	55.3	59.5	93.3	—	201.0
Mantle width		8.2	13.7	26.0	24.5	26.3	27.4	29.2	30.6	39.2	39.8	39.3	48.4	43.3	58.6
Head width		9.0	12.9	18.6	20.5	19.0	20.8	22.7	21.9	26.7	23.6	21.0	26.0	31.9	28.5
Funnel length		4.7	7.9	14.8	14.4	19.4	18.2	15.5	19.8	20.3	22.7	25.0	29.3	29.2	35.5
Free funnel length		2.0	3.8	6.8	7.8	13.3	10.9	8.4	14.5	14.3	12.4	12.2	15.8	15.3	23.2
Funnel organ limb (medial)		InD	4.6	8.7	8.2	10.7	12.3	11.3	13.8	12.5	18.6	15.5	15.3	17.3	19.5
Funnel organ limb (lateral)		InD	4.3	8.0	8.1	9.6	11.7	10.3	12.9	12.0	17.1	10.8	14.2	15.5	17.7
Shallowest web depth		A: 3.4	A: 7.0	A: 9.7	A: 12.4	A: 11.0	A: 20.0	A: 13.0	A: 13.4	A: 20.5	A: 13.2	A: 11.2	A: 13.8	A: 22.0	A: 19.0
Deepest web depth		D, E: 5.5	D: 15.0	D: 26.6	D: 24.0	D: 26.0	D: 31.0	D: 33.0	D: 29.7	E: 40.5	D: 38.5	D: 49.0	D: 45.4	D: 44.0	D: 58.2
Arm lengths (L/R):	1	13 14	40 38	79 80	65 68	85 92	89 88	91 99	112 113	135 135	115 117	134 123	136 139	148 168	187 182
	2	17 17	40 41	88 87	72 69	89 d	99 94	103 104	125 125	147 148	d d	163 156	168 166	d 182	214 224
	3	17 16H	42 36H	89 78H	74 64H	d 74H	101 87H	111 90H	126 98H	149 112H	127 110H	158 136H	176 125H	164 126H	225 153H
	4	15 15	39 37	89 90	72 77	97 100	d 107	d 102	128 132	161 159	122 105	159 168	156 157	181 d	215 d
Arm width		2.0	3.1	6.2	6.2	6.0	7.1	6.2	7.3	4.8	4.2	4.1	4.9	10.0	6.5
Sucker diameter		1.0	1.7	3.5	4.0	4.2	4.6	4.6	5.8	6.3	5.2	6.5	6.7	7.5	9.8
Sucker count:	R3	InD	82	85	84	84	80	84	85	78	81	80	87	82	73
	L3	InD	127	—	—	d	160	—	176	188	149	159	159	—	18
Gill lamellae count:	R	8–8	8–8	9–9	9–9	9–9	8–8	9–9	9–9	9–9	9–9	9–9	9–9	9–9	9–9
	L	8–9	8–8	9–9	9–9	9–9	8–8	9–9	9–9	9–9	9–9	9–9	9–9	9–9	9–9
Ligula length		InD	0.9	3.7	4.3	3.7	3.6	6.2	6.9	6.5	6.2	7.2	6.7	8.4	10.2
Calamus length		InD	InD	1.0	1.0	1.0	0.9	0.7	1.3	1.7	1.2	1.9	1.4	2.4	3.0
Spermatophore number		InD	InD	InD	InD	4	2	InD	InD	4	2	6	3	3	6
Spermatophore length		—	—	—	—	84.0	91.6	d	—	124.0	d	d	d	130.0	d
Spermatophore width		—	—	—	—	1.0	1.0	—	—	1.3	d	d	d	1.4	d
Spermatophore resevoir length		—	—	—	—	44.2	55.0	—	—	69.0	d	d	d	66.0	d

Table 2. Counts and measurements (mm) for 9 females of *Amphioctopus* cf *kagoshimensis*. (d=damaged, InD=indistinct, A–E=web sectors from dorsal sector)

Museum Reg. No.	AMS C159278	AMS C159277	AMS C159276	MV F60120	MV F60117	MV F60116	MV F60121	MV F60115	MV F82878
Maturity	Submature	Mature	Mature	Mature	Mature	Mature	Mature	Mature	Mature
Mantle length	30.6	32.3	40.9	43.1	44.5	55.7	61.5	67.3	72.1
Total length	112	123	153	170	154	200	216	222	252
Weight (g)	—	—	—	23.5	21.9	35.1	75.5	83.7	91.1
Mantle width	19.2	23.6	36.3	22.0	25.9	29.5	38.3	31.5	43.3
Head width	16.6	16.8	19.3	17.8	17.3	22.0	22.4	22.9	26.1
Funnel length	—	12.4	15.2	15.6	15.2	17.3	25.9	25.3	29.8
Free funnel length	—	6.8	7.5	11.2	10.7	11.5	16.3	19.6	18.7
Funnel organ limb (medial)	8.0	11.1	10.1	9.0	InD	12.8	InD	InD	InD
Funnel organ limb (lateral)	7.0	10.3	9.3	8.0	InD	11.6	InD	InD	InD
Shallowest web depth	A: 10.0	A: 9.0	A: 11.9	A: 10.0	A: 8.1	A: 14.0	A: 15.0	A: 18.0	A: 20.0
Deepest web depth	D: 22.0	C: 23.3	D: 25.0	D: 26.0	D: 26.4	C: 32.0	D: 36.0	D: 37.0	D: 43.0
Arm lengths (L/R): 1	60 61	70 70	84 87	99 105	88 86	d 118	133 131	135 122	147 166
2	68 71	73 73	93 94	112 d	96 95	128 131	143 148	140 137	154 172
3	73 76	74 73	98 105	119 d	102 102	134 140	144 146	138 146	163 172
4	75 78	81 70	99 100	120 111	104 98	131 137	142 149	d 149	170 165
Arm width	4.7	5.3	6.1	5.8	5.0	7.0	9.0	9.0	8.7
Sucker diameter	2.6	3.0	3.3	2.8	3.4	4.1	4.3	5.6	5.4
Sucker count: R3	—	—	—	d	152	188	172	182	208
L3	—	—	—	—	—	—	—	—	—
Gill lamellae count: R	9–9	9–9	d	9–9	9–9	9–9	9–9	9–9	8–9
L	9–9	9–9	d	9–9	8–9	9–9	9–9	9–9	8–9
Egg number	0	0	>1000	>1000	>1000	>1000	>1000	>1000	>1000
Egg length	—	—	3.4	3.4	3.3	2.5	3.8	3.0	2.9
Egg width	—	—	1.0	0.8	0.7	0.4	0.8	0.6	0.7

bered starting from the dorsal (front) pair. Web sectors are designated by capital letters starting from the dorsal (front) sector as "A". Unless otherwise stated data below is presented as ranges and means (latter in italics) for 20 eastern Australian specimens (12 mature males and 8 mature females). Tables 1–2 include counts and measurements for three additional specimens not presented in data below (1 immature and 1 submature male, 1 submature female).

Small to medium-sized robust species (Fig. 1A); mantle length (ML) to at least 87 mm, total length to at least 335 mm; weight to at least 200 g. Mantle ovoid (M: width 58.0–*63.7*–68.6% of ML; F: width 46.8–*61.7*–88.8% of ML), mantle walls moderately muscular. Head narrower than mantle (M: 31.1–*42.9*–52.4% of ML, 48.6–*67.5*–83.7% of mantle width; F: 34.0–*40.7*–52.0% of ML, 53.2–*67.3*–80.9% of mantle width). Eyes large and slightly pronounced. Stylets absent. Mantle aperture moderately wide, approximately half circumference of body at level of opening. Funnel broad based and muscular, approximately 40% of mantle length (M: 35.2–*38.9*–45.2% of ML; F: 31.1–*37.3*–42.1% of ML), free portion usually greater than half funnel length (M: 45.9–*58.5*–73.2% of funnel length; F: 49.3–*64.5*–77.5% of funnel length). Funnel organ W shaped with broad limbs (Fig. 1B). Outer limbs slightly shorter in length than median limbs (M: outer limbs 69.7–*90.9*–98.8% of median limbs; F: outer limbs 88.9–*91.1*–92.8% of median limbs). Funnel organ occupies approximately 60–70% of funnel length (M: 52.2–*62.7*–81.9% of funnel length; F: 57.7–*71.9*–89.5% of funnel length).

Table 3. Comparison of *A.* cf *kagoshimensis* with other non-ocellate members of the genus *Amphioctopus*.
[m=male, f=female, AL=arm length, HAL=hectocotylised arm length, LL=ligula length, ML=mantle length (eye to posterior tip)].

	A. cf *kagoshimensis*	*A. kagoshimensis*	*A. marginatus*	*A. aegina*
Synonyms:	—	—	—	*dollfusi* *hardwickei*
Misidentifications:	—	*granulatus* *aegina*	*aegina*	*rugosus*
Distribution:	eastern Australia + north NZ	southern Japan to Taiwan	Indian Ocean, western Pacific	Indian Ocean, western Pacific
Affinity:	subtropical	subtropical	tropical	tropical
Mantle length:	to 87 mm	to 86 mm	to 80 mm	to 90 mm
Total length:	to 335 mm	to 295 mm	to 280 mm	to 300 mm
Arm length:	2.0–2.8 x ML	2.4, 2.6 x ML	2.0–2.8 x ML	2–3 x ML
Web depth:	21.8–31.2% AL	21.4, 25.6% AL	26.3–33.3% AL	20.0–32.8% AL
Normal arm sucker count:	149–188 (m), 152–208 (f)	157, 164 (m), 169 (f)	127–152 (both)	96–130 (both)
Hectocotylised arm sucker count:	73–87	68–88	61–84	55–70
Ligula length:	4.1–7.0% HAL	5, 6.7% HAL	1.6–3.6% HAL	4–6% HAL
Calamus length:	11.3–29.4% LL	17% LL	37.9–65.0% LL	19–25% LL
Enlarged suckers:	10–12 slightly enlarged	none obvious	4–5 slightly enlarged	2–3 enlarged
Male sucker diameter:	to 11.5% ML	to 9.0% ML	to 14.5% ML	to 16.6% ML
Spermatophores:	no internal teeth (unarmed)	no internal teeth (unarmed)	no internal teeth (unarmed)	internal teeth (armed)
Spermatophore length:	84–130 mm	117–160 mm	37–68 mm	25–51 mm
Spermatophore length versus ML:	174–215% ML	160, 186% ML	73–116% ML	58–115% ML
Colour pattern:	Cross around eye, reticulate markings produced by dark grooves.	Cross around eye, reticulate markings produced by dark grooves.	White triangle under eye, dark purple leading edges of arms in contrast to white-blue suckers.	Longitudinal pale stripe on dorsal mantle. Dark circular reticulations.
Skin sculpture:	Polygonal patches over all surfaces with distinct grooves	Polygonal patches over all surfaces with distinct grooves	Oval to elongate patches in irregular longitudinal rows	Circular raised bumps with indistinct grooves

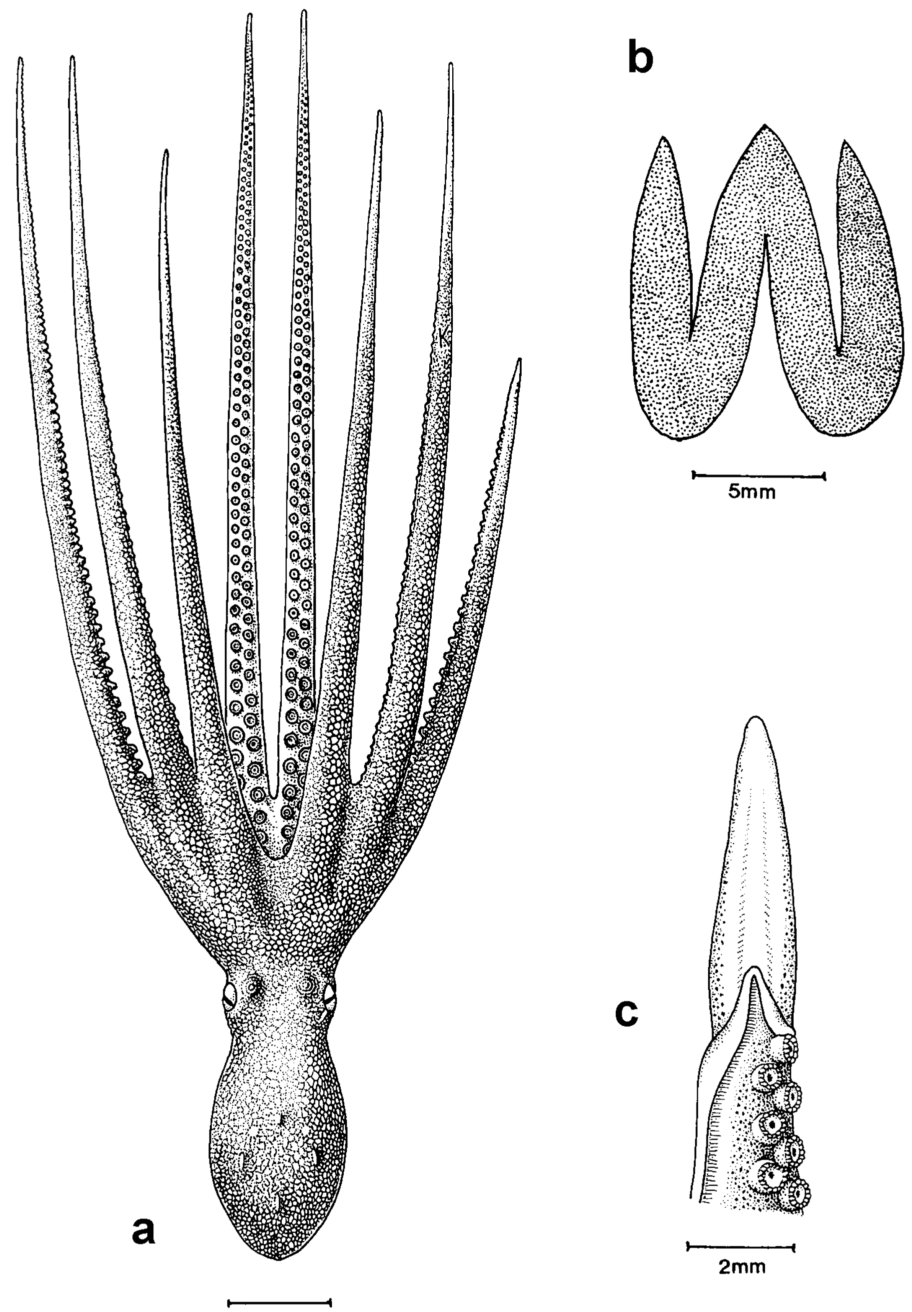

Fig. 1. *Amphioctopus* cf *kagoshimensis*. A. Dorsal view of 50.5 mm ML male (MV F660121): illustration: K. Nolan. B. Funnel organ of 43.4 mm ML male (MV F60113). C. Copulatory organ of 50.5 mm ML male (MV F60121).

Arms moderate length, typically two to three times mantle length (M: 2.0–*2.4*–2.8 X ML; F: 2.2–*2.5*–2.8 X ML). Arms robust at base (M: 6.1–*11.7*–16.4% of ML; F: 11.2–*13.6*–16.4% of ML), roughly circular in cross section and tapering to long fine tips in distal half. Arms approximately equal in length, dorsal pair slightly shorter (arm formula typically 4=3=2>1). Suckers forming two rows are of moderate size, slightly elevated with distinct radial cushions. Considerable increase in sucker diameter between first and second proximal suckers in both sexes. Mature males possess slightly larger suckers from second to 14th suckers on arms 2 and 3 (M: 8.0–*10.1*–11.5% of ML; F: 7.0–*7.7*–9.3% of ML). Approximately 150–210 suckers on intact arms of mature animals (M: 149–*167*–188 suckers on normal 3rd arm; F: 152–*180*–208 suckers on 3rd arms). Webs of moderate depth, slightly shallower in females (M: deepest web 22.5–*27.4*–31.2% of longest arm; F: deepest web 21.8–*24.6*–28.8% of longest arm). Ventro-lateral web deepest, dorsal web distinctly shorter (web formula typically D>C=E>B>A or D=E>C>B>A). Web margins well developed on ventral edges of arms, extending along approximately 80% of arm length.

Third right arm of males hectocotylised. Modified arm approximately twice mantle length (1.6–*1.9*–2.1 X ML) and around 80% length of opposite arm (68.0–*80.3*–87.6% of opposite arm). Ligula moderate-size (4.1–*5.8*–7.0% of arm length), elongate and slightly flattened (Fig. 1C). Ligula groove wide and shallow. Floor of groove with raised longitudinal medial rib and fine transverse ridges. Calamus distinct, raised, approximately one quarter of ligula length (11.3–*23.6*–29.4% of ligula). Spermatophore groove well developed and wide with fine transverse creases. Spermatophore guide distinct with a ridge of elevated square papillae. Approximately 80 suckers on hectocotylised arm (73–*82*–87).

Gills with 8–9 lamellae on both inner and outer demibranchs, plus terminal lamella.

Digestive tract illustrated in Figure 2A. Anterior salivary glands extend along approximately one third of buccal mass from posterior margin on dorsal surface. Posterior salivary glands moderate sized (similar in length to buccal mass, approximately 40% of digestive gland length). Crop diverticulum present, moderately small. Stomach bipartite. Caecum coiled in single whorl, lacks striations. Digestive gland approximately ovoid. Muscular intestine reflexed approximately one third along length from proximal end. Ink sac well developed, embedded in ventral surface of digestive gland. Anal flaps present. Beaks illustrated in Figures 2B–D. Upper beak with a hooked rostrum, concave on cutting edge, and moderate hood (Fig. 2B). Lower beak with blunt rostrum showing two to three blunt processes when viewed from ventral aspect, hood narrow, widely spread wings and moderately flared lateral walls (Figs. 2C–D). Radula with seven teeth and two marginal plates in each transverse row (Fig. 4F,H). Rhachidian tooth with 1–2 lateral cusps, typically 1, on each side of short robust medial cone. Lateral cusps in symmetrical seriation, migrating from lateral to medial position over 2–3 transverse rows. First lateral teeth unicuspidate with cusp towards lateral edge. Second lateral teeth unicuspidate and long with curved base. Lateral marginal teeth long and curved. Marginal plates oblong and plain.

Male genitalia illustrated in Figure 3A. Terminal organ ("penis") in mature males very long and recurved with robust bilobed diverticulum. Spermatophores (Fig. 3B), very long, around twice mantle length (84.0–*107.4*–130 mm, 174.3–*199.1*–215.3% of ML [n=4]), and fine (1.0–*1.2*–1.4 mm, 1.9–*2.2*–2.3% of ML [n=4]), produced in low numbers (2–*4*–6 in storage sac [n=8]). Spermatophore surface rippled at oral end. Oral cap simple bearing long cap thread. Sperm reservoir very long, approximately 55% of total spermatophore length (50.8–54.8–60.0% of total spermatophore length [n=4]), containing loosely coiled sperm cord forming approximately 40 irregular whorls.

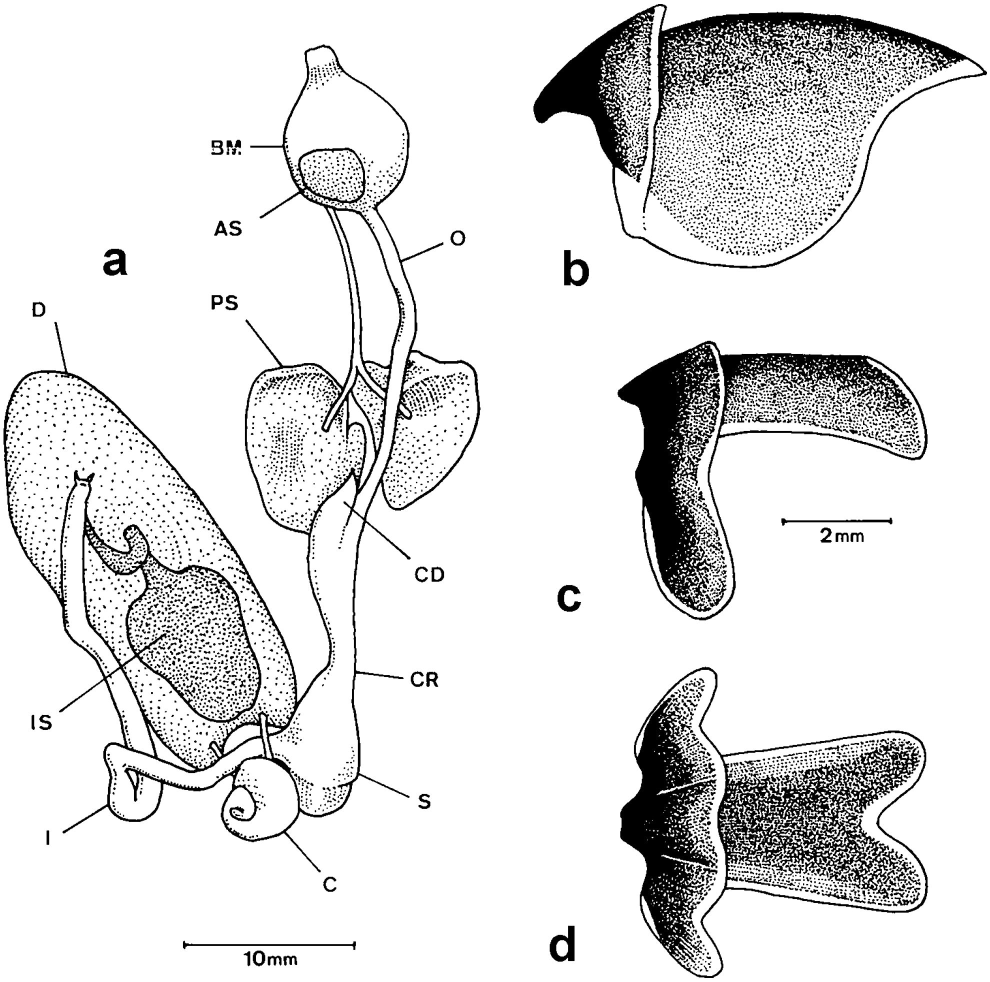

Fig. 2. *Amphioctopus* cf *kagoshimensis*. A. Digestive tract of 43.4 mm ML male (MV F60113): AS=anterior salivary glands, BM=buccal mass, C=caecum, CD=crop diverticulum, CR=crop, D=digestive gland, I=intestine, IS=ink sac, O=oesophagus, PS=posterior salivary gland, S=stomach. B–D. Beaks of same specimen. B. Upper beak, lateral view. C. Lower beak, lateral view. D. Lower beak, ventral view.

Female genitalia illustrated in Fig 3C. Mature ovary ovoid (Fig. 3C). Distal oviducts very long and robust, reflexed at different points along length in different specimens. Proximal oviducts very short. Oviducal glands large divided into approximately 20 braiding chambers. Eggs moderately small, ovarian eggs to 3.8 mm long (2.5–*3.2*–3.8 mm, 4.0–*6.1*–8.3% of ML [n=7]), moderately wide (0.4–*0.7*–1.0 mm, 0.7–*1.4*–2.4% of ML) and produced in large numbers (~60,000 in one female). Approximately four follicular folds on immature ovarian eggs.

Colour in life variable, typically evenly cream to white mottled with red brown blotches (Figs 4A, C–E). Diagnostic lattice of dark grooves between raised patches on dorsal faces of arms and oral surface of dorsal web (Fig. 4B). Transverse pair of dorsal white spots (*sensu* Packard & Sanders, 1971) on dorsal mantle, slightly closer to eyes than posterior margin (Fig. 4C–D). Dark maroon longitudinal bar through each eye, bordered by thin white lines (Fig. 4G).

When alarmed, several individuals displayed an ill-defined dark blotch on either side of arm

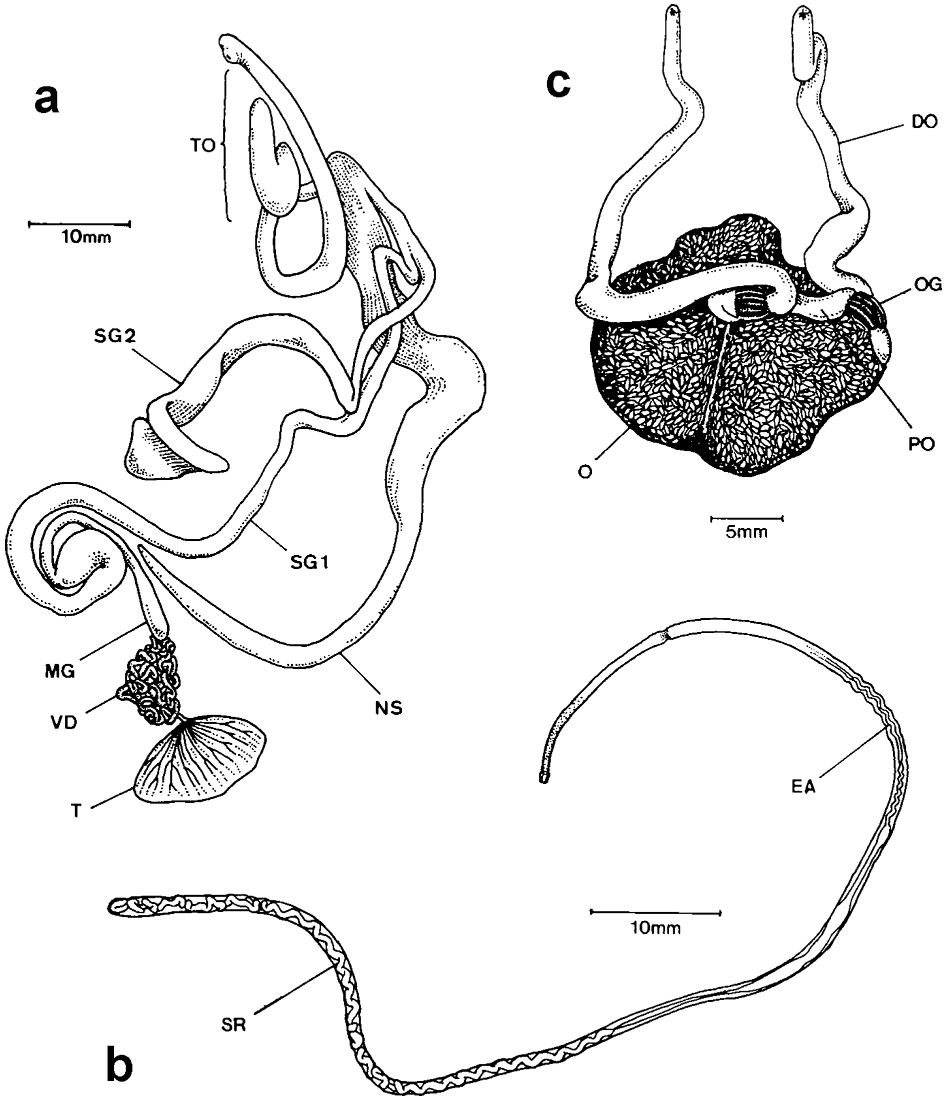

Fig. 3. *Amphioctopus* cf *kagoshimensis*. A. Male reproductive tract of 43.4 mm ML male (MV F60113): MG=mucilagenous gland, NS=Needham's sac, SG1=spermatophoric gland, SG2=accessory spermatophoric gland, T=testis, TO=terminal organ ("penis"), VD=vas deferens. B. Spermatophore from 74.6 mm ML (MV F60116): EA=ejaculatory apparatus; SR=sperm reservoir. C. Ovary of 55.7 mm ML female (MV F60116): DO=distal oviducts; O=ovary; OG=oviducal gland; PO=proximal oviduct.

crown in approximate position of false-eye spots (ocelli) of true ocellate species (Figs 4A,C). No evidence of this dark spot was visible on preserved specimens.

Entire body, arms and arm crown sculptured in distinct patch and groove system (Figs 4A,E). Patches generally pentagonal or hexagonal containing up to eight small erectile papillae. Sculpturing extends to oral surface of dorsal web. Patches on ventral body smaller than dorsal ones, patches on ventral arm crown larger in diameter than those on dorsum. Frontal white patch containing erectile papilla located between and slightly below eyes, white in some colour patterns. Pattern of longitudinal raised skin ridges on dorsal body, four largest arranged in cross shape

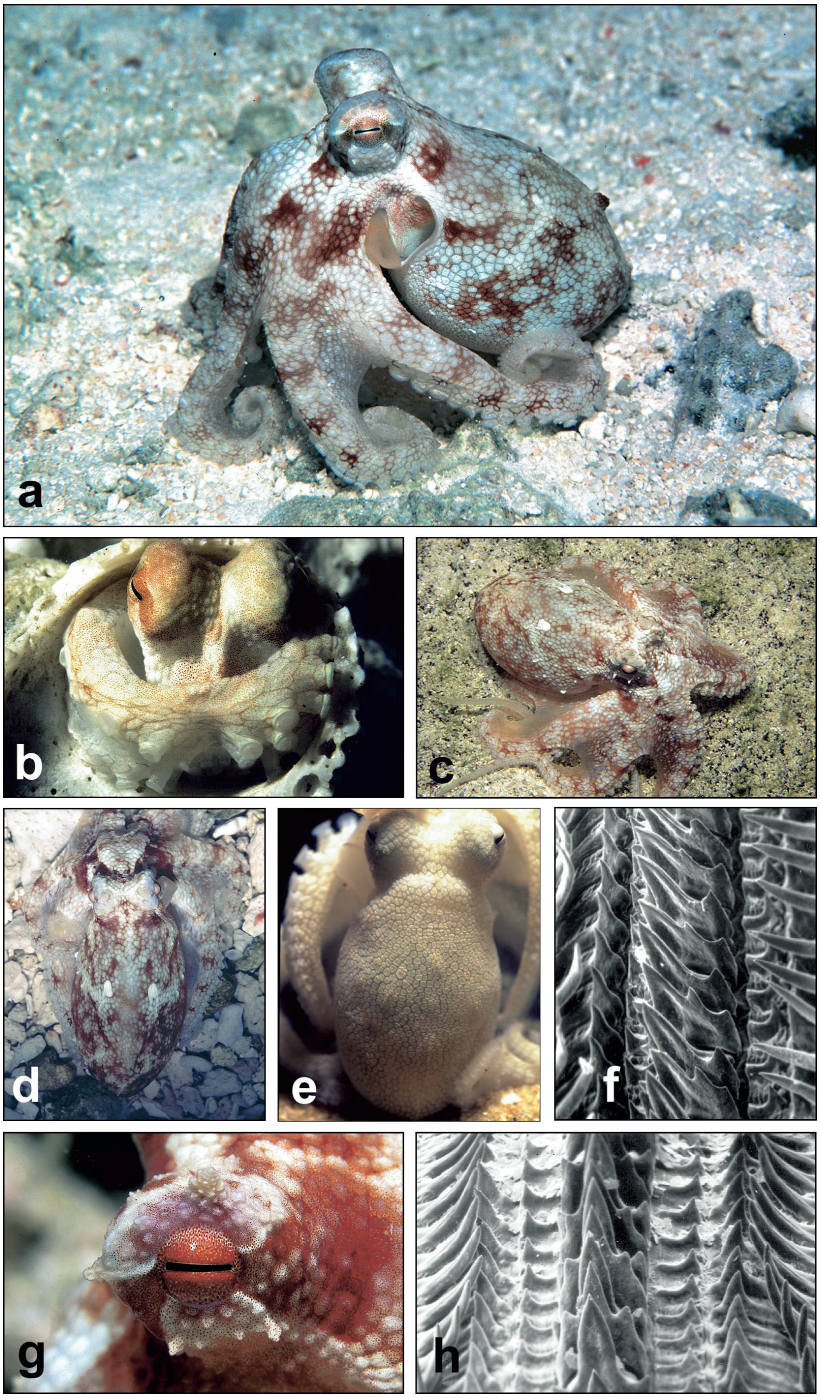

Fig. 4. Photographs of *Amphioctopus* cf *kagoshimensis*. A–F. Colour patterns and skin sculpture of live *Amphioctopus* cf *kagoshimensis* at One Tree Island, Queensland. A. Lateral view showing reticulate pattern on mantle and temporary false-eye spot on arm crown below eye. B. Frontal view of animal in gastropod shell showing dark reticulations on arm faces. C. Dorsal view showing temporary false-eye spot. D. Dorsal view showing "dorsal white spots". E. Dorsal view showing patch and groove skin texture. F. Lateral view of radula of 43.3 mm ML male (MV F60113). G. Close-up of eye showing dark eye bar bounded by cross of white lines. H. Dorsal view of radula of 43.1 mm ML female (MV F60120).

(Fig. 1A). Each ridge consists of four or more patches raised together. Large erectile papilla and smaller secondary papillae above each eye (Fig. 4G).

Juvenile and submature specimens (10.6 mm and 20.1 mm ML males) possessed two longitudinal rows of large dark chromatophores (founder chromatophores) on aboral surfaces of all arms. Characteristic dorsal white spots, dark eye-bar and raised ridges in cross arrangement on dorsum all clearly visible in smallest specimens.

Preserved specimens typically cream-brown with dark lattice pattern visible on dorsal arm faces and arm crown. White borders to dark eye-bar visible as four white lines radiating for short distance from eye. Preservation technique can cause considerable variation in extent of sculpturing, freezing resulting in smooth-skinned specimens.

Sexual dimorphism not marked in this species. Both sexes attain approximately equal maximum size. Mature males possess slightly enlarged suckers on arms 2 and 3 to level of seventh sucker pair (M: 8.0–*10.1*–11.5% of ML; F: 7.0–*7.7*–9.3% of ML).

Distribution: *Amphioctopus* cf *kagoshimensis* is reported here from eastern Australia between Tathra in southern New South Wales (36°50′S, 150°00′E) and One Tree Island, Queensland (23°30′S, 152°05′E). This octopus has been collected at depths between 1 and 115 m. O'Shea (1999) reports this *octopus* under the name *Octopus* cf *rugosus* (Bosc, 1792) from the northern tip of the north island of New Zealand (~34°N, 173°E), at depths between 23 and 50 m.

Life History: Observations of more than 10 live animals at One Tree Island found that *Amphioctopus* cf *kagoshimensis* occupies permanent lairs in live coral or coral rubble often bordering sand substrata, both in the lagoon and on sand in inter-reef areas. Lairs were easily recognised by the large number of clean mussel and nerite shells scattered around the lair mouth. Retreating individuals were observed closing the entrances to lairs with pieces of dead coral. On emergence, coral pieces form a ring around the opened lair. One very small specimen (10.6 mm ML male, MV F60119) was collected in an octopus pot from 24 m, hiding under a small bivalve shell.

This octopus appears to have crepuscular activity patterns. Active, foraging animals were encountered at 0600, 1900 and 1905 hr. Other animals were encountered in mouths of lairs, often half emerged at 0445–0650 hr, and 1745–1820 hr. Eight specimens were flushed from deep within lairs with copper sulphate solution between 1015–1630 hr and one at 2000 hr. These lairs were blocked with pieces of dead coral.

It is possible that pair-bonding occurs in this octopus. One pair of specimens, one of each sex were found in dual lairs 40 cm apart. The female was gravid with eggs. Both lairs were surrounded by very large numbers of nerite and bivalve shells, suggesting extended occupancy. Small numerous eggs (to 3.8 mm) indicate that juveniles are likely to enter the plankton on hatching.

Amphioctopus cf *kagoshimensis* has a diet including molluscan and crustacean prey. Fresh bivalve shells, particularly mussels, were regularly encountered surrounding lairs. Gastropod shells, particularly *Polinisia* sp., also made up a large proportion of discarded shells. The lair of one small specimen was surrounded exclusively by small bivalves. Evidence of drilling was visible towards the spire of most gastropod remains. The stomach of one specimen was full of crustacean remains.

Amphioctopus cf *kagoshimensis* is harvested on a small scale as trawl bycatch from southern

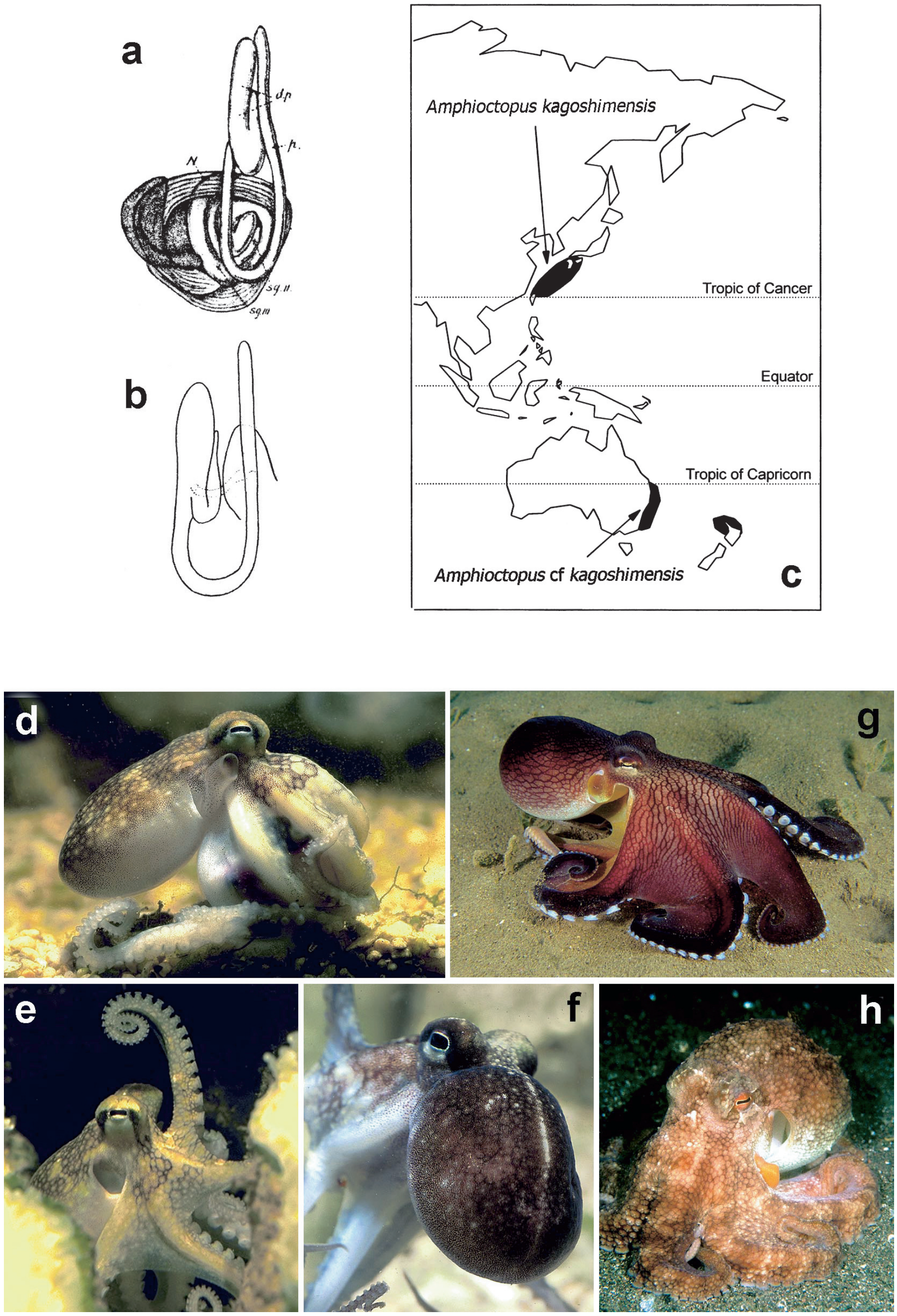

Fig. 5. A. Male reproductive tract of *A. kagoshimensis* showing long recurved terminal organ (as drawn by Sasaki, 1929 under the name, *O. granulatus*). B. Terminal organ of syntype of *A. kagoshimensis* (from Adam, 1960). C. Distributions of *A.* cf *kagoshimensis* and *A. kagoshimensis*. D–F. *Amphioctopus aegina* (Singapore, photos: MN). G. *Amphioctopus marginatus* (Sulawesi, Indonesia, photo: MN). H. *Amphioctopus kagoshimensis* (Osesaki, Japan, photo R. Kuiter).

Queensland to Sydney and is sold for both human consumption and as bait.

Discussion

Systematics

Strong morphological similarities link the southern hemisphere octopus treated here with the northern hemisphere species, *Amphioctopus kagoshimensis* (Ortmann, 1888). The latter taxon was originally described from Kagoshima, southern Japan (31°36′N, 130°33′E) and has since been treated by a number of workers under inappropriate names (including *O. granulatus* non Lamarck, 1798: Wülker, 1910, Sasaki, 1929, and in part under *O. aegina* non Gray, 1849: Robson, 1929, Roper *et al*., 1984, Okutani *et al*., 1987).

Both taxa share similar form in size (total length to around 300 mm), gill counts (8–9 lamellae per demibranch), arm length (2–3 times mantle length) and web depths (20–30% of arm length). The skin of both taxa is sculptured in regular polygonal patches separated by a distinct network of grooves and the eye is bordered by a cross of four white lines (Figures 4G). They also share long spermatophores (1.5–2 times mantle length) and a distinctive greatly elongated and recurved terminal organ or 'penis' (Figures 3A, 5A–B).

Morphological features of *A. kagoshimensis* and *A.* cf *kagoshimensis* are compared to related members of the genus (*A. aegina* Gray, 1849 and *A. marginatus* Taki, 1964) in table 3. Live images of these taxa are presented in figures 4 and 5. Norman & Hochberg (2005a) and Huffard & Hochberg (2005) discuss the genus *Amphioctopus* and its member taxa.

Biogeography

Amphioctopus cf *kagoshimensis* occurs off both Australia and northern New Zealand. In Australia it ranges from the southern Great Barrier Reef to southern New South Wales, from 23°30′S to 36°50′S. O'Shea's (1999) reports this species under the name *Octopus* cf *rugosus* from northern New Zealand based on four specimens collected between 34°23.5′S and 34°49′S. The waters across these latitudinal ranges are considered subtropical (Wilson & Allen, 1987). The distribution of *A. kagoshimensis* occurs at similar latitudes in the north-west Pacific Ocean, from Sendai Bay, Japan (~38°N) south to Taiwan (~25°N). Figure 5C summarizes the known distributions of these two taxa.

This disjunct pattern of closely-related taxa separated by thousands of kilometres of intervening tropical waters has been reported for other taxonomic groups, particularly fishes. Such a distribution is often referred to as 'bipolar', 'amphitropical' or 'antitropical' (Hubbs, 1952, Ekman, 1953). Hubbs (1952) reported a number of fish genera with members represented in northern and southern temperate waters but not in the intervening tropical climes.

Randall (1981) published a list individual fish species with isolated populations split between the temperate fringes of northern and southern hemispheres. Briggs (1987) summarized the theories that have been generated to account for such antitropical distributions in single species. Three theories attempted to describe mechanisms of current or recent gene flow to account for single species with such disjunct populations.

• *Transgression during past glaciations:*

Darwin (1859) is attributed as the first to suggest that cool water currents may have traversed the equator during past glaciations. Berg (1933) developed this concept further, suggesting that single species with antitropical distributions were maintained through gene flow between isolated populations during cooler glacial periods. Berg suggested such exchange was possible as recently as the late Pleistocene.

• *Tropical submergence*

Ekman (1953) attributed a second theory, that of isothermic submergence, back to the 19th century Antarctic explorer, Sir James Ross. This theory suggests that cold water organisms traverse equatorial latitudes by moving into deeper cooler waters, following isothermic depth contours. This theory proposes a corridor of gene flow through deeper water without established populations present in these corridors.

• *Relict theory*

Theel (1885) proposed that the disjunct populations witnessed in antitropical species are remnants of a once widely-distributed species. Springer (1967) used a "fairy-ring mushroom" analogy to describe this process, where a species starts from a central area and spreads as an ever-enlarging ring around a central area that no longer harbours the species. The disappearance of the intervening stock may have resulted from factors such as emergence of new competitors, predation, disease or increases in temperature.

The relevance of the proposed theories is dependent on the validity of the initial reports of single species with antitropical distributions. Many of the prior reports can be reassessed or interpreted in other ways. Three categories of taxa emerge:

- Pelagic species with the capacity to cover large distances over their lifetime, such as members of the family Carangidae, e.g., *Pseudocaranx dentex* (Randall *et al*., 1990).
- Species which occur in the intervening latitudes but have not been detected until recently due to limited sampling effort. E.g., the deep water squalid shark *Cirrhigaleus barbifer* was originally reported as being antitropical (Garrick and Paul, 1971), it has since been recorded at depth in intervening tropical latitudes (Last & Stevens, 1994).
- Closely related shallow-water subtropical or temperate species being interpreted as a single species.

Increased interest over recent years in wild animal observations and photography is providing insights into many of the reported "antitropical" fishes. Consistent differences in colour patterns have been detected for numerous 'species' with supposed antitropical distributions. Species such as *Microcanthus strigatus* and *Arothron firmamentum* have sufficiently different colour patterns between Japanese and Australian "populations" that their taxonomic status is being questioned (R. Kuiter, pers. comm.). Where the morphology of particular groups has been examined in greater detail, such supposed antitropical species have proven to be complexes of related species. For example, recent research into the 'antitropical' labrid *Bodianus vulpinus* has split records of this species into at least four related species which occur around the cooler fringes of the tropical Pacific Ocean (Gomon, in press).

Cryptic sibling species may not be detected due to a number of factors. For particular groups, poor taxonomy may prevent recognition of closely-related species. Records of single antitropical species should be treated with caution for groups with limited diagnostic characters (e.g., moray eels such as *Lycondontis eurostus*, Randall, 1981) or for those families in need of major revision (e.g, the velvetfish, *Aploactis aspera*, Randall, 1981).

Other "antitropical" records may result from use of diagnostic keys developed for different regions of the world, with insufficient resolution to separate morphologically similar taxa. Further "antitropical" records may be the product of taxonomic decisions based on limited material or information. Randall (1981) lists instances of decisions being based on second hand reports or even single photographs (e.g., for *Cheilodactylus vittatus*). In some instances, expectation of single species with disjunct temperate distributions may have lead to a culture of lumping closely-related species.

Molecular analyses may be appropriate tools to clarify reports of single species with antitropical distributions. Molecular studies of a mole crab, *Emerita analoga*, from the Eastern Pacific Ocean indicated an absence of recent gene flow between disjunct Californian and Chilean populations (Tam *et al*., 1996). The authors predicted that "many marine invertebrates with antitropical distributions similar to *E. analoga* may consist of sibling species".

The distributional pattern reported here for the Australasian octopus (*A*. cf *kagoshimensis*) and the related *A. kagoshimensis* are reflected in the distributions of a number of other taxa. Examples of sibling species pairs which occur in the shallow subtropical waters of Australia and southern Japan include:

- Fishes:

  Family Labridae: *Pseudolabrus luculentus* and *P. japonicus* (Kuiter, pers. comm)
  Suezichthys devesi and *S. gracilis* (Kuiter, 1993)
  Family Gobiidae: *Trimma necopina* and *T. macrophthalma* (Kuiter, 1993)
  Family Acanthuridae: *Prionurus microlepidotus* and *P. scalprus* (Kuiter, 1993)
  Family Siganidae: *Siganus nebulosus* and *S. fuscescens* (Kuiter, 1993)
  Family Tetraodontidae: *Canthigaster callisterna* and *C. rivulata* (Kuiter, 1993)
- Bivalve molluscs:

  Family Mytilidae: *Xenostrobus atratus* and *X. pulex* (Wilson & Allen, 1987)

We believe that the related Australasian and Japanese *octopus*es treated here will similarly prove to be genetically-isolated and distinct species. It is unlikely that we are dealing with a single widespread species as:

- distributions in each hemisphere match the distributions of many species considered subtropical transition zone endemics (see Wilson & Allen, 1987).
- extensive sampling throughout intervening tropical waters and examination of all major museum and reference collections of octopuses from this region have failed to uncover such taxa.

It is similarly unlikely that we are dealing with a single species which submerges into deeper cooler water in lower latitudes. Examination of affinities and depth distributions of octopuses in tropical latitudes has found a considerable faunal shift at the limits to the continental shelf, around 200 m (Norman *et al*., 1997). Familiar shallow-water genera such as *Octopus sensu strictu*. and *Amphioctopus* are replaced at this depth by a very different suite of unrelated octopuses, primarily the deeper-water genera *Scaeurgus*, *Pteroctopus* and *Benthoctopus*.

Further resolution of the taxonomic status of the Australasian *octopus* will only be possible with the emergence of additional well-preserved material of *O. kagoshimensis*. Molecular studies may be the most appropriate avenue to resolve the status of these two taxa and determine the nature of their phylogenetic relationship.

Of the theories coined to explain single species with antitropical distributions, one may be relevant regardless of the taxonomic status of these related taxa. The relict theory of Theel (1885) proposed that taxa remain as relicts on the margins of a larger ancestral distribution. This process may account for the Australian-Japanese pairs of subtropical species reported here. It may also account for the marginalised distributions around the periphery of the tropical Indo-Pacific found in other species groups. As mentioned above, re-examination of the labrid fish *Bodianus vulpinus* found a ring of related species around the periphery of the tropical Pacific Ocean (Gomon, in press). Similar patterns occur in cardinalfishes, family Apogonidae (Kuiter, pers. comm.).

Representatives of another group of octopuses also possess such a marginalised distribution. Members of *Octopus sensu strictu* (also known as the *Octopus vulgaris* species group, Robson, 1929) are characterised by large body size, lateral arms longer than the dorsal pair, lateral webs deeper than dorsal pair, enlarged suckers on arms 2 and 3 in mature males, a small modified arm tip in mature males (<5% of arm length) skin sculpture including a diamond of large conical primary papillae on the dorsal mantle and colour patterns incorporating dorsal and frontal white spot complexes (*sensu* Packard & Sanders, 1971). Members of this species group are present in the subtropical waters abutting the tropical Indo-Pacific region, represented by at least one species in Australia and New Zealand (treated under the name *O. tetricus* Gould, 1852), an Asian species from Taiwan to Japan, and another from Cape Town to Durban in South Africa (the latter two species currently being treated under the name *O. vulgaris* Cuvier, 1797). These *octopus*es may be the relicts of ancestors once occupying much of the Indo-Pacific or equatorial Tethyan Sea regions.

In conclusion, it is likely that more cryptic species-pairs will emerge around the margins of tropical oceans, these closely-related forms being potential relicts of a wider distributed ancestry. At this stage the mechanisms and timing of such marginalisation remain unknown.

Acknowledgments

The authors would like to thank the National Science Museum, Tokyo for support through their "*Cooperation with the Museums in Asia and the Pacific Rim for Collection Building and Natural History Studies*", enabling exchange visits by the authors between Tokyo and Museum Victoria. The authors are also grateful for the input of J. Finn, R. Kuiter, M. Gomon, C.C. Lu, M. Dunning, C. Myers, M. Harvey, K. Matsuura, W. Ponder, J. Hooper and B. Rudman. Additional thanks to K. Nolan, R. Condon, R. Fenwick, M. Turner, K. Graham, F. G. Hochberg, D. Paul, C. Rowley and J. Clark.

References

Adam, W., 1960. Cephalopoda from the Gulf of Aqaba. Contributions to the knowledge of the Red Sea, No. 16. *Bulletin of the Sea Fisheries Research Station, Haifa*, (26): 1–26, 1 pl.

Berg, L. S., 1933. Die bipolare Vebreitung der Organismen und die Eiszeit. *Zoogeografica*, **1**: 444–484.

Bosc, L., 1792. *Sepia rugosa*. *Actes de la Sociéte d'Histoire Naturelle, Paris*. **1**(1): 24, Figs. 1–2, pl. 5.

Briggs, J. C., 1974. Marine Zoogeography. (McGraw-Hill, New York).

Briggs, J. C., 1987. Biogeography and plate tectonics. (Elsevier, New York).

Chaitiamvong, S., 1993. Identification of cephalopods found in the Gulf of Thailand. Marine Life History Research Group, Bangkok Marine Fisheries Development Centre, Technical Report, **23**: 1–78.

Chikuni, S., 1987. Potential yield of marine fishery resources in southeast Asia. Symposium on the exploitation and management of marine fishery resources in southeast Asia. FAO RAPA Report, 1987(10): 16–28.

Chotiyaputta, C., 1993. Cephalopod resources of Thailand. pp. 71–80. In: Okutani, T., R. K. O'Dor and T. Kubodera (Eds), *Recent Advances in Fisheries biology*. (Tokai University Press: Tokyo).

Darwin, C., 1859. On the origin of species by means of natural selection. (John Murray, London).

Davie, P., 1998. Wild Guide to Moreton Bay. (Queensland Museum, Brisbane).

Dong, Z., 1979. A preliminary report of the cephalopods from the Xisha waters, Guangdong Province, China. *Studia Marina Sinica*, **15**: 71–74. In Chinese with English summary.

Dong, Z., 1987. Fauna Sinica. Phylum Mollusca, class Cephalopoda. (Science Press: Beijing, China).

Ekman, S., 1953. Zoogeography of the Sea. (Sidgwick and Jackson, London).

Garrick, J. A. F. & L. J. Paul, 1971. *Cirrhigaleus barbifer* (fam. Squalidae), a little known Japanese shark from New Zealand waters. *Zoological Publications of Victoria University, Wellington* 55.

Gomon, M. F., J. C. M. Glover & R. H. Kuiter, 1994. The fishes of Australia's south coast. (State Print, Adelaide).

Gomon, M. F. (in press). A revision of the labrid fish genus Bodianus with descriptions of eight new species. *Records of the Australian Museum*.

Hardy, G. S., 1980. A redescription of the antitropical pufferfish *Arothron firmamentum* (Plectognathi: Tetraodontidae). *New Zealand Journal of Zoology*, **7**: 115–125.

Hubbs, C. L., 1952. Antitropical distribution of fishes and other organisms. Symposium on problems of bipolarity and of pantemperate faunas. Proceedings of the Seventh Pacific Science Congress (Pacific Science Association), **3**: 324–329.

Huffard, C. L. & F. G. Hochberg, 2005. Description of a new species of the genus *Amphioctopus* (Mollusca: Octopodidae) from the Hawai'ian Islands. *Molluscan Research*, **25**(3): 113–128.

Kuiter, R. H., 1993. Coastal fishes of south-eastern Australia. (Crawford House Press, Bathurst).

Lamarck, J. B., 1798. Extrait d'un memoire sur les genres de la seche, der Calmar et du Poulpe, vulgairement nomenies Polypes de mer. *Bulletin Société du Philomathematique, Paris*, **2**: 129–131.

Last, P. R. & J. D. Stevens, 1994. Sharks and Rays of Australia. (CSIRO, Australia).

Li, F., 1983. Studies on the cephalopod fauna of the Taiwan Strait. *Taiwan Strait*, **2**(1): 103–109.

Nateewathana, A., 1997. The octopod fauna (Cephalopoda: Octopoda) of the Andaman Sea, Thailand. *Phuket Marine Biological Center Special Publication*, **17**(2): 407–452.

Nateewathana, A. & M. D. Norman, 1999. On three new species of ocellate *octopus*es (Cephalopoda: Octopoda) from Thai waters. *Phuket Marine Biological Center Special Publication*, **19**(2): 445–462.

Norman, M. D., 1991. *Octopus cyanea* Gray, 1849 (Mollusca: Cephalopoda) in Australian waters: description, distribution and taxonomy. *Bulletin of Marine Science*, **49**(1–2): 20–38.

Norman, M. D., 1992. *Ameloctopus litoralis* gen. & sp. nov. (Cephalopoda: Octopodidae), a new shallow-water *octopus* from tropical Australian waters. *Invertebrate Taxonomy*, **6**: 567–582.

Norman, M. D., 1993a. Four new species of the *Octopus macropus* group (Cephalopoda: Octopodidae) from the Great Barrier Reef Australia. *Memoirs of Museum of Victoria*, (1992) **53**(2): 267–308.

Norman, M. D., 1993b. Ocellate octopuses (Cephalopoda: Octopodidae) of the Great Barrier Reef, Australia: description of two new species and redescription of *Octopus polyzenia* Gray, 1849. *Memoirs of Museum of Victoria*, (1992) **53**(2): 309–344.

Norman, M. D., 1993c. Systematics and biogeography of the shallow-water octopuses (Cephalopoda: Octopodinae) of the Great Barrier Reef, Australia. (Unpublished Ph.D. thesis, University of Melbourne).

Norman, M. D., 1993d. *Octopus ornatus* Gould, 1852 (Cephalopoda: Octopodidae) in Australian waters: morphology, distribution and life history. *Proceedings of the Biological Society of Washington*, **106**(4): 645–660.

Norman, M. D., 2000. Cephalopods: a world guide. (IKAN Publishing, Frankfurt). 320 pp.

Norman, M. D., 2001. New octopus species from Queensland, Australia. *Memoirs of the Queensland Museum*, **46**(2): 677–690.

Norman, M. D., R. Boucher. & F. G. Hochberg, 2004. The Shark club Octopus, *Galeoctopus lateralis*, a new genus and species of deep-water octopus from the western Pacific Ocean (Cephalopoda: Octopodidae). *Journal of Molluscan Studies*, **70**: 247–256.

Norman, M. D. & J. Finn, 2001. Revision of the *Octopus horridus* species group with description of two member species from the Great Barrier Reef, *Australia. Invertebrate Taxonomy*, **15**: 13–35.

Norman, M. D. & F. G. Hochberg, 1994. Shallow-water octopuses (Cephalopoda: Octopodidae) of Hong Kong territorial waters. 141–160. In: Morton, B. (ed) The Malacofauna of Hong Kong and southern China III, Proceedings of the Third International Workshop on the Malacofauna of Hong Kong and southern China (Hong Kong University Press).

Norman, M. D. & F. G. Hochberg, 2005a. The current state of octopus taxonomy. Proceedings of the International Workshop and Symposium of Cephalopod International Advisory Council, Phuket, 2003. *Phuket Marine Biological Center Special Publication*, **66**: 127–154.

Norman, M. D. & F. G. Hochberg, 2005b. The "Mimic Octopus" (*Thaumoctopus mimicus* n. gen. et sp.), a new octopus from the tropical Indo-West Pacific (Cephalopoda: Octopodidae). *Molluscan Research*, **25**(2): 57–70.

Norman, M. D., F. G. Hochberg, & R. Boucher-Rodoni, 2005. A revision of the deep-water octopus genus *Scaeurgus* (Cephalopoda: Octopodidae) with description of three new species from the south-west Pacific Ocean. *Journal of Molluscan Studies*, **71**: 319–337.

Norman, M. D., F. G. Hochberg, & R. Boucher-Rodoni, 2004. *Microeledone mangoldi* n. gen. and n. sp., a deep-water pygmy octopus from the Norfolk Ridge, New Caledonia (Cephalopoda: Octopodidae). *Molluscan Research*, **24**(3): 193–209.

Norman, M. D., F. G. Hochberg & C. C. Lu, 1997. Mollusca: Cephalopoda: Mid-depth octopuses (200–1000 m) of the Banda and Arafura Seas (Octopodidae and Alloposidae). In: A. Crosnier & P. Bouchet (eds), Résultats des Campagnes MUSORSTOM, Volume 16. *Bulletin de Museum National d'Histoire Naturelle, Paris*, **172**: 357–383.

Norman, M. D. & C. C. Lu, 2000. Preliminary checklist of the cephalopods of the South China Sea. Special edition on the Biodiversity of the South China Sea, *Bulletin of the Raffles Museum, Singapore*, **8**: 539–567.

Norman, M. D. & M. J. Sweeney, 1997. The shallow-water octopuses (Cephalopoda: Octopodinae) of the Philippine Islands. *Invertebrate Taxonomy*, **11**: 89–140.

Norman, M. D. & A. Reid, 2000. A guide to octopuses, cuttlefishes, squids and nautiluses of Australasian waters. (CSIRO and Gould League of Victoria, Melbourne). 96 pp.

Okutani, T., M. Tagawa & H. Horikawa, 1987. Cephalopods of continental shelf and slope around Japan. (Japan Fisheries Resource Conservation Association, Tokyo).

O'Shea, S. 1999. The marine fauna of New Zealand: Octopoda (Mollusca: Cephalopoda). *National Institute of Water and Atmospheric Research Biodiversity Memoir*, **112**: 1–280.

Packard, A. & G. D. Sanders, 1971. Body patterns of *Octopus vulgaris* and maturation of the response to disturbance. *Animal Behaviour*, **19**: 780–790.

Randall, J. E. 1981. Examples of antitropical and antiequatorial distribution of Indo-West-Pacific fishes. *Pacific Science*, **35**(3): 197–209.

Randall, J. E., G. R. Allen & R. C. Steene, 1990. Fishes of the Great Barrier Reef and Coral Sea. (Crawford House Press, Bathurst).

Robson, G. C., 1929. A monograph of the Recent Cephalopoda. Part I. Octopodinae. (British Museum: London).

Roper, C. F. E., M. J. Sweeney, & C. E. Nauen, 1984. FAO species catalogue. Volume 3, Cephalopods of the world: an annotated and illustrated catalogue of species of interest to fisheries. FAO Fisheries Synopsis, (125)3: 1–277.

Roper, C. F. E. & G. L. Voss, 1983. Guidelines for taxonomic descriptions of cephalopod species. *Memoirs of the Museum of Victoria*, **44**: 49–63.

Salman, A., T. Katagan & S. Von. Boletzky, 1999. New cephalopod molluscs in the eastern Mediterranean: previously unnoted species or recent migrants? *Vie et milieu*, **49**(1): 11–17.

Sasaki, M., 1929. A monograph of the dibranchiate cephalopods of the Japanese and adjacent waters. *Journal of the College of Agriculture, Hokkaido Imperial University*, **20**(supplement): 1–357.

Springer, V. G., 1967. Revision of the circumtropical shorefish genus Entomacrodus (Bleniidae: Salariinae). Proceedings of the U.S. National Museum, **122**: 1–150.

Stranks, T. N., 1988a. Systematics of the family Octopodidae (Mollusca: Cephalopoda) of south-eastern Australia. M.Sc. thesis. (University of Melbourne, Victoria).

Stranks, T. N., 1988b. Redescription of *Octopus pallidus* (Cephalopoda: Octopodidae) from south-eastern Australia. *Malacologia*, **29**(1): 275–287.

Stranks, T. N., 1990. Three new species of Octopus (Mollusca: Cephalopoda) from south-eastern Australia. *Memoirs of the Museum of Victoria*, **50**(2): 457–465.

Stranks, T. N. & M. D. Norman, 1993. Review of the *Octopus australis* complex (Cephalopoda: Octopodidae) and description of a new species. *Memoirs of the Museum of Victoria*, (1992) **53**(2): 345–373.

Taki, I., 1965. Cephalopoda: 307–326. In: OKADA *et al*., eds, New Illustrated Encyclopedia of the Fauna of Japan, vol. 2.

Tam, Y. K., I. Kornfield & F. P. Ojeda, 1996. Divergence and zoogeography of mole crabs, *Emerita* spp (Decapoda, Hippidae) in the Americas. *Marine Biology*, **125**(3): 489–497.

Theel, H., 1885. Report on the Holothuroidea. In: Voyage of H.M.S. Challenger. Part II. *Zoology*, **14**: 1–290.

Toll, R. B. & G. L. Voss, 1998. The systematic and nomenclatural status of the Octopodinae described from the West Pacific region. Smithsonian Contributions to *Zoology*, **586**: 489–520.

Voss, G. L. & G. R. Williamson, 1972. Cephalopods of Hong Kong. Hong Kong Government Press: Hong Kong. 138 pp. [Title page dated 1971, actual publication date 1972].

Wilson, B. R. & G. R. Aallen, 1987. Major components and distribution of marine fauna: 43–68. In: Dyne, G.R. and D.W. Watson (eds). Fauna of Australia. General articles. Vol. 1A. (Australian Government Publishing Service: Canberra).